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The ichneumon-fly genus *Banchus* (Hymenoptera) in the Old World

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Synopsis

This paper provides the first comprehensive account of the genus *Banchus* (Ichneumonidae, Banchinae) in the Old World. Twenty-three species are recognized, described and keyed. Seven of the species are new. Geographical distributions and data on biology and hosts are summarized. Known hosts are Lepidoptera (mainly of the family Noctuidae) and *Banchus* species are known to play an important role in the control of some pest species in Europe and North America. The taxonomic treatment includes 11 new synonymies, one provisional synonymy, three new combinations, one revised combination, two revised statuses, three lectotype designations and four nomina dubia.

Introduction

Banchus has had a chequered history. Taxonomists found it difficult to assign to one of the five traditional subfamilies of the Ichneumonidae, sometimes placing it in the Ophioninae and sometimes in the Pimplinae. As originally defined by Fabricius (1798; 1804) the genus included members of the families Braconidae, Cephidae, Pompilidae, Proctotrupidae and Ibaliidae, as well as the Ichneumonidae. This exotic assortment was reduced by Gravenhorst (1829) to a grouping resembling the genus as understood at present. The main error in his treatment was the transposition of the sexes. Developments in the following 150 years were mainly concerned with description of new species, splitting the genus and faunistic studies. Much of this work was of poor quality; no one made a comprehensive study and those describing and keying species failed to appreciate all but the most superficial characters. A real advance in our understanding of the taxonomy of *Banchus* came only with publication of the revision of the Nearctic species by Townes & Townes in 1978.

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Fig. 1 *Banchus palpalis*, male, habitus.

BANCHUS Fabricius

Banchus Fabricius, 1798: 209, 233. Type-species: *Banchus pictus* Fabricius, by subsequent designation (Curtis, 1836: 588).
Corynephanus Wesmael, 1849: 631. Type-species: *Banchus monileatus* Gravenhorst, by monotypy.
Cidaphurus Foerster, 1869: 159. Type-species: *Ichneumon volutatorius* Linnaeus, by subsequent monotypy (Woldstedt, 1877: 439).
Nawaia Ashmead, 1906: 184. Type-species: *Nawaia japonica* Ashmead, by monotypy.

Diagnosis. Moderately-built ichneumonids (Fig. 1), fore wing length 7·7–14·3 mm. Frons simple. Margin of clypeus with a median notch. Genal carina joining hypostomal carina above base of mandible. Upper tooth of mandible much wider than lower tooth and longer, its apex truncate and weakly subdivided. Lower tooth pointed. Maxillary palp with segment 4 more or less widened and flattened distally, especially in males. Labium not elongate. Antennal flagellum long, tapered to a slender apex. In males, flagellum with poorly- to well-developed specialized setae (flag setae), 2 to 4 per segment, often arising from a poorly- to well-marked, shallow trough on the dorsal surface. Epicnemial carina absent. Scutellum produced posteriorly into a spine, although it is sometimes reduced to a very weak tubercle or even absent. Propodeum short, its posterior transverse carina strong laterally, weak or obsolete medially. Pleural carina present, at least in part. Tarsal claws pectinate. Laterotergites of segments 2 and 3 of gaster about 0·7 times as deep as long. Gaster more or less compressed, relatively strongly so in most females. Ovipositor very short, its sheath about 0·1 times as long as hind tibia.

Remarks. The genus comprises 47 valid, described species. One is Holarctic in distribution, a further 24 occur in the Nearctic (Townes & Townes, 1978) and another 22 are found in the Palaearctic and the mountains of the Oriental region.

Banchus is the largest of a group of five genera united by the structure of the mandible. The mandible is of an unusual, almost tridentate form unlikely to have arisen more than once within the Banchinae. A mandible similar in structure is found only in the Diplazontinae (in which subfamily it occurs in all species). The other genera in the *Banchus*-group are: *Rhynchobanchus* (with 3, possibly 4, Palaearctic species); *Banchopsis* (1 Palaearctic and 1 Oriental species); *Ceratogastra* (1 Palaearctic and 1 Nearctic species) and; *Philogalleria* (7 Australian species and 1 species in Argentina which possibly deserves a separate genus). Within this group the most important discriminant characters are the form of the claws, the presence or absence of the epicnemial carina, the extent of the propodeal carinae, the form of the frons, the position of cross-vein 2m-cu in the fore wing, and the relative sizes of the coxae.

The tribe Banchini, as currently recognized (Townes, 1970: 45; Townes & Townes, 1978: 378), includes two disparate elements – the *Banchus*-group of genera and *Exetastes* and its allies. Cushman (1937), Perkins (*in* Beirne, 1941) and Beirne (1941) all supported separation of the two groups on the basis of adult and larval characters. Cushman and Perkins associated the *Exetastes*-group more closely with the tribe Lissonotini. Townes (1944) on the other hand linked the two groups as the Banchini, separate from the Lissonotini, mainly on the basis of a rather weak character in the hind wing venation. Townes has consistently maintained this position. Viktorov (1967) supported Cushman's (1937) conclusion, citing several characters of *Exetastes* which distinguish it from the *Banchus*-group. Aubert (1978) has gone further, placing *Exetastes* in a tribe of its own, Exetastini. As with many ichneumonid subfamilies the generic and tribal classification of the Banchinae, although workable, is in need of closer study. Townes' (1970) treatment and key fail to take account of the structure of the mandible in *Philogalleria* (of which Townes may have then seen only one specimen).

Taxonomy

Despite its long period of gestation this study, based on the examination of 3421 specimens of Old World *Banchus*, cannot be regarded as definitive. It has raised as many taxonomic questions as it has answered. The lack of specimens from some problem areas (taxonomic as well as geographic), coupled with an inadequate knowledge of most aspects of the biology of the genus, has effectively prevented discrimination of all of the species. A conservative approach was adopted and some of the morphospecies recognized undoubtedly comprise complexes of two or more 'biological' species. With the material and resources available further splitting could not be justified on scientific grounds.

Apart from obvious species-pairs or very small groups it is difficult to deduce anything of the phylogenetic relationships of the species within the genus. As noted by Townes & Townes (1978) in their revision of North American *Banchus*, the characters which distinguish species do not correlate in ways which indicate clear-cut species-groups. Specialization by reduction (an obvious example is in the length of the scutellar spine) is probably one of the complicating factors. The best that can be done is to suggest trends of specialization for individual characters.

Many species show considerable sexual dimorphism (including colour patterns). The most obvious morphological differences are in the shape of the gaster, the antennae and the maxillary palps. The specializations in the female seem to be associated with oviposition and in the male with mate-finding and courtship. In some species the overall colour pattern is the same in male and female, in others it is completely different, for example, in *B. falcatorius* and *B. volutatorius* the females are largely black with reddish legs while the males are conspicuously marked with yellow. This female colour pattern, although still aposematic, probably renders her less conspicuous while searching for hosts (which, in *B. falcatorius*, probably occurs very low in the vegetation at soil level). As a general rule males have a yellowish face with a median black stripe and females a black face, sometimes with yellowish orbital marks, and there are often also differences in the colour of the antennae.

The characters which have been used in this study are discussed below. The formal descriptions of species in the systematic section of the paper are restricted largely to the characters used in the keys. When comparing specimens with figures allowance should be made for some variation.

Head. The overall shape of the head is important in distinguishing species. The characters most easily used are the relative width of the face and the size of the malar space. These are measured as indicated in Figs 2 and 3. The shape of the head behind the eyes varies between species but is much more difficult to use as a distinguishing character. The maxillary palps are specialized in many species (Figs 11–32, 103–123). The relative lengths of the two terminal segments are important and in males the way in which the fourth segment is widened and flattened is characteristic. The antennae vary in length and in the shape of the terminal segments, both characters being difficult to use in keys.

In the male the distal half of the antenna bears specialized setae ('flag setae') on its dorsal surface (Figs 124–129). The development of these varies greatly between species. In the most primitive cases the setae are not easily distinguished from others on the antenna. In the most specialized forms the setae (two, three or four per segment) are erect, widened and flattened and arise from a shallow polished trough. All segments do not bear these setae, there is a zone (which varies in position between species) in which they are best developed and proximally and distally to this the setae become progressively less modified. The descriptions given for each species apply only to the zone bearing the most modified setae. The shape and number per segment are subject to some variation, but together with the form of the male maxillary palps these setae give the best 'key' characters for a species. Both are probably important in courtship.

Thorax and propodeum. The scutellum bears a spine on its posterior apex (Figs 33–58). The primitive condition, it is supposed, is to have a well-developed spine. The length of the spine is impossible to measure accurately because of the lack of reference points, and there is variation within species. Nonetheless it is still useful taxonomically. The lower postero-lateral corners of the mesothorax in some species are formed into weak tubercles which, although relatively constant in their development, are difficult to use comparatively. In the descriptions the 'posterior part of the propodeum' refers to the posterior transverse carina and the area behind and enclosed by it. The posterior transverse carina itself is often obsolete or absent medially.

The measured proportions of the hind femur (as shown in Fig. 5) are used to represent the general proportions of the legs as a whole. The length of the fore wing (measured from the tip of the tegula to the tip of the wing) is used as a measure of overall size.

Gaster. The form of the gaster in the female offers a number of very useful characters. However, their practical value is much reduced by the very variable amounts of distortion found in dry specimens. Allowance must be made for this in comparing specimens with descriptions and figures, particularly those of the apex of the gaster (Figs 82–102). The distortion most affects the amount of compression of the posterior half of the gaster, the telescoping of segments and the compression and profile of sternite 6 (the subgenital plate) which in some species has a weaker, less sclerotised portion on its posterior margin. The form of tergite 1 is not subject to distortion and it offers useful characters in males and females (Figs 59–81), although subject to some variation (compare Figs 65 and 66 of male and female *gudrunae*). The proportions of tergite 1 are measured as indicated in Fig. 4.

Sculpture and colour. The development of microsculpture and puncturation on the thorax, coxae and gaster varies between species but variation within species and difficulties of description limit its value. Colour patterns are subject to variation but are easily observed. Care was taken to ensure that such variation was taken into account in construction of those parts of the keys relying on colour.

Biology and hosts

Townes & Townes (1978) state that *Banchus* is a genus of open shrubby country and that females fly rather low and males higher and faster. However, there are few published observations on the habits and habitats of individual species. Adults have been collected from flowers. The black and yellow and/or reddish colour patterns may be aposematic (Townes & Townes note that specimens give off a strong pungent odour when captured). *B. falcatorius* has been recorded as the prey of an asilid fly.

Most species probably are univoltine and adults are on the wing for some period during late spring or early summer. A few species (e.g. *B. dilatatorius*) occur in early spring. These probably pass the winter as adults or pharate adults within the cocoon. In Europe three species (*B. zonatus, B. gudrunae* and *B. moppiti*) have been taken in late autumn, winter and early spring. Of these three, *B. zonatus* and *B. gudrunae* are Mediterranean in distribution whilst the few known specimens of *B. moppiti* come from localities as scattered as Great Britain, Switzerland and Spain. There appears to be a similar pattern in the species in the eastern Palaearctic and mountains of the Oriental region, with some specimens of the more southern species occurring in the period from October to May. However, some of these species might not be univoltine.

Courtship behaviour in *B. hastator* is described by van Veen (1982): when the male encounters a female he orientates himself face to face and starts fanning with his wings, probably creating an airstream along the female and himself. The gaster of the male is also raised and at intervals these actions are interrupted by an attempt to mount the female. Using the tips of the antennae the male gently strokes the legs and sides of the thorax of the female. If the female is receptive copulation takes place.

The hosts of *Banchus* are Lepidoptera. All of the reliable observations relate to species of Noctuidae, though species of seven other lepidopterous families are also recorded. Whether or not any or all of the non-noctuid records should be rejected is difficult to assess. In the Nearctic species *B. flavescens* it has been shown that females oviposited readily in the larvae of its usual host *Mamestra configurata* Walker and also in *Scotogramma trifolii* (Rottemburg) and *Trichoplusia ni* (Hübner), but had to be induced to attack *Autographa californica* (Speyer), *A. falcifera* (Kirby) and *Heliothis ononis* (Denis & Schiffermüller) by an immediately preceding exposure to *M. configurata* larvae (Arthur & Ewen, 1975; Ewen & Arthur, 1976). All these hosts are noctuids and in addition to the reluctance of the females to oviposit in some species the parasite failed to develop in any except *M. configurata*, because of successful host defence reactions. Van Veen (1982), working with *B. hastator* in the Netherlands, found 'that an antennal contact of a few strokes with the cuticle of the host's skin was sufficient to reject a strange host by walking away or to a susceptible instar of *P[anolis] flammea* [the usual host] immediately by an acute sting reaction'. He unfortunately does not identify the 'strange host'. All these results could be used to support a contention that *Banchus* species are probably monophagous on species of Noctuidae, but for one species, *B. volutatorius*, there are reliable rearings from at least three noctuid species (*Anarta myrtilli* (Linnaeus), *Lacanobia oleracea* (Linnaeus) and *Xestia xanth-*

ographa (Denis & Schiffermüller)), so judgement must be reserved. The host records from two Hymenoptera (Maneval, 1935) can probably be dismissed out of hand.

The larvae normally develop as solitary internal parasites and it is usually suggested that oviposition is into an early instar host larva. In experiments, van Veen (1982) has demonstrated a preference for early instar larvae in *B. hastator*, although females will attack all larval instars except the last (the fifth) (van Veen, 1982; Błedowski & Kraińska, 1926). The larval development of *B. hastator* was studied in detail by Błedowski & Kraińska (1926). The head sclerites of the final larval instar of four species are illustrated by Short (1978). Short's work should be used with caution: his figures of *Banchus* show why. The illustrations of *B. femoralis* and *B. hastator* show differences which might be thought significant; however, both specimens are of the same species (*B. hastator*, of which *femoralis* is a synonym) and one figure shows the view from outside the head capsule while the other shows the view from within! Other figures are given by Beirne (1941) and Barron (1976).

The full-grown *Banchus* larva kills and leaves the host larva after it has left its foodplant and entered the soil to pupate (this has been reported in several species). Cocoons of *Banchus* are elongate-ovoid, the silk dense and almost black. The adult emerges through a hole cut next to one end.

Barron (1976) records a species of *Banchus* (from Maryland) parasitized by *Euceros medialis* Cresson (Hymenoptera: Ichneumonidae).

Systematic list of hosts

The list below includes all the hosts of *Banchus* detailed elsewhere in this paper. Those details can be accessed via the index.

LEPIDOPTERA
ZYGAENIDAE
  Zygaena ephialtes (Linnaeus)
NYMPHALIDAE
  Melitaea didyma (Esper)
THYATIRIDAE
  Achlya flavicornis (Linnaeus)
  Habrosyne pyritoides (Hufnagel)
GEOMETRIDAE
  Opisthograptis luteolata (Linnaeus)
SPHINGIDAE
  Deilephila elpenor (Linnaeus)
  Deilephila porcellus (Linnaeus)
  Hyloicus pinastri (Linnaeus)
  Smerinthus ocellata (Linnaeus)
NOTODONTIDAE
  Phalera bucephala (Linnaeus)
LYMANTRIIDAE
  Dasychira fascelina (Linnaeus)
  Euproctis similis (Fuessly)
  Leucoma salicis (Linnaeus)
NOCTUIDAE
  Acronicta megacephala (Denis & Schiffermüller)
  Agrochola circellaris (Hufnagel)
  Agrochola helvola (Linnaeus)
  Agrotis exclamationis (Linnaeus)
  Agrotis segetum (Denis & Schiffermüller)
  Anarta myrtilli (Linnaeus)
  Aporophyla lutulenta (Denis & Schiffermüller)
  Aporophyla lutulenta luenebergensis (Freyer)
  Atethmia ambusta (Denis & Schiffermüller)
  Bena prasinana (Linnaeus)
  Blepharita adusta (Esper)

Ceramica pisi (Linnaeus)
Euxoa nigricans (Linnaeus)
Hadena compta (Denis & Schiffermüller)
Hadena rivularis (Fabricius)
Heliothis viriplaca (Hufnagel)
Lacanobia contigua (Denis & Schiffermüller)
Lacanobia oleracea (Linnaeus)
Lacanobia suasa (Denis & Schiffermüller)
Lycophotia porphyrea (Denis & Schiffermüller)
Mamestra brassicae (Linnaeus)
Panolis flammea (Denis & Schiffermüller)
Phlogophora meticulosa (Linnaeus)
Xestia xanthographa (Denis & Schiffermüller)

HYMENOPTERA
DIPRIONIDAE
Diprion pini (Linnaeus)
ICHNEUMONIDAE
Ophion luteus (Linnaeus)

Nomenclatural summary

agathae **sp. n.**
altaiensis Meyer, 1927 (nomen dubium)
cerinus Chandra & Gupta, 1977
crefeldensis Ulbricht, 1916
  croaticus Hensch, 1928
dilatatorius (Thunberg, 1822) **stat. rev.**
  acuminator (Fabricius, 1787) (homonym) **syn. n.**
  compressus (Fabricius, 1787) (homonym)
  sibiricus Meyer, 1927 **syn. n.**
falcatorius (Fabricius, 1775)
  variegator (Fabricius, 1775)
  intersectus (Geoffroy, 1785)
  aries (Christ, 1791)
  labiatus (Schrank, 1802)
  histrio (Schrank, 1802) (homonym)
  tricolor (Schrank, 1802)
  falcator Fabricius, 1804
  sachalinensis (Matsumura, 1911)
  luteofasciatus Ulbricht, 1911
  nobilitator Morley, 1915
  sanguinator Meyer, 1922
  lavrovi Meyer, 1927
  nigromarginatus Constantineanu & Pisică, 1960
  propitius Kuslitzky, 1979 (provisional synonymy)
flavomaculatus (Cameron, 1904)
gudrunae **sp. n.**
hastator (Fabricius, 1793)
  pungitor (Thunberg, 1822)
  reticulator (Thunberg, 1822) **syn. n.**
  femoralis Thomson, 1897
  kolosovi Meyer, 1925 **syn. n.**
insulanus Roman, 1937
japonicus (Ashmead, 1906)
mauricettae **sp. n.**
moppiti **sp. n.**
nox Morley, 1913
palpalis Ruthe, 1859 **stat. rev.**
  spinosus Cresson, 1865 **syn. n.**

formidabilis Provancher, 1874 **syn. n.**
groenlandicus Aurivillius, 1890 **syn. n.**
alticola (Ashmead, 1901) **syn. n.**
pictus Fabricius, 1798
cultratus (Gmelin, 1790) (homonym)
mutillatus (Christ, 1791) (homonym)
zagoriensis Hensch, 1928
bipunctatus Hensch, 1928
russiator Aubert, 1981 **syn. n.**
poppiti **sp. n.**
punkettai **sp. n.**
sanjozanus Uchida, 1929
tholus **sp. n.**
tumidus Chandra & Gupta, 1977
turcator Aubert, 1981
volutatorius (Linnaeus, 1758)
venator (Linnaeus, 1758)
umbellatarum (Schrank, 1786) **syn. n.**
certator (Thunberg, 1822) (homonym)
monileatus Gravenhorst, 1829 **syn. n.**
farrani Curtis, 1836
calcaratus Szépligeti, 1910
alticola Schmiedeknecht, 1910 (homonym)
obscurus Meyer, 1926
zonatus Rudow, 1883
algericus Schmiedeknecht, 1910 **syn. n.**

Species excluded from *Banchus*

Andricus villosulus (Gravenhorst) (nomen dubium) **comb. n.**
Banchus robustus Rudow, 1883 (nomen dubium)
Cephus pygmeus (Linnaeus, 1767)
spinipes (Panzer, 1800)
viridator (Fabricius, 1804)
Earinus elator (Fabricius, 1804) **comb. n.**
Exetastes fornicator (Fabricius, 1781)
Exetastes tomentosus (Gravenhorst, 1829)
Ibalia leucospoides (Hochenwarth, 1785)
cultellator (Fabricius, 1793)
Ichneumon vigilatorius Panzer, 1804 (nomen dubium) **comb. rev.**
Lissonota histrio (Fabricius, 1798)
Megarhyssa quadrator (Schellenberg, 1802) **comb. n.**
Phytodietus armillatus (Morley, 1913)
Pompilus (Episyron) annulatus (Fabricius, 1793)
Proctotrupes gravidator (Linnaeus, 1758)
Theronia atalantae (Poda, 1761)
varius (Fabricius, 1793)

Format, material examined and depositories

In the systematic section the species are arranged in alphabetical order. For each (except *altaiensis*) information is under the following headings.

Synonymy. When types have not been available for study (because of loss or destruction or because they could not be obtained on loan) the inclusion of a nominal species in a synonymy is based on consideration of the original description and/or it is substantiated by reference to a published treatment or is considered more fully under 'Nomenclature'.

Nomenclature. This includes discussion of synonymies, type-restrictions, etc. It takes up a considerable amount of space (and it took up a lot of time) because the nomenclatural problems associated with work on European species are related to human historical and sociological factors rather than biological ones.

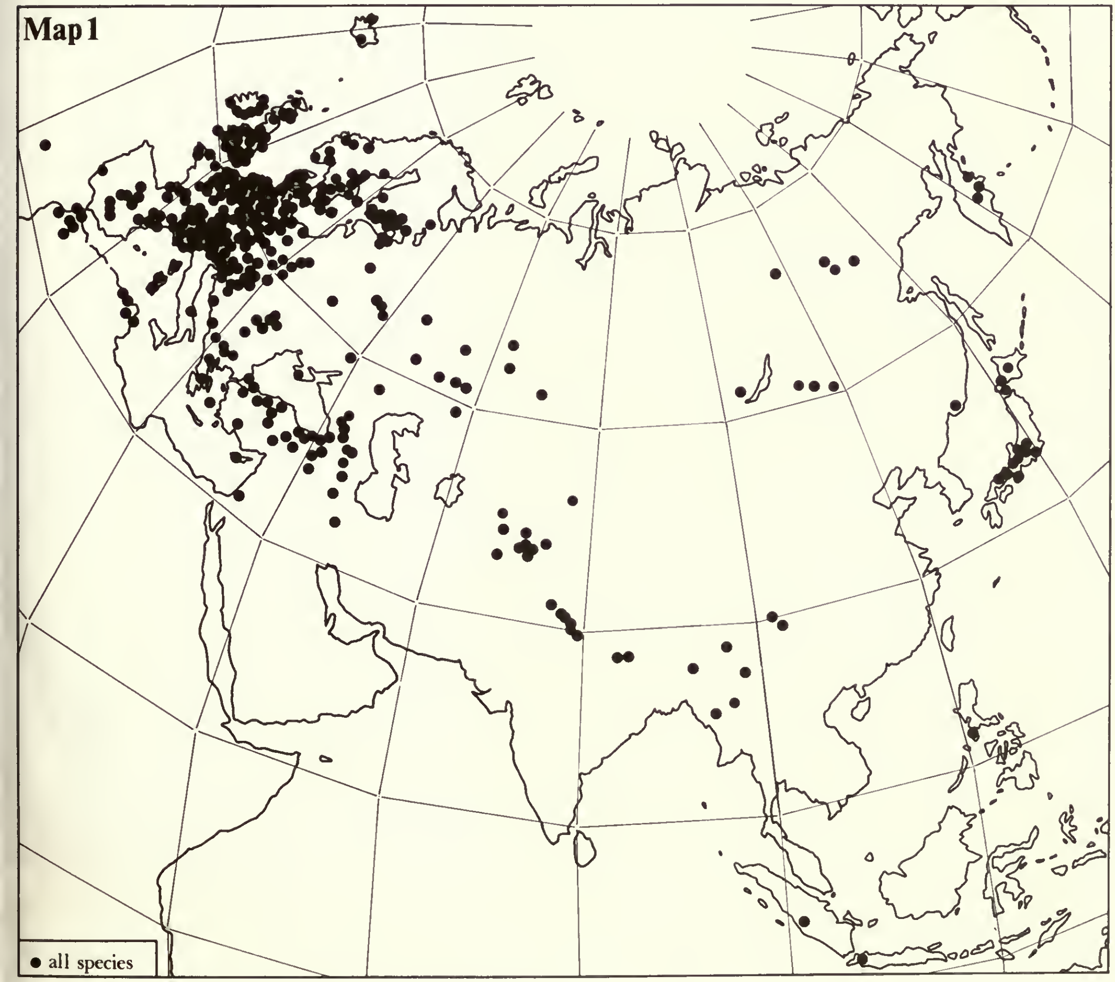
Description. The descriptions for females and males are separate. The characters included are mainly those used in the keys, the ones which apply equally to both sexes are given for the female only (except where the female is not known). The characters, including details of measurements, are discussed in the 'Taxonomy' section above.

Remarks. These include brief notes on recognition and relationships of the species and discussion of its taxonomy.

Biology and hosts. This is a brief summary based on data associated with material examined and information gleaned from the literature. Names of hosts have been up-dated to conform with current usage.

Distribution. As given this is based entirely on data taken from specimens examined, as are the distribution maps. Map 1 shows the distribution of the genus (that is, the combined distributions of all the species) in the Old World for comparison with the distributions of individual species (Maps 2–11). The records in the literature are not reliable and only a few references are made to them (Aubert (1978) should be consulted for more details of these).

Material examined. Except for new species and those known from only a few specimens, the data under 'material examined' are restricted to totals of specimens, the names of countries (and



Map 1 Distribution of *Banchus* in the Old World.

larger islands) from which they come and the depositories in which they are to be found. All specimens on which this revision is based bear my determination labels. Some detail of collecting localities is presented in the distribution maps for each species. However, a feature of much European material is inadequate locality data on labels and there are no points on the maps for perhaps a third of all the specimens examined. Dates of collection are also often lacking; for instance, in an attempt to relate morphological to seasonal variation in *Banchus pictus* only 90 of the 184 specimens to hand could be utilized because the rest had no date of collection.

The names of depositories are abbreviated as in the list below.

AC	Collection of J. Aubert, Paris, France
ANS	Academy of Natural Sciences, Philadelphia, U.S.A.
BC	Collection of R. Bauer, Grossschwarzenlohe, B.R.D.
BMNH	British Museum (Natural History)
BRI	Biosystematics Research Institute, Ottawa, Canada
CM	Castle Museum, Norwich, England
EIHU	Entomological Institute, Hokkaido University, Sapporo, Japan
FSA	Faculté des Sciences Agronomique de l'État, Gembloux, Belgium
GC	Collection of V. Gupta, University of Florida, Gainsville, U.S.A.
HC	Collection of R. Hinz, Einbeck, B.R.D.
IBMPP	All-Union Institute of Biological Methods of Plant Protection, Kishinev, U.S.S.R.
IEAU	Istituto di Entomologia Agraria dell'Università, Sassari, Italy
IEE	Instituto Espanõl de Entomología, Madrid, Spain
IEUB	Istituto di Entomologia, Università degli studi di Bologna, Bologna, Italy
IP	Institut für Pflanzenschutzforschung, Eberswalde, D.D.R.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
ITZ	Institut voor Taxonomische Zoölogie, Zoölogisch Museum, Amsterdam, Netherlands
IZPAN	Instytut Zoologiczny, Polska Akademia Nauk, Warsaw, Poland
JC	Collection of R. Jussila, Paattinen, Finland
JKC	Collection of J. Kolarov, Sadovo, Bulgaria
JPM	Jena Phyletisches Museum, Jena, D.D.R.
KC	Collection of K. Kusigemati, Kagoshima, Japan
KHC	Collection of K. Horstmann, Würzburg, B.R.D.
LELW	Laboratorium voor Entomologie van de Landbouwhogeschool, Wageningen, Netherlands
LSL	Linnean Society, London, England
MCSN	Museo Civico di Storia Naturale, Genoa, Italy
MHN	Museum d'Histoire Naturelle, Geneva, Switzerland
MIZS	Museo ed Istituto di Zoologia Sistematica, Turin, Italy
MLSU	Zoological Museum, Moscow Lomonosov State University, Moscow, U.S.S.R.
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin, D.D.R.
MUM	Manchester University Museum, Manchester, England
NC	Collection of A. Nakanishi, Fukuoka, Japan
NM	Naturhistorisches Museum, Vienna, Austria
NMB	Naturhistorisches Museum, Basle, Switzerland
NMV	National Museum of Victoria, Melbourne, Australia
NR	Naturhistoriska Riksmuseet, Stockholm, Sweden
PC	Collection of C. Pisică, Iasi, Rumania
RNH	Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
RSM	Royal Scottish Museum, Edinburgh, Scotland
SC	Collection of H. Schnee, Markkleeberg, D.D.R.
SMT	Staatliches Museum für Tierkunde, Dresden, D.D.R.
TAU	Department of Zoology, Tel-Aviv University, Tel-Aviv, Israel
TC	Collection of H. & M. Townes, American Entomological Institute, Ann Arbor, U.S.A.
TM	Természettudományi Múzeum, Budapest, Hungary
UL	Université Laval, Quebec, Canada
UM	University Museum, Oxford, England
USNM	U.S. National Museum of Natural History, Washington, U.S.A.
UU	Department of Entomology, University of Uppsala, Uppsala, Sweden
UZI	Universitetets Zoologiska Institutionen, Lund, Sweden

UZM	Universitetets Zoologisk Museum, Copenhagen, Denmark
VRC	Collection of G. van Rossem, Ede, Netherlands
ZC	Collection of K. Zwart, Wageningen, Netherlands
ZI	Zoological Institute, Wrocław, Poland
ZIL	Zoological Institute, Leningrad, U.S.S.R.
ZIM	Zoological Institute and Museum, Sofia, Bulgaria
ZMU	Zoological Museum of the University, Helsinki, Finland
ZPZ	Zavod Za Poljoprivednu Zoologiju, Zagreb, Yugoslavia
ZSBS	Zoologische Sammlung des Bayerischen Staates, Munich, B.R.D.

Keys to species

The keys to females and males are separate. Sexing specimens of *Banchus* is not always straightforward. The short, broad ovipositor sheaths are sometimes mistaken for the male genitalia. The most reliable way to sex specimens is to examine the last visible tergites and sternites of the gaster: in females they are relatively long (Figs 6–10) and in males they are short (Fig. 1).

Males (the males of *cerinus* and *insulanus* are unknown)

1 Maxillary palp (Figs 104, 114) with segment 5 less than 0·2 as long as segment 4; segment 4 long and cylindrical, with only its extreme apex sharply expanded and flattened 2

– Maxillary palp (Figs 103, 105–113, 115–123) with segment 5 more than 0·4 as long as segment 4; segment 4 gradually and evenly widened and flattened from base to apex or more sharply expanded from near base 3

2 Hind femur less than 6·2 times as long as deep; entirely reddish yellow in colour. Gaster usually entirely black, the segments sometimes brownish or yellowish on their posterior margins, very rarely as conspicuous yellow bands on tergites 1, 2 and 3. Scutellar spine usually long (more than 0·8 as long as scutellum) (Fig. 47) .... **palpalis** Ruthe (p. 30)

– Hind femur more than 6·5 times as long as deep; black, yellow proximally and distally and sometimes dorsally. Gaster with each segment black anteriorly and yellow posteriorly. Scutellar spine short (about 0·3 as long as scutellum) (Fig. 34) .... **crefeldensis** Ulbricht (p. 15)

3 Antennal flag setae well developed (Figs 126–129): upright, flattened, 2 or 3 (rarely 4) per segment, arising from a more or less well-defined and polished trough 4

– Antennal flag setae not or only poorly differentiated (as in Fig. 124, or at most as in Fig. 125 but shorter): at 60 degrees or less to the segment surface, not flattened, 2 per segment, never arising from a trough 17

4 Antennal flag setae 3 (occasionally 4) per segment (Fig. 129) 5

– Antennal flag setae 2 per segment (Figs 126–128) (very rarely a few segments with 3 setae) 7

5 Scutellar spine long (about 0·8 as long as scutellum) (Fig. 44) .... **mauricettae** sp. n. (p. 28)

– Scutellar spine short (about 0·3 as long as scutellum) to absent (Figs 33, 37, 38) 6

6 Hind femur less than 5·3 times as long as deep, usually entirely reddish yellow in colour but can be darkened medially. Malar space more than 0·6 times basal width of mandible **falcatorius** (Fabricius) (p. 19)

– Hind femur about 6·1 times as long as deep, yellow in colour with the median part black. Malar space about 0·5 times basal width of mandible .... **agathae** sp. n. (p. 14)

7 Tergite 1 of gaster at least 2·1 times as long as broad 8

– Tergite 1 of gaster at most 2·0 times as long as broad 11

8 Hind femur at least 7·0 times as long as deep. Tergite 3 of gaster with a crease separating laterotergite along its whole length .... **gudrunae** sp. n. (p. 23)

– Hind femur less than 6·5 times as long as deep. Tergite 3 of gaster with a crease separating laterotergite on only about its anterior 0·5 9

9 Meoscutum shining, with only weak microsculpture between punctures. Scutellar spine at most about 0·5 as long as scutellum (Fig. 39) .... **flavomaculatus** (Cameron) (p. 23)

– Mesoscutum not shining, with well-developed microsculpture between punctures. Scutellar spine at least about 0·7 as long as scutellum (Figs 46, 52) 10

10 Hind femur about 6·0 times as long as deep. Antennal flagellum black with underside of segment 1 and distal section reddish yellow. Segments of gaster each black anteriorly and yellow posteriorly, with junction of the two areas reddish .... **nox** Morley (p. 30)

– Hind femur at most 5·6 times as long as deep. Antennal flagellum reddish, darkened dorsally (especially first few segments and distal third). Segments of gaster each reddish with some blackish anteriorly, especially on tergites 1 and 2 .... ***sanjozanus*** Uchida (p. 37)

11 Maxillary palp (Figs 110, 116, 122) with segment 5 about 0·5 as long as segment 4 12

– Maxillary palp (Figs 105, 113, 121, 123) with segment 5 more than 0·7 as long as segment 4 14

12 Antennal flagellum black ventrally. Hind femur more than 6·2 times as long as deep. Gaster with tergite 1 at most 1·65 times as long as broad; tergite 3 with a crease separating the laterotergite on at least its anterior 0·8 .... ***japonicus*** (Ashmead) (p. 26)

– Antennal flagellum yellowish ventrally. Hind femur at most 6·1 times as long as deep. Gaster with tergite 1 at least 1·60 times as long as broad; tergite 3 with a crease separating the laterotergite on its anterior 0·5 or less 13

13 Hind femur reddish yellow, usually entirely, rarely darkened ventrally; at most 5·4 times as long as deep. Hind tibia and segment 1 of hind tarsus reddish yellow, the tibia and sometimes the tarsal segment distally blackish .... ***volutatorius*** (Linnaeus) (p. 40)

– Hind femur yellow, black-marked ventrally and internally; at least 5·6 times as long as deep. Hind tibia and segment 1 of hind tarsus blackish, the tibia partly reddish yellow ventrally ***poppiti*** sp. n. (p. 35)

14 Malar space at most 0·6 times basal width of mandible. Antennal flagellum with its proximal 0·6 orange .... ***turcator*** Aubert (p. 39)

– Malar space more than 0·6 times basal width of mandible. Antennal flagellum with at least its dorsal surface entirely brownish or blackish 15

15 Antennal flagellum yellowish ventrally (and posterior margins of gastral tergites 1, 2 and 3 yellow) or, if antennal flagellum is black ventrally, the posterior margins of gastral tergites 1, 2 and 3 yellowish brown or reddish brown. Hind coxa entirely black ***dilatatorius*** (Thunberg) (p. 17)

– Antennal flagellum blackish ventrally. Posterior margins of gastral tergites 1, 2 and 3 yellow. Hind coxa black, usually with at least a dorsal yellow spot 16

16 Tergite 1 of gaster at most 1·6 times as long as broad. Hind femur at most 5·5 times as long as deep. Fore wing length at most 10·0 mm .... ***moppiti*** sp. n. (p. 28)

– Tergite 1 of gaster more than 1·6 times as long as broad. Hind femur more than 5·3 times as long as deep. Fore wing length more than 10·5 mm .... ***zonatus*** Rudow (p. 41)

17 Tergite 1 of gaster with a strong median swelling in front of level of spiracles, the anterior face of swelling at almost 90 degrees to its dorsal surface (Figs 77, 78). Scutellar spine long (at least 0·7 as long as scutellum) (Figs 53, 54) 18

– Tergite 1 of gaster at most weakly swollen at level of spiracles (Figs 64, 73, 75). Scutellar spine moderately long (about 0·6 as long as scutellum) to very small (Figs 41, 49, 51) 19

18 Segment 4 of maxillary palp relatively weakly expanded (Fig. 119); uniformly reddish yellow in colour .... ***tholus*** sp. n. (p. 37)

– Segment 4 of maxillary palp considerably expanded from the base (Fig. 120); bi-coloured ***tumidus*** Chandra & Gupta (p. 38)

19 Maxillary palp (Fig. 117) with segment 5 about 0·6 as long as segment 4; segment 4 considerably widened and flattened. Hind femur about 6·0 times as long as deep .... ***punkettai*** sp. n. (p. 36)

– Maxillary palp (Figs 109, 115) with segment 5 about 0·8 as long as segment 4; segment 4 slightly or moderately widened and flattened. Hind femur less than 5·7 times as long as deep 20

20 Posterior part of propodeum entirely black. Hind coxa almost always entirely black. Segments of gaster each black, usually with the posterior margin brownish yellow. Segment 4 of maxillary palp relatively slightly widened (Fig. 109). Antennal flag setae poorly differentiated and very small (Fig. 124) .... ***hastator*** (Fabricius) (p. 24)

– Posterior part of propodeum almost always with yellow marks. Hind coxa black, often with a yellow dorsal patch. Segments of gaster each black anteriorly, broadly yellow posteriorly. Segment 4 of maxillary palp relatively more widened (Fig. 115). Antennal flag setae at about 60 degrees to the segment surface, small (as in Fig. 125 but setae shorter) ***pictus*** Fabricius (p. 33)

Females (the female of *sanjozanus* is not included in the key)

1 Maxillary palp (Figs 13, 24) with segment 5 at most about 0·5 as long as segment 4; segment 4 relatively very long and slender 2

– Maxillary palp (Figs 11, 12, 14–23, 25–32) with segment 5 at least 0·7 as long as segment 4; segment 4 variable in proportions, but much less slender 3

2 Hind femur less than 6·0 times as long as deep; reddish yellow in colour, sometimes darkened ventrally. Gaster usually entirely black, posterior edges of some segments may be brownish. Scutellar spine long (usually more than 0·8 as long as scutellum) (Fig. 47) ***palpalis*** Ruthe (p. 30)

– Hind femur more than 6·3 times as long as deep; black and yellow (proximally and distally and sometimes dorsally). Gaster with each segment black anteriorly and yellow posteriorly. Scutellar spine short (about 0·3 as long as scutellum) (Fig. 34) .... ***crefeldensis*** Ulbricht (p. 15)

3 Posterior part of propodeum entirely black 4

– Posterior part of propodeum with at least some yellow or reddish marks 9

4 Malar space at least 0·8 times basal width of mandible. Width of lower face at least 1·1 times vertical length of eye. Hind femur mainly black .... ***dilatatorius*** (Thunberg) (p. 17)

– Malar space at most 0·7 times basal width of mandible. Width of lower face at most 1·0 times vertical length of eye. Hind femur entirely reddish yellow or with more or less extensive black areas 5

5 Tergite 7 of gaster (Fig. 85) elongate, subacute, its upper surface rounded posteriorly **falcatorius** (Fabricius) (p. 19)

– Tergite 7 of gaster (Figs 88, 89, 95, 101) of normal length, subtruncate, its upper surface not markedly rounded posteriorly 6

6 Hind femur more than 6·0 times as long as deep. Tergite 3 of gaster with a crease separating laterotergite along its whole length .... ***insulanus*** Roman (p. 26)

– Hind femur at most 5·5 times as long as deep. Tergite 3 of gaster with a crease separating laterotergite on less than its anterior 0·5 7

7 Tergite 1 of gaster at least 1·8 times as long as broad. Hind femur entirely reddish yellow ***volutatorius*** (Linnaeus) (p. 40)

– Tergite 1 of gaster at most 1·7 times as long as broad. Hind femur reddish yellow with more or less extensive black areas 8

8 Tergites of gaster each black anteriorly, broadly yellow posteriorly, the boundary between the two areas sharply defined .... ***pictus*** Fabricius (p. 33)

– Tergites of gaster each black, grading posteriorly, to a greater or lesser extent, into a brownish and sometimes yellowish marginal area .... ***hastator*** (Fabricius) (p. 24)

9 Tergite 7 of gaster (Figs 84, 92, 102) relatively elongate, subacute, its upper surface rounded posteriorly AND width of lower face at least 1·0 times vertical length of eye 10

– Tergite 7 of gaster (Figs 6, 82, 86, 87, 90, 91, 93, 95–100) of normal length, subtruncate, its upper surface not markedly rounded posteriorly AND/OR width of lower face at most 0·9 times vertical length of eye 12

10 Antennal flagellum yellowish orange in colour, with the base of segment 1 and the distal segments dark .... ***dilatatorius*** (Thunberg) (p. 17)

– Antennal flagellum black, brownish distally 11

11 Tergite 7 of gaster (Fig. 102) more elongate. Hind femur at least 5·3 times as long as deep. Fore wing length at least 11·0 mm .... ***zonatus*** Rudow (p. 41)

– Tergite 7 of gaster (Fig. 92) less elongate. Hind femur at most 5·2 times as long as deep. Fore wing length at most 10·8 mm .... ***moppiti*** sp. n. (p. 28)

12 Tergite 1 of gaster with a strong median swelling in front of level of spiracles, the anterior face of the swelling at almost 90 degrees to its dorsal surface (Figs 77, 78) ***tholus*** sp. n. (p. 37) and ***tumidus*** (Chandra & Gupta) (p. 38)
(It has proved impossible to separate reliably the females of these two species. See notes under *tumidus*.)

– Tergite 1 of gaster at most weakly swollen in front of level of the spiracles (Figs 6, 59, 63, 65, 66, 68, 69, 71, 73, 74, 75, 79) 13

13 Antennal flagellum entirely black. Hind femur largely black (yellow or reddish proximally and distally) or yellow with a black area medially (which extends onto its dorsal surface) 14

– Antennal flagellum reddish, orange, or yellow, at least on its proximal 0·5, or dark dorsally (black or brownish) and paler ventrally (yellow or reddish). If antennal flagellum is dark (blackish or brownish dorsally and dark reddish ventrally) then hind femur reddish with a black ventral mark, which does not reach to dorsal surface 16

14 Tergite 3 of gaster with a crease separating laterotergite along its whole length. Hind femur more than 6·6 times as long as deep. Hind tibia yellow, with its distal 0·2 blackish ***gudrunae*** sp. n. (p. 23)

– Tergite 3 of gaster with a crease separating laterotergite on only its anterior 0·5. Hind femur at most 6·5 times as long as deep. Hind tibia yellow with its distal 0·2 blackish or black with a median yellowish band 15

15 Hind tibia yellow with its distal 0·2 black. Hind femur about 5·4 times as long as deep **agathae** sp. n. (p. 14)

– Hind tibia black with a median yellowish band. Hind femur more than 5·5 times as long as deep **japonicus** (Ashmead) (p. 26)

16 Hind femur entirely yellow or entirely reddish 17

– Hind femur black and yellow or black and reddish, at least reddish with a ventral black mark 18

17 Hind femur more than 6·0 times as long as deep. Tergite 1 of gaster more than 2·5 times as long as broad .... **cerinus** Chandra & Gupta (p. 15)

– Hind femur less than 5·5 times as long as deep. Tergite 1 of gaster less than 2·5 times as long as broad .... **mauricettae** sp. n. (p. 28)

18 Tergites of gaster each black anteriorly, broadly to narrowly yellow posteriorly, the boundary between the two areas sharply defined 19

– Tergites of gaster (at least 1, 2 and 3) each black anteriorly, reddish or yellow posteriorly, if yellow with an intermediate reddish band grading into the black and into the yellow 21

19 Hind tibia and tarsus mainly blackish, tibia and segment 1 of tarsus slightly lighter proximally. Tergites of gaster each only narrowly yellow posteriorly........ **poppiti** sp. n. (p. 35)

– Hind tibia, on at least its proximal 0·5, and tarsus yellow. Tergites of gaster each broadly to relatively narrowly yellow posteriorly 20

20 Gaster (about as in Figs 7, 8) relatively less compressed posteriorly; tergite 7 and sternite 6 (Fig. 100) subtruncate. Antennal flagellum entirely yellowish orange (at least its proximal 0·7), sometimes with a very small dark mark dorsally on segment 1 .... **turcator** Aubert (p. 39)

– Gaster relatively more compressed posteriorly; tergite 7 and sternite 6 (Fig. 95) more acute. Antennal flagellum yellowish orange, sometimes with proximal section dark dorsally and almost always with at least proximal 0·5 of segment 1 blackish dorsally ... **pictus** Fabricius (p. 33)

21 Tergites of gaster each black anteriorly (at least 1, 2 and 3), reddish posteriorly. Tergite 1 of gaster at least 2·25 times as long as broad 22

– Tergites of gaster each black anteriorly, yellow posteriorly and with an intermediate reddish band. Tergite 1 of gaster at most 2·25 times as long as broad .... **punkettai** sp. n. (p. 36)

22 Posterior part of propodeum entirely reddish. Gaster with tergites 1 to 5 each black anteriorly **flavomaculatus** (Cameron) (p. 23)

– Posterior part of propodeum black, with an irregular reddish yellow band along posterior transverse carina. Gaster with only tergites 1, 2 and 3 black anteriorly .... **nox** Morley (p. 30)

Systematic section

Banchus agathae sp. n.

(Figs 11, 33, 59, 82, 103)

[*Banchus pictus* Fabricius; Bischoff, 1930: 225. Misidentification (and wrong sex).]

DESCRIPTION. Female. Width of lower face 0·90 times vertical length of eye. Malar space 0·60 times basal width of mandible. Maxillary palp as in Fig. 11. Antenna with apical segments as long as broad. Scutellar spine (Fig. 33) about 0·3 as long as scutellum. Mesopleuron and mesoscutum shining, only very weakly sculptured, with strong punctures, on the mesopleuron separated by much less than their diameter. Hind femur 5·40 times as long as deep. Fore wing length 10·1 mm. Tergite 1 of gaster 2·00 times as long as broad, its dorsal profile as in Fig. 59. Gaster compressed from the posterior of segment 3, reaching just beyond the tips of the fore wings (when folded back). Tergite 3 with a crease along its anterior 0·5 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 82.

Colour: black and yellow. Face yellow with a median black stripe. Antenna black with scape and pedicel yellow ventrally. Maxillary palp yellowish with dark marks, including distal 0·7 of segment 4 and all of segment 5. Posterior part of propodeum yellow, narrowly black posteriorly. Hind coxa black with a yellow dorsal patch and distal margin narrowly yellow. Hind femur black, yellow proximally and distally. Segments of gaster each black anteriorly, very narrowly yellow posteriorly.

Male. Width of lower face 0·90 times vertical length of eye. Malar space 0·45 times basal width of mandible. Maxillary palp as in Fig. 103; segment 4 flattened and considerably widened; segment 5 about 0·7 as long as 4. Antennal flag setae (similar to Fig. 129, but the setae only about half as long) upright, short, flattened, 3 per segment, arising from a polished trough. Hind femur 6·10 times as long as deep. Fore wing length 8·5 mm. Tergite 1 of gaster 1·80 times as long as broad. Tergite 3 with a crease along its anterior 0·5 separating the laterotergite.

Colour: black and yellow. Antenna black with scape, pedicel and proximal and distal parts of flagellum yellow ventrally. Maxillary palp with segments 1 yellowish, 2 and 3 reddish, 4 and 5 blackish. Posterior part of propodeum yellow, narrowly black posteriorly. Hind coxa black with a yellow dorsal spot and narrow postero-ventral margin. Hind femur yellow, black medially. Segments of gaster each black anteriorly, yellow posteriorly.

REMARKS. The male should be readily recognized by the form of the antennal flag setae. The female is keyed to a large extent on colour characters but the form of the posterior part of the gaster is also important.

BIOLOGY AND HOSTS. Unknown. The specimens were taken in July and August.

DISTRIBUTION (Map 2, p. 16). Known from only two specimens collected in the Pamir.

MATERIAL EXAMINED

Holotype ♂, **U.S.S.R.**: Pamir, Umss-Tugai, 25.vii.1928 (*Rickmers*) (ZSBS).
Paratype ♀, **U.S.S.R.**: Pamir, Maz, 3580 m, 15.viii.1928 (*Reinig*) (MNHU).

Banchus altaiensis Meyer nomen dubium

Banchus altaiensis Meyer, 1927*b*: 295. Type(s) ♂, U.S.S.R. (destroyed).

This species was described from material, probably only one specimen, collected in the Altai mountains. The description does not fit adequately any of the species from Central Asia known to me and I hesitate to identify it with any species not proven to occur there. Its identification will have to wait until more extensive collections have been made in the area.

Banchus cerinus Chandra & Gupta

(Figs 6, 12)

Banchus cerinus Chandra & Gupta, 1977: 185. Holotype ♀, INDIA (GC) [examined].

DESCRIPTION. Female. Width of lower face 0·85 times vertical length of eye. Maxillary palp as in Fig. 12. Antenna with apical segments longer than broad. Scutellar spine of moderate length. Mesopleuron and mesoscutum weakly coriaceous, with dense, fairly small punctures. Hind femur 6·25 times as long as deep. Fore wing length 14·3 mm. Tergite 1 of gaster 2·75 times as long as broad, its dorsal profile as in Fig. 6. Gaster subcylindrical, only weakly compressed posteriorly, not reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·6 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 6.

Colour: mainly yellow, with black marks. Face yellow with a black mark between and just below antennal sockets. Antenna yellow with distal half of flagellum and an externo-lateral mark on pedicel blackish. Maxillary palp yellowish. Posterior part of propodeum yellow. Hind coxa yellow, blackish distally. Hind femur yellow. Segments of gaster yellow, with basal third of tergites 1, 2 and 3 and of sternite 2 black.

Male. Unknown.

REMARKS. A pale-coloured species with relatively long appendages. Its closest relatives seem to be *tholus* and *tumidus*.

DISTRIBUTION (Map 4, p. 20), BIOLOGY AND HOSTS. The species is known only from the holotype, which was collected amongst mixed bushes in coniferous forest in the NW. Himalayas (Gupta, 1975: (appendix) 50).

MATERIAL EXAMINED (1 ♀)

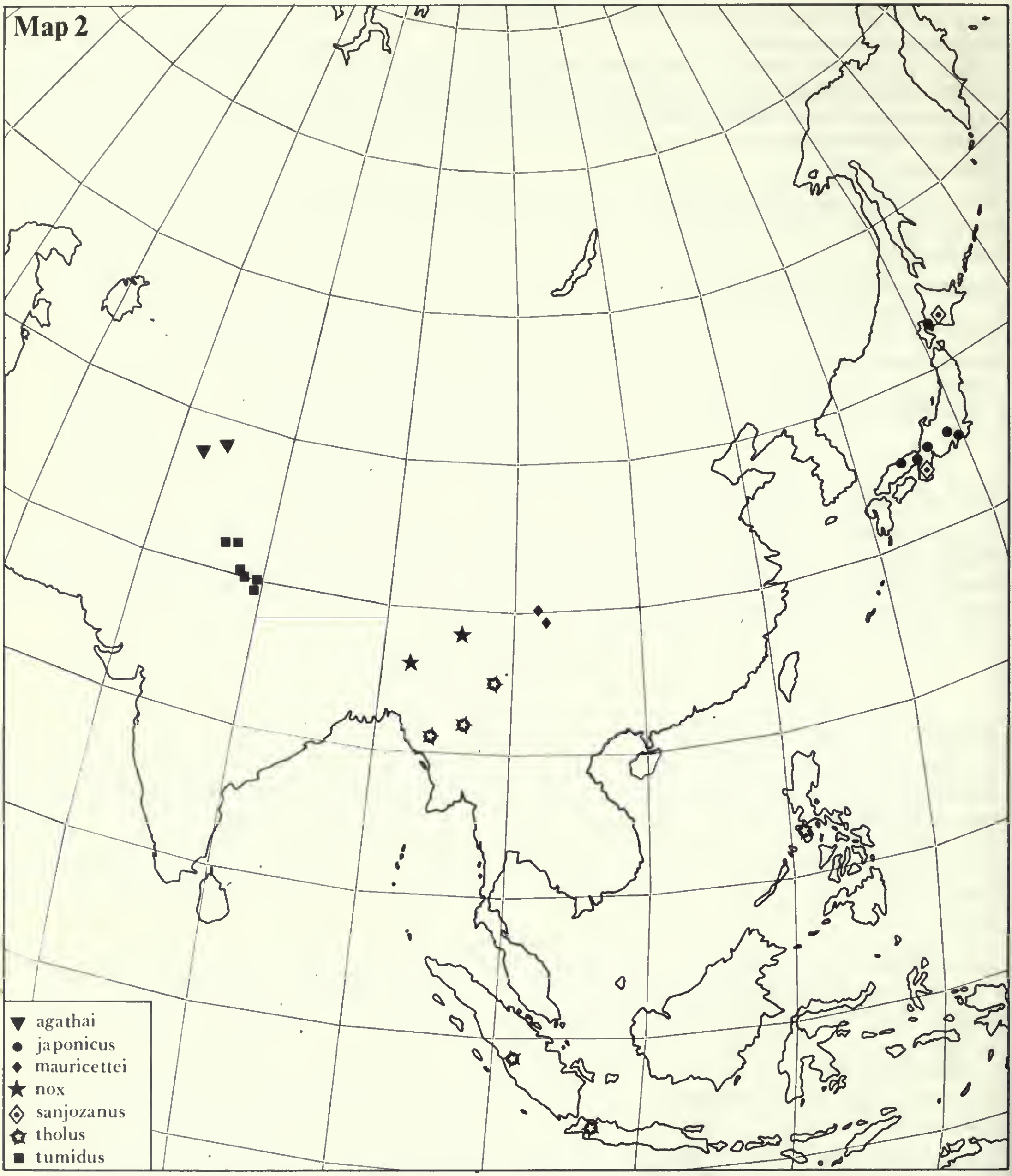
India: 1 ♀ (holotype), Himachal Pradesh, Ahla, 2286 m, 18.vii.1971 (*Gulati*) (GC).

Banchus crefeldensis Ulbricht

(Figs 4, 13, 34, 60, 83, 104, 125)

Banchus crefeldensis Ulbricht, 1916: 12. Holotype ♂, WEST GERMANY (A. Ulbricht coll., Krefeld) [examined].

Banchus croaticus Hensch, 1928: 99. Lectotype ♀, YUGOSLAVIA (ZPZ), designated by Horstmann, 1982*a*: 82 [examined].



Map 2 Distribution of *Banchus agathae, B. japonicus, B. mauricettae, B. nox, B. sanjozanus, B. tholus* and *B. tumidus*.

Description. Female. Width of lower face 0·90–1·00 times vertical length of eye. Malar space 0·60–0·75 times basal width of mandible. Maxillary palp as in Fig. 13. Antenna with apical segments longer than broad. Scutellar spine (Fig. 34) about 0·3 as long as scutellum. Mesopleuron and mesoscutum strongly coriaceous, with moderately strong punctures, on mesopleuron separated by about their diameter. Hind femur 6·35–7·50 times as long as deep. Fore wing length 9·9–10·7 mm. Tergite 1 of gaster 1·80–2·00 times as long as broad, its dorsal profile as in Fig. 60 (male). Gaster compressed from segment 4, reaching about to tips of fore wings (when folded back). Tergite 3 with a crease along its entire length separating laterotergite. Tergite 7 and sternite 6 as in Fig. 83.

Colour: black and yellow. Face black with broad yellow orbital stripes and a vertical yellow mark below each antennal socket. Antenna entirely black except for a yellow patch on underside of scape, and rarely also on pedicel. Maxillary palp blackish with part or all of segment 2 and proximal 0·7 of segments 3 and 4 reddish yellow. Posterior part of propodeum yellow anteriorly, black posteriorly. Hind coxa black with a yellow dorsal patch. Hind femur black, yellow proximally and distally and sometimes dorsally. Segments of gaster each black anteriorly and broadly yellow posteriorly.

Male. Width of lower face 0·90–1·00 times vertical length of eye. Malar space 0·55–0·70 times basal width of mandible. Maxillary palp as in Fig. 104; segment 4 narrow and cylindrical, flattened and widened only at its extreme distal apex; segment 5 less than 0·2 as long as 4. Antennal flag setae (Fig. 125) at about 50 degrees, not flattened, 2 or 3 per segment, not arising from a trough. Hind femur 6·60–7·65 times as long as deep. Fore wing length 9·1–10·8 mm. Tergite 1 of gaster 1·80–2·10 times as long as broad (Fig. 4). Tergite 3 with a crease along its entire length separating laterotergite.

Colour: black and yellow. Antenna black, with scape and pedicel yellow ventrally. Maxillary palp blackish with segments 2 wholly and 3 and 4 proximally reddish yellow. Posterior part of propodeum black with a variable amount of yellow anteriorly, ranging from a very broad band along posterior transverse carina to a small median spot to absent entirely. Hind coxa black, usually with a yellow dorsal patch. Hind femur black, yellow proximally and distally and sometimes dorsally. Segments of gaster each black anteriorly, yellow posteriorly (on at least tergites 2 and 3 relatively broadly so).

REMARKS. Like the related *B. palpalis*, this is a very distinctive species; it is readily recognized by the structure of the maxillary palps and its coloration.

BIOLOGY AND HOSTS. Dates of collection range from mid-February (in Spain and Portugal) to mid-May (in Scotland and Ireland). Stelfox (1936: 63) records males flying in numbers round ivy (*Hedera helix*) and gorse (*Ulex europaeus*) in Ireland. Specimen labels indicate capture of males on *Betula* and around *Buxus* and females from pine.

I have seen 11 reared specimens, 3 without a satisfactory host identification, the remaining 8 (including both sexes) from *Aporophyla lutulenta* (Denis & Schiffermüller) or *A. lutulenta* 'subspecies' *lueneburgensis* (Freyer) (Noctuidae). The named hosts were collected at Bussum, Netherlands; Aviemore, Great Britain; and Bremen and near Hamburg, West Germany.

DISTRIBUTION (Map 3, p. 18). Widely distributed in Europe but not found in Scandinavia or the U.S.S.R. In Great Britain it is restricted to the Scottish Highlands.

MATERIAL EXAMINED (40 ♀, 79 ♂)

Austria, Belgium, France, Great Britain, Hungary, Ireland, Italy, Netherlands, Portugal, Spain, Switzerland, Tunisia, Turkey, West Germany, Yugoslavia (BMNH, FSA, IEE, IRSNB, LELW, MHN, MNHN, NM, NMB, NR, RNH, UM, USNM, ZC, ZSBS).

***Banchus dilatatorius* (Thunberg) stat. rev.**

(Figs 2, 14, 35, 36, 61, 84, 105)

Ichneumon acuminator Fabricius, 1787: 268. Type(s) ♂, EAST GERMANY (lost). [Junior primary homonym of *Ichneumon acuminator* Müller, 1776: 157.] **Syn. n.**

Ichneumon compressus Fabricius, 1787: 381. Holotype ♀, SWEDEN (UZM) [examined]. [Junior primary homonym of *Ichneumon compressus* Sulzer, 1776: 190.]

Ichneumon dilatatorius Thunberg, 1822: 279; 1824: 360. Holotype ♀, GERMANY (UU) [not examined].

Banchus sibiricus Meyer, 1927*b*: 294. Syntypes ♀, ♂, U.S.S.R. (destroyed). **Syn. n.**

NOMENCLATURE. In most of the literature this species is referred to by the invalid name *compressus*.

Although *Ichneumon acuminator* has been placed previously in *Banchus* it has never been identified. The description fits certain males of *dilatatorius* if one allows that Fabricius failed to observe the pale colour of the underside of the antennae.

The description of *Banchus sibiricus* fits well specimens from Kamchatka (which include those identified by Roman (1931: 29) as *lavrovi* var.) which are considered conspecific with *dilatatorius* but are discussed under 'Remarks' below. The identity of the female from Rumania determined as *sibiricus* by Constantineanu & Pisică (1959: 190) is not known.

DESCRIPTION. Female. Width of lower face 1·15–1·25 times vertical length of eye. Malar space 0·80–1·00 times basal width of mandible (Fig. 2). Maxillary palp as in Fig. 14. Antenna with apical segments about as broad as long. Scutellar spine (Figs 35, 36) very small or virtually absent. Mesopleuron and mesoscutum coriaceous, with strong punctures, on mesopleuron separated by less than diameter. Hind femur 4·35–4·85

Map 3 Distribution of *Banchus crefeldensis*.

times as long as deep. Fore wing length 8·7–11·5 mm. Tergite 1 of gaster 1·30–1·40 times as long as broad, its dorsal profile as in Fig. 61. Gaster strongly compressed from posterior of tergite 3, reaching beyond tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·3 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 84.

Colour: black and yellow (the yellow often rather creamy). Face black with yellow orbital marks. Antenna with scape and pedicel black, scape, and usually pedicel, yellowish or reddish ventrally. Flagellum yellowish orange, with base of segment 1 and distal segments dark. Maxillary palp blackish, entirely or with segments 2 and 3 brownish. Posterior part of propodeum black, entirely or, more usually, with a yellow band along posterior transverse carina, the band usually not extensive and narrowly absent medially. Hind coxa black. Hind femur black, narrowly yellowish proximally and usually widely yellowish distally. Segments of gaster each black anteriorly, yellow posteriorly, the yellow bands usually less than 0·3 of length of segments.

Male. Width of lower face 1·10–1·25 times vertical length of eye. Malar space 0·85–0·95 times basal width of mandible. Maxillary palp as in Fig. 105; segment 4 only slightly flattened and widened distally; segment 5 about 0·9 as long as 4. Antennal flag setae (similar to Fig. 126) upright, flattened, relatively narrow, 2 per segment, arising from a polished trough. Hind femur 4·35–5·00 times as long as deep. Fore wing length 8·6–10·7 mm. Tergite 1 of gaster 1·25–1·55 times as long as broad. Tergite 3 with a crease along its anterior 0·3 separating laterotergite.

Colour: black and yellow. Antenna blackish or brownish dorsally, yellow or yellowish ventrally (except for apex of flagellum which is dark). Maxillary palp blackish or brownish. Posterior part of propodeum black, entirely or with a yellow band (sometimes broken medially) along posterior transverse carina. Hind coxa black. Hind femur yellow with a black mark on interno-lateral and ventral surface, and sometimes also dorsally near base. Segments of gaster each black anteriorly, yellow posteriorly, the yellow bands usually less than 0·3 of length of segment.

REMARKS. This species is distinctive and easily identified. The very wide face is a conspicuous feature. However, the poor characters used in earlier keys led to confusion with other species in several of the collections examined.

The details of colour given in the description above do not apply fully to all of the material examined. One female from Iran (AC) has the yellow coloration much more extensive than in any other specimens seen. All the specimens from Kamchatka (1 ♀ (MLSU) and 4 ♀, 2 ♂ (NR)) have yellow absent but with reddish in place of the yellow on the legs and on the face of the male, and with the margins of some or all of tergites 1, 2 and 3 of the gaster narrowly to broadly reddish brown. Other than in these colour characters the Iranian and Kamchatka specimens do not differ much from 'typical' *dilatatorius*. It is impossible to decide whether or not they represent extremes of colour variation or distinct species. Unfortunately the character which might enable a decision to be reached, the male flag setae, cannot be investigated. Of the two male specimens one lacks the head completely and the other lacks both antennae. The Kamchatka specimens match the description of *B. sibiricus* which was described from Irkutsk (see 'Nomenclature' above). The material from Mongolia identified by Momoi (1973: 242–243) as *lavrovi* might also be this dark form of *dilatatorius*. I could not examine these Mongolian specimens because Momoi has so far failed to return them to Budapest (Zombori, pers. comm.). The six specimens in Stockholm (NR) had been identified by Roman (1931: 29) as *lavrovi* var.

BIOLOGY AND HOSTS. This is an early spring species with most records relating to the period from late March to late April. The earliest dates of collection (7 and 13 March) come from sand dune areas in the Netherlands. The label on one female records that it was found on catkins of *Salix caprea*. I have seen no reared specimens of this species, although the following hosts are recorded in the literature: *Blepharita adusta* (Esper) (Noctuidae) (Bajári, 1960: 260); *Euxoa nigricans* (Linnaeus) (Noctuidae) (Schmiedeknecht, 1910: 1926; Meyer, 1934: 228); *Phlogophora meticulosa* (Linnaeus) (Noctuidae) (Györfi, 1944: 106); *Euproctis similis* (Fuessly) (Lymantriidae) (de Gaulle, 1907: 19); and *Leucoma salicis* (Linnaeus) (Lymantriidae) (Leonardi, 1928: 83).

DISTRIBUTION (Map 4, p. 20). Western and central Europe, mainly north of 50 degrees N. (but with very few records from the area bordering the Atlantic (France, the British Isles and Norway) and only a few from Denmark and Sweden); the European Alps; and with some scattered records in the western U.S.S.R., north-west Iran and the Soviet Far East (see 'Remarks' above).

MATERIAL EXAMINED (86 ♀, 96 ♂)

Austria, Belgium, Czechoslovakia, Denmark, East Germany, Finland, France, Great Britain, Hungary, Iran, Italy, Netherlands, Sweden, Switzerland, U.S.S.R., West Germany (AC, BMNH, BRI, HC, IP, IRSNB, ITZ, LELW, MNHN, MHN, MIZS, NMB, NR, RNH, SMT, USNM, UZI, UZM, ZC, ZIL, ZMU, ZSBS).

Banchus falcatorius (Fabricius)

(Figs 5, 9, 10, 15, 37, 38, 62, 85, 106, 129)

Ichneumon falcatorius Fabricius, 1775: 332. Holotype ♂, DENMARK (UZM) [examined].

Ichneumon variegator Fabricius, 1775: 339. LECTOTYPE ♂, SWEDEN (UZM), here designated [examined].

Ichneumon intersectus Geoffroy, 1785: 414. Type(s) ♂, FRANCE (lost) (Horstmann, 1982*b*: 243).

Ichneumon aries Christ, 1791: 339. Type(s) ♀, no type-locality (lost).

Ichneumon labiatus Schrank, 1802: 264. Syntypes ♀ [not ♂ as stated by Schrank], WEST GERMANY (lost).

Ichneumon histrio Schrank, 1802: 265. Syntypes ♂, WEST GERMANY and FRANCE (lost) (Horstmann, 1982*b*: 243). [Junior primary homonym of *Ichneumon histrio* Christ, 1791: 356.]

Ichneumon tricolor Schrank, 1802: 286. Syntypes ♂, WEST GERMANY (lost).

Banchus falcator Fabricius, 1804: 128. [Unjustified emendation of *Ichneumon falcatorius* Fabricius, 1775.]

Corynephanes sachalinensis Matsumura, 1911: 92. Lectotype ♂ [not ♀ as stated by Matsumura], U.S.S.R. (EIHU), designated by Townes, Momoi & Townes, 1965: 236 [examined].

Banchus falcatorius var. *luteofasciatus* Ulbricht, 1911: 151. Type(s) ♀, HUNGARY (?lost).

Banchus nobilitator Morley, 1915: 138. Holotype ♀, U.S.S.R. (BMNH) [examined].

Banchus falcatorius var. *sanguinator* Meyer, 1922: 139. Holotype ♂, U.S.S.R. (destroyed).

Banchus lavrovi Meyer, 1927*b*: 294. Syntypes ♀, ♂, U.S.S.R. (destroyed).

Banchus falcatorius var. *nigromarginatus* Constantineanu & Pisică, 1960: 710. Syntypes 3 ♀, RUMANIA (?Constantineanu coll.) [not examined].

Banchus propitius Kuslitzky, 1979: 351. Holotype ♂, MONGOLIA (ZIL) [not examined]. [Provisional synonymy.]

Map 4 Distribution of *Banchus cerinus, B. dilatatorius* and *B. turcator*.

Nomenclature. *Ichneumon labiatus* was listed by Dalla Torre (1901: 63) in the synonymy of *compressus* (= *dilatatorius*). However, as noted by Gravenhorst (1829: 390) the description applies to *B. falcatorius*. Schrank misdetermined the sex of his species.

Ichneumon tricolor has been synonymised usually with *compressus* (= *dilatatorius*) (e.g. Aubert, 1978: 153). The description and the figure to which Schrank refers (Schaeffer, 1768: pl. 116, fig. 5), differ from that species in the coloration of the gaster. However, they fit the male of *B. falcatorius* and there can be little doubt about the identity of the two species. This synonymy was first proposed by Gravenhorst (1829: 396).

The synonymy of *sanguinator* might be questioned. I have seen no male of *B. falcatorius* as red as described by Meyer; the most reasonable explanation of the colour is that the specimen had suffered from overlong exposure to cyanide in a killing jar.

The description of *lavrovi* fits specimens from the northern part of the eastern Palaearctic and here included in *falcatorius*. One such specimen determined as *lavrovi* by Meyer himself has been examined. The oldest name applying to this form of *falcatorius* is *nobilitator* Morley.

In terms of *falcatorius* as recognized in this revision (see 'Remarks' below) I have thought it best provisionally to synonymize the species, *propitius*, recently described by Kuslitzky (1979).

Description. Female. Width of lower face 0·95–1·00 times vertical length of eye. Malar space 0·60–0·70 times basal width of mandible. Maxillary palp as in Fig. 15. Antenna with apical segments just longer than broad. Scutellar spine (Fig. 37) minute or absent (but see 'Remarks'). Mesopleuron and mesoscutum coriaceous, with moderately strong punctures, on mesopleuron separated by less than their diameter. Hind femur 4·25–4·70 times as long as deep. Fore wing length 10·1–11·2 mm. Tergite 1 of gaster 1·45–1·70 times as long as broad, its dorsal profile as in Fig. 62. Gaster (Figs 9, 10) strongly compressed, reaching beyond tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·3 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 85.

Colour: mainly black, with legs largely reddish and usually some reddish and very rarely yellow on the gaster. Face black, often with very small reddish or yellowish orbital spots. Antenna dark brown or blackish dorsally, brown or reddish ventrally. Maxillary palp reddish with segments 4 apically and 5 wholly dark. Posterior part of propodeum entirely black. Hind coxa black, very rarely with a postero-ventral reddish spot. Hind femur reddish yellow, entirely or, in a few specimens, blackish medially. Segments of gaster black, rarely entirely so, usually with variable reddish marks on segments 1, 2 and 3 and more rarely on other segments. Very rarely reddish areas grade to yellow posteriorly.

Male. Width of lower face 0·95–1·10 times vertical length of eye. Malar space 0·65–0·75 times basal width of mandible. Maxillary palp as in Fig. 106; segment 4 considerably widened and flattened; segment 5 about 0·5 as long as 4. Antennal flag setae (Fig. 129) upright, long, flattened and considerably widened, 3 (sometimes 4) per segment, arising from a polished trough. Hind femur (Fig. 5) 4·45–5·25 times as long as deep. Fore wing length 9·2–11·7 mm. Tergite 1 of gaster 1·40–1·70 times as long as broad. Tergite 3 with a crease along its anterior 0·3 separating the laterotergite.

Colour: black, yellow and reddish. Antenna black dorsally (and ventrally at distal apex of flagellum), yellow ventrally. Maxillary palp with segment 1 yellow, segments 2 and 3 wholly and 4 proximally reddish yellow, segment 4 distally and 5 wholly brown or blackish. Posterior part of propodeum yellow anteriorly, black posteriorly, the yellow sometimes reduced to a pair of latero-median spots or entirely absent. Hind coxa black, usually with a yellowish or reddish patch postero-ventrally and sometimes also dorsally. Hind femur reddish yellow, almost always entirely but in a few specimens blackish medially. Gaster with tergite 1 black anteriorly, reddish and then yellow posteriorly; tergites 2 and 3 each reddish anteriorly, yellow posteriorly (with some blackish laterally); remaining tergites black, 4, 5 and 6 each with a postero-median yellow spot.

REMARKS. *B. falcatorius* has several specialized features and it is the species in which sexual dimorphism is most marked. There is also some geographical variation in characters; for instance, specimens from the eastern part of the range have the hind femur darkened medially and a few specimens from Turkey have a well-developed spine on the scutellum. More than one species might be included in the taxon here recognized, but in the limited material from the eastern Palaearctic available for study no clear-cut segregates could be recognized.

Although the sex association in this species is not in doubt, interesting confirmation comes from the discovery of four gynandromorph specimens in the extensive material examined. These were the only gynandromorphs found (or at least recognized) during the present study. Details of the specimens are as follows.

Italy: Piemonte, Susa, 24.vi.1872 (*Gribodo*) (MCSN). Head male (unfortunately the antennal flagella are missing), thorax and abdomen female. Italy: Cadore, Valle del Boite (IEUB). Head female, thorax and propodeum apparently mainly female but with yellow marks on the left of the mesoscutum and scutellum (male characters), gaster apparently male (including the genitalia) but with some bilateral asymmetry in colour anteriorly. ?locality [illegible] (*Giraud coll.*) (MNHN). Head (including antennae and palps) male on the left and female on the right, prothorax and anterior of mesothorax mainly female but partly male on left, posterior of mesothorax and remainder of body female. Interestingly this specimen had been labelled (anonymously) as a hybrid between *falcatorius* and *monileatus* [= *palpalis*]. Denmark: Ordrup, 19.viii.1877 (*Drewsen*) (UZM). Head (including appendages) female, remainder male except that the dark colour of the left fore and mid coxae suggests some female influence.

BIOLOGY AND HOSTS. This species is on the wing from early June to mid August (with a few records for late May and late August). The adults have often been collected from umbellifer flowers. One female is labelled as being the prey of *Dasypogon teutonus* (Diptera; Asilidae).

Despite the abundance of specimens in collections there are very few reared examples, and not all of those have an attached host name or host remains. The most reliable host data relate to *Agrotis segetum* (Denis & Schiffermüller) (Noctuidae) and this is certainly an important host species. It is (or was) a major pest of root crops (particularly various beets and carrots) and its association with *B. falcatorius* was the subject of research in the U.S.S.R. in the 1920s and 30s (Kosobutzkii, 1928; Meyer, 1927*a*, 1928; Pospelov, 1924; Samoilova, 1936). The long, knife-like gaster of the female is undoubtedly adapted to enable it to reach the host larvae, which feed at soil level. Other hosts recorded on specimen labels are: *Deilephila porcellus* (Linnaeus) and *D. elpenor* (Linnaeus) (Sphingidae), *Dasychira fascelina* (Linnaeus) (Lymantriidae), *Acronicta megacephala* (Denis & Schiffermüller) (Noctuidae) and *Melitaea didyma* (Esper) (Nymphalidae). The last named host record seems unlikely to be accurate, but it is difficult to judge the others (all the specimens are without locality or date !). Other hosts recorded in the literature are: *Agrotis exclamationis* (Linnaeus) (Noctuidae) (Meyer, 1927*a*: 81) and, erroneously, two Hymenoptera (*Diprion pini* (Linnaeus) (Diprionidae) and *Ophion luteus* (Linnaeus) (Ichneumonidae) (Maneval, 1935: 74)).

Distribution (Map 5, p. 22). Most of the Palaearctic, but few specimens seen from large areas of the U.S.S.R. and further east than the Caucasus none from south of 50 degrees N. In the more southern parts of its range in the western Palaearctic it is apparently restricted to higher altitudes.

Material examined (652 ♀, 806 ♂)

Austria, Belgium, Bulgaria, Corsica, Czechoslovakia, Denmark, East Germany, Finland, France, Great Britain, Greece, Italy, Netherlands, Norway, Poland, Rumania, Sakhalin, Spain, Sweden, Switzerland, Turkey, U.S.S.R., West Germany, Yugoslavia (AC, BC, BMNH, BRI, CM, EIHU, FSA, HC, IEE, IEUB, IP, IRSNB, ITZ, IZPAN, JC, JKC, KHC, LELW, MCSN, MHN, MNHN, MNHU, MUM, NMB, NR, PC, RNH, SC, SMT, UM, USNM, UZI, UZM, VRC, ZIL, ZIM, ZMU, ZC, ZSBS).

Map 5 Distribution of *Banchus falcatorius* and *B. flavomaculatus*.

Banchus flavomaculatus (Cameron)

(Figs 16, 39, 63, 86, 107)

Cidaphurus flavomaculatus Cameron, 1904: 346. Lectotype ♀ [not ♂ as stated by Cameron and by Morley, 1913], INDIA (BMNH), fixed by Morley, 1913: 255.

NOMENCLATURE. The lectotype and one paralectotype female (BMNH) are the only known syntype specimens. Both bear labels 'Cidaphurus flavomaculatus Cam. Simla' in Cameron's handwriting. The lectotype has, in addition, Nurse's typewritten data label 'Simla 5.97.'. It is unfortunate that Cameron's original description applies better to the paralectotype because it is not conspecific with the lectotype and is *B. punkettai*.

DESCRIPTION. Female. Width of lower face 0·75–0·80 times vertical length of eye. Malar space 0·50–0·55 times basal width of mandible. Maxillary palp as in Fig. 16. Antenna with apical segments about as broad as long. Scutellar spine (Fig. 39) varying from very short to about 0·5 as long as scutellum. Mesopleuron and mesoscutum shining, weakly coriaceous, with moderate punctures, on mesopleuron separated by about or a little more than their diameter. Hind femur 5·60–5·65 times as long as deep. Fore wing length 8·8–9·2 mm. Tergite 1 of gaster 2·25–2·35 times as long as broad, its dorsal profile as in Fig. 63. Gaster strongly compressed from posterior of segment 3, reaching to about tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·4 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 86.

Colour: black and reddish, with some yellow marks. Face reddish, yellowish laterally and with a black median stripe. Antenna blackish dorsally, scape and pedicel yellowish ventrally, flagellum brown ventrally. Maxillary palp reddish yellow, segments 4 distally and 5 wholly dark. Posterior part of propodeum entirely reddish. Hind coxa black with large dorsal and postero-ventral reddish patches. Hind femur reddish with a black stripe ventrally. Segments of gaster black anteriorly, very broadly reddish posteriorly.

Male. Width of lower face 0·80 times vertical length of eye. Malar space 0·60 times basal width of mandible. Maxillary palp as in Fig. 107; segment 4 considerably widened and flattened; segment 5 about 0·5 as long as 4. Antennal flag setae (similar to Fig. 126, but setae slightly longer) upright, long, flattened, 2 per segment, arising from a polished trough. Hind femur 5·25 times as long as deep. Fore wing length 8·3 mm. Tergite 1 of gaster 2·30 times as long as broad. Tergite 3 with a crease along its anterior 0·5 separating laterotergite.

Colour: black and yellow, with some reddish, especially on legs. Antenna black dorsally, scape and pedicel yellow ventrally, underside of flagellum reddish yellow proximally and distally, black medially. Maxillary palp with segments 1 brownish, 2 reddish yellow, 3 brownish and 4 and 5 blackish. Posterior part of propodeum entirely yellow. Hind coxa black, with a yellow dorsal spot contiguous interno-laterally with a postero-ventral spot. Hind femur reddish yellow with a black mark ventrally. Segments of gaster each black anteriorly, yellow posteriorly, the yellow tending to reddish, especially on sternites.

REMARKS. See 'Remarks' under *nox*.

BIOLOGY AND HOSTS. Virtually unknown. Adults have been collected in May and October. The specimens collected at Simla by Gupta and Joseph were from coniferous and deodar forest (Gupta, 1971: (appendix) 2, 3, 54).

DISTRIBUTION (Map 5, p. 22). Along the southern flank of the Himalayas at about 2000 m.

MATERIAL EXAMINED (11 ♀, 2 ♂).

India: 1 ♀, Himachal Pradesh, Simla, v.1897 (*Nurse*) (BMNH) (lectotype); 4 ♀, 1 ♂, Himachal Pradesh, Simla, 2133 m, 1 & 10.x.1962, 3.x.1966 (*Gupta, Joseph*) (GC); 1 ♀, Uttar Pradesh, Khurpatal, 11.x.1978 (*Gupta*) (GC); 1 ♀, 1 ♂, Uttar Pradesh, Mussoorie, 2100 m, 1.x.1962, 21.x.1972 (*Gupta, Khana*) (GC); 3 ♀, Uttar Pradesh, Nainital, 1938 m, 2–10 & 12.x.1978 (*Gupta*) (GC). **Nepal**: 1 ♀, 3·2 km SE. of Sikha, 2100–2400 m, 23.v.1954 (*Quinlan*) (BMNH).

***Banchus gudrunae* sp. n.**

(Figs 17, 40, 65, 66, 87, 108)

DESCRIPTION. Female. Width of lower face 0·75–0·85 times vertical length of eye. Malar space 0·45–0·55 times basal width of mandible. Maxillary palp as in Fig. 17. Antenna with apical segments longer than broad. Scutellar spine (Fig. 40) about 0·7 as long as scutellum. Mesopleuron and mesoscutum coriaceous, with moderately strong punctures, on mesopleuron separated by about their diameter. Hind femur 6·75–7·20 times as long as deep. Fore wing length 9·7–10·7 mm. Tergite 1 of gaster 2·00–2·50 times as long as broad, its dorsal profile as in Figs 65 (male), 66 (female). Gaster compressed from tergite 4, reaching about to tips of fore wings (when folded back). Tergite 3 with a crease along its whole length separating laterotergite. Tergite 7 and sternite 6 as in Fig. 87.

Colour: black and yellow. Face yellow with a black median stripe. Antenna black (sometimes slightly brownish distally), scape, and sometimes pedicel, with a yellow patch beneath. Maxillary palp reddish yellow with segment 1 and distal parts of 4 and 5 blackish. Posterior part of propodeum yellow, narrowly black posteriorly. Hind coxa black with a yellow dorsal patch. Hind femur yellowish with proximal half largely black. Segments of gaster each black anteriorly, yellow posteriorly, the yellow bands relatively wide.

Male. Width of lower face 0·80–0·90 times vertical length of eye. Malar space 0·45–0·65 times basal width of mandible. Maxillary palp as in Fig. 108; segment 4 flattened and widened distally; segment 5 about 0·5 as long as 4. Antennal flag setae (similar to Fig. 127, but with setae slightly shorter and very much broader) upright, relatively short, flattened and very broad, 2 (occasionally 3) per segment, arising from a polished trough. Hind femur 7·00–7·45 times as long as deep. Fore wing length 8·8–10·0 mm. Tergite 1 of gaster 2·10–2·40 times as long as broad. Tergite 3 with a crease along its whole length separating laterotergite.

Colour: black and yellow. Antenna black dorsally, scape and pedicel yellow ventrally, flagellum brownish ventrally. Maxillary palp reddish yellow, segment 1 dorsally narrowly black, segment 4 distally and 5 wholly blackish. Posterior part of propodeum yellow, very narrowly black posteriorly. Hind coxa black with a large yellow dorsal patch. Hind femur yellow, blackish on its proximal 0·3, especially ventrally and laterally. Segments of gaster each black anteriorly, very broadly yellow posteriorly.

REMARKS. This species has a number of characters which make relating it to any others in the Palaearctic difficult. The form of the male palp suggests a relationship with *palpalis* and *crefeldensis* but the flag setae are of a very much more specialized kind and the female palp is not specialized in the same way.

BIOLOGY AND HOSTS. Unknown. Dates of collection of adults range from the middle of November to the middle of January.

DISTRIBUTION (Map 6, p. 27). Known only from the island of Cyprus.

MATERIAL EXAMINED

Holotype ♂, **Cyprus**: Polemedia Hills, 14.xii.1948 (*Mavromoustakis*) (BMNH).

Paratypes 10 ♀, 9 ♂. **Cyprus**: 6 ♀, 3 ♂, Polemedia Hills, 14 & 20.xii.1948 (*Mavromoustakis*) (BMNH); 3 ♀, Palodkia, 5 & 12.i.1949 (*Mavromoustakis*) (BMNH); 1 ♀, Limassol, 4.i.1940 (*Mavromoustakis*) (USNM); 4 ♂, Zakaki Marshes, 29.xi.1946 (*Mavromoustakis*) (TC); 1 ♂, near Limassol, 18.xi.1946 (*Mavromoustakis*) (TC); 1 ♂, Paphos district, near Panayia, 900 m, 29.xi.1946 (*Mavromoustakis*) (TC).

Banchus hastator (Fabricius)

(Figs 18, 41, 64, 88, 109, 124)

Ichneumon hastator Fabricius, 1793: 167. Holotype ♀, EUROPE (UZM) [examined].

Ichneumon pungitor Thunberg, 1822: 265; 1824: 320. [Replacement name for *Ichneumon hastator* Fabricius.]

Ichneumon reticulator Thunberg, 1822: 265; 1824: 321. Type(s) ♂, SWEDEN (lost). **Syn. n.**

Banchus femoralis Thomson, 1897: 2411. Lectotype ♀, SWEDEN (UZI), designated by Townes, Momoi & Townes, 1965: 237 [examined].

Banchus kolosovi Meyer, 1925: 10. Syntypes 3 ♀, U.S.S.R. (destroyed). **Syn. n.**

NOMENCLATURE. This species until recently has been referred to by the junior synonym *femoralis*. It is dealt with in a relatively large number of non-taxonomic papers so the name change is particularly unfortunate. A further source of confusion is the incorrect use of the name *hastator* by Townes & Townes (1978) (see nomenclatural notes under *palpalis*).

Ichneumon pungitor is a junior objective synonym of *hastator*. It was proposed apparently because of the secondary homonymy in *Ichneumon*, in Thunberg's work, with *Foenus hastator* Fabricius, 1804 [which, incidentally, was miss-spelled as *vastator* by Thunberg (1822: 262; 1824: 315)]. The status of *pungitor* as a replacement name has not been recognized previously and it had been placed incorrectly in the synonymy of *B. volutatorius* (Linnaeus) (e.g. Aubert, 1978: 158).

Ichneumon reticulator has not been identified since its description. Roman (1912: 277) reported that there were no specimens in Thunberg's collection and suggested that the species was a *Banchus*. The description fits some males of *hastator*, with which it is here synonymised.

After its description, except for an entry in the *Zoological Record, B. kolosovi* was not referred to (even by Meyer) until Aubert (1978: 166) noted its existence. Aubert miss-spelled the name as *kozlovi*. The description fits particularly dark specimens of *hastator*, with which it is here synonymised. Notwithstanding Meyer's comments on *kolosovi* and *femoralis*, it seems that he realised his mistake because in his treatment of the genus (1934: 229) he mentions, under *femoralis*, material from Sverdlovsk (the type-locality of *kolosovi*) collected by Kolosov. This is presumably the type-material of *kolosovi*. No material collected by Kolosov is noted under other *Banchus* species by Meyer.

DESCRIPTION. Female. Width of lower face 0·85–0·90 times vertical length of eye. Malar space 0·50–0·65 times basal width of mandible. Maxillary palp as in Fig. 18. Antenna with apical segments longer than broad. Scutellar spine (Fig. 41) about 0·2 as long as scutellum. Mesopleuron and mesoscutum coriaceous, usually fairly weakly so, with moderate punctures, on mesopleuron separated by about their diameter. Hind femur 4·50–5·15 times as long as deep. Fore wing length 8·8–10·9 mm. Tergite 1 of gaster 1·50–1·70 times as long as broad, its dorsal profile as in Fig. 64. Gaster weakly compressed, reaching about to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·3 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 88.

Colour: mainly black, with yellow and reddish, particularly on legs. Face black with yellow orbital marks, which are usually small but are sometimes large and with a pair of very small reddish marks in centre of face. Antenna with scape and pedicel black, scape, and usually pedicel, yellow ventrally. Flagellum brown dorsally, reddish ventrally, darker at extreme base and apex. Maxillary palp reddish with segment 1 black and segments 2 proximally, 4 distally and 5 wholly darker. Posterior part of propodeum entirely black. Hind coxa black. Hind femur reddish or yellowish proximally and distally, medially varying from reddish dorsally and blackish ventrally to all blackish. Segments of gaster black, sometimes almost entirely except for brownish posterior margin of sternites 1 and 6 and tergite 7, but usually with posterior margins of further segments narrowly yellowish and with the yellow grading into a wider brownish band.

Male. Width of lower face 0·90–1·00 times vertical length of eye. Malar space 0·50–0·65 times basal width of mandible. Maxillary palp as in Fig. 109; segment 4 only slightly widened and flattened; segment 5 almost as long as 4. Antennal flag setae (Fig. 124) relatively poorly differentiated, small, not flattened, 2 per segment, not arising from a trough. Hind femur 4·60–5·50 times as long as deep. Fore wing length 7·2–10·7 mm. Tergite 1 of gaster 1·45–1·80 times as long as broad. Tergite 3 with a crease along its anterior 0·3 separating laterotergite.

Colour: mainly black, with some reddish and yellow, particularly on legs. Antenna black dorsally, scape and pedicel yellow ventrally, flagellum reddish ventrally. Maxillary palp with segment 1 blackish or blackish and yellow, 2 and 3 reddish, 4 and 5 blackish or brownish. Posterior part of propodeum entirely black. Hind coxa black (in a single specimen with a small yellowish dorsal spot and the postero-ventral margin reddish). Hind femur reddish or yellowish proximally and distally, medially varying from reddish dorsally and blackish ventrally to all blackish. Gaster sometimes almost entirely black except for brownish posterior margins of some segments, but usually with posterior margins of segments narrowly yellowish with adjacent brownish bands.

REMARKS. This is an isolated species, with few obvious specializations. The primitive condition of the antennal flag setae in the male is particularly notable.

BIOLOGY AND HOSTS. The species is an important parasite of *Panolis flammea* (Denis & Schiffermüller) (Noctuidae), which is sometimes a serious pest in pine forests. *B. hastator* is univoltine and adults occur in May, June and early July. Reared specimens have emergence dates in March and April also. Some details of the biology and ecology of the species have been investigated as a result of the association with an economically important host. Most of the work has been connected with its effect as a natural control agent (Friederichs, 1936; Habermehl, 1922, 1924; Pfeffer, 1933; Scheidter, 1934; Schwerdtfeger, 1952; Smits van Burgst, 1927) but has included studies of embryonic and larval development and morphology (Beirne, 1941; Błedowski & Kraińska, 1926; Shevyrev, 1913), courtship, host identification and host-stage preferences, egg-laying and the reproductive system (van Veen, 1982).

There are many specimens reared from *P. flammea* in collections. Apart from that species, the following species are recorded as hosts on specimen labels: *Blepharita adusta* (Esper) (Noctuidae) (1 ♀, 2 ♂, Germany (*Smits van Burgst coll.*) LELW); *Deilephila porcellus* (Linnaeus) (Sphingidae) (1 ♂, no locality (*Adkin*) BMNH); *Hyloicus pinastri* (Linnaeus) (Sphingidae) (1 ♀, Poland (*Mazur*) IZPAN) and *?Achlya flavicornis* (Linnaeus) (Thyatiridae) (1 ♀, Great Britain (*Lyle*) BMNH). While one might cast doubt on these records it is difficult to investigate them critically. Kolubajiv (1934: 114, 116) records *Lymantria dispar* (Linnaeus) (Lymantriidae) as a host.

DISTRIBUTION (Map 6, p. 27). Widely distributed in northern Europe as far east as Leningrad, perhaps extending further east to the Urals (if my synonymy of *kolosovi* is correct (see 'Nomenclature' above)). It also occurs in the European Alps and I have seen single individuals collected in Corsica and Yugoslavia.

Material examined (113 ♀, 151 ♂)

Belgium, Corsica, Denmark, East Germany, Finland, France, Great Britain, Ireland, Netherlands, Poland, Sweden, Switzerland, U.S.S.R., West Germany, Yugoslavia (AC, BC, BMNH, BRI, HC, IP, IRSNB, ITZ, IZPAN, LELW, KC, MNHN, MUM, NMB, NR, RNH, RSM, SC, SMT, UM, USNM, UZI, UZM, VRC, ZC, ZIL, ZMU, ZSBS).

Banchus insulanus Roman

(Figs 19, 42, 67, 89)

Banchus insulanus Roman, 1937: 18. Holotype ♀, Madeira (NR) [examined].

Description. Female. Width of lower face 0·85 times vertical length of eye. Malar space 0·55 times basal width of mandible. Maxillary palp as in Fig. 19. Antenna with apical segments longer than broad. Scutellar spine (Fig. 42) indistinct. Mesopleuron and mesoscutum coriaceous, with moderate punctures, on mesopleuron separated by more than their diameter. Hind femur 6·55 times as long as deep. Fore wing length 9·3–9·5 mm. Tergite 1 of gaster 1·65 times as long as broad, its dorsal profile as in Fig. 67. Gaster only weakly compressed, not reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its entire length separating laterotergite. Tergite 7 and sternite 6 as in Fig. 89.

Colour: mainly black, with yellow and reddish marks. Face black with irregular, yellow orbital marks. Antenna black. Maxillary palp blackish. Posterior part of propodeum black. Hind coxa black with a small yellow dorsal patch. Hind femur yellowish, blackish ventrally and posteriorly on its proximal 0·5. Segments of gaster blackish, in one specimen with only posterior 0·5 of tergite 3 and posterior 0·3 of tergite 7 reddish; in the other specimen with posterior 0·7 of tergite 2, almost all of tergite 3, posterior 0·5 of tergite 4, and tergites 5 and 6 laterally, reddish.

Male. Unknown (but see 'Remarks').

Remarks. The specimen described as the male by Hellén (1949: 13) proved, on examination, to be a female. The material collected in 1959 and supposedly including both sexes (Hellén, 1961: 37) cannot be found in Hellén's collection (A. Albrecht, pers. comm.).

The relationships of the species are not at all obvious from the characters of the female.

Biology and hosts. Unknown. Adults have been collected in May and July–August.

Distribution (Map 6, p. 27). Known only from the island of Madeira.

Material examined (2 ♀)

Madeira: 1 ♀, 25 Fontes, Rabacal, 17.vii–4.viii.1935 (*Lunblad*) (NR) (holotype); 1 ♀, Ribeiro Frio, 3.v.1938 (*Frey*) (ZMU).

Banchus japonicus (Ashmead)

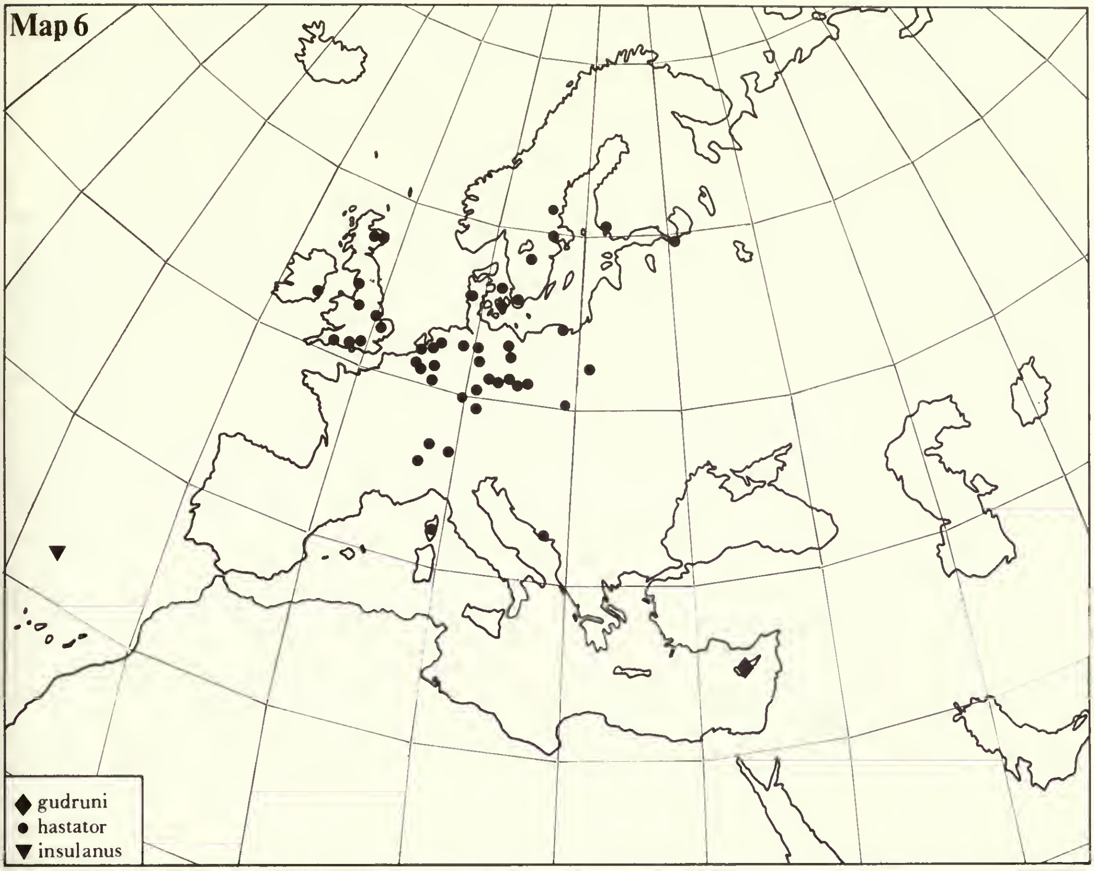
(Figs 20, 43, 68, 90, 110)

Nawaia japonica Ashmead, 1906: 185. LECTOTYPE ♀, Japan (USNM), here designated [examined].

Nomenclature. Ashmead described this species from two specimens, also stating 'Type. – Cat. No. 7259, U.S.N.M.', thus giving the impression that one was the holotype. However, both specimens are labelled 'Type No. 7259 U.S.N.M.' and must be considered as syntypes. Other labels include 'Nawaia japonica Ashm' on one specimen and 'Nawaia japonica Ash. Paratype' on the other, the latter on a similar label but in a different hand and obviously more modern than the former. The specimen labelled as paratype also bears a label '47' and is in much better condition than the other. I have labelled and hereby designate it as lectotype.

Description. Female. Width of lower face 0·80–0·90 times vertical length of eye. Malar space 0·35–0·45 times basal width of mandible. Maxillary palp as in Fig. 20. Antenna with apical segments about as long as broad. Scutellar spine (Fig. 43) about 0·3 as long as scutellum. Mesopleuron and mesoscutum shining and only weakly coriaceous, with moderate punctures, on mesopleuron separated by about their diameter. Hind femur 5·55–6·50 times as long as deep. Fore wing length 9·2–12·1 mm. Tergite 1 of gaster 1·45–1·85 times as long as broad, its dorsal profile as in Fig. 68. Gaster only weakly compressed, reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·5 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 90.

Colour: black and yellow. Face yellow with a broad median black stripe and sometimes a black mark below each antennal socket. Antenna black, with a small yellow mark on scape. Maxillary palp blackish, with a longitudinal yellow stripe ventrally on segments 1 and 2. Posterior part of propodeum yellow,



Map 6 Distribution of *Banchus gudrunae, B. hastator* and *B. insulanus.*

entirely or with a black area postero-medially. Hind coxa black with a yellow dorsal patch. Hind femur blackish, yellow proximally and distally. Segments of gaster black with posterior margins broadly yellow and with a pair of yellow spots on tergite 2 and usually also on 1 and 3.

Male. Width of lower face 0·90 times vertical length of eye. Malar space 0·35–0·45 times basal width of mandible. Maxillary palp as in Fig. 110; segment 4 flattened and considerably widened; segment 5 about 0·5 as long as 4. Antennal flag setae (similar in appearance to Fig. 126, but with setae longer) upright, long, flattened, 2 per segment, arising from trough which is not polished. Hind femur 6·25–6·75 times as long as deep. Fore wing length 9·3–10·3 mm. Tergite 1 of gaster 1·50–1·65 times as long as broad. Tergite 3 with a crease along almost its entire length separating laterotergite.

Colour: black and yellow. Antenna black with scape, pedicel and proximal end of flagellar segment 1 yellow ventrally. Maxillary palp with segment 1 yellow, 2 and 3 brownish yellow to blackish, 4 and 5 black. Posterior part of propodeum yellow, entirely or with small black marks posteriorly. Hind coxa black and yellow. Hind femur yellow with a black mark ventrally and interno-laterally, usually extending also to dorsal surface. Segments of gaster black with posterior margins broadly yellow and with a pair of yellow spots on tergite 2 and usually also on 1 and 3.

REMARKS. Although *japonicus* has been confused with *poppiti* the two species are easily separated.

BIOLOGY AND HOSTS. Unknown. Adults have been collected in May and June.

DISTRIBUTION (Map 2, p. 16). Japan. Recorded also from Korea (Kim, 1955: 493), from which country the only species of *Banchus* examined is *B. palpalis*.

MATERIAL EXAMINED (6 ♀, 6 ♂)

Japan: 1 ♀, Gifu, Fujishiro (*Nawa*) (USNM) (lectotype); 1 ♀, Gifu, Gifu-yama (*Nawa*) (USNM) (paralectotype); 1 ♀, Hokkaido (*Uchida*) (TC); 1 ♀, 3 ♂, Hokkaido, Mt Soranuma, 26.vi.1965 and

15.vi.1968 (*Kusigemati*) (KC); 1 ♂, Hokkaido, Toya-ko, 14.vi.1967 (*Miyazaki*) (KC); 1 ♀, Honshu, Tokyo, Komaba, 9.v.1916 (*Hirayama*) (EIHU); 1 ♂, Honshu, Hyogo Pref., Ryuzoji, Sasayama, 5.v.1965 (*Nakanishi*) (NC); 1 ♀, Honshu, Tottori Pref., Mt Daisen, 12.vi.1963 (*Nakanishi*) (NC); 1 ♂, Honshu, Yatsugatake, 2.vi.1967 (*Kocha*) (KC).

***Banchus mauricettae* sp. n.**

(Figs 21, 44, 69, 91, 111)

DESCRIPTION. Female. Width of lower face 0·90–0·95 times vertical length of eye. Malar space 0·55 times basal width of mandible. Maxillary palp as in Fig. 21. Antenna with apical segments longer than broad. Scutellar spine (Fig. 44) about as long as scutellum. Mesopleuron and mesoscutum coriaceous, with moderate to strong punctures, on mesopleuron separated by a little more than their diameter. Hind femur 5·20–5·30 times as long as deep. Fore wing length 10·5–10·6 mm. Tergite 1 of gaster 1·90–2·35 times as long as broad, its dorsal profile as in Fig. 69 (male). Gaster moderately compressed, not quite reaching tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·6 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 91.

Colour: yellowish red with black and yellow marks. Face yellowish red with orbits yellow and sometimes with a blackish median stripe. Antenna entirely reddish yellow except for extreme apex of flagellum and scape and pedicel dorsally, which are blackish. Maxillary palp reddish yellow with segments 4 distally and 5 wholly dark. Posterior part of propodeum reddish, entirely or with black marks posteriorly. Hind coxa varying from reddish with black patches to almost entirely black. Hind femur entirely reddish. Segments of gaster entirely reddish or with some black anteriorly.

Male. Width of lower face 0·85–0·90 times vertical length of eye. Malar space 0·60–0·65 times basal width of mandible. Maxillary palp as in Fig. 111; segment 4 flattened and widened; segment 5 about 0·8 as long as 4. Antennal flag setae (similar in appearance to Fig. 129, but with setae only two-thirds as long) upright, fairly short and broad, 3 (occasionally 4) per segment, arising from a polished trough. Hind femur 5·95–6·20 times as long as deep. Fore wing length 11·2–12·3 mm. Tergite 1 of gaster 2·20–2·35 times as long as broad. Tergite 3 with a crease along its anterior 0·6 separating laterotergite.

Colour: yellow, reddish and black. Antenna blackish dorsally, scape and pedicel yellow ventrally, flagellum reddish yellow ventrally. Maxillary palp reddish yellow with segments 4 distally and 5 wholly blackish. Posterior part of propodeum entirely yellow. Hind coxa largely reddish yellow, blackish or brownish antero-ventrally and dorso-posteriorly. Hind femur reddish, sometimes with a blackish mark ventrally. Segments of gaster each black, reddish and yellow (from anterior to posterior), the area of black reduced or absent on posterior segments.

REMARKS. This is a distinctive species; its relationships are difficult to discern.

BIOLOGY AND HOSTS. Unknown. Dates of collection are in June and July.

DISTRIBUTION (Map 2, p. 16). The Szechuen province of China. Altitudes given on data labels range from 300–4500 m.

MATERIAL EXAMINED

Holotype ♂, **China**: Szechuen, Yao-Gi, 1200–2400 m, 3.vii.1929 (*Graham*) (USNM).

Paratypes 4 ♀, 10 ♂. **China**: 1 ♀, 2 ♂, Szechuen, Yao-Gi, 1200–2400 m, 3 & 16.vii.1929 (*Graham*) (USNM); 2 ♂, Szechuen, near Mupin, 600–2400 m, 28.vi & 22.vii.1929 (*Graham*) (USNM); 1 ♂, Szechuen, Ningyuenfu, 1800–3240 m, 24–26.vii.1928 (*Graham*) (USNM); 1 ♂, Szechuen, Mt Omei, 840 m, vi.1937 (*Graham*) (USNM); 1 ♂, Szechuen, Suifu, 300–450 m, 1–21.vi.1928 (*Graham*) (USNM); 2 ♂, Szechuen, 14·5 km SW. of Tatsienlu, 2550–3900 m, 25–27.vi.1923 (*Graham*) (USNM); 1 ♂, Szechuen, U Long Kong, near Tatsienlu, 3000–4500 m, 25–30.vi.1923 (*Graham*) (USNM); 2 ♀, Szechuen, Yachow, v–vi.1928 (*Graham*) (USNM); 1 ♀, Szechuen, Yachow to Mupin, 600–1500 m, 23–27.vi.1929 (*Graham*) (USNM).

***Banchus moppiti* sp. n.**

(Figs 22, 45, 70, 92, 113, 127)

DESCRIPTION. Female. Width of lower face 1·10–1·20 times vertical length of eye. Malar space 0·85–1·00 times basal width of mandible. Maxillary palp as in Fig. 22. Antenna with apical segments about as broad as long. Scutellar spine (Fig. 45) about 0·6 as long as scutellum, usually downcurved at the tip. Mesopleuron and mesoscutum coriaceous, usually strongly so, with strong punctures, on mesopleuron separated by much less than their diameter. Hind femur 4·75–5·20 times as long as deep. Fore wing length 8·2–10·8 mm. Tergite 1 of gaster 1·60–1·80 times as long as broad, its dorsal profile as in Fig. 70. Gaster compressed from segment 4, reaching just beyond tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·3 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 92.

Colour: black and yellow. Face black with yellow orbital stripes, usually broad but varying considerably in width. Antenna black, usually with a small yellow patch on underside of scape. Maxillary palp blackish. Posterior part of propodeum black with a broad yellow stripe along posterior transverse carina. Hind coxa black, usually with a small yellow dorsal patch. Hind femur black, yellow proximally and distally and usually dorsally. Segments of gaster each black anteriorly, broadly yellow posteriorly.

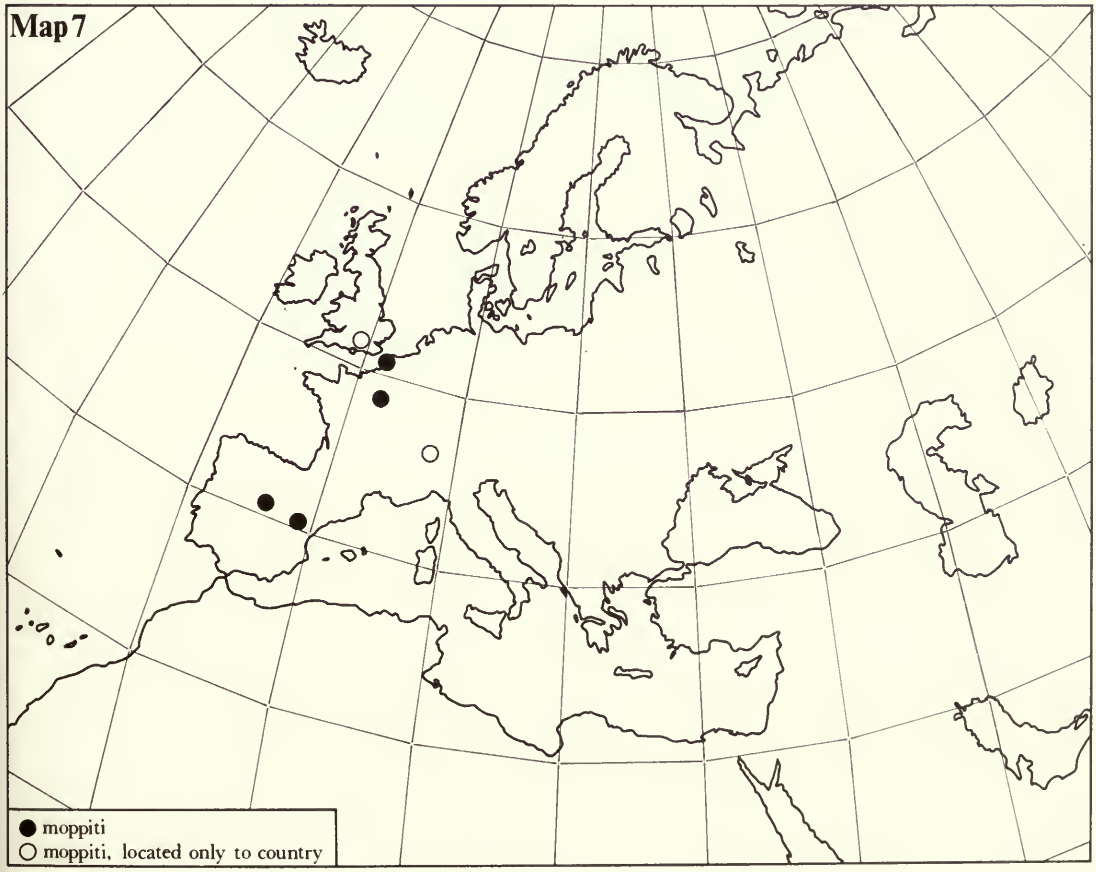
Male. Width of lower face 1·10–1·20 times vertical length of eye. Malar space 0·75–0·95 times basal width of mandible. Maxillary palp as in Fig. 113; segment 4 flattened and widened; segment 5 not quite as long as 4. Antennal flag setae (Fig. 127) upright, relatively short, flattened and widened, 2 per segment, arising from a polished trough. Hind femur 4·80–5·50 times as long as deep. Fore wing length 8·5–10·9 mm. Tergite 1 of gaster 1·45–1·60 times as long as broad. Tergite 3 with a crease along its anterior 0·3 separating laterotergite.

Colour: black and yellow. Antenna black with scape and pedicel yellow ventrally. Maxillary palp blackish. Posterior part of propodeum yellow anteriorly, black posteriorly. Hind coxa black, usually with a yellow dorsal spot and sometimes also a postero-lateral one. Hind femur yellow with an extensive black mark, extending ventrally and laterally. Segments of gaster each black anteriorly, yellow posteriorly.

REMARKS. This species seems closely related to *zonatus*. Its generally much smaller size and relatively shorter appendages (and gaster in females) readily differentiate it.

BIOLOGY AND HOSTS. Unknown. The specimens were collected early in the year (in February, March and April) with the exception of a female taken in October.

DISTRIBUTION (Map 7, p. 29). The few known specimens come from widely scattered localities in western Europe.



Map 7 Distribution of *Banchus moppiti*.

MATERIAL EXAMINED

Holotype ♀, **Spain**: Madrid, Cercedilla, 22.x.1978 (*Noyes*) (BMNH).

Paratypes 6 ♀, 4 ♂. **France**: 1 ♂, Vincennes, 20.ii.1885 (*de Gaulle* coll.) (MNHN); 1 ♂, Boulogne, 22.iii (*Giraud* coll.) (MNHN). **Great Britain**: 1 ♀ (*Desvignes* coll.) (BMNH). **Spain**: 4 ♀, 2 ♂, Teruel, 15.iii.82 (*Hiendlmayr* coll.) [note – only 1 ♀ of these 6 specimens has the locality and date but all are identically mounted and set] (ZSBS). **Switzerland**: 1 ♀, 7.iv.1861 (*Sichel* coll.) (MNHN).

Banchus nox Morley

(Figs 23, 46, 71, 93, 112)

Banchus nox Morley, 1913: 255. Holotype ♂, INDIA (BMNH) [examined].

NOMENCLATURE. The species misidentified as *nox* by Chandra & Gupta (1977: 182) is *B. punkettai*.

DESCRIPTION. Female. Width of lower face 0·80 times vertical length of eye. Malar space 0·55 times basal width of mandible. Maxillary palp as in Fig. 23. Antenna with apical segments longer than broad. Scutellar spine (Fig. 46) about 0·7 as long as scutellum. Mesopleuron and mesoscutum coriaceous, with moderate punctures, on mesopleuron separated by a little more than their diameter. Hind femur 6·40 times as long as deep. Fore wing length 11·2 mm. Tergite 1 of gaster 2·70 times as long as broad, its dorsal profile as in Fig. 71 (male). Gaster strongly compressed from posterior of segment 3, not reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·4 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 93.

Colour: black and reddish, with some yellow marks. Face black with very broad yellow orbital marks which also extend beneath antennal sockets. Antenna dark brown, blackish dorsally, scape and pedicel yellowish ventrally. Maxillary palp reddish yellow, with segment 1 dorsally and segment 4 distally blackish. Posterior part of propodeum blackish with an irregular reddish yellow band along posterior transverse carina. Hind coxa black with a large reddish dorsal patch. Hind femur reddish with a black stripe ventrally. Segments of gaster reddish, tergites 1, 2 and 3 black anteriorly.

Male. Width of lower face 0·85 times vertical length of eye. Malar space 0·50 times basal width of mandible. Maxillary palp as in Fig. 112; segment 4 flattened and considerably widened; segment 5 about 0·6 as long as 4. Antennal flag setae (similar to Fig. 126, but setae slightly longer) upright, long, flattened, 2 per segment, arising from a polished trough. Hind femur 6·05 times as long as deep. Fore wing length 9·7 mm. Tergite 1 of gaster 2·15 times as long as broad. Tergite 3 with a crease along its anterior 0·5 separating laterotergite.

Colour: black and yellow, with some reddish, especially on legs. Antenna black dorsally, scape and pedicel yellow ventrally, underside of flagellum with segment 1 and distal part reddish yellow, remainder black. Maxillary palp with segment 1 yellowish, 2 and 3 wholly and 4 proximally reddish yellow, 4 distally and 5 wholly brownish. Posterior part of propodeum yellow, narrowly black postero-medially. Hind coxa black, with a yellow dorsal spot contiguous interno-laterally with a postero-ventral spot. Hind femur reddish with a black mark ventrally. Segments of gaster each black anteriorly, yellow posteriorly, with junction of the two areas reddish.

REMARKS. Closely related to *flavomaculatus*. The aggregate differences between these taxa warrant their separation, but this will need to be reassessed when more material becomes available for study.

BIOLOGY AND HOSTS. The only two known specimens were collected in October and November, the male on flowers of *Spiraea* (Morley, 1913: 255).

DISTRIBUTION (Map 2, p. 16). Assam, between 1800 and 2400 m.

MATERIAL EXAMINED (1 ♀, 1 ♂)

India: 1 ♂, Assam, Shillong, Khasi Hills, 1800 m, x.1903 (*Turner*) (BMNH) (holotype); 1 ♀, Assam, Mishmi Hills, Delai Valley, Cha Che, 2200–2400 m, 21.xi.1936 (*Steele*) (BMNH).

Banchus palpalis Ruthe

(Figs 1, 24, 47, 72, 94, 114)

[*Banchus monileatus* Gravenhorst, 1829: 393; in part. Misidentification.]

Banchus palpalis Ruthe, 1859: 377. Syntypes 2 ♂, ICELAND (lost).

Banchus spinosus Cresson, 1865: 274. Holotype ♀ [not ♂ as stated by Cresson], U.S.A. (ANS) [not examined]. **Syn. n.**

Banchus formidabilis Provancher, 1874: 61. Holotype ♀, CANADA (UL) [not examined]. **Syn. n.**

Banchus (Corynephanus) groenlandicus Aurivillius, 1890: 30. Lectotype ♂, GREENLAND (NR), designated by Townes, 1961: 104 [examined]. **Syn. n.**

Cidaphurus alticola Ashmead, 1901: 148. Holotype ♀ [not ♂ as stated by Ashmead], U.S.A. (USNM) [not examined]. **Syn. n.**

NOMENCLATURE. For almost 150 years the name *monileatus* was applied consistently to this species. However, two species were mixed in Gravenhorst's original material and a series of unfortunate events culminated in Townes & Townes (1978: 532) designating as lectotype of *monileatus* a female which was *volutatorius*, rather than the species as it had been identified previously. In addition, as a result of misinformation about my examination of the holotype of *hastator*, Townes & Townes incorrectly synonymized *monileatus* with that species. Female *volutatorius* and *palpalis* superficially are strikingly similar, so much so that Aubert (1978: 156), without realising that he was examining *volutatorius*, commented that Townes' lectotype differed from *volutatorius* only in certain details! When he originally examined Gravenhorst's syntypes (in 1964) Townes probably checked the identity of the species and then made the mistake of selecting the specimen in best condition for designation as lectotype without re-checking it. Under the *International Code* the lectotype designation has priority over the previous restriction of the taxonomic species.

Thus *monileatus* becomes a junior synonym of *volutatorius* while the species previously known as *monileatus* must take the next available name – *palpalis*. The name *hastator* correctly applies to the species previously known by the junior synonym *femoralis*.

The identity of *palpalis* was established by Roman (1928: 24; 1930: 285) and Fitton (1978*a*: 76).

Banchus spinosus, B. formidabilis and *Cidaphurus alticola* are included in the synonymy of *palpalis* on the basis of their treatment in Townes & Townes (1978).

DESCRIPTION. Female. Width of lower face 0·80–0·90 times vertical length of eye. Malar space 0·65–0·75 times basal width of mandible. Maxillary palp as in Fig. 24. Antenna with apical segments longer than broad. Scutellar spine (Fig. 47) long, more than 0·8 as long as scutellum (in a very few specimens only 0·3 as long as scutellum). Mesopleuron and mesoscutum coriaceous, with fine to moderate punctures, on mesopleuron separated by a little more than their diameter. Hind femur 5·00–5·95 times as long as deep. Fore wing length 9·8–11·5 mm. Tergite 1 of gaster 1·65–2·15 times as long as broad, its dorsal profile as in Fig. 72 (male). Gaster compressed from posterior of segment 3, not quite reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·4 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 94.

Colour: almost entirely black except for mainly reddish legs and a few small yellowish marks. Face black with yellow orbital marks, usually very small and sometimes absent. Antenna black, entirely or with yellowish marks ventrally on scape and pedicel. Maxillary palp yellowish or brownish with segments 1 and 5 wholly and 3 and 4 distally blackish. Posterior part of propodeum entirely black. Hind coxa black. Hind femur reddish yellow, usually entirely, rarely darkened ventrally. Segments of gaster black, sternites and posterior edges of tergites 6 and 7 sometimes brownish.

Male (Fig. 1). Width of lower face 0·90–0·95 times vertical length of eye. Malar space 0·60–0·70 times basal width of mandible. Maxillary palp as in Fig. 114; segment 4 narrow and cylindrical, flattened and widened only at its extreme distal apex; segment 5 less than 0·2 as long as 4. Antennal flag setae (similar to Fig. 125, but setae slightly longer and showing signs of flattening) at about 50 degrees, very weakly flattened, 3 per segment, not arising from a trough. Hind femur 5·35–6·10 times as long as deep. Fore wing length 9·8–11·4 mm. Tergite 1 of gaster 1·90–2·25 times as long as broad. Tergite 3 with a crease along its anterior 0·5 separating laterotergite.

Colour: black, with some yellow and with legs mainly reddish yellow. Antenna black, scape and pedicel yellow ventrally, proximal and distal parts of flagellum often brownish yellow ventrally. Maxillary palp with segments 1 and 2 wholly and 3 and 4 proximally reddish yellow, 3 and 4 distally and 5 wholly blackish. Posterior part of propodeum usually entirely black, sometimes with a transverse yellow mark (or marks) immediately behind posterior transverse carina. Hind coxa sometimes entirely black, usually with an externo-lateral reddish yellow mark and sometimes also dorsal and/or ventral yellowish spots. Hind femur entirely reddish yellow. Segments of gaster black, sometimes brownish or yellowish on their posterior margins, very rarely with conspicuous yellow bands on tergites 1, 2 and 3.

REMARKS. Easily identified from the structure of the maxillary palps. Nonetheless, it is confused with female *volutatorius* by incompetent or overconfident identifiers. Its presumed sister-species is *crefeldensis*.

The males with well-developed yellow marking and conspicuous yellow bands on the gaster come mainly, but not exclusively, from the southern parts of the range. In North America, where the geographical variation in colour may be more consistent and also applies to females, this form has been recognized as a separate 'subspecies' (Townes & Townes, 1978: 533).

Biology and hosts. Adults normally occur from mid-June to mid-August, with one record from Switzerland as early as 22 May and one from Yugoslavia as late as September. In Europe the usual host seems to be *Blepharita adusta* (Esper) (Noctuidae), from which I have seen 39 reared specimens. Of these, 34, possibly 35, come from a single mass rearing (with the only data: Germany (*Smits van Burgst* coll.) (LELW)). In Great Britain *Blepharita adusta* is more common in the north (Bretherton, Goater & Lorimer, 1983) and the records of *palpalis* show a similar pattern.

Hosts recorded in the literature are: *Panolis flammea* (Denis & Schiffermüller) (Noctuidae) (Smits van Burgst, 1927: 239), *Lacanobia oleracea* (Linnaeus) (Noctuidae) (Meyer, 1934: 231) and *Deilephila porcellus* (Linnaeus) (Sphingidae) (Leonardi, 1928: 87). The record from *L. oleracea*, at least, can probably be dismissed as having resulted from the misidentification of female *volutatorius*.

Distribution (Map 8, p. 32). The only Holarctic species of *Banchus*. Very widely distributed; in the more southern parts of its range it occurs at higher altitudes (for example, altitudes of 1800 to 2100 m are recorded for the specimens from Austria, Yugoslavia, Bulgaria, Greece and Turkey).

Map 8 Distribution of *Banchus palpalis* (the North American records are taken from Townes & Townes, 1978).

Material examined (103 ♀, 88 ♂)

Belgium, Bulgaria, Canada, Denmark, East Germany, Finland, France, Great Britain, Greece, Iceland, Ireland, Italy, Japan, Korea, Netherlands, Poland, Sweden, Switzerland, Turkey, West Germany, U.S.A., U.S.S.R., Yugoslavia (BC, BMNH, BRI, EIHU, FSA, HC, IEUB, IRSNB, IZPAN, JC, JKC, KC, LELW, MHN, MNHN, MNHU, MUM, NC, NR, RNH, USNM, UZM, VRC, ZC, ZI, ZMU, ZSBS).

Banchus pictus Fabricius

(Figs 25, 49, 50, 73, 95, 115)

Ichneumon cultratus Gmelin, 1790: 2708. Type(s) [?sex], Europe (destroyed). [Junior (by first reviser choice of Gravenhorst, 1829: 382, 1006) primary homonym of *Ichneumon cultratus* Gmelin, 1790: 2699.]

Ichneumon mutillatus Christ, 1791: 358. Type(s) ♂, no type-locality (lost). [Junior primary homonym of *Ichneumon mutillatus* Gmelin, 1790: 2716.]

Banchus pictus Fabricius, 1798: 234. Lectotype ♀, Germany (UZM), designated by Townes, Momoi & Townes, 1965: 238 [examined].

Banchus zagoriensis Hensch, 1928: 100. ?Syntypes 2 ♀, 1 ♂, Yugoslavia (ZSBS) [examined].

Banchus bipunctatus Hensch, 1928: 101. Holotype ♂, Yugoslavia (ZPZ) [examined].

Banchus russiator Aubert, 1978: 157. [Unavailable name published conditionally (Article 15 of the *Code*).]

Banchus russiator Aubert, 1981: 18. Holotype ♀, U.S.S.R. (AC) [examined]. **Syn. n.**

Nomenclature. The synonymy of *I. cultratus* with *pictus* was queried by Aubert (1978: 157) but he gave no reasons for so doing and I can find none.

The description of *Ichneumon mutillatus* Christ fits well the male of *pictus* and the synonymy, proposed by Gravenhorst (1829: 383) but queried by Aubert (1978: 157), is accepted. The Christ name is unavailable because of its homonymy with *I. mutillatus* Gmelin, which is a replacement name for *I. mutillarius* Fabricius, 1787: 271 (a junior homonym of *I. multillarius* Fabricius, 1775: 342).

I did not succeed in obtaining on loan material from the Hensch collection. However, Dr K. Horstmann was able to visit Zagreb in 1980 and in the course of his work on the species of Ichneumonidae described by Hensch he made the types of the *Banchus* species available to me. Unfortunately the specimen tentatively selected for designation as lectotype of *B. zagoriensis* had the date of collection 28 August 1928 and could not therefore have been a syntype as the description was published on 1 September 1928 (Horstmann, 1982*a*: 82). Three specimens labelled as cotypes (= syntypes) of *B. zagoriensis* are present in the Bauer collection (ZSBS). Because they bear no dates of collection and because the cotype labels were almost certainly added by Bauer and not Hensch (Horstmann, pers. comm.) they are only tentatively regarded as syntypes. Selection and designation of a lectotype for *B. zagoriensis* is best deferred until the other material in the Hensch collection can be examined. The identity of the species is not in doubt.

Description. Female. Width of lower face 0·80–0·95 times vertical length of eye. Malar space 0·40–0·50 times basal width of mandible. Maxillary palp as in Fig. 25. Antenna with apical segments slightly longer than broad. Scutellar spine (Figs 49, 50) ranging from very small to about 0·6 as long as scutellum. Mesopleuron and mesoscutum coriaceous, with strong punctures, on mesopleuron separated by less than their diameter. Hind femur 5·00–5·50 times as long as deep. Fore wing length 8·1–10·6 mm. Tergite 1 of gaster 1·45–1·65 times as long as broad, its dorsal profile as in Fig. 73. Gaster compressed, reaching just beyond tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·2 to 0·3 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 95.

Colour: black and yellow. Face yellow, with a black median stripe (rarely rather wide). Antenna with scape and pedicel black dorsally, yellow ventrally. Flagellum orange, sometimes slightly darker dorsally, almost always with segment 1 proximally blackish and distal segments dark. Maxillary palp reddish yellow, with segment 1 black and sometimes segments 2 proximally and 4 distally darkened. Posterior part of propodeum yellow anteriorly, black posteriorly; the yellow area varying considerably in extent, from covering almost all of the area to being divided by the black area medially, reduced to a pair of spots, or (very rarely) entirely absent. Hind coxa black, entirely or with a yellow dorsal patch. Hind femur medially black (sometimes brownish red, especially dorsally), yellow proximally and distally. Segments of gaster each black anteriorly, broadly yellow posteriorly.

Male. Width of lower face 0·85–1·00 times vertical length of eye. Malar space 0·45–0·55 times basal width of mandible. Maxillary palp as in Fig. 115; segment 4 moderately widened and flattened; segment 5 about 0·9 as long as 4. Antennal flag setae (similar to Fig. 125, but setae shorter) at about 60 degrees, short, not flattened, 2 per segment, not arising from a trough. Hind femur 5·05–5·65 times as long as deep. Fore wing length 8·1–10·3 mm. Tergite 1 of gaster 1·45–1·70 times as long as broad. Tergite 3 with a crease along its anterior 0·3 separating laterotergite.

Colour: black and yellow. Antenna with scape and pedicel black dorsally, yellow ventrally. Flagellum reddish orange, dorsally darker (blackish at base and apex). Maxillary palp blackish, sometimes entirely, but usually with segments 2 and 3 wholly and 4 and 5 proximally yellowish brown. Posterior part of propodeum black, entirely or with a pair of antero-lateral yellow patches (rarely the yellow more extensive, very rarely posterior part of propodeum entirely yellow). Hind coxa black, often with a dorsal yellow patch. Hind femur medially black (sometimes brownish red, especially dorsally), yellow proximally and distally. Segments of gaster each black anteriorly, broadly yellow posteriorly.

REMARKS. Specimens of *turcator* have been confused with *pictus*. The two species can be distinguished using the characters given in the key.

The morphospecies *pictus*, as here defined, has variations in time of occurrence of adults, length of the scutellar spine, and sex ratios which need further investigation and explanation.

There are two distinct periods of occurrence of adults. When this was noted 184 specimens were to hand. Of these 90 had a date of collection, 48 were captured between 10 April and 3 June and 42 between 1 July and 2 October (most of the latter batch after 10 August). The length of the scutellar spine varies from very small to about 0·6 as long as the scutellum. Although there is continuous variation in the length of the spine most of the specimens with a short spine were collected in the first period and most of those with a longer spine in the second. The sex ratio of the 48 specimens collected in the first period was 1·18 ♀: 1 ♂ and of the 42 in the second period 4·25 ♀: 1♂.

Three possible biological explanations of these observations are that (1) *pictus* is bivoltine, with the generations varying slightly in morphology and more distinctly in sex ratio; (2) the early and late summer groups represent separate species; or (3) that one species has a partial second generation and a second species (possibly parthenogenetic) occurs in late summer.

If two species were involved diligent study should have revealed variation in some morphological characters, colour, geographical distribution, or host or other biological data correlated with date of capture or length of scutellar spine. None was found. Assignment of the 94 specimens without a date of capture to two subjective classes – with short or long scutellar spine – gave groups which varied in sex ratio in the same way as the early and late summer groups (short spine, 58 specimens, 1·55 ♀: 1 ♂; long spine, 36 specimens, 5 ♀: 1 ♂). The only other relevant evidence comes from two reared specimens: two larvae of the noctuid *Agrochola helvola* (Linnaeus) collected near Sheffield, Great Britain (*Ford*) (UM) on 13 June 1969 proved to be parasitized. The parasite larvae emerged in August 1969 and spun cocoons. The resulting adults (1 ♀ 1 ♂) did not emerge until early May 1970.

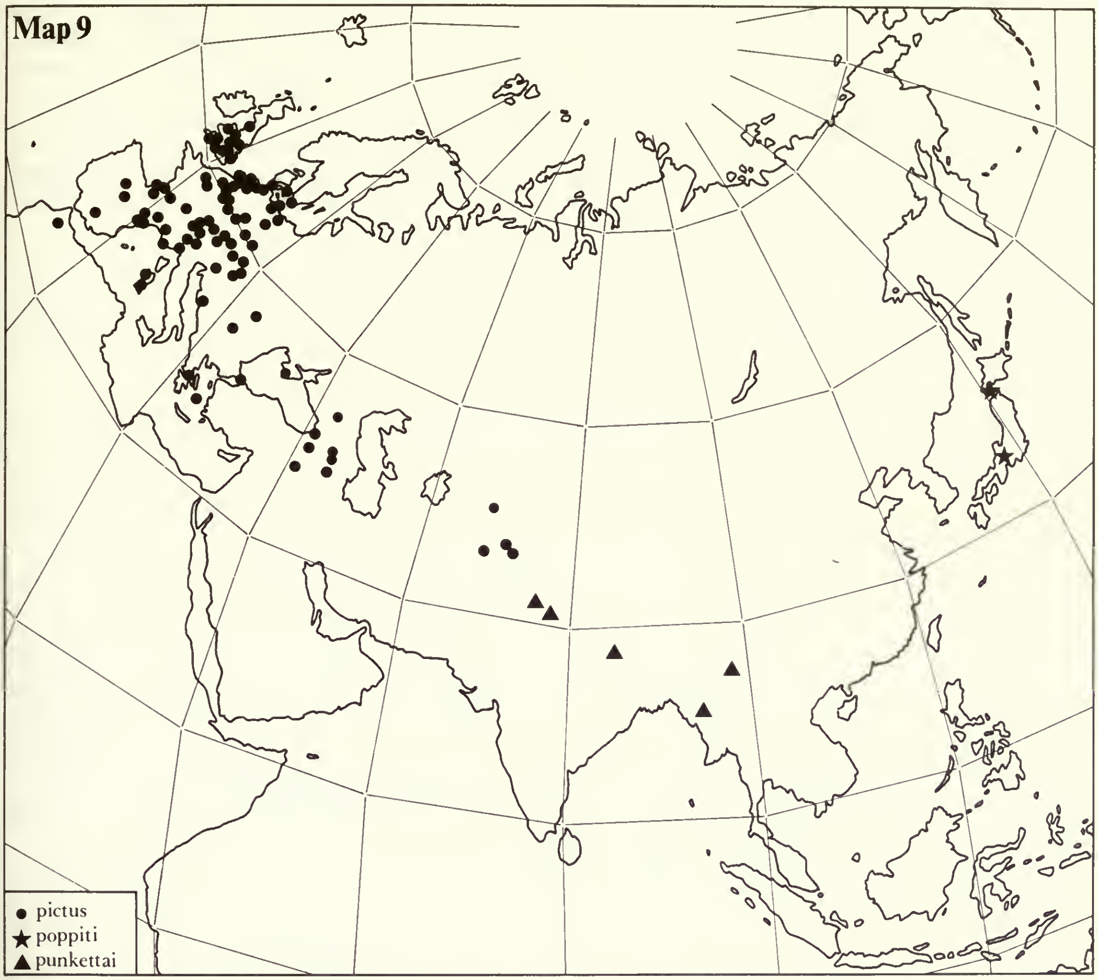
None of this evidence gives unambiguous support to any of the three suggested explanations of the observations. Even the one year life-cycle of the specimens reared in Sheffield could be explained by postulating univoltinism in the northern part of the range of the species and bivoltinism in the south (although no evidence of this was found). However, the balance *is* perhaps in favour of the involvement of more than one species, if only because there is no undisputed evidence of bivoltinism in any other species of *Banchus*. The poor quality and quantity of the available data and the possible complexity of the situation mean that the problem remains unresolved – a fruitful field for future study.

BIOLOGY AND HOSTS. For information on phenology see 'Remarks' above. I have seen only three reared specimens of *pictus*, from *Agrochola helvola* (Linnaeus) (Noctuidae) (all from Great Britain (*Lyle* and *Ford*) BMNH and UM). There are several hosts noted in the literature, but as black-and-yellow *Banchus* are frequently misidentified as *pictus* they should be treated with caution. The recorded hosts are: *Agrochola circellaris* (Hufnagel) (Noctuidae) (Habermehl, 1922: 269), *Agrotis segetum* (Denis & Schiffermüller) (Noctuidae) (Bajári, 1960: 261), *Atethmia ambusta* (Denis & Schiffermüller) (Noctuidae) (Schmiedeknecht, 1910: 1928), *Lycophotia porphyrea* (Denis & Schiffermüller) (Noctuidae) (de Gaulle, 1907: 119), *Hadena rivularis* (Fabricius) (Noctuidae) (Wagner, 1929: 11), *Phalera bucephala* (Linnaeus) (Notodontidae) (Leonardi, 1928: 83) and *Smerinthus ocellata* (Linnaeus) (Sphingidae) (Meyer, 1934: 228).

DISTRIBUTION (Map 9, p. 35). Widely distributed in the western Palaearctic as far north as 56°N in the west, and extending south-east as far as the Pamirs.

MATERIAL EXAMINED (162 ♀, 75 ♂).

Austria, Belgium, Czechoslovakia, Denmark, East Germany, France, Great Britain, Greece, Hungary, Italy, Morocco, Netherlands, Poland, Portugal, Rumania, Sardinia, Spain, Sweden, Switzerland, Turkey, U.S.S.R., West Germany, Yugoslavia (AC, BMNH, BRI, CM, FSA, HC, IBMPP, IEAU, IEE, IP, IRSNB, KHC, LELW, MCSN, MHN, MIZS, MLSU, MNHN, MUM, NM, NMB, NR, PC, RNH, RSM, TM, UM, USNM, UZI, UZM, VRC, ZC, ZIL, ZMU, ZSBS).



Map 9 Distribution of *Banchus pictus, B. poppiti* and *B. punkettai.*

Banchus poppiti sp. n.

(Figs 26, 48, 74, 96, 116)

Description. Female. Width of lower face 0·90 times vertical length of eye. Malar space 0·55–0·65 times basal width of mandible. Maxillary palp as in Fig. 26. Antenna with apical segments longer than broad. Scutellar spine (Fig. 48) about 0·4 as long as scutellum. Mesopleuron and mesoscutum coriaceous, with moderate punctures, on mesopleuron separated by about their diameter. Hind femur 5·25–5·65 times as long as deep. Fore wing length 10·3–11·1 mm. Tergite 1 of gaster 1·65 times as long as broad, its dorsal profile as in Fig. 74 (male). Gaster very weakly compressed, not reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·4 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 96.

Colour: black and yellow, the margins of some yellow areas slightly reddish. Face black with yellow orbital stripes. Antenna with scape and pedicel black dorsally, yellow ventrally. Flagellum orange ventrally, dark dorsally. Maxillary palp yellowish with segments 1 dorsally, 4 distally, and 5 wholly dark. Posterior part of propodeum yellow, entirely or with posterior margin black. Hind coxa black with a large yellow dorsal patch. Hind femur black, narrowly reddish yellow proximally and distally. Segments of gaster black, narrowly yellow posteriorly.

Male. Width of lower face 0·95 times vertical length of eye. Malar space 0·50–0·65 times basal width of mandible. Maxillary palp as in Fig. 116; segment 4 flattened and widened; segment 5 about 0·5 as long as 4.

Antennal flag setae (similar to Fig. 127, but with setae narrower) upright, flattened, 2 per segment, arising from a polished trough. Hind femur 5·60–6·10 times as long as deep. Fore wing length 11·1–11·2 mm. Tergite 1 of gaster 1·65–1·90 times as long as broad. Tergite 3 with a crease along its anterior 0·4 separating laterotergite.

Colour: black and yellow, the margins of some yellow areas slightly reddish. Antenna black dorsally, yellow ventrally. Maxillary palp yellow with segments 4 distally and 5 wholly blackish. Posterior part of propodeum yellow, entirely or narrowly black postero-medially. Hind coxa black with very large dorsal and ventral yellow patches. Hind femur yellow, black-marked ventrally and internally, tending to reddish distally. Segments of gaster each black anteriorly, black posteriorly.

REMARKS. This species has not previously been differentiated from *japonicus*.

BIOLOGY AND HOSTS. Unknown. Adults have been collected in May and June.

DISTRIBUTION (Map 9, p. 35). Japan.

MATERIAL EXAMINED

Holotype ♂, **Japan**: Hakodate, 12.vi.1926 (*Malaise*) (NR).

Paratypes 2 ♀, 1 ♂. **Japan**: 1 ♀, 1 ♂, Hakodate, 12.vi.1926 (*Malaise*) (NR); 1 ♀, Mt Mino, 6.v.1929 (*Teranishi*) (TC).

Banchus punkettai **sp. n.**

(Figs 27, 51, 75, 97, 117)

[*Banchus nox* Morley; Chandra & Gupta, 1977: 182. Misidentification.]

DESCRIPTION. Female. Width of lower face 0·75–0·80 times vertical length of eye. Malar space 0·45–0·60 times basal width of mandible. Maxillary palp as in Fig. 27. Antenna with apical segments just broader than long. Scutellar spine (Fig. 51) about 0·5 as long as scutellum. Mesopleuron and mesoscutum shining, only very weakly sculptured, with strong punctures, on mesopleuron separated by less than their diameter. Hind femur 5·60–6·10 times as long as deep. Fore wing length 8·6–9·7 mm. Tergite 1 of gaster 1·80–2·25 times as long as broad, its dorsal profile as in Fig. 75. Gaster strongly compressed from posterior of segment 3, reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·3 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 97.

Colour: black and yellow, with some reddish, especially on legs. Face yellow with a black median stripe, the stripe sometimes rather wide but with reddish yellow patches remaining below antennal sockets. Antenna brown, often rather darker dorsally and distally, with scape and pedicel blackish dorsally and yellowish ventrally. Maxillary palp reddish yellow with distal parts of segments 4 and 5 dark. Posterior part of propodeum yellowish with a black patch medio-posteriorly, the yellow area sometimes reduced to a band along posterior transverse carina. Hind coxa black with a yellow dorsal patch and a red postero-ventral patch. Hind femur reddish with a blackish ventral stripe. Segments of gaster each black anteriorly, yellow posteriorly, with junction between two colours reddish. Tergite 1 also with posterior margin black and yellow area reduced to two lateral and/or one median spot(s).

Male. Width of lower face 0·90 times vertical length of eye. Malar space 0·65 times basal width of mandible. Maxillary palp as in Fig. 117; segment 4 flattened and considerably widened; segment 5 about 0·6 as long as 4. Antennal flag setae (similar to Fig. 124) relatively poorly differentiated, at about 50 degrees, very short, not flattened, 2 per segment, without a polished trough. Hind femur 6·05 times as long as deep. Fore wing length 8·6 mm. Tergite 1 of gaster 1·90 times as long as broad. Tergite 3 with a crease along its anterior 0·5 separating laterotergite.

Colour: black and yellow, with some reddish, especially on legs. Antenna black dorsally, scape, pedicel and proximal flagellar segments yellow ventrally, remainder of flagellum brownish yellow ventrally. Maxillary palp with segment 1 yellow, 2 and 3 reddish yellow, 4 and 5 blackish. Posterior part of propodeum yellow, black postero-medially. Hind coxa black, with a dorsal yellow spot which is contiguous interno-laterally with a postero-ventral spot. Hind femur reddish, black ventrally and with a separate dorsal blackish area. Segments of gaster each black anteriorly, yellow posteriorly, the junction between the two colours very narrowly reddish.

REMARKS. The colour pattern of this species is very similar to two other species, *flavomaculatus* and *nox*, found in the same area. The males are easily identified using the flag setae but the females are more difficult to separate.

Biology and hosts. Virtually unknown. Adults have been collected in April and May. The specimens collected by Kamath and Gupta came from mixed vegetation in coniferous forest (Gupta, 1975: (appendix) 20, 22).

Distribution (Map 9, p. 35). Along the southern flank of the Himalayas and south-east into Burma, between about 2000 and 3000 m.

Material examined

Holotype ♂, **Nepal**: 27°56'N, 85°00'E, 3030 m, 23–29.v.1967 (*Can. Nepal Exped.*) (BRI).

Paratypes 13 ♀. **Burma**: 5 ♀, NE., Kambaiti, 2000 m, 4, 6 & 7.iv.1934 (*Malaise*) (NR); 1 ♀, Mt Victoria, 2800 m, 27.iv.1938 (*Heinrich*) (TC). **India**: 1 ♀, Himachal Pradesh, Dalhousie, 2132 m, 29.iv.1971 (*Ram*) (GC); 1 ♀, Himachal Pradesh, Kalatop, 2438 m, 8.v.1971 (*Kamath*) (GC); 1 ♀, Himachal Pradesh, Simla (*Nurse*) (BMNH) (paralectotype of *Cidaphurus flavomaculatus* Cameron). **Nepal**: 2 ♀, 27°56'N, 85°00'E, 3030 m, 23–29.v.1967 (*Can. Nepal Exped.*) (BRI); 2 ♀, 28°00'N, 85°00'E, 21–23.v.1967 (*Can. Nepal Exped.*) (BRI).

Banchus sanjozanus Uchida

(Figs 52, 76, 118)

Banchus volutatorius var. *sanjozanus* Uchida, 1929: 184. Holotype ♂, Japan (EIHU) [examined].

Description. Female. See 'Remarks'.

Male. Width of lower face 0·86 times vertical length of eye. Malar space 0·50–0·60 times basal width of mandible. Maxillary palp as in Fig. 118; segment 4 flattened and considerably widened; segment 5 about 0·6 as long as 4. Antennal flag setae (similar to Fig. 128) upright, long, flattened, 2 per segment, arising from a polished trough. Scutellar spine (Fig. 52) about as long as scutellum. Mesopleuron and mesoscutum coriaceous, with moderately fine punctures, on mesopleuron separated by a little more than their diameter. Hind femur 5·15–5·60 times as long as deep. Fore wing length 10·2–10·4 mm. Tergite 1 of gaster 2·10–2·22 times as long as broad, its dorsal profile as in Fig. 76. Tergite 3 with a crease along its anterior 0·4 separating laterotergite.

Colour: black and reddish, with some yellow. Face entirely reddish yellow or yellow with a narrow median black stripe. Antenna with scape and pedicel blackish dorsally, yellow or reddish yellow ventrally. Flagellum reddish, darkened dorsally, especially first few segments and distal 0·3. Maxillary palp with segments 1, 2 and 3 reddish yellow, 4 and 5 blackish. Posterior part of propodeum reddish, entirely or with posterior margin narrowly black. Hind coxa blackish with a large (but not sharply defined) reddish dorsal patch and at least some reddish ventrally. Hind femur reddish with a blackish ventral mark. Segments of gaster each reddish, with some blackish anteriorly, especially on tergites 1 and 2.

Remarks. Closely related to *volutatorius*. I have seen no females which I can associate with the males, although females were recorded by Uchida (1931: 52).

Biology and hosts. Unknown. Adults have been collected in August.

Distribution (Map 2, p. 16). Japan.

Material examined (2 ♂)

Japan: 1 ♂, Sanjodake, Yamato, 9.viii.1913 (*Isshiki*) (EIHU) (holotype); 1 ♂, Hokkaido, Mt Yubari, 11.viii.1966 (*Kusigemati*) (KC).

Banchus tholus **sp. n.**

(Figs 28, 53, 77, 98, 119)

Description. Female. Width of lower face 0·70–0·80 times vertical length of eye. Malar space 0·65–0·85 times basal width of mandible. Maxillary palp as in Fig. 28. Antenna with apical segments longer than broad. Scutellar spine (Fig. 53) about as long as scutellum. Mesopleuron shining, very weakly sculptured, with moderate punctures, separated by more than their diameter. Hind femur 6·60–7·05 times as long as deep. Fore wing length 10·8–12·2 mm. Tergite 1 of gaster 1·90–2·20 times as long as broad, its dorsal profile as in Fig. 77. Gaster subcylindrical, only weakly compressed apically, not reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its whole length separating laterotergite. Tergite 7 and sternite 6 as in Fig. 98.

Colour: variable, from brown and yellowish cream to largely reddish orange (see 'Remarks' below). Face yellowish to reddish orange with orbits yellow. Antenna blackish, with scape, pedicel, and sometimes base of flagellum, yellowish or reddish ventrally. Maxillary palp entirely reddish yellow. Posterior part of propodeum pale yellow cream with a postero-median brown area or entirely reddish. Hind coxa yellowish cream and brown or entirely reddish. Hind femur entirely reddish. Segments of gaster reddish with segment 1 pale cream or yellowish anteriorly, and sometimes with segments 1 to 4 each with a dark brownish transverse median band.

Male. Width of lower face 0·80 times vertical length of eye. Malar space 0·70 times basal width of mandible. Maxillary palp as in Fig. 119; segment 4 moderately widened and flattened; segment 5 about as long as 4. Antennal flag setae not differentiated (antennae in poor condition and proper observation difficult). Hind femur 7·15 times as long as deep. Fore wing length 11·5 mm. Tergite 1 of gaster 1·60 times as long as broad. Tergite 3 with a crease along its whole length separating laterotergite.

Colour: brown and yellowish cream, with some reddish. Antenna brownish dorsally, brownish yellow ventrally. Maxillary palp entirely reddish yellow. Posterior part of propodeum reddish yellow, narrowly dark brownish postero medially. Hind coxa yellowish cream and brown. Hind femur entirely reddish. Segments of gaster reddish, with segment 1 pale creamy yellow anteriorly and 1 and 2 more or less brownish medially.

REMARKS. The females show a considerable range of variation in colour, the specimens from Burma resembling those of *tumidus*, while those from the Philippines are almost entirely reddish orange. The specimens from Sumatra and Java have an intermediate coloration. Unfortunately only a single male (from Burma) is known. The females might represent more than one species. See also 'Remarks' under *B. tumidus*.

BIOLOGY AND HOSTS. Virtually unknown. Adults have been collected in December, March, April, May and June. The specimen from Mount Data was collected in oak forest.

DISTRIBUTION (Map 2, p. 16). On mountains in Burma, Sumatra, Java and the Philippines.

MATERIAL EXAMINED

Holotype ♂, **Burma**: NE., Kambaiti, 1800 m, 11.vi.1934 (*Malaise*) (NR).

Paratypes 10 ♀. **Burma**: 1 ♀, Mt Victoria, 1400 m, iii.1938 (*Heinrich*) (GC) (paratype of *Banchus tumidus* Chandra & Gupta); 2 ♀, Maymyo, 800 m, xii.1937 (*Heinrich*) (TC) (paratypes of *Banchus tumidus* Chandra & Gupta). **Sumatra**: 1 ♀, Sungei Kumbang, Korinchi, 1370 m, iv.1914 (*Robinson & Klass*) (BMNH). **Java**: 1 ♀, Gedeh, Tjibodas, 1700 m, xii.1935 (*Lieftinck*) (TC). **Philippines**: 4 ♀, Mindoro, Ilong, Mt Halcon, 1370 m, 9, 10 & 11.v.1954 (*Townes*) (TC); 1 ♀, Mt Data, 2380 m, 31.xii.1952 (*Townes*) (TC).

Banchus tumidus Chandra & Gupta

(Figs 29, 54, 78, 99, 120)

Banchus tumidus Chandra & Gupta, 1977: 183. Holotype ♀, INDIA (GC) [examined].

DESCRIPTION. Female. Width of lower face 0·75–0·80 times vertical length of eye. Malar space 0·65–0·75 times basal width of mandible. Maxillary palp as in Fig. 29. Antenna with apical segments longer than broad. Scutellar spine (Fig. 54) about as long as scutellum. Mesopleuron shining, only very weakly sculptured, with moderate punctures, separated by more than their diameter. Hind femur 6·80–7·05 times as long as deep. Fore wing length 10·5–11·9 mm. Tergite 1 of gaster 1·85–1·95 times as long as broad, its dorsal profile as in Fig. 78. Gaster subcylindrical, only weakly compressed posteriorly, not reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its whole length separating laterotergite. Tergite 7 and sternite 6 as in Fig. 99.

Colour: yellowish cream, reddish and brown. Face yellowish. Antenna dark brown, with scape, pedicel and base of flagellum yellowish ventrally. Maxillary palp entirely reddish yellow. Posterior part of propodeum yellowish cream with a postero-median brown area. Hind coxa yellowish cream and brown. Hind femur entirely reddish. Segments of gaster reddish yellow, with segment 1 pale anteriorly and segments 1 to 4 each with a brownish transverse median band.

Male. Width of lower face 0·80–0·85 times vertical length of eye. Malar space 0·60–0·70 times basal width of mandible. Maxillary palp as in Fig. 120; segment 4 very considerably widened and flattened; segment 5 about 0·76 as long as 4. Antennal flag setae not differentiated. Hind femur 6·70–6·90 times as long as deep. Fore wing length 10·8 mm. Tergite 1 of gaster 1·70–1·75 times as long as broad. Tergite 3 with a crease along its whole length separating laterotergite.

Colour: creamy yellow and brown. Antenna dark brown dorsally, yellow ventrally. Maxillary palp reddish yellow with segment 4 partly blackish (Fig. 120). Posterior part of propodeum reddish yellow, brownish postero-medially. Hind coxa creamy yellow and brown. Hind femur entirely reddish. Segments of gaster reddish yellow, with segment 1 pale cream anteriorly and 1 and 2 brownish medially.

REMARKS. This species is very closely related to *tholus*. The males are easily distinguished on the form of the maxillary palp, but not otherwise. The females are impossible to separate on morphological characters; those placed here as *tumidus* have segment 4 of the maxillary palp very weakly bicoloured (it is strongly bicoloured in males). The females of *tholus* show a much wider range of variation in colour and the division between the two species was made largely on the basis of geography. See also 'Remarks' under *tholus*.

BIOLOGY AND HOSTS. Virtually unknown. Adults have been collected in April, May, June, September and November.

DISTRIBUTION (Map 2, p. 16). On the southern flank of the western Himalayas between 600 and 2000 m.

MATERIAL EXAMINED (9 ♀, 2 ♂)
India: 1 ♀, Uttar Pradesh, Kumaon Himalaya, Jeolikote, 1219 m, 12.ix.1965 (*Tikar*) (GC) (holotype); 1 ♀, Himachal Pradesh, Khajjiar, 1920 m, 24.vi.1965 (*Joseph*) (GC); 1 ♀, Himachal Pradesh, Khajjiar, 1828 m, 30.iv.1971 (*Ram*) (GC); 2 ♀, Himachal Pradesh, Manali, 1828 m, 17 & 20.v.1970 (*Ram & Gulati*) (GC); 1 ♀, Uttar Pradesh, 1949 (*Bianchi*) (TC); 2 ♀, Uttar Pradesh, Dehra Dun, 600 m, 27.xi.1965 (*Gupta*) (GC); 1 ♂, Uttar Pradesh, Kumaon Hills, Bhowali, 1700 m, 5–8.vi.1968 (*Gupta*) (GC); 1 ♂, Uttar Pradesh, Dehra Dun, 7.iv.1967 (*Tikar*) (GC); 1 ♀, Uttar Pradesh, Gharwal Himalaya, Phata, 1524 m, 12.v.1967 (*Kamath*) (GC).

Banchus turcator Aubert

(Figs. 30, 55, 79, 100, 121)

Banchus turcator Aubert, 1978: 157. [Unavailable name published conditionally (Article 15 of the *Code*).]
Banchus turcator Aubert, 1981: 18. Holotype ♂, TURKEY (AC) [examined].

DESCRIPTION. Female. Width of lower face 0·90–1·00 times vertical length of eye. Malar space 0·50–0·55 times basal width of mandible. Maxillary palp as in Fig. 30. Antenna with apical segments longer than broad. Scutellar spine (Fig. 55) usually very small, sometimes absent or reasonably well developed. Mesopleuron and mesoscutum strongly coriaceous, with moderate to strong punctures, on mesopleuron separated by slightly less than their diameter. Hind femur 4·70–5·60 times as long as deep. Fore wing length 8·0–10·7 mm. Tergite 1 of gaster 1·45–1·90 times as long as broad, its dorsal profile as in Fig. 79. Gaster relatively weakly compressed, reaching about to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·3 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 100.

Colour: mainly black and yellow, the yellow areas on the appendages tending to reddish. Face varying from yellow with a black median stripe to black with yellow orbital stripes. Antenna with scape and pedicel black dorsally, yellow ventrally. Flagellum entirely orange except that it is dark at extreme apex. Maxillary palp reddish yellow, with segments 1 and 5 wholly, 2 proximally and 4 distally dark. Posterior part of propodeum black with a yellow band (sometimes interrupted medially) along posterior transverse carina. Hind coxa black, entirely or with a yellow dorsal patch. Hind femur black, yellow or reddish yellow proximally and distally, the yellowish area sometimes extending along most of dorsal surface. Segments of gaster each black anteriorly, yellow (sometimes broadly so) posteriorly.

Male. Width of lower face 0·90–1·05 times vertical length of eye. Malar space 0·45–0·55 times basal width of mandible. Maxillary palp as in Fig. 121; segment 4 flattened and considerably widened; segment 5 about as long as 4. Antennal flag setae (similar to Fig. 127, but setae more widened toward their apices) upright, flattened and widened, 2 per segment, arising from a polished trough. Hind femur 4·60–5·30 times as long as deep. Fore wing length 8·7–10·0 mm. Tergite 1 of gaster 1·55–1·65 times as long as broad. Tergite 3 with a crease along its anterior 0·3 separating laterotergite.

Colour: black and yellow, with some reddish. Antenna with scape and pedicel black dorsally, yellow ventrally. Flagellum orange, darkened distally. Maxillary palp with segment 1 yellowish (sometimes partly darkened), 2 and 3 wholly and 4 proximally reddish yellow, 4 distally and 5 wholly blackish or brownish. Posterior part of propodeum black with a yellow band along posterior transverse carina, the band sometimes broken medially, reduced to two lateral spots or even absent. Hind coxa black, usually with a ventral and sometimes also a dorsal yellow spot. Hind femur yellowish red with a large medial black area. Segments of gaster each black anteriorly, yellow posteriorly.

REMARKS. This species has been confused with *pictus* in collections. It is, however, quite unrelated as shown, for instance, by the rather different flag setae.

BIOLOGY AND HOSTS. Unknown. Adults have been collected in April, May and June.

DISTRIBUTION (Map 4, p. 20). Turkey and in the mountains of Tadzhikistan.

MATERIAL EXAMINED (5 ♀, 9 ♂)

Turkey: 1 ♂, Gürün, 12–15.vi.1976 (*Heinrich*) (AC) (holotype); 1 ♀, Alem-Dağ, 600 m, 26–30.vi., (*Demelt*) (FSA); 1 ♂, Antalya, Termessus, 9.v.1968 (*Hallin*) (NR); 1 ♀, Erzurum, 20 km İspir to İkizdere rd, 1700 m, 2.vi.1962 (*Guichard & Harvey*) (BMNH); 1 ♂, Gümüşane, near Maden, 1800 m, 29.v.1962 (*Guichard & Harvey*) (BMNH); 1 ♀, Isik-Dağ, 1200 m, vi.1966 (*Ressl.*) (FSA); 1 ♀, Istanbul, 20.iv.(*de Gaulle* coll.) (MNHN); 1 ♂, Kızılcahamam, 1000 m, 26–28.v.1964 (FSA); 1 ♀, 1 ♂, Nevşehir, Urgüp, 4 & 6.vi.1978 (*Schwarz*) (AC); 1 ♂, Zara Taiger (UZM). **U.S.S.R.**: 2 ♂, Gissarskiy Khrebet, K-K chanch-ov on Aliche, 25.iv.1960 (*Malyavin*) (MLSU); 1 ♂, Khorog region, Shugnansk Khrebet, 2600 m, 5.vi.1956 (*Zhelokhovtsev*) (MLSU).

Banchus volutatorius (Linnaeus)

(Figs 3, 7, 8, 31, 56, 80, 101, 122, 128)

Ichneumon volutatorius Linnaeus, 1758: 562. Lectotype ♂, EUROPE (LSL), fixed by Roman, 1932: 14 [examined].

Ichneumon venator Linnaeus, 1758: 564. Type(s) ♀, EUROPE (lost).

Ichneumon umbellatarum Schrank, 1786: 261. Type(s) ♀ [not ♂ as stated by Schrank], WEST GERMANY (lost). **Syn. n.**

Ichneumon certator Thunberg, 1822: 266; 1824: 322. Holotype ♀, SWEDEN (UU) [not examined].

Banchus monileatus Gravenhorst, 1829: 393. Lectotype ♀, POLAND (ZI), designated by Townes & Townes, 1978: 532 [examined]. **Syn. n.**

Banchus farrani Curtis, 1836: 588. Lectotype ♂, IRELAND (NMV), designated by Fitton, 1976: 322 [examined].

Banchus calcaratus Szépligeti, 1910: 186. Holotype ♀, HUNGARY (TM) [examined].

Banchus volutatorius var. *alticola* Schmiedeknecht, 1910: 1931. Syntypes ♀, ♂, EAST GERMANY (?MNHU) [not examined]. [Junior secondary homonym of *Cidaphurus alticola* Ashmead, 1901: 148.]

Banchus obscurus Meyer, 1926: 263. Type(s) ♀ [not ♂ as stated by Meyer], U.S.S.R. (destroyed).

NOMENCLATURE. The identity of *venator* was established by Fitton (1978*b*: 375).

Gravenhorst (1829: 389) synonymised *I. umbellatarum* with *B. falcatorius* but subsequently it has been included in the synonymy of *B. compressus* (= *dilatatorius*) (e.g. Aubert, 1978: 152 [with the date given incorrectly as 1802]) without, however, being used as the valid name for that species, despite its seniority. The description does not fit *dilatatorius*; it could apply to some females of *falcatorius* or *volutatorius*. I consider that it best fits certain females of *volutatorius*, with which it is here synonymised.

Although the types of var. *alticola* were not located a male determined by Schmiedeknecht, and from the type-locality, was examined (ZSBS).

Meyer undoubtedly mistook the sex of the type-material (probably a single specimen) of *obscurus* because the face coloration cannot apply to any male *Banchus*. The description fits perfectly the female of *volutatorius* and the host recorded by Meyer (*Lacanobia oleracea*) is one of those known for this species.

DESCRIPTION. Female. Width of lower face 0·85–0·90 times vertical length of eye (Fig. 3). Malar space 0·55–0·60 times basal width of mandible. Maxillary palp as in Fig. 31. Antenna with apical segments longer than broad. Scutellar spine (Fig. 56) distinct, often almost 0·5 as long as scutellum. Mesopleuron and mesoscutum coriaceous, with moderate punctures, on mesopleuron separated by about their diameter. Hind femur 4·85–5·35 times as long as deep. Fore wing length 8·1–9·8 mm. Tergite 1 of gaster 1·80–2·05 times as long as broad, its dorsal profile as in Fig. 80. Gaster (Figs 7, 8) moderately compressed, not reaching to tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·4 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 101.

Colour: predominantly black, with legs largely reddish. Face black, occasionally with brownish orbital marks. Antenna black, with scape, pedicel and proximal flagellar segments reddish brown ventrally. Maxillary palp black, with segments 2 and 3 wholly and 4 proximally reddish or brownish. Posterior part of propodeum black, often entirely, sometimes with reddish areas (of varying extent) on segments 1, 2 and 3 (in extreme cases with posterior margins of these segments narrowly yellowish).

Male. Width of lower face 0·90–1·00 times vertical length of eye. Malar space 0·45–0·60 times basal width of mandible. Maxillary palp as in Fig. 122; segment 4 considerably widened and flattened; segment 5 about 0·5 as long as 4. Antennal flag setae (Fig. 128) upright, very long, flattened and widened, 2 per segment, arising from a polished trough. Hind femur 4·85–5·40 times as long as deep. Fore wing length 8·0–9·9 mm. Tergite 1 of gaster 1·65–2·00 times as long as broad. Tergite 3 with a crease along its anterior 0·4 separating laterotergite.

Colour: black and yellow, with some reddish. Antenna black with flagellum yellowish ventrally except at its distal apex. Maxillary palp with segment 1 yellow, 2 and 3 wholly and 4 proximally reddish yellow, 4 distally and 5 wholly blackish. Posterior part of propodeum black or with a yellow mark or marks along (usually just anterior to) posterior transverse carina. Hind coxa black, entirely or with small yellow marks externo-laterally and/or postero-ventrally. Hind femur reddish yellow, rarely with a blackish ventral mark. Segments of gaster each black anteriorly, yellow posteriorly, tergites 1, 2 and 3 very broadly yellow and with anterior area often partly (sometimes largely) reddish.

REMARKS. The male is similar, superficially, to *falcatorius* but can be separated readily by the number of flag setae and the lack (usually) in *falcatorius* of a distinct spine on the scutellum. The female has a gaster which is quite unlike that of *falcatorius* and would not be confused with it. The female is, however, frequently confused with *palpalis*, although the maxillary palp is different in form and *volutatorius* generally has a much shorter scutellar spine.

BIOLOGY AND HOSTS. Adults have been collected mainly in the period from mid-June to early August, but there are a few records as early as mid-April and as late as September. However, there is no evidence of two generations in the distribution of the records and information from rearings also indicates that *volutatorius* is univoltine. I have seen 58 reared specimens, many with detailed and reliable host data. The hosts (in decreasing order of number of rearings and reared specimens) are: *Anarta myrtilli* (Linnaeus) (Noctuidae), 12 ♀, 11 ♂ from 12 rearings, Great Britain, Germany, the Netherlands and Switzerland; *Lacanobia oleracea* (Linnaeus) (Noctuidae), 14 ♀, 1 ♂ from 5 rearings, Great Britain; *Mamestra brassicae* (Linnaeus) (Noctuidae), 1 ♀, 1 ♂ from 2 rearings, Great Britain; *Hadena compta* (Denis & Schiffermüller) (Noctuidae), 3 ♀, 1 ♂ from 1 rearing, Denmark; *Ceramica pisi* (Linnaeus) (Noctuidae), 1 ♀, 1 ♂ from 1 rearing, Great Britain; *Heliothis viriplaca* (Hufnagel) (Noctuidae), 2 ♂ from 1 rearing, Germany; *Xestia xanthographa* (Denis & Schiffermüller) (Noctuidae), 1 ♂ from 1 rearing, Great Britain; *Habrosyne pyritoides* (Hufnagel) (Thyatiridae), 1 ♀ from 1 rearing, Germany; *Opisthograptis luteolata* (Linnaeus) (Geometridae), 1 ♀ from 1 rearing, Germany; and *Zygaena ephialtes* (Linnaeus) (Zygaenidae), 1 ♂ from 1 rearing, Germany.

The literature additionally records these noctuid hosts: *Agrotis segetum* (Denis & Schiffermüller) (Meyer, 1927*a*: 81), *Lycophotia porphyrea* (Denis & Schiffermüller) (Leonardi, 1928: 83; Meyer, 1934: 231); *Lacanobia suasa* (Denis & Schiffermüller) and *L. contigua* (Denis & Schiffermüller) (Ljungdhal, 1918: 82; Meyer, 1934: 231); and *Bena prasinana* (Linnaeus) (Hedwig, 1939: 22). Zorin & Zorina (1929) give some biological information on the association with *Lacanobia oleracea*.

DISTRIBUTION (Map 10, p. 42). Widespread in northern and central Europe, extending into Turkey, and in the U.S.S.R. occurring as far south as Alma-Ata and as far east as the Chitinskaya Oblast.

MATERIAL EXAMINED (486 ♀, 301 ♂)

Austria, Belgium, Denmark, East Germany, Finland, France, Great Britain, Hungary, Ireland, Netherlands, Norway, Poland, Rumania, Sweden, Switzerland, Turkey, U.S.S.R., West Germany (AC, BC, BMNH, BRI, CM, FSA, HC, IBMPP, IEUB, IP, ITZ, IZPAN, JC, KHC, LELW, MHN, MLSU, MNHN, MUM, NMB, NR, PC, RNH, RSM, TM, UM, USNM, UZI, UZM, VRC, ZC, ZI, ZIL, ZIM, ZMU, ZSBS).

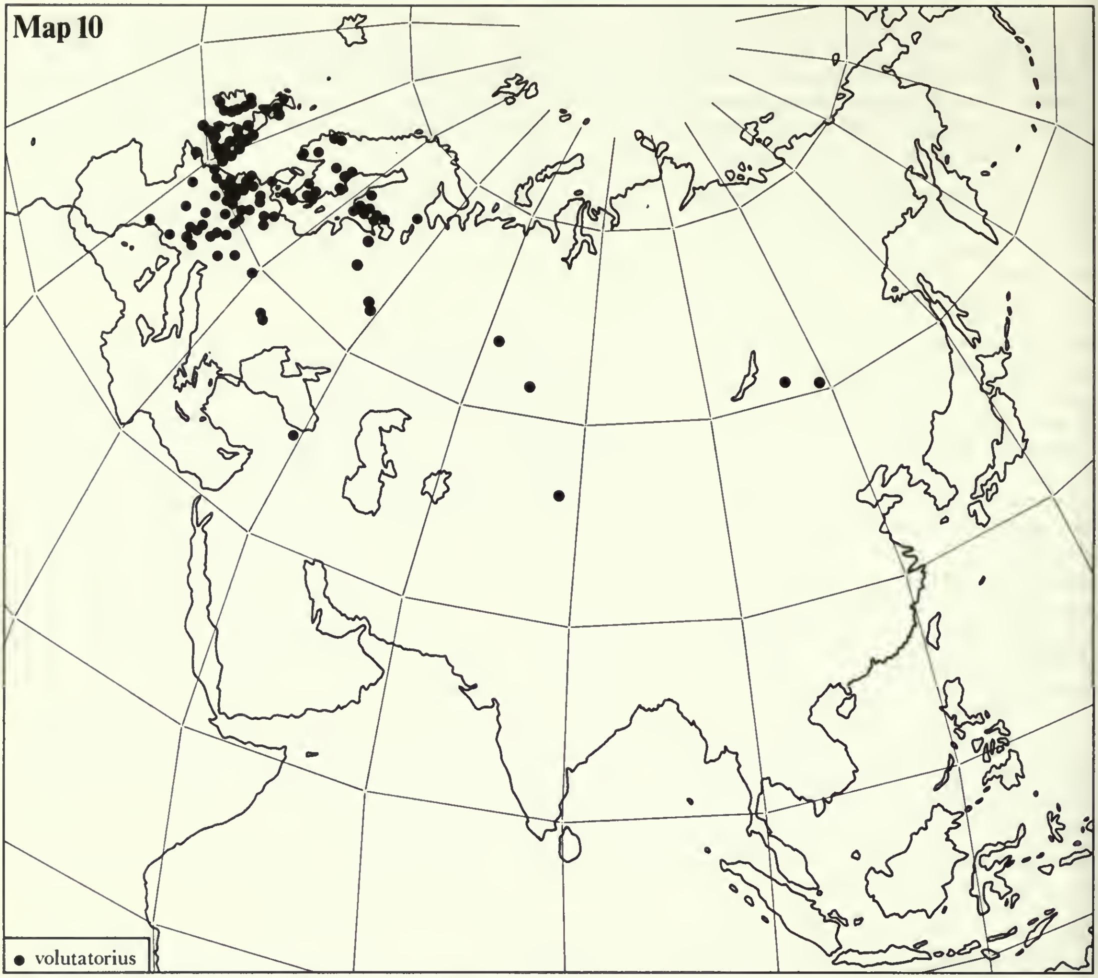
Banchus zonatus Rudow

(Figs 32, 57, 58, 81, 102, 123, 126)

Banchus zonatus Rudow, 1883*a*: 57. Type(s) ♀, EUROPE 'Sudeuropa' (?JPM) [not examined].
Banchus algericus Schmiedeknecht, 1910: 1927. Holotype ♀, ALGERIA (MNHU) [examined]. **Syn. n.**

NOMENCLATURE. Apart from some exaggeration of size, the description of *zonatus* fits perfectly, and only, the female of this species. The synonymy is further confirmed by the type-locality 'Vaterland Sudeuropa' (the species was not described from Germany as stated by Aubert, 1978: 166). It has not been possible to obtain on loan material from the Rudow collection. Rudow's methods and the poor condition of his collection were criticized during his lifetime. The collection, still neglected, was seen recently by Horstmann (pers. comm.), who made notes on its contents, including the fact that three specimens stand as *B. zonatus*. However, nothing is known of the status or identity of these specimens.

DESCRIPTION. Female. Width of lower face 1·00–1·15 times vertical length of eye. Malar space 0·75–0·95 times basal width of mandible. Maxillary palp as in Fig. 32. Antenna with apical segments broader than long. Scutellar spine (Figs 57, 58) about 0·5 as long as scutellum or almost absent (see 'Remarks'). Mesopleuron and mesoscutum coriaceous with moderately strong punctures, on mesopleuron separated by less than their diameter. Hind femur 5·30–6·15 times as long as deep. Fore wing length 11·1–13·5 mm.



Map 10 Distribution of *Banchus volutatorius*.

Tergite 1 of gaster 1·35–1·65 times as long as broad, its dorsal profile as in Fig. 81. Gaster strongly compressed from posterior part of segment 3, reaching beyond tips of fore wings (when folded back). Tergite 3 with a crease along its anterior 0·4 separating laterotergite. Tergite 7 and sternite 6 as in Fig. 102.

Colour: black and yellow. Face yellow with a black median stripe. Antenna black (sometimes brownish distally), scape with a yellow patch beneath. Maxillary palp dark brown or black. Posterior part of propodeum black with a yellow stripe along posterior transverse carina. Hind coxa black, usually with a yellow dorsal patch. Hind femur black, yellow at extreme base, distally, and often dorsally. Segments of gaster each black anteriorly, yellow posteriorly.

Male. Width of lower face 1·00–1·20 times vertical length of eye. Malar space 0·60–0·90 times basal width of mandible. Maxillary palp as in Fig. 123; segment 4 flattened and slightly widened; segment 5 about 0·8 as long as 4. Antennal flag setae (Fig. 126) upright, moderately long, flattened, 2 per segment, arising from a polished trough. Hind femur 5·35–6·65 times as long as deep. Fore wing length 10·5–14·0 mm. Tergite 1 of gaster 1·65–1·90 times as long as broad. Tergite 3 with a crease along its anterior 0·4 separating laterotergite.

Colour: back and yellow. Antenna black, scape and pedicel (and sometimes flagellum segment 1 proximally) yellow ventrally, flagellum sometimes slightly brownish ventrally. Maxillary palp blackish or brownish. Posterior part of propodeum yellow anteriorly, black posteriorly, the yellow varying from a stripe along posterior transverse carina to covering almost entire area. Hind coxa black with a dorsal and often a postero-ventral yellow patch. Hind femur yellow, blackish laterally and ventrally towards base.

Map 11 Distribution of *Banchus zonatus*.

Segments of gaster each black anteriorly, yellow posteriorly, the yellow less variable in extent than in females, occupying about 0·5 of each tergite.

REMARKS. This is the largest species of the genus and the appearance of the females in particular is very striking. *B. zonatus* seems to be most closely related to *dilatatorius* and *moppiti*.

The specimens from the eastern Mediterranean (Cyprus and Israel) consistently have the scutellar spine very small or virtually absent and it is possible that they represent a separate species. However, this is difficult to investigate without additional material. There are no specimens from peninsular Italy, Greece or Turkey in collections.

BIOLOGY AND HOSTS. Unknown. Dates of collection range from early September to mid-December. There is a single male with a date in March, unfortunately without an intelligible locality but with the intriguing data 'Salix caprea'.

DISTRIBUTION (Map 11, p. 43). A 'Mediterranean' species. Meyer (1927*b*: 291) records the species from the Caucasus but I have seen no specimens to substantiate this north-eastward extension of its distribution.

MATERIAL EXAMINED (28 ♀, 21 ♂)

Algeria, Cyprus, France, Israel, Italy, Morocco, Spain, Tunisia (AC, BMNH, FSA, IEE, MHN, MNHN, MNHU, NR, TAU, TC, UZM).

Species excluded from *Banchus*

The following Old World species were described incorrectly in *Banchus*.

Banchus armillatus Morley, 1913: 254. Holotype ♂, NICOBAR ISLANDS (BMNH) [examined].

Identity. *Phytodietus armillatus* (Morley). In Kaur & Jonathan's (1979) treatment of Oriental *Phyto-*

dietus the holotype runs to *P. alasuffuscus* Kaur & Jonathan. However, it differs in some details, particularly in the degree of constriction of tergite 1 of the gaster.

Banchus elator Fabricius, 1804: 128. LECTOTYPE ♂, AUSTRIA (UZM), here designated (selected by G. E. J. Nixon) [examined].
Identity. Earinus elator (Fabricius) **comb. n.** (Braconidae) (see Nixon, 1986, in press).

Banchus histrio Fabricius, 1798: 234. Lectotype ♂, EAST GERMANY (UZM), designated by Horstmann, 1982*b*: 243 [not examined].
Identity. Lissonota histrio (Fabricius) (Horstmann, 1982*b*: 243).

Banchus quadrator Schellenberg, 1802: 21. Type(s) ♀, SWITZERLAND (lost).
Identity. Megarhyssa quadrator (Schellenberg) **comb. n.** Schellenberg's description and figures are obviously of a rhyssine (Pimplinae). The species concerned corresponds to that named as *M. citraria* (Olivier) in the BMNH collection. The two recent catalogues (Oehlke, 1967; Aubert, 1969) covering European *Megarhyssa* differ in so many details that it is not clear what name is the valid one for this species. Whatever it is, *quadrator* will be a junior synonym. Gravenhorst's invitation (1829: 959) to compare *quadrator* with *M. superba* (Schrank) has been overlooked by all who have dealt subsequently with the European Rhyssini.

Banchus robustus Rudow, 1883*b*: 246. Type(s) ♀, EAST GERMANY (?JPM) [not examined].
Identity. Unknown, it remains a nomen dubium. It is excluded from *Banchus* because of the length of the ovipositor: 'Legestachel fast halb so lang als Hinterlieb'.

Banchus spinipes Panzer, 1800: 17. Type(s) ♀, GERMANY (lost).
Identity. Junior synonym of *Cephus pygmeus* (Linnaeus) (Cephidae) (Muche, 1981: 283).

Banchus tomentosus Gravenhorst, 1829: 376, Holotype ♀, EAST GERMANY (ZI) [examined].
Identity. Exetastes tomentosus (Gravenhorst) (Townes, Momoi & Townes, 1965: 235).

Banchus villosulus Gravenhorst, 1807: 267. Syntypes [?number] [?♀], no type-locality (lost).
Identity. The description of this species fits a cynipoid rather than an ichneumonid. Gravenhorst himself compared it to *Ibalia* and did not refer to it in any of his subsequent works on ichneumonids. It is unlikely that any type-material will be found. The general nature of the description makes application of the name to a particular species difficult, but it is desirable to formally transfer the name to the Cynipoidea so that workers on that group can consider its identity. The species is here placed as a nomen dubium in *Andricus* (**comb. n.**) (Cynipidae), to the agamic females of which the description seems best to apply.

Banchus viridator Fabricius, 1804: 127. Syntypes ♀, AUSTRIA (UZM) [one of four putative syntypes examined].
Fabricius cited *Banchus spinipes* Panzer as a synonym of his new species *viridator*. I can see no reason for him not to have used Panzer's name for the species. Whatever the reasons, it complicates consideration of the name. It could be treated as an independent species, as published in synonymy, or as a replacement name (in which case the type-specimens would be those of *B. spinipes* rather than those cited above).
Identity. Junior synonym of *Cephus pygmeus* (Linnaeus) (Cephidae) (Muche, 1981: 283).

The following species have been placed incorrectly in *Banchus* at some time.

Ichneumon annulatus Fabricius, 1793 is a pompilid, *Pompilus (Episyron) annulatus* (Fabricius) (Schulz, 1912: 73).

Ichneumon cultellator Fabricius, 1793 is a junior synonym of *Ibalia leucospoides* (Hochenwarth) (Ibaliidae) (Kerrich, 1973: 73).

Ichneumon fornicator Fabricius, 1781 is a species of *Exetastes* (Townes, Momoi & Townes, 1965: 229).

Ichneumon gravidator Linnaeus, 1758 is a species of *Proctotrupes* (Proctotrupidae) (Fitton, 1978*b*: 378; Townes & Townes, 1981: 179).

Ichneumon varius Fabricius, 1793 is a junior synonym of *Theronia atalantae* Poda (Aubert, 1978: 167).

Ichneumon vigilatorius Panzer, 1804 was synonymised with *Banchus falcatorius* by Gravenhorst (1829: 390). This was later rejected in favour of synonymy with *compressus* (Aubert, 1978: 153) but was reinstated by Horstmann (1982*b*: 238). However, Schaeffer's illustration (1767: pl. 61, fig. 6), to which Panzer's description and name refer, clearly shows an ichneumonid with segment 1 of the gaster strongly petiolate and which probably belongs in the Ichneumoninae. Although I cannot find an ichneumonine with all details of the colour pattern correct, I think it best to place the species as a nomen dubium in *Ichneumon* (**comb. rev.**).

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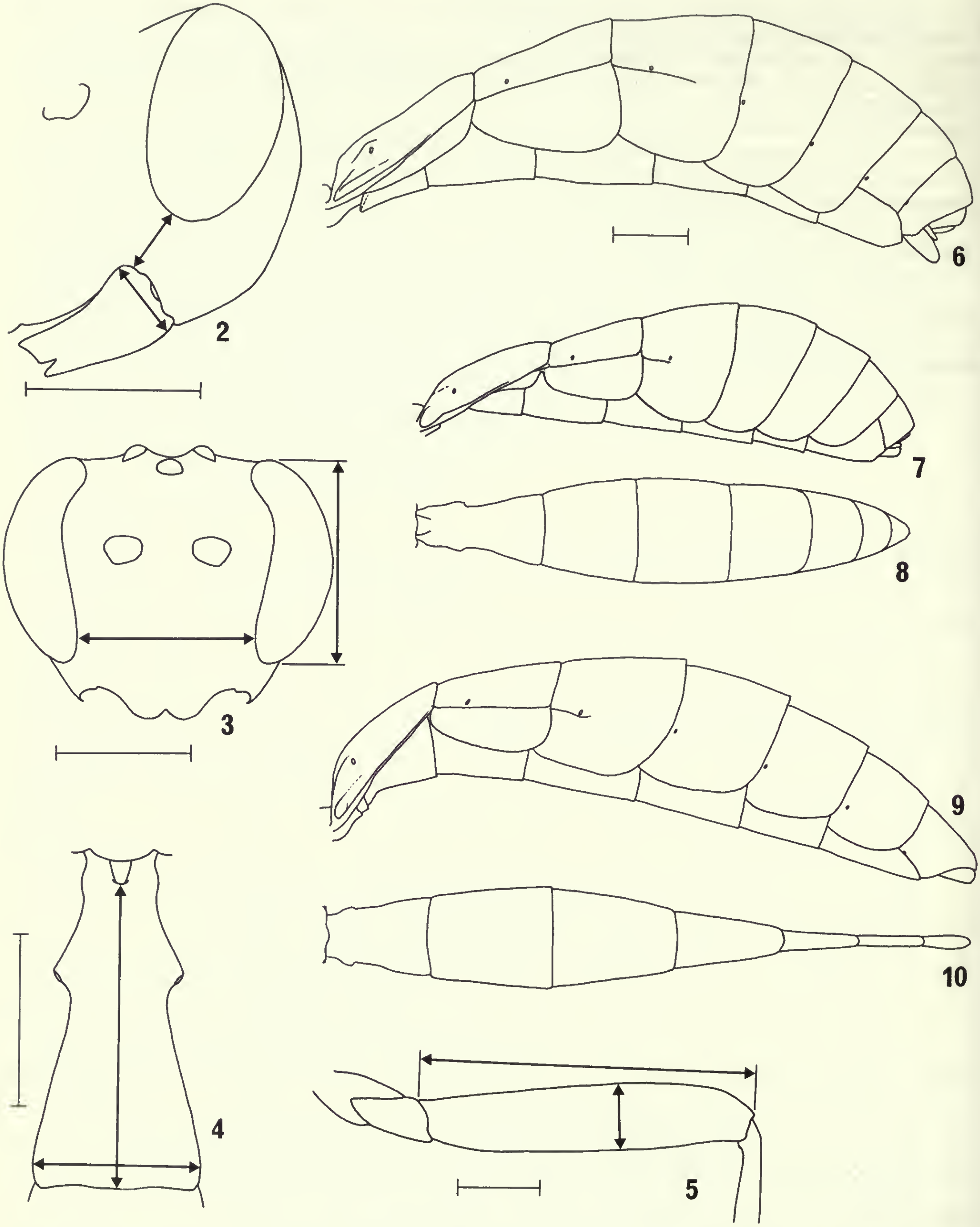
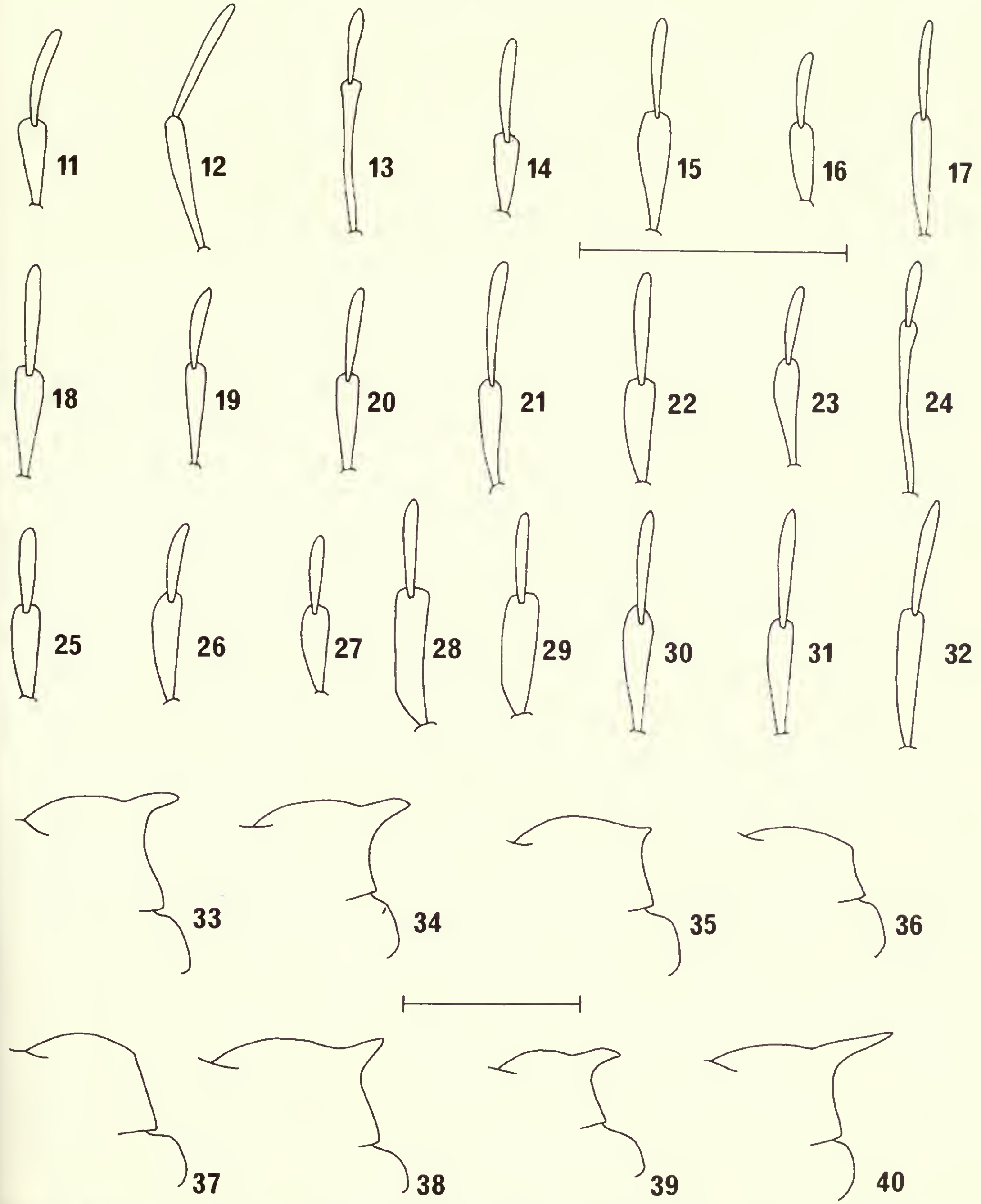
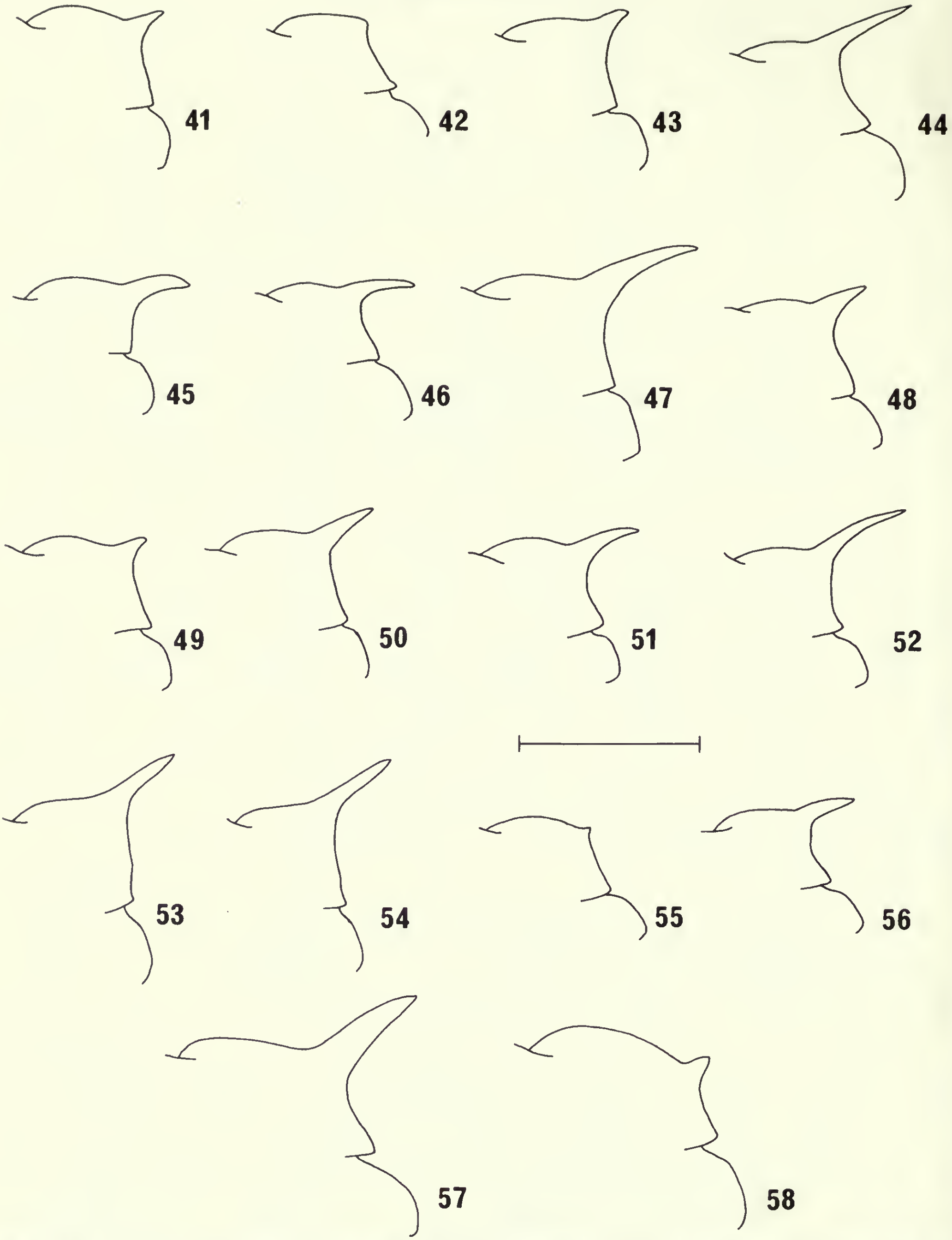


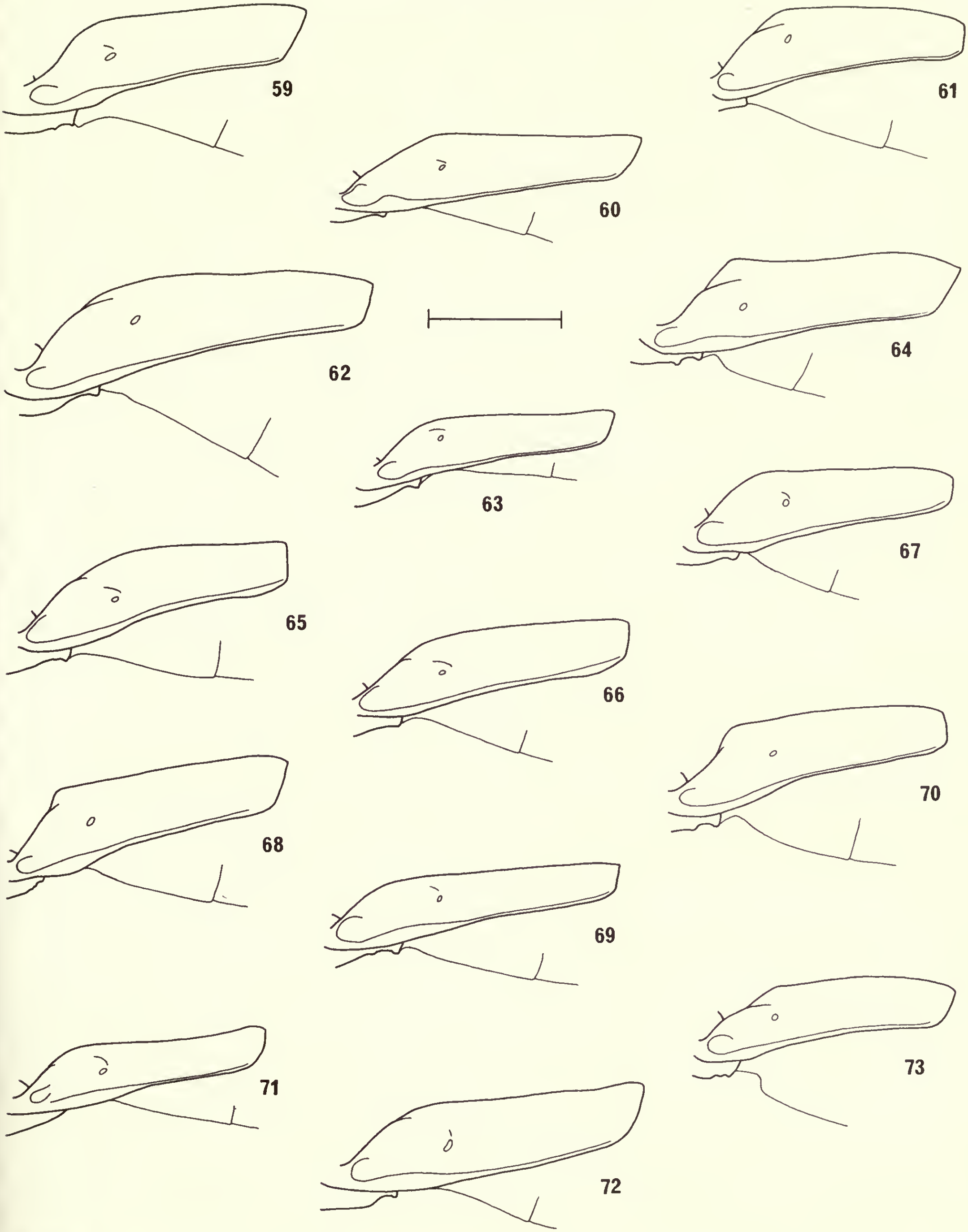
Figs 2–10 2–5, measurements used in descriptions, of (2) malar space, *dilatatorius*, female; (3) face, *volutatorius*, female; (4) gaster tergite 1, *crefeldensis*, male; (5) hind femur, *falcatorius*, male. 6–10, female gaster of (6) *cerinus*, lateral; (7) *volutatorius*, lateral; (8) *volutatorius*, dorsal; (9) *falcatorius*, lateral; (10) *falcatorius*, dorsal. Scale lines represent 1 mm.



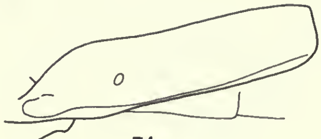
Figs 11–40 11–32, segments 4 and 5 of female maxillary palp, right, of (11) *agathae*; (12) *cerinus*; (13) *crefeldensis*; (14) *dilatatorius*; (15) *falcatorius*; (16) *flavomaculatus*; (17) *gudrunae*; (18) *hastator*; (19) *insulanus*; (20) *japonicus*; (21) *mauricettae*; (22) *moppiti*; (23) *nox*; (24) *palpalis*; (25) *pictus*; (26) *poppiti*; (27) *punkettai*; (28) *tholus*; (29) *tumidus*; (30) *turcator*; (31) *volutatorius*; (32) *zonatus*. 33–40, outline of scutellum, left lateral, of (33) *agathae*; (34) *crefeldensis*; (35, 36) *dilatatorius*; (37, 38) *falcatorius*; (39) *flavomaculatus*; (40) *gudrunae*. Scale lines represent 1 mm.



Figs 41–58 Outline of scutellum, left lateral, of (41) *hastator*; (42) *insulanus*; (43) *japonicus*; (44) *mauricettae*; (45) *moppiti*; (46) *nox*; (47) *palpalis*; (48) *poppiti*; (49, 50) *pictus*; (51) *punkettai*; (52) *sanjozanus*; (53) *tholus*; (54) *tumidus*; (55) *turcator*; (56) *volutatorius*; (57, 58) *zonatus*. Scale line represents 1 mm.



Figs 59–73 Gaster tergite 1, left lateral, of (59) *agathae* ♀; (60) *crefeldensis* ♂; (61) *dilatatorius* ♀; (62) *falcatorius* ♀; (63) *flavomaculatus* ♀; (64) *hastator* ♀; (65) *gudrunae* ♂; (66) *gudrunae* ♀; (67) *insulanus* ♀; (68) *japonicus* ♀; (69) *mauricettae* ♂; (70) *moppiti* ♀; (71) *nox* ♂; (72) *palpalis* ♂; (73) *pictus* ♀. Scale line represents 1 mm.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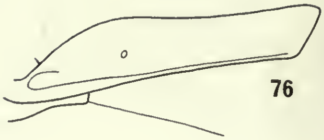
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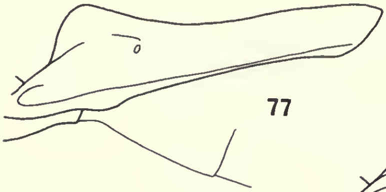
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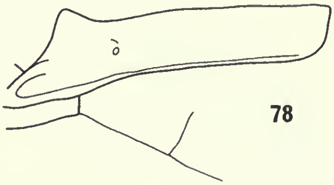
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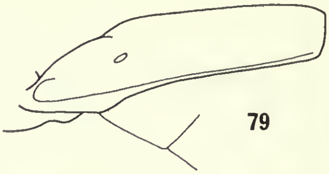
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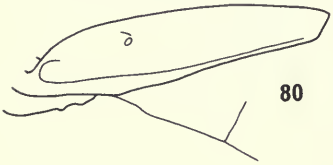
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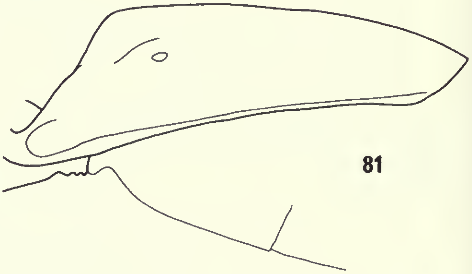
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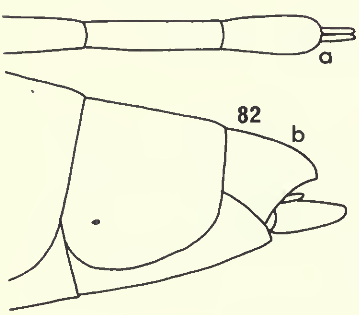
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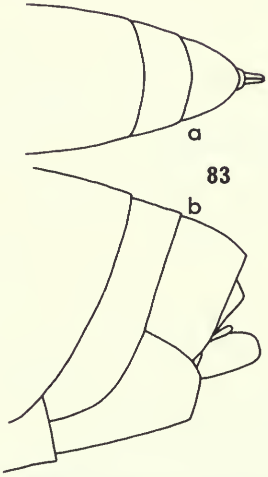
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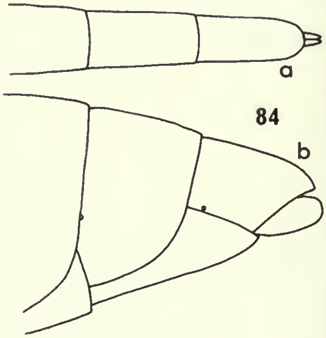
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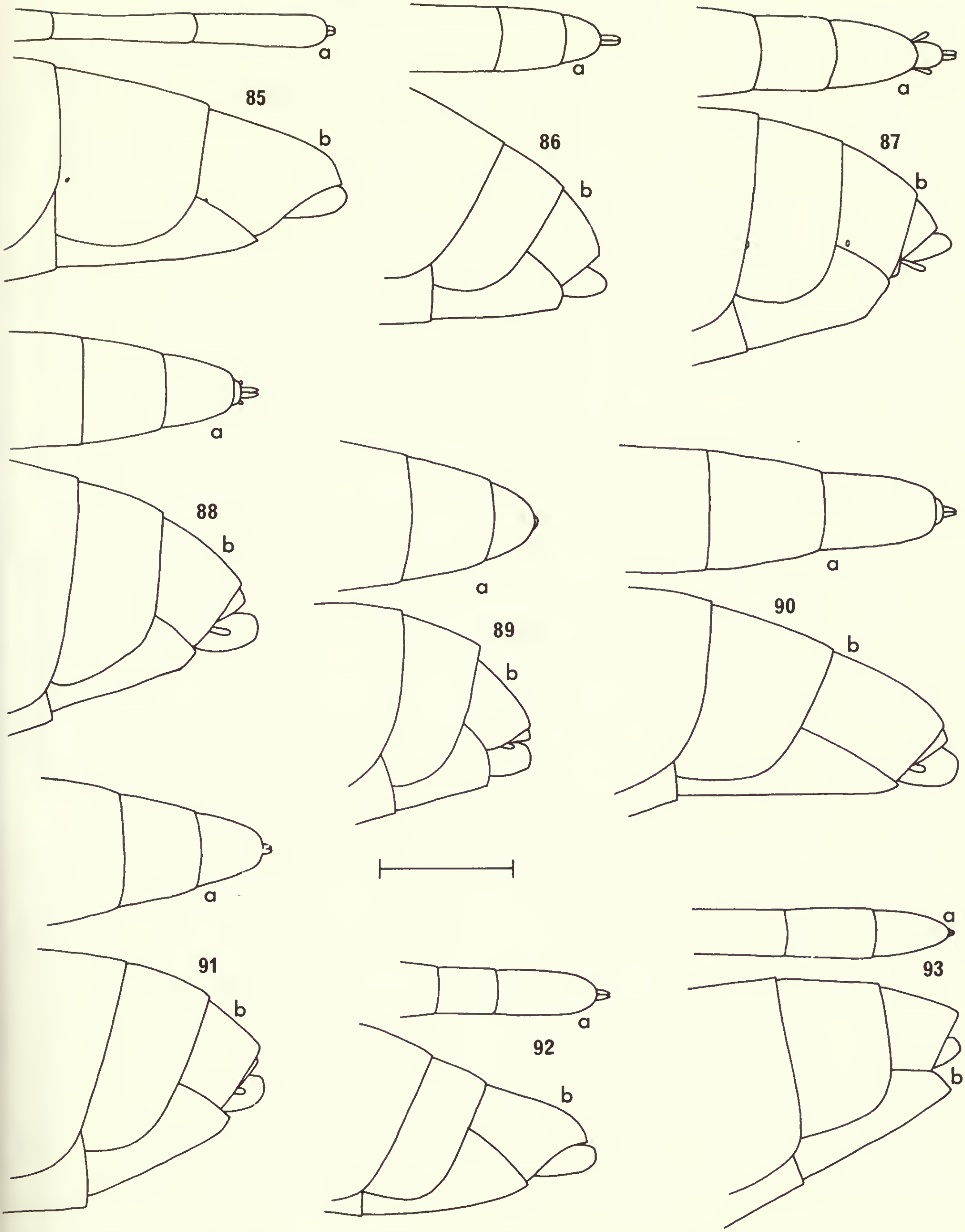

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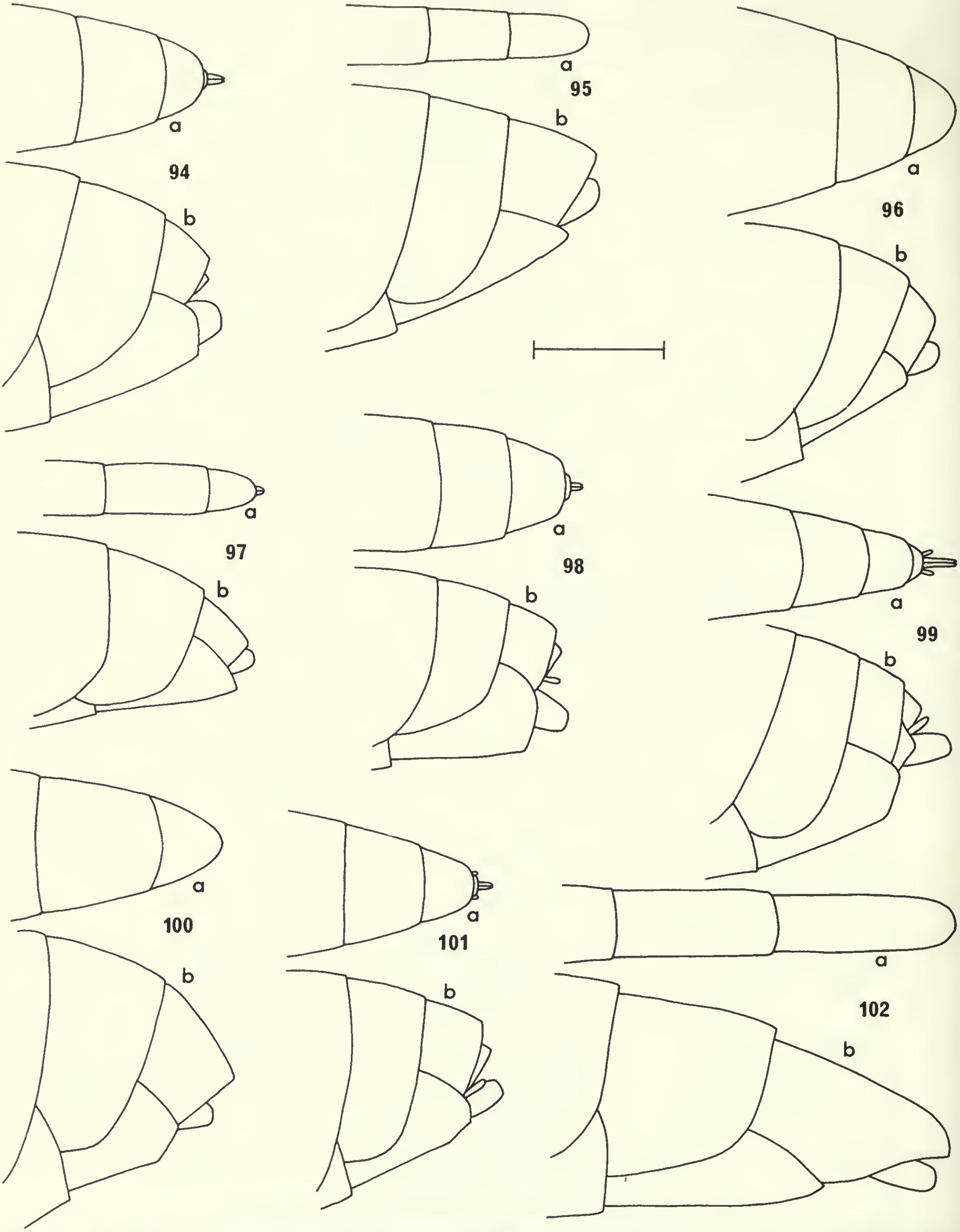

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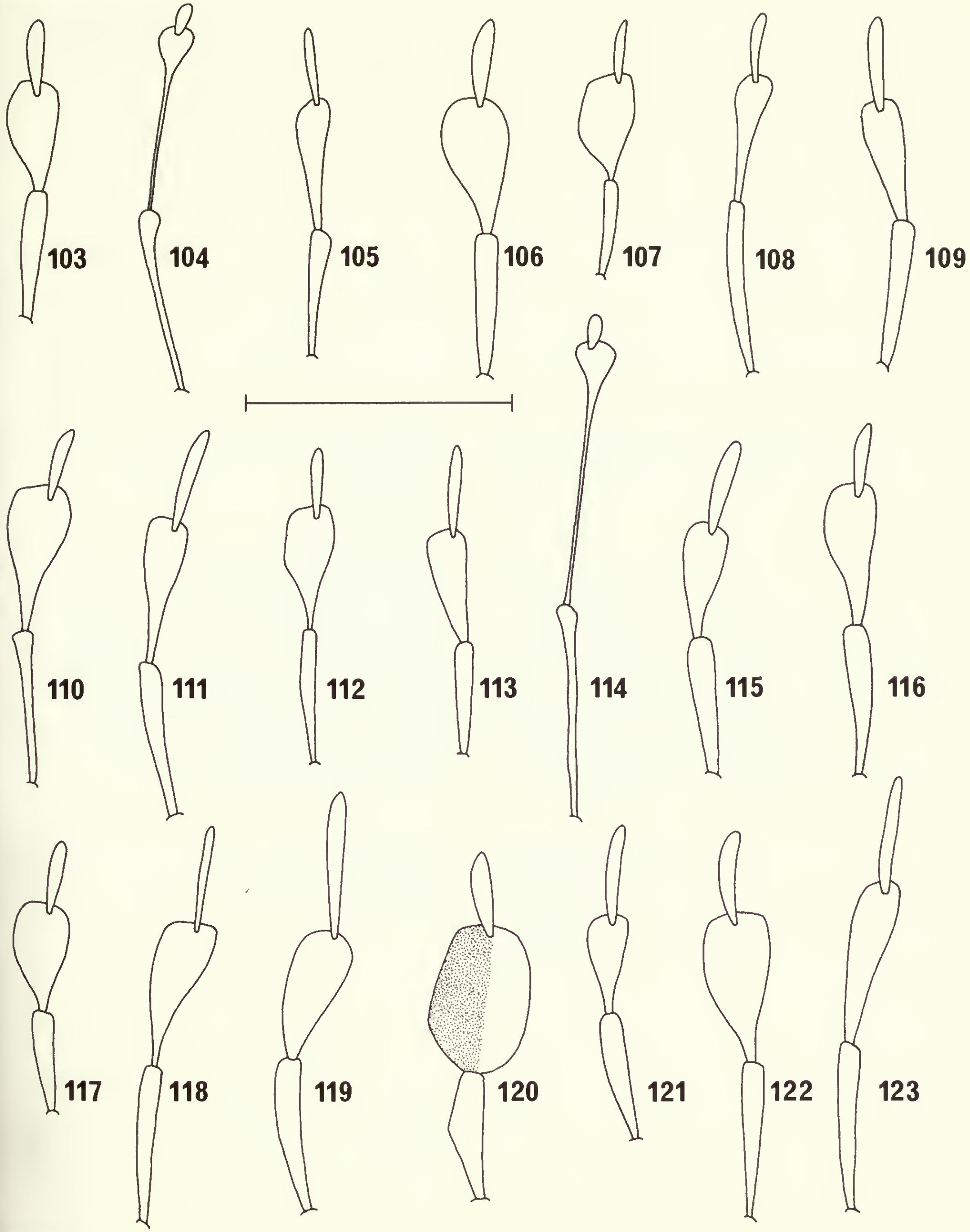

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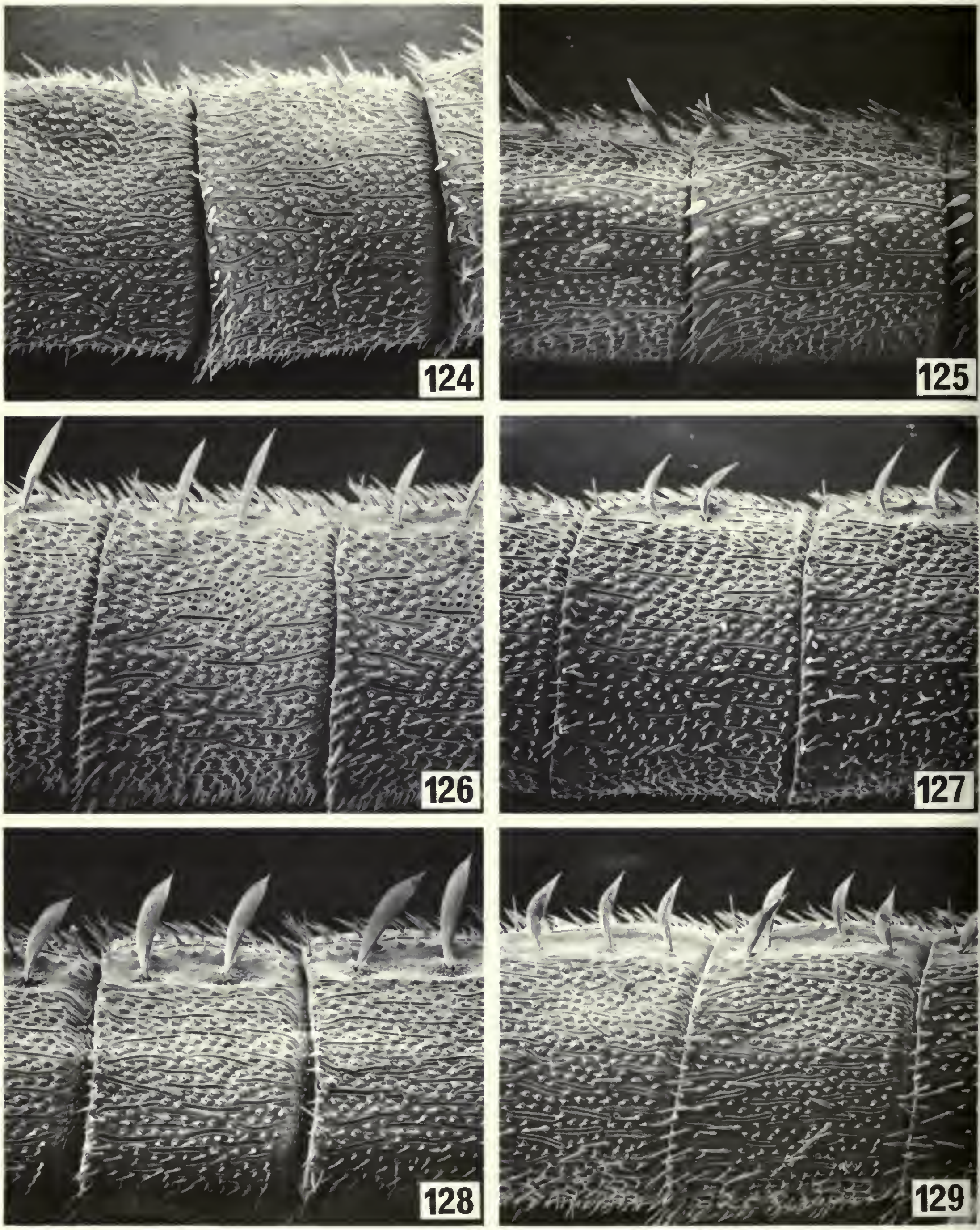

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British Museum (Natural History)

An introduction to the Ichneumonidae of Australia

I. D. Gauld

In the important field of biological and integrated control of pests the parasitic Hymenoptera are of particular significance, and this work considers one of the largest families of Parasitica, the Ichneumonidae. The group has received little attention in Australia – though it has already been utilized successfully in curtailing the ravages caused by accidentally introduced pests. For selective control programmes to be effective, however, a sound knowledge of the biology of both the pest and its parasites is essential – and a sound taxonomic base is vital for the development of such knowledge.

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Ian D. Gauld

Entomology series
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Synopsis

An attempt is made to reconstruct the phylogeny of the genera of the ichneumonid subfamily Ophioninae using both parsimony and compatibility methods of analysis. The problems of phylogenetic analysis of highly homoplastic data are discussed and the strengths and weaknesses of the various methods evaluated. It was concluded that there is no wholly adequate objective method of analysing highly homoplastic data, but it is suggested that analysis may be undertaken using subjective evaluation of characters supporting conflicting patterns. Within the Ophioninae five major evolutionary lineages are recognized, the *Ophion, Sicophion, Eremotylus, Thyreodon* and *Enicospilus* genus-groups. The largest, the *Enicospilus* genus-group, is subdivided into five subgroups, the *Orientospilus, Ophiogastrella, Stauropoctonus, Leptophion* and *Enicospilus* subgroups. A scenario for the possible evolution of the subfamily is suggested. Thirty-two genera are recognized, one of which, *Janzophion*, is described as new. *Rictophion* is treated as a synonym of *Euryophion, Ophionopsis* is treated as a synonym of *Dictyonotus*, and *Aulophion* treated as a synonym of *Stauropoctonus*. The majority of genera are shown to be holophyletic, but *Ophion* and *Enicospilus* are thought to be paraphyletic, though for purposes of classificatory convenience they are retained as valid genera. Diagnostic descriptions of the genera are given and the inter-relationships of their component species are discussed.

Introduction

Ophionines are mostly quite large, slender, orange-brown ichneumonids that can frequently be observed flying around lights at night in virtually any part of the world. In temperate regions there are rather few species, but in the tropics there are very large numbers of taxa, and ophionines form a conspicuous component of the ichneumonid fauna. Almost all members of the subfamily are nocturnal or crepuscular, though in drier areas a few are diurnally active. Males of many species fly at dusk, but most females are not active until an hour or two after dark.

Ophionines are solitary protelean endoparasites of holometabolous insect larvae. The hosts of the vast majority of species are not known, but what records there are usually refer to species parasitizing lepidopterous larvae, most often exposed, solitary larvae, and in particular species of the families Noctuidae, Geometridae and Lymantriidae. Larvae of a wide range of other families are also attacked, but there are extremely few records of ophionines parasitizing Microlepidoptera or Rhopalocera. One Nearctic species is exceptional in that it is known to parasitize coleopterous larvae (Townes, 1971).

Oviposition is usually into the host larva. The parasitoid egg is apparently free in the host's haemocoel where it hatches to produce a caudate first instar larva (Moutia & Curtois, 1952). Species attacking mature larvae undergo rapid development, but species (e.g. *Enicospilus americanus*) that oviposit in very young larvae have a protracted first larval instar (Price, 1975). Several species are apparently host specific (Janzen, pers. comm.), whilst others (e.g. *Thyreodon atriventris*) parasitize a variety of taxonomically related hosts. Some temperate species seem to attack a number of different hosts in a similar niche, whilst a few species are bivoltine, with different generations attacking different hosts (Brock, 1982). A few species seem to attack a wide range of hosts (Gauld & Mitchell, 1981). The parasitoid larva completes development just prior to host-pupation, often after the host has constructed a cocoon. The ichneumonid larva spins a characteristic fibrous, ovoid cocoon which is generally dark brown with a pale equatorial band. Species may remain as mature larvae or even adults in this cocoon for the greater part of the year in seasonal habitats.

The research potential of Ophioninae

The ease with which ophionines may be collected (using m.v. light-traps) makes them particularly suitable for zoogeographic and ecological study. Large samples may be collected in terrain where sweep netting and Malaise trapping yield poor results, or, as in the case of rain forest canopy, where collecting can only be achieved by cumbersome, expensive and (for fast-flying insects) unproven techniques. Unlike Lepidoptera, which are similarly easy to collect, most tropical ophionines are readily separable without recourse having to be made to time-consuming genitalic preparation. Illustrated keys are available to facilitate identification of most Old World tropical species (Gauld, 1977; Gauld & Mitchell, 1978; 1981).

The aim of the present work

If the Ophioninae is to be used as a serious vehicle for zoogeographic study then it is necessary to have an understanding of the phylogenetic inter-relationships of the genera, as many authors contend that biogeographic speculations are valid only when related to the evolutionary history of a group (Mackerras, 1962; Nelson & Platnick, 1981). As little has been published on the phylogeny of Ophioninae, a cladistic study of the group is necessary before much of the distributional data available can be interpreted in an evolutionary manner. The aim of the present study is to investigate the phylogeny of the Ophioninae using a variety of modern cladistic techniques, and to relate the results to what is known about the distribution and biology of the group in general.

Terminology

The morphological terminology in this work follows that proposed by Richards (1956) and interpreted for the Ophioninae by Gauld & Mitchell (1978; 1981). Specialist terms, relevant to only some ophionines, are defined in these works. Family-group names used conform with the directives of the *International Code of Zoological Nomenclature* and with various *Opinions* of the International Commission. Some recent authors (e.g. Townes, 1969; 1971) have chosen to disregard certain of these opinions and have not followed the *Code* when forming family-group names (see Fitton & Gauld, 1976).

Material examined

The majority of specimens examined are contained in the collections of the British Museum (Natural History) (BMNH), but valuable additional material was furnished by the Australian National Insect Collection (ANIC), Canberra, the Bernice P. Bishop Museum (BPBM), Hawaii, the Canadian National Collection (CNC), Ottawa, the Gupta Collection (GC), the Musée Royal de l'Afrique Centrale (MRAC), Tervuren, the Muséum National d'Histoire Naturelle (MNHN), Paris, the Taiwan Agricultural Research Institute (TARI), Taichung, the Townes Collection (TC), Ann Arbor, the United States National Collection (USNM), Washington and the Zoological Institute (ZI), Leningrad. The types of virtually all Old World species have been examined and exhaustive lists of material examined are contained in recent revisionary studies (Gauld, 1977; Gauld & Mitchell, 1978; 1981; Gauld & Carter, 1983).

Discussion of methodology

The present work is an attempt to elucidate the phylogeny of the Ophioninae and therefore only phylogenetic methods of data analysis have been used. These methods are based on ideas initially expounded by Hennig (1966). Although Hennig made a major contribution to systematic philosophy, he greatly underestimated the difficulty that would occur in phylogenetic analyses due to morphologically undetectable evolutionary parallelism and character-state reversal (i.e. homoplasy). Such events result in there being incompatible character sets in taxonomic data. An estimation of the extent of incompatibility can be made using the simple test outlined by Le Quesne (1969) (see also Gauld & Mound, 1982; Underwood & Gauld, in prep.), and such incompatibilities are far from uncommon in most real data.

In the past decade two main approaches have been adopted by cladists in an attempt to resolve conflicting character sets – parsimony methods, which seek to minimize the number of character-state transformations, and compatibility methods, which seek to find a series of nesting groups supported by the largest number of compatible characters (Felsenstein, 1982). For simple data sets where there is a low incidence of homoplasy, these methods yield very similar results (e.g. Gauld, 1983), but as the frequency of homoplasy increases so the methods usually give increasingly different results.

Parsimony methods have gained wide acceptance in the literature, with the shortest rooted Wagner tree often being uncritically presented as the best phylogenetic hypothesis. Simultaneously, many authors have criticized compatibility analysis either for producing numerous apparent best solutions (Kluge, 1976), or as being less useful at producing congruent phylogenies from different developmental stages (e.g. Mickevich, 1978; Rohlf & Sokal, 1980) (but see also Rohlf *et al.,* 1983). However, Felsenstein (1981; 1982) stated that both methods can be justified as maximum likelihood methods, but under somewhat different circumstances. If homoplasy is expected to be scattered at random throughout all characters then a parsimony method is favoured, but if homoplasy is expected to be concentrated in certain characters then compatibility is supported. Felsenstein (*op. cit.*) continues by noting that both methods require both homoplasy to be rare and characters to have a low rate of change. In the case of Ophioninae, homoplasy demonstrably is not rare, suggesting results obtained by either method should be viewed circumspectly. The additional assumption necessary for parsimony methods to approach maximum likelihood, that is that homoplasy is randomly scattered across all characters, contradicts the consensus of opinion of most practising entomological taxonomists. Both parsimony and compatibility methods were used, with caution, in this study.

Choice of parsimony method utilized

Of the parsimony methods available at the start of this study, the program selected was PHYLIP (package for inferring phylogenies) written by Dr J. Felsenstein. This program offers four routines for dealing with non-polymorphic, discrete state data: (a) the Camin-Sokal parsimony method; (b) the Dollo parsimony method; (c) the Wagner parsimony method and (d) a mixed method allowing a, b or c to be specified for each character. The Camin-Sokal and Dollo methods were not used in the present study. Neither gives as short a tree as that obtained by the Wagner method as both place additional constraints on the ‘tree-growing’ method (Felsenstein, 1982), the former by not allowing reversal, the latter by not permitting forward parallelism.

In the insects being studied there is virtually no evidence at all for either of the additional *a priori* assumptions these methods necessitate. Indeed there is some biological evidence to suggest that these extra assumptions are unwarranted for ichneumonids. Dollo parsimony may justifiably be invoked for treating complex structures (such as the vertebrate eye), but virtually all characters used in the present study involve small changes in simple structures. Very often the derived state involves reduction of a structure, and observation of other ichneumonid taxa suggests that certain of these apomorphies (such as reduction of extent of occipital carina) have been developed in parallel in numerous different evolutionary lineages. Even when the apomorphic state is the development of a novel structure (such as an alar sclerite), the evidence strongly suggests (as the feature occurs in a few otherwise specialized species of several different genera) parallel development in closely related lineages.

Reversal is more difficult to demonstrate, but clearly it does occur. For example, the alar sclerites apparently have been lost by some *Enicospilus* species on oceanic islands (Gauld & Carter, 1983) and the posterior transverse carina of the propodeum, which is absent in most *Enicospilus* species, has been redeveloped in some members of the otherwise highly specialized *E. signativentris* species-complex (Gauld & Mitchell, 1981).

Because of the objections to the Camin-Sokal and Dollo methods the option employed in this study was that which necessitates no extra *a priori* assumptions, the Wagner method. Cladograms were rooted using a hypothetical all zero ancestor, as use of any outgroup taxon is liable to introduce more incidences of homoplasy.

The advantages and disadvantages of the parsimony method

The major advantage of the parsimony method seemed to be that, because of its 'averaging procedure' (see below), generally all species of a particular genus were associated. As ophionine genera are polythetic, compatibility methods invariably exclude certain taxa (see Davies & Boratyński, 1979).

Despite its widespread acceptance there are serious flaws in parsimony methodology when applied to complex data sets. (There are also philosophical objections (see Pratt, 1972; Felsenstein, 1981; Friday, 1982; Panchen, 1982), but these are beyond the discussion of the present work.) One, and perhaps the most obvious methodological flaw, is that because the method considers each character as an identical piece of binary information, and is attempting only to minimize transformation, a large set of coincidental 'bad' characters will be favoured at the expense of even a very slightly smaller set of 'good' characters. This is best illustrated in the case of some Hawaiian genera of ophionines (taxa 924-6 in the following study) and *Ophiogastrella* (taxa 910-11). In both cases, the sets of characters responsible for positioning these taxa in the Wagner analysis are composed of characters that are likely to be highly homoplastic in other taxa. Although a traditional taxonomist intuitively recognizes these as poor characters (and taxonomist's intuitive judgement may be very good, see Davies, 1981) and has no confidence in them as indicators of phylogenetic affinity, it was not found to be possible to translate this subjective bias into an objective taxonomic weighting scheme. Without an objective weighting scheme the averaging procedure adopted by the Wagner method has the effect of reducing the number of transformation steps of many 'weak' characters at the expense of 'moderately good' ones (Strauch, 1984).

Although some hybrid parsimony/compatibility trees produced in this study were longer than the shortest Wagner tree (mainly because certain characters appear to have been 'written-off', i.e. allowed to have a large number of transformations) it is noteworthy that these cladograms were supported by more characters with minimal or nearly minimal homoplasy. This can best be illustrated by reference to two alternative cladograms produced during this study, the most parsimonious 235-step one and the favoured 239-step one (Gauld, unpubl. PhD). The numbers of characters with various numbers of transformation steps are shown in Fig. 1.

A second disadvantage of the parsimony method is that a multiplicity of almost equally parsimonious cladograms may be generated from the same data set by the same procedure (Strauch, 1984), but altered merely by re-ordering the input order of the taxa (e.g. Figs 21–24). In this study it soon became apparent, when rearrangements are practised, that certain taxa are prone to 'hopping', i.e. moving from one lineage to another in different reconstructions. Taxon 906 was found to be such an OTU – its final position in a cladogram depended solely upon the position in which it was entered into the analysis. This was presumed to operate in the following manner: taxon 906 is almost equally associated (see Appendix 3) with three separate lineages, *Simophion*, the *Thyreodon* complex and the *Enicospilus* complex. This equality of association is so pronounced that once the taxon has linked to one or other of the alternatives (the first encountered) it does not share enough derived features with any other taxon to disassociate itself. Thus if the first three taxa entered are 905 (*Simophion*), 906 and 940 (a more distantly related taxon), 906 remains associated with 905, whilst if the first three taxa entered are 935 (one of the *Thyreodon* complex), 906 and 940, 906 remains associated with the *Thyreodon* complex. Some programs attempt to circumvent this problem by computing an 'advancement index' for ordering the taxon input, but I fail to see the intellectual justification for this.

A third disadvantage of the parsimony method is that it is not possible to predict, from any given data set, the actual minimum tree length (Felsenstein, 1982; Day, 1983). This means that, for large data sets, in practice one is guessing that the minimum length tree obtained is the shortest possible. This study shows that for highly homoplastic data, a number of equally short, quite different cladograms may be obtained. It appears to be merely an *act of faith* that a slightly

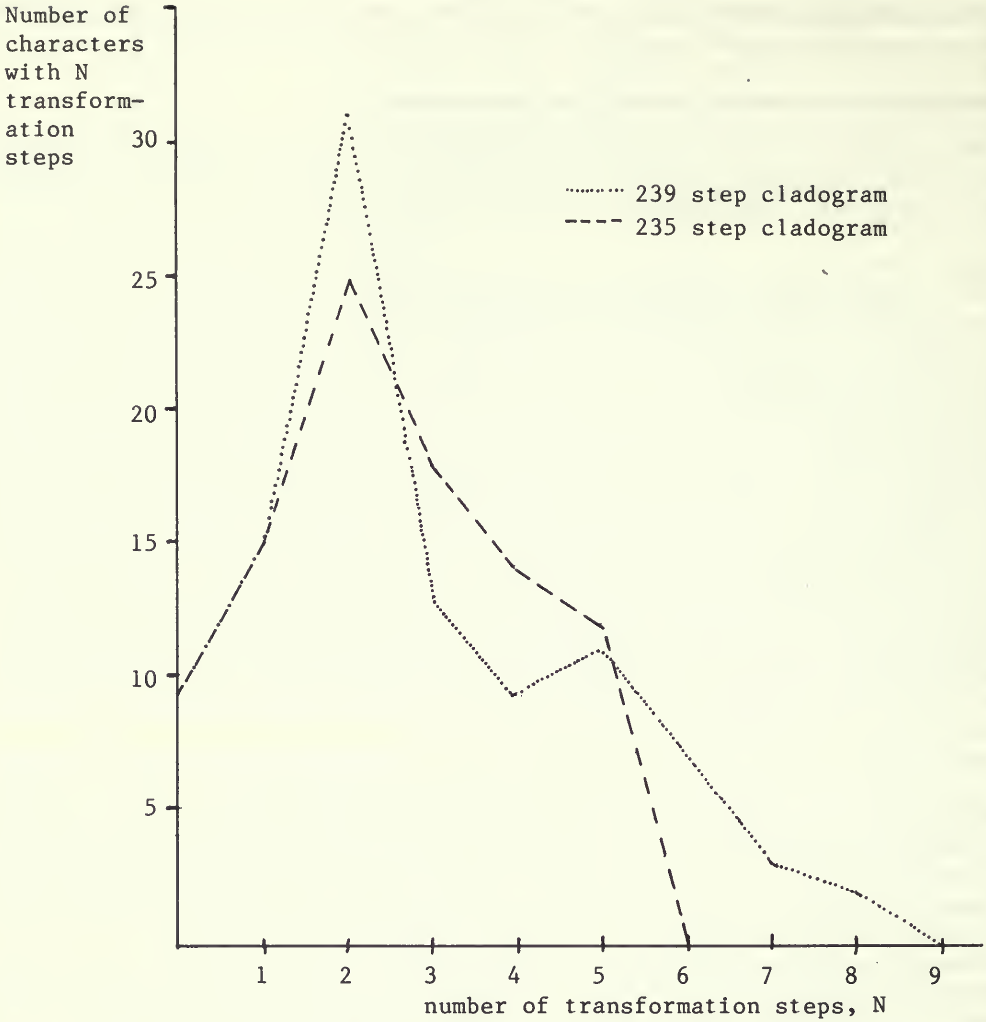


Fig. 1 A comparison of the incidences of transformation required to fit all characters to the most parsimonious 242-step cladogram and a favoured 249-step cladogram (From Gauld, unpubl. PhD thesis). It is noteworthy that the latter, although 7 steps longer, is supported by more minimally homoplastic characters.

shorter and yet totally different arrangement does not exist, a rather disconcerting observation if one accepts the principle of parsimony as paramount in phylogenetic reconstruction.

Compatibility methods utilized

Felsenstein's package, PHYLIP, provides an option for producing compatible character sets. This option, CLIQUE, was used to find the largest cliques for various sets of taxa considered in this study. A second program (written by Dr G. Underwood) was developed by Underwood and Gauld during the course of this study. This program was developed from the work of Le Quesne (1969; 1972) and involves calculating the probability of incompatibility between two characters on a null hypothesis of random distribution of states of both. This value was then used to calculate for each character a coefficient of character-state randomness (herein called the O/E value). Typically the output of this program, LEQU.BAS, consists of a list of characters with their observed incompatibilities, calculated expected number of incompatibilities, and O/E values tabulated; the characters are ranked by O/E value as a postscript (e.g. Tables 2, 6). A facility has been incorporated so that multistate characters which have been coded in binary fashion and numbered as decimal increments (e.g. 1·1, 1·2), and cannot logically fail, are not compared.

Included also in LEQU.BAS is a labelling feature. This is based on an idea given by Guise *et al.* (1982) for counting frequencies of each of the four possible character-state combinations (0,0; 0,1; 1,0; 1,1) for each character pair. If a pair of characters fail the test (because all four combinations are found in the data) on account of a single occurrence of one combination, the taxon having this combination is labelled. The results of this operation are printed in the form of a table (e.g. Appendix 4). The figure in brackets adjacent to the taxon is the total number of labels the taxon has received. The taxa most frequently labelled will be the ones with the most discordant character sets. A particularly high label score for a species for any one character strongly suggests homoplasy for that character with respect to other taxa in the set. Some care is needed in the interpretation of results as characters with very unequal character-state distribution (either only two 0 or two 1 scores) often have high label values. These are easily recognized as equally high scores are given for the two taxa with the minority states. Even these values can sometimes be seen to be unusually high (i.e. suggestive of homoplasy) if the character label values are compared with the label values of similarly uninformative characters.

Value of LEQU.BAS for overcoming some problems of compatibility analysis

Two major disadvantages with compatibility analysis are: (1) a maximum character set is often far too small to allow full resolution of data (Felsenstein, 1982) and (2) the data set may yield a number of more or less equally large cliques (Kluge, 1976). LEQU.BAS is of some value in overcoming both these problems.

As the largest compatible character set is generally very small, it is useful to have a way of ordering characters. Homoplastic characters that would be eliminated from any compatible set are not all equally bad; some are far more discordant than others. For example, allowance of just one incidence of parallelism or reversal may be enough to make certain characters compatible with a cladogram, whereas others will necessitate the invocation of multiple incidences of homoplasy to achieve congruence. It can be seen from the hypothetical data set 1 (Tables 1–3) that LEQU.BAS offers a way of grading characters from slightly to extremely homoplastic. Eight taxa, A–H, exhibit 18 binary characters (Table 1). Characters 1–12 support the nested set (((AB)C)((DE)(F(GH)))). Characters 13–18 are differentially homoplastic, 13 and 14 requiring one extra transformation to fit the specified cladogram, 15 and 16 requiring two extra transformations and 17 and 18 needing three extra. Analysing these data with LEQU.BAS gave the results presented in Table 2. It can be seen that the six homoplastic characters are ranked in order of the extra number of transformations required to make them fit the specified cladogram. Several taxa are highly labelled for certain characters, suggesting homoplasy. For example, character 15, which is present in the apomorphic state in B and C, but is plesiomorphic in A, is highly labelled for A, suggesting a reversal may have occurred.

Table 1 Character state matrix for hypothetical data set 1. A–H represent taxa, 1–18 their independent characters. 0 = plesiomorphic, 1 = apomorphic.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
A	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0
B	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1
C	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1
D	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0
E	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	1
F	0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	1	1	1
G	0	0	0	0	1	1	0	0	1	1	1	1	1	0	1	0	1	0
H	0	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	0	1

Table 2 Result of LeQuesne test on hypothetical data set 1. The number in italics is the character number, the second column is the number of observed failures, the third column the number of expected failures and the final column in each case the ratio of observed over expected failures. Characters with a low O/E value are considered to be good characters, and are ranked in the final line higher than those with high O/E scores.

Character number:	failures observed	expected	O/E ratio	Character number:	failures observed	expected	O/E ratio	Character number:	failures observed	expected	O/E ratio
1 :	3	8.68	0.35	*2* :	3	8.68	0.35	*3* :	5	12.21	0.41
4 :	5	12.21	0.41	*5* :	5	12.21	0.41	*6* :	5	12.21	0.41
7 :	2	8.68	0.23	*8* :	2	8.68	0.23	*9* :	4	12.21	0.33
10 :	4	12.21	0.33	*11* :	3	8.68	0.35	*12* :	3	8.68	0.35
13 :	7	12.21	0.57	*14* :	8	13.09	0.61	*15* :	10	12.21	0.82
16 :	13	13.09	0.99	*17* :	16	13.09	1.22	*18* :	16	12.21	1.31

Grand totals- failures observed	expected	O/E ratio
57	100.63	0.57

Ranking ratios

7 8 9 10 1 2 11 12 3 4 5 6 13 14 15 16 17 18

Although there is a clear relationship between the number of extra transformations required to make a character 'fit' a favoured cladogram and that character's O/E value, the O/E value also varies with information value of the character, i.e. the number of 1 scores in relation to 0 scores. For example, in data set 1, character 14 may be modified so it has the following distribution of 1 states in taxa A–H, 11100000, 11001000 or 10001001. These require one, two and three transformations, respectively, and have O/E values of 0·41, 0·90 and 1·24. However, if the number of transformations necessary is kept constant (at say two) and the number of derived states varied, the following relationship may be observed: 10001000 (O/E = 1·41), 11001000 (O/E = 0·90), 11011000 (O/E = 0·61), 11100010 (O/E = 0·53), 11100011 (O/E = 0·50), 11100111 (O/E = 0·23). Similar variations of character 16 (requiring three transformations) produced values with the range 0·74–1·24 (the largest being for 10010001), whilst a range of 1·16–1·35 was found for a character requiring four transformations. Thus a homoplastic character with a high proportion of derived states supporting various subgroups in the definitive cladogram may have a lower O/E value than a less homoplastic, but less informative character.

Kluge (1976) pointed out that compatibility analysis may produce a large number of equally large cliques. From his data set of 139 binary characters he obtained six almost equally large cliques of 80 or 81 characters. Kluge remarked that not only is there no reason to prefer one to any other of the sets, but also pointed out that the most primitive species in each of the cliques did not correspond to the most primitive as assessed on the basis of the best documented characters. To consider Kluge's objections necessitates re-examining his data. Of his six largest cliques, it is apparent that no less than 76 characters are common to all sets. The six dendrograms supported by these cliques are essentially similar, differing mostly in the relative order of the most primitive taxa (im–ti in Kluge's fig. 7a) so a great deal of information is common to all, and

Table 3 Labels matrix derived from hypothetical data set 1. The column to the right of the taxon letter is the total number of times that taxon is solely responsible for a character failing the LeQuesne test. For further details see text.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
A (21)	3	3	3	3	3	3	-	-	-	-	-	-	1	-	8	2	6	7
B (6)	3	3	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2	2
C (8)	-	-	2	2	2	2	-	-	-	-	-	-	-	4	-	4	-	-
D (5)	-	-	-	-	-	-	2	2	-	-	-	-	1	-	-	-	2	3
E (7)	-	-	-	-	-	-	2	2	-	-	-	-	1	-	2	-	4	3
F (5)	-	-	-	-	-	-	-	-	1	1	-	-	5	1	1	1	-	-
G (12)	-	-	-	-	-	-	-	-	2	2	3	3	-	1	1	4	2	6
H (8)	-	-	-	-	-	-	-	-	1	1	3	3	-	-	-	2	4	2

this agrees with Kluge's preferred phylogenetic arrangement. Most of the differences between cliques (and between the dendrograms supported by these and the preferred arrangement) involve relatively uninformative characters. It is mathematically demonstrable that the probability of chance compatibility of a particular character with any other set of characters is inversely proportional to the information value of the character. Therefore, one criterion of which clique to select is to favour that with the highest information value.

However, in practice one frequently finds that the subsets which are not common to all the similar-sized cliques comprise equally poorly informative characters. In such cases the average O/E value for a clique is a useful indicator of the degree to which the clique is consistent with slightly homoplastic (and hence excluded) characters which are not normally considered in a compatibility analysis. For example, consider the hypothetical data set 2 (Tables 4, 5). There are two equally large, equally informative cliques:

A (10) [1, 2, 3, 4, 5, 6, 7, 8, 9, 10] Average O/E value = 0·308
B (10) [1, 2, 3, 4, 5, 6, 7, 8, 9, 14] Average O/E value = 0·323
$A \cap B = \{1, 2, 3, 4, 5, 6, 7, 8, 9\}$

Table 4 Character state matrix for hypothetical data set 2. Conventions follow table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
J	1	1	0	0	1	1	0	0	0	1	1	1	1	1
K	1	1	0	0	1	1	0	0	0	1	1	1	1	0
L	1	1	0	0	1	1	0	0	0	0	0	1	1	0
M	1	1	0	0	1	1	0	0	0	0	0	0	0	1
N	1	1	0	0	0	0	0	0	0	0	0	0	0	0
O	0	0	1	1	0	0	1	1	0	0	1	0	0	0
P	0	0	1	1	0	0	1	1	1	0	0	1	0	0
Q	0	0	1	1	0	0	1	1	1	0	0	0	1	0

Table 5 Results of LeQuesne test on hypothetical data set 2. Conventions follow table 2.

Character number:	failures observed	expected	O/E ratio	Character number:	failures observed	expected	O/E ratio	Character number:	failures observed	expected	O/E ratio
1	3	9.86	0.30	2	3	9.86	0.30	3	3	9.86	0.3
4	3	9.86	0.30	5	3	10.63	0.28	6	3	10.63	0.28
7	3	9.86	0.30	8	3	9.86	0.30	9	2	6.89	0.29
10	1	6.89	0.15	11	11	9.86	1.12	12	12	10.63	1.13
13	12	10.63	1.13	14	4	6.89	0.58				

Ranking ratios

10 6 5 9 1 2 3 4 7 8 14 11 12 13

These sets differ in one character, possession of either 10 or 14. Character 10 supports J + K whereas 14 supports J + M. No other character that is compatible offers support for one or other of these alternatives but some homoplastic characters do support J + K (plus other taxa also) reinforcing the J + K grouping suggested by character 10. No homoplastic character reinforces the J + M suggestion. This reinforcement can be detected by differences in the values of the O/E ratio, as character 10 scores 0·15 whereas character 14 scores 0·58. This difference in O/E value is responsible for the difference in average O/E values of the two cliques A and B, and it thus seems reasonable to prefer the clique with the lowest average O/E value. This method offers a simple objective procedure for selecting one of a number of large cliques as 'most favourable', as it will be the one reinforced by most secondary characters.

In the present study compatibility analysis was found to give, up to a point, results that were similar to conventional taxonomic assessment. Frequently, characters considered important in generic classification by traditional taxonomists were found to be the intersect of the largest cliques.

The operational procedure adopted in this study

This study was commenced by tentative recognition of groups of taxa from the shared derived character matrix (Appendix 3). The rigidity of these groups was tested using Underwood's FOURS program (Underwood, 1982) and then further analyses using the compatibility and parsimony methods outlined above. Resulting cladograms were compared and differences subjectively evaluated by appraisal of characters supporting different options. The various groups were gradually related to each other until the majority of taxa had been placed. The remaining unplaced taxa all exhibited confusing affinities. To facilitate their placement a number of hypothetical taxonomic units were proposed to represent the various genera already placed in the analysis. The data set comprising hitherto unplaced taxa and HTUs was analysed using parsimony and compatibility techniques, and the resulting cladograms subjectively evaluated.

An apologia for subjectivity in cladistic analysis

In recent years there has been a great deal of intellectual activity devoted to making taxonomy more 'scientifically respectable' by attempting to remove subjectivity. Phenetic methods were the first to be claimed as objective taxonomic procedures (Sokal & Sneath, 1963), but these methods were essentially a movement away from evolutionary taxonomy (Nelson & Platnick, 1981) and have largely been eclipsed by the development of numerical cladistics. Despite the seeming objectivity of such numerical methods, they are really only objective ways of analysing largely subjective data, as character selection is a highly subjective procedure (Pratt, 1972). Furthermore, the claim by many cladists that their favoured numerical methods (parsimony analyses) are scientific (in the Popperian sense) is flawed by the assumption that parsimony *per se* is a criterion for formulation of a scientific hypothesis (i.e. the least falsified hypothesis is accepted – Gaffney, 1979), as is eloquently shown by Panchen (1982). A phylogenetic hypothesis derived from a cladistic analysis rests on the supposition (or hypothesis) that a particular derived character-state is a genuine synapomorphy which thus indicates commonality of descent of two or more taxa. In a highly homoplastic data set, for every character that is accepted as a genuine synapomorphy, others are rejected as showing false patterns. Farris (1969) defends parsimony in such cases, on the grounds that hierarchic correlations are more likely to occur among cladistically reliable characters than among cladistically unreliable characters (i.e. random variables). This is true only if cladistically unreliable characters vary randomly and is not a corollary of the generally accepted statement that random variables are cladistically unreliable characters. Clearly it is untrue; most taxonomists can cite examples of suites of characters being size related, habitat related, associated with a particular biological strategy and so forth. How then is a taxonomist supposed to choose between competing character sets if not by 'biggest is best' criteria? I think this can only be done at present, subjectively. Competing character sets are examined in the light of a taxonomist's knowledge of the variability of characters over a much wider group of organisms. Highly variable features (such as the number of ribs or vertebrae in some birds – Strauch, 1984 – or the form of mammalian teeth – Butler, 1982) are rejected as unlikely to be indicative of phylogenetic affinity. Other sets clearly comprise adaptive features associated with certain habitats and these may likewise be rejected. It is noteworthy that very many cladistic analyses seem to have been undertaken on data sets that have initially been subjectively edited (with no explanation) by discarding characters which are presumably thought to have no phylogenetic value. In this work I have tried to explain my reasons for rejecting certain character sets in preference to others.

The holophyly of the subfamily

A prerequisite to meaningful cladistic analysis is the establishment of the holophyly of the group being studied. The holophyly of the Ophioninae is supported by the following apomorphies.

(a) Possession of a spurious vein extending from the vannal notch to the tornus of the fore wing. This feature, first recognized by Perkins (1959), is an autapomorphy of the subfamily.

(b) Possession of numerous setae on the labial sclerite of the final instar larva (Short, 1978). This feature is also an autapomorphy of the subfamily.

(c) Presence of a single radio-medial cross vein (? 3*r–m*) far distal to 2*m–cu*. This unusual condition is elsewhere only found in isolated genera of the Campopleginae, Tersilochinae and Anomaloninae (Townes, 1970; 1971; Gauld, 1976). In none of these taxa is the cross vein as far distal to 2*m–cu* as is the case in ophionines.

(d) Possession of a sinuous pectinal comb on the tarsal claws. Many ichneumonids have a few scattered pectinal teeth on the tarsal claws but very few have a strongly developed sinuous comb like that found in virtually all ophionines.

(e) Total loss of glymmae. These structures are present in at least some members of virtually all other subfamilies. No trace has ever been observed in ophionines.

(f) Enlargement of ocelli and related nocturnal specializations (Gauld & Huddleston, 1976). The pale colour, enlarged ocelli and eyes, long antennae and slender legs are features found in many nocturnal ichneumonoids, but this suite of characters is apparently an apomorphic feature of the Ophioninae.

The systematic position of the subfamily

The subfamily Ophioninae belongs to the Ichneumonidae, a holophyletic group of apocrite Hymenoptera (Königsmann, 1978). Virtually nothing has been published about the phylogenetic relationships of ichneumonid taxa and, if a reasonable assessment is to be made of character polarity in Ophioninae, it is necessary to attempt to place the group in relation to some other subfamilies.

From study of Cretaceous fossil ichneumonoids (Townes, 1973*a* & *b*; Rasnitsyn, 1983), comparison with putative ancestral groups (such as siricids and cephids) and examination of primitive extant Apocrita (e.g. Megalyridae, Stephanidae, some Braconidae), it can be deduced that primitive ichneumonoid features are likely to include: possession of an un-notched (possibly long) ovipositor; possession of a gaster that is broadly attached to the propodeum and has a free first sternite; possession of an areolated propodeum; possession of notaular grooves; possession of simple or basally lobate claws. Study of the biological evolution of parasitoids (e.g. Shaw, 1983) suggests that the ectoparasitic habit is primitive with respect to endoparasitism, and as both types occur in the Ichneumonidae (Clausen, 1940; Gauld, 1984*b*), one expects that the most primitive taxa will be found amongst ectoparasitoids. Some authors (e.g. Cushman, 1926; Telenga, 1969; Achterberg, 1976; 1984) suggest that primitive ichneumonoids are likely to have been parasites of xylophagous coleopterous larvae, as are archaic extant parasitoids such as orussids (Quinlan & Gauld, 1981; Middlekauf, 1983). These data suggest that the most primitive extant ichneumonids are to be found amongst the Pimplinae, Labeninae and perhaps also Tryphoninae. This hypothesis is supported by studies of larval morphology (Short, 1978) and is concomitant with the informal higher classificatory scheme outlined by Townes (1969).

Compared with the Pimplinae and Labeninae, the Ophioninae appears to be a rather specialized subfamily. It seems to belong to a large, holophyletic group of taxa that includes the subfamilies Ophioninae, Campopleginae, Cremastinae, Tersilochinae, Banchinae and Ctenopelmatinae. The holophyly of this group is suggested by the following apomorphies:

(a) possession of a dorsal subapical notch on the ovipositor;
(b) possession of similar female reproductive tract (Pampel, 1913);
(c) having endoparasitic larvae which lack a labral sclerite and possess a Y-shaped prelabial sclerite (see also Fig. 2).

Two of the included taxa, the Ctenopelmatinae and Banchinae, usually possess a plesiomorphic first gastral segment which is broadly attached to the propodeum, has a more or less centrally positioned pair of spiracles and a free sternite. In the Ophioninae, Campopleginae, Cremastinae and Tersilochinae this segment is specialized. It is more slender, has the tergite and sternite intimately fused and is lengthened anteriorly so that the spiracles are nearer to the posterior end. Furthermore, all these taxa possess apomorphic, laterally compressed gasters, suggesting they constitute a holophyletic clade.

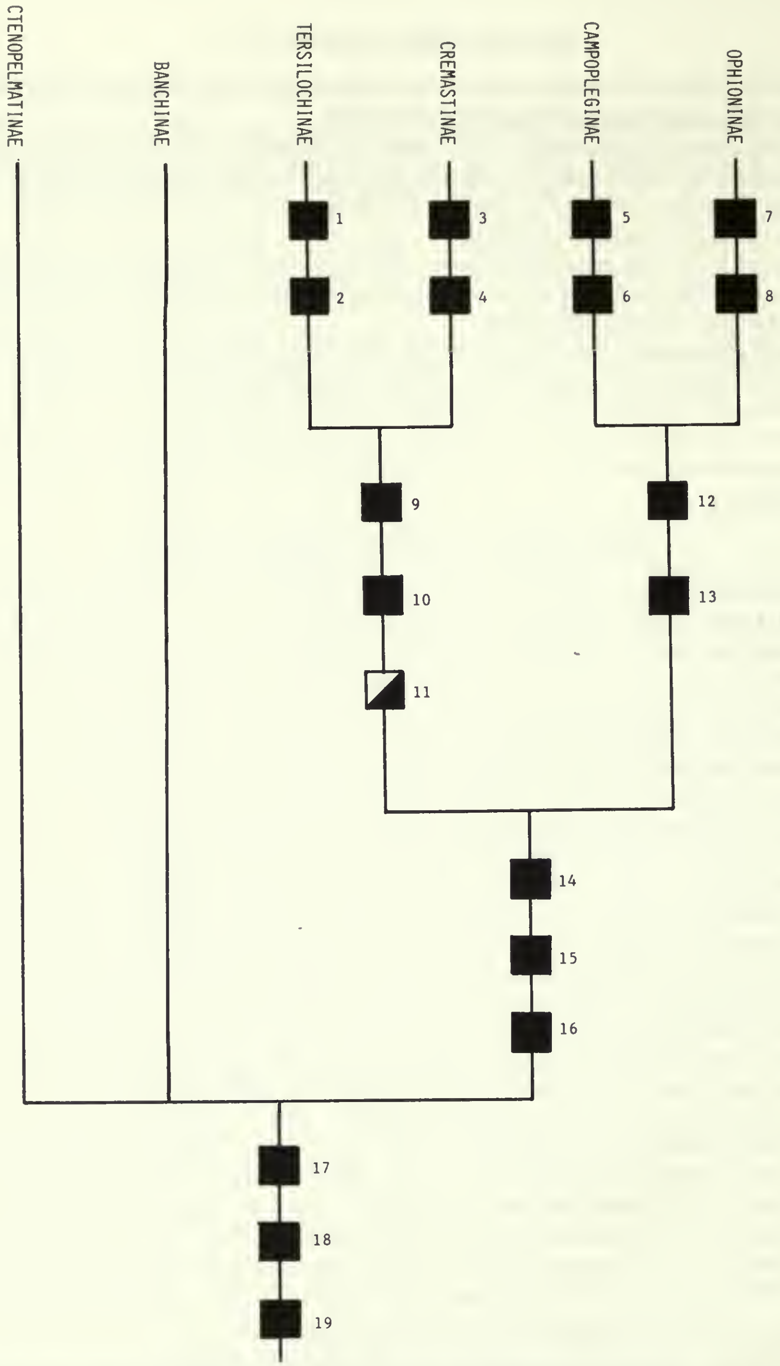


Fig. 2 Cladogram showing putative phylogenetic inter-relationship of the ophionoid group of ichneumonid subfamilies. The apomorphic features supporting this arrangement are: 1, possession of a fringed clypeus; 2, fusion of *Rs* with *M* in central part of fore wing; 3, development of sclerotized bridge between tibial spurs; 4, possession of striae on tergite 2 of gaster; 5, loss of distal abscissae of veins in hind wing; 6, fusion of areae superomedia and petiolaris; 7, development of spurious vein in fore wing; 8, loss of 2*r–m* in fore wing; 9, enlargement of pterostigma; 10, reduction of length of *Rs* in hind wing; 11, development of sinuous apex to ovipositor; 12, possession of expanded larval labial sclerite; 13, development of tubular petiole with reduced glymmae (note this is developed in parallel in some tersilochines); 14, gaster laterally compressed; 15, petiolar spiracle near hind end of tergite; 16, tergite and sternite 1 intimately associated; 17, possession of a dorsal subapical notch on ovipositor; 18, possession of a similarly modified female reproductive tract (see Pampel, 1913); 19, endoparasitic larva with a Y-shaped prelabial sclerite.

Within this clade two apparent groups are recognizable. One comprises the Tersilochinae + Cremastinae and is supported by two apomorphies, possession of an enlarged pterostigma and strongly shortened vein *Rs* in the hind wing. In addition both these taxa share a number of developmental trends (underlying synapomorphies of Saether, 1979), most notably, the development of a sinuous ovipositor apex and the presence of dorsally convergent eyes in males. The second group, Ophioninae + Campopleginae, is supported by a larval specialization, the possession of an expanded labial sclerite. The petioles of these two taxa are similarly modified, although this development appears to have been paralleled in some tersilochines (primitive tersilochines have a more 'cremastine-like' petiole). Most ophionines and campoplegines possess an apomorphic short, straight ovipositor; even when it is long it is very similar in the two groups, being robust and up-curved.

For the purposes of this study the Ophioninae is considered to be the sister-group of the Campopleginae, and the Campopleginae + Ophioninae is treated as the sister-group of the Cremastinae + Tersilochinae (Fig. 2).

Polarity determination and character coding

The polarity of the majority of characters has largely been determined by the method of out-group comparison (Watrous & Wheeler, 1981) using as out-groups the taxa mentioned above. Unfortunately this method does not work for all characters, usually because both states occur in both the group under study and the out-groups. In these cases the polarity assignment is based on unsatisfactory criteria such as common equals primitive, but this is stated in the discussion.

In many cases in the Ichneumonidae, character-states are progressive steps in the loss of ancestral features such as the occipital carina, propodeal carinae or segments of the palp. Such characters can be arranged in simple transformation series, from plesiomorphic to the most derived state. For example, for maxillary palps – 5-segments to 4-segments to 3-segments. Such transformation series may simply be scored in binary form as two characters –

	8·1	8·2
maxillary palp 5-segmented	0	0
maxillary palp 4-segmented	1	0
maxillary palp 3-segmented	1	1

where 0 = plesiomorphic and 1 = apomorphic. Hence 8·1 represents reduction from 5 to 4 segments and 8·2 further reduction to 3. Such characters are obviously not independent for it is impossible to have a 0,1 coding as, if extreme reduction is observed, it is assumed that an intermediate stage has been passed through.

In other cases a particular structure may have been modified in one of several ways. For example, in the Ichneumonidae generally the mandible is bidentate equally, so in the Ophioninae teeth of the same length must be considered a plesiomorphic feature. Although the lower tooth is fairly constant in size, the upper may either be lengthened or shortened. Such a bifurcate series can be scored as two binary characters –

	4·1	4·2
mandible equally bidentate	0	0
upper tooth enlarged	1	0
upper tooth reduced	0	1

Thus character 4·1 represents enlargement of the upper tooth, whilst 4·2 represents reduction. Clearly a 1,1 coding cannot exist for such character pairs. All transformation series in the characters dealt with below have been treated in similar fashion.

From the very large number of characters exhibited by the Ophioninae a number have been selected which show the greatest range of variation between the different genera. Included are all characters previously considered to be diagnostic of genera, and a number of additional features that have been found to be useful in delineating species-groups (e.g. in Gauld &

Mitchell, 1978). Many other characters, features in which a single species differs from others in a species-complex, were excluded from this analysis. These characters, such as the shape of the alar sclerites, form of the microsculpture of the alitrunk, density of hairs on the wing surface, general colour pattern, relative length of the mid tibial spurs etc., show a considerable range of variation within the species of any single genus and, in most cases, this range of variation is repeated in many genera. Such characters were considered to be unlikely to make significant contribution to resolving the phylogeny of the genera.

Characters used in the study

In the following section considerable space has been allocated to explaining the rationale involved in character scoring and polarity determination. Although this practice is not usual in all cladistic studies (characters are frequently relegated to an appendix) it is considered to be important in the present work. It is upon these scores that the results of any numerical analysis depend; consequently, this section is seminal to the entire work.

The characters and their polarity

1·1, 1·2 Occipital carina. A complete occipital carina is plesiomorphic (0,0). It may be centrally interrupted (1,0) or absent (1,1).

2 Mandibular axis. The plesiomorphic condition is for the axis of articulation of the mandible to be at 90° to the longest axis of the head. In a few ophionines the head is narrowed and the mandibular axis tilted almost into the vertical plane (1).

3 Mandibular swelling. A flat outer mandibular surface is plesiomorphic for ichneumonids; the swelling present near the mandibular base of some ophionines is apparently a derived feature (1).

4·1, 4·2 Mandibular teeth. The relative lengths of the teeth vary considerably in ichneumonids, but equally bidentate appears to be the plesiomorphic state (0). In ophionines the alternative specializations are – upper tooth elongate (1,0) and upper tooth reduced (0,1).

5·1, 5·2 Torsion of the mandibles. The plesiomorphic condition for ichneumonids is to have the teeth of the mandible aligned in the same plane as the mandibular axis (Figs 38, 39). Many ophionines have the mandible twisted from 5–50° so that the lower tooth is directed forwards (Fig. 40). In a few species the mandible is exceptional in being twisted more than 70° so that, when closed, the lower tooth occludes the internal, upper one. This torsion is here considered a serial development, from untwisted (0,0) through slightly twisted (1,0) to exceptionally twisted (1,1). The selective advantage of this torsion is not clearly understood, but it is suggested that it is important in facilitating egress from certain types of cocoon. It is noteworthy that not only do all species of the huge and successful genus *Enicospilus* have such mandibles, but the totally unrelated tryphonine genus *Netelia* (which is also nocturnal and has a similar host range) also has twisted mandibles.

6·1, 6·2 Shape of the clypeal margin in anterior aspect. The shape of the clypeus is often characteristic of a group of ichneumonids. For example, in the pimplines it is usually bilobate, in the anomalonines convex with a central tooth, whilst in the ichneumonines it is usually flat and truncated. The weakly convex condition found in many ophionines, campoplegines and cremastines is considered plesiomorphic. In the Ophioninae the clypeus may be modified one of two ways – either being strongly concave (1,0), or centrally produced and pointed (0,1).

7·1, 7·2 Clypeal profile. It is difficult to assign polarity to this character, but the widespread condition in the subfamily and in the closely related out-groups was assumed to be plesiomorphic. This is the possession of a virtually flat clypeus (0,0) (Fig. 39). The clypeus may be modified in one of two ways – either flared outwards (1,0) (Fig. 44) or with a groove present parallel to the margin, so that the actual margin is sharp (0,1) (Fig. 38).

8·1, 8·2 Number of maxillary palp segments. The plesiomorphic condition for the Hymenoptera is 6-segmented palps, but in the Ichneumonidae the number is reduced to 5. Fusion may occur between the distal two or three segments leading to a reduction in apparent segment number to 4 or 3. This character is scored as a transformation series, 5-segmented being 0,0, 4 being 1,0 and 3 being 1,1.

9 Shape of central segments of maxillary palp. In most primitive ichneumonids, virtually all members of the out-groups and many ophionines, the maxillary palp segments are slender and elongate. This is considered to be plesiomorphic. In a few ophionines the central segments are specialized, being globose.

10 Maxillae. The maxillae of most ichneumonids resemble those of the more primitive mandibulate hexapods (Richards, 1956). A few ophionines have the maxillae specialized, unusually elongated so that the galea projects below the mandibles. This apomorphic condition is found in species inhabiting dry areas and is presumed to be an adaptation to feeding from certain flowers.

11 *Labium.* Like the maxillae, the labium is remarkably unspecialized in most ichneumonids. A few eremic ophionines possess greatly elongated glossae, an apomorphy that presumably has a similar function to character 10.

12 *Ocelli.* The majority of ophionines exhibit a set of features, the so-called ophionoid facies (Gauld & Huddleston, 1976), common to nocturnal Hymenoptera. These features are here regarded as apomorphies of the entire Ophioninae. They include possession of greatly enlarged ocelli. The majority of species in the out-groups, being diurnally active, lack this specialization. Consequently the possession of enlarged ocelli must, within the Ophioninae, be regarded as a plesiomorphy. In a few areas where competition from other ichneumonids is low, e.g., remote islands, deserts, tops of high mountains, several ophionines have adopted a diurnal habit. This is presumed to be a secondary feature as several species retain some nocturnal features. However, these diurnal species have small ocelli, and in these cases small ocelli are considered apomorphic. Polarity determination of this character can be questioned as it is based on an *a posteriori* inference.

13 *Frontal grooves.* Most ichneumonids, including almost all members of the out-groups, have the lateral part of the frons flat. In some ophionines a groove is present on either side, parallel to the inner orbit. Possession of this groove is regarded as a specialization.

14·1, 14·2 *Flagellum length.* In most ichneumonids the flagellum is setaceous and consists of a large number of more or less identical segments (flagellomeres). In the majority of ophionines there are between 45 and 65 such segments, and the flagellum is about as long as the fore wing. This is considered, because of its common occurrence within the group, to be the plesiomorphic condition. The flagellum appears to be modified in one of two ways. Either the segments may be very short and transverse (scored 1,0) or the number may be greatly increased (to between 75 and 95) so the flagellum is very much longer than the fore wing (0,1). A short flagellum is found in many species inhabiting hot, dry areas, and is perhaps an attempt at reducing an evaporative surface. A very long flagellum is found in species inhabiting humid areas, particularly rain forest canopies. Similarly shortened or elongated antennae can be observed in other groups, e.g. the Anomaloninae (Gauld, 1976).

15·1, 15·2 *Spiracular sclerite.* In most ichneumonids, including the majority of species in the closely related out-groups, the spiracular sclerite is exposed and is clearly visible near the upper hind corner of the pronotum (Fig. 42). This is considered to be plesiomorphic. A large number of ophionines have the upper corner of the pronotum somewhat broadened and notched to partially occlude the spiracular sclerite (1,0), whilst in a few species this flap completely covers the sclerite (1,1) (Fig. 43).

16·1, 16·2 *Notauli.* The notauli are grooves in the mesoscutum that appear to extend backwards from the anterior margin, and at their most extreme, reach the scuto-scutellar groove. The presence of these grooves seems to be a plesiomorphic feature (0,0), as they are well developed in many sawflies and are visible in many fossil apocritans. However, notauli are not present in all members of the out-groups so some doubt remains about the correct polarity of this character. The majority of ophionines only have vestigial notauli impressed at the extreme anterior margin of the mesoscutum (1,0), whilst in several they are absent entirely (1,1).

17 *Pronotal crest.* The plesiomorphic condition for ichneumonids is possession of a more or less flat pronotum dorsally. In several ophionines a crest is present to protect the neck region, possibly against attacks by asilids which habitually kill Hymenoptera by piercing the cervical region. The presence of this crest is regarded as an apomorphy.

18·1, 18·2 *Mesopleural furrow.* The plesiomorphic condition of the ichneumonid mesopleuron is for it to be relatively flat with a small pit (the episternal scrobe) near to the middle of the mesopleural suture (Townes, 1969). Amongst ophionines two specializations have apparently arisen – the presence of a diagonal groove from the pit to just below the subalar prominence (1,0) or possession of a groove from the pit to the upper end of the epicnemial carina (0,1).

19 *Epicnemial carina.* It is a plesiomorphic feature for ichneumonids to have this carina complete, extending laterally from the medioventral line to near the subalar prominence. In a number of taxa the lateral portion of this carina is lost (1).

20·1, 20·2 *Scutellar carinae.* These carinae are of sporadic occurrence throughout the Ichneumonidae but in many of the more primitive groups such as Pimplinae they are not developed. In the majority of species in the out-groups these carinae are absent, suggesting that their absence in ophionines may be a plesiomorphic feature. When present these carinae may be short, reaching to or not quite to the centre (1,0), or they may be virtually complete, reaching 0·8 or more of the length of the scutellum (1,1).

21·1, 21·2 Metanotal protuberances. The hind rim of the metanotum of most ophionines, as well as most campoplegines and cremastines, is unspecialized. In a few ophionines a small lateral tooth is discernible (1,0), whilst in some taxa this tooth is apparently enlarged to form a protuberance that extends back almost to the propodeal spiracle (1,1).

22·1, 22·2 Propodeal anterior area. The anterior part of the propodeum (Fig. 50), immediately behind the metanotum, is, in ichneumonids, characteristically depressed to form a transverse groove which is often somewhat broadened medially behind the postscutellum. This presumably plesiomorphic state is found widely in Ophioninae and in virtually all members of the out-groups. Two modifications from this pattern have been observed. In some species the groove is broadened (lengthened) and striate, and thus forms a broad shallow concavity, almost as if the insect had been stretched (Fig. 51) (1,0). The other adaptation is for the groove to be much deeper and present as a U-shaped furrow (Fig. 52) (0,1).

23 Propodeal spiracle. In the majority of ophionines and members of the out-groups the propodeal spiracle is oval or even subcircular, with the longest axis 4 or less times as long as the shortest. A few ophionines have very large, very elongate spiracles which are 8 or more times as long as broad. This is considered to be an apomorphic development.

24·1, 24·2 Anterior transverse carina of the propodeum. The presence of this carina, like the other propodeal carinae, is a plesiomorphic feature of ichneumonids as they are complete in fossils (Townes, 1973*b*). The reduction of this carina is a progressive feature and has been coded as follows – complete (0,0), present only centrally (1,0), absent (1,1).

25·1, 25·2 Posterior transverse carina of the propodeum. Coded as for character 24 for the same reasons.

26 Longitudinal propodeal impression. The plesiomorphic condition for ichneumonids is to have the dorsum of the propodeum more or less flat. In a few ophionines a deep longitudinal impression is present and this is considered to be an apomorphic feature.

27·1, 27·2, 27·3 Posterior transverse carina of the mesosternum. This carina is usually complete in campoplegines and cremastines and thus a complete carina is here considered plesiomorphic for the Ophioninae. The carina is usually lost at two points on either side of the midline, before the mid coxae, so that central and lateral vestiges remain (1,0,0). Sometimes the central vestige is completely lost so only lateral traces remain (1,1,0). In a few species reduction seems to have occurred by loss of only the central part so two broad lateral portions remain (0,0,1).

28·1, 28·2 Lateromedian longitudinal carina of the propodeum. Coded as for character 24 for the same reasons.

29·1, 29·2 The thyridium. This is a moderately large indentation found on the second gastral tergite. In its plesiomorphic condition it is close to the anterior margin of the tergite (0,0), but in a number of ophionines it can be seen to have been displaced posteriorly, leaving a scar between itself and the tergal margin (0,1). In a few taxa the thyridium is absent (1,0).

30 Epipleuron of tergite 2. This is a difficult feature to determine the polarity of as within the out-groups both conditions occur widely. In most ophionines it is upturned, and in a few otherwise specialized taxa it is pendant. The latter condition is tentatively considered to be apomorphic.

31 Profile of tergite 2. Tergite 2 is laterally compressed in ophionines and members of the closer out-groups (Fig. 2). In profile it is much longer than posteriorly deep. In a few ophionines it is quadrate and this is considered to be an apomorphic development.

32 Position of spiracles on tergite 1. The plesiomorphic condition for ophionines and members of the out-groups is for the spiracles to be at or behind the level of the margin of the sternite. In a few taxa the spiracles are situated before the sternite margin, a presumed apomorphic condition (1).

33 Presence of an umbo on tergite 2. The umbo is a convex area on the midline at the anterior margin of tergite 2. It is typically present in many ophionines and members of the out-groups. The apomorphic state (1) is where this structure has been lost.

34 Ovipositor length. The length of the ovipositor varies a great deal between ichneumonid taxa. Probably the ancestral condition for the family was long, but almost every evolutionary lineage shows reduction. Virtually all ophionines have short straight ovipositors resembling those of many campoplegines (Townes, 1970), and thus this condition is considered to be plesiomorphic. The long ovipositors found in a few taxa are considered to be apomorphic features (1).

35 Ovipositor sheath. The ovipositor sheaths (valvulae 3) of ichneumonids are almost always slender, just wide enough to enclose the ovipositor. In a few ophionines the sheaths are very stout. This is considered to be an apomorphic development (1).

36·1, 36·2, 36·3 Position of 1m–cu *in relation to* Cu_{1a} *in the fore wing.* In most ichneumonids these two veins are quite widely separated and are often at least as far apart as 0·75 of the length of Cu_{1b}. With some reservation this is considered to be the plesiomorphic state (0,0,0). In many ophionines these veins are separated by about 0·5 times the length of Cu_{1b} (1,0,0), in a number of species by about 0·25 times (1,1,0), whilst in a very few instances the veins are practically contiguous (1,1,1).

37 Length of second discal cell. The plesiomorphic condition for ichneumonids generally, including ophionines, is for the length of the second discal cell (measured along Cu_{1a}) to exceed 1·10 times the length of the first subdiscal cell (measured along Cu_1). In a number of ophionines the second discal cell is unusually short, being less than the length of the first subdiscal cell. This is considered to be an apomorphic feature (1).

38 Presence of a ramellus. The ramellus on 1*m–cu* in the fore wing is apparently a remnant of the vein that divided the first discal from the submarginal cell (the two are confluent in all extant ichneumonids though present in fossil forms (Townes, 1973*b*)). The retention of this stub is tentatively considered to be a plesiomorphic feature, but I have some doubts about the polarity assignment for similar reasons to those stated in 47·1 below.

39 Base of Rs+2r *in fore wing.* In the majority of ophionines and members of the out-groups this vein is emitted from the pterostigma at about 30° to the fore margin of the wing; the base of the vein is straight (Fig. 3). In some ophionines the angle of emission is greater (40°+) and the vein is rather sharply bent basally (Fig. 4). This is considered to be an apomorphic feature (1).

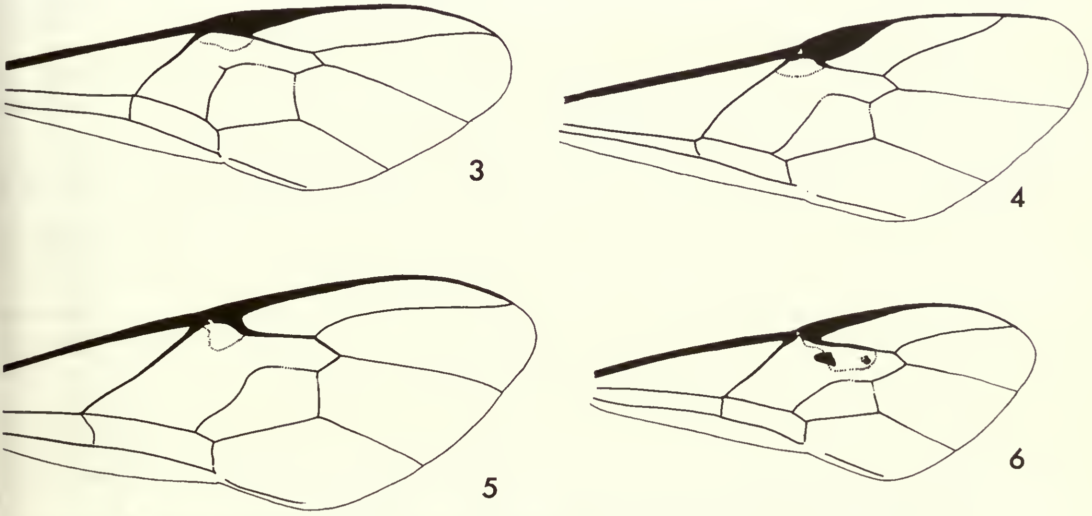
40 Shaft of Rs+2r *in fore wing.* The plesiomorphic condition for Hymenoptera generally is for this vein to be centrally straight; this condition is found widely in out-groups and many ophionines (Fig. 3). In some ophionines the vein is markedly sinuous just before the centre and this (Fig. 6) is considered to be an apomorphic development (1).

41 Position of confluence of Rs *and* R_1 *in fore wing.* In virtually all ophionines and many members of the out-groups these veins meet at the extreme distal apex of the wing so the marginal cell is very long. In a few ophionines the confluence of these veins is more proximal on the fore margin of the wing, away from the tip, so the marginal cell is correspondingly shorter (Fig. 4). This is considered to be an apomorphic feature (1).

42·1, 42·2 Shape of pterostigma. In most ichneumonids the pterostigma is quite broadly triangular and this plesiomorphic condition prevails in most species in the out-groups. In some ophionines the pterostigma is still broad (0,0) but in many it is not abruptly narrowed distally but evenly tapered (1,0) (Figs 4, 6). In a few the pterostigma is much more slender and elongately tapered (1,1) (Fig. 5).

43·1, 43·2 Position of distal abscissa of Cu_1 *in hind wing.* It is very difficult to assign polarity to this character as all stages from Cu_1 close to *M* to Cu_1 close to 1*A* can be found in members of the out-groups. Furthermore, in most Campopleginae this vein is lost. However, in some of the more primitive ichneumonids the usual condition is for this vein to be closer to *M* than to 1*A*. This is tentatively assumed to be the plesiomorphic condition (0,0). The derived states, treated as a transformation series are: intermediate between *M* and 1*A* (1,0) and closer to 1*A* than to *M* (1,1).

44·1, 44·2 Shape of Rs *in hind wing.* The plesiomorphic condition of this vein in ichneumonids generally, including many ophionines, is for it to be straight (0,0). In many ophionines it is quite distinctly



Figs 3–6 Fore wings: 3, *Ophion*; 4, *Simophion*; 5, *Stauropoctonus*; 6, *Enicospilus*.

concave whilst in a few taxa it is exceptionally curved so that the distal portion is parallel to the fore margin of the wing. These two derivations are treated as a transformation series and coded 1,0 and 1,1 respectively.

45·1, 45·2 Glabrous area in fore wing. All primitive ichneumonids, most taxa in the out-groups, and virtually all lower Hymenoptera have the membrane of the fore wing uniformly hirsute close to vein *Rs+2r*. This is treated as the plesiomorphic condition (0,0). In most ophionines a small glabrous area is present in the discosubmarginal cell near where the pterostigma emits *Rs+2r*. This is considered apomorphic (1,0). A further specialization is for this area to be very extensive, reaching at least 0·3 of the way along *Rs+2r* (1,1).

46 Alar sclerites. The possession of alar sclerites is an unusual apomorphic feature of certain ophionines. Other than in this subfamily these sclerites are only found in two species of ichneumonid (and then in different positions). Elsewhere in the Hymenoptera alar sclerites are apparently only found in some pepsine pompilids (M. C. Day, pers. comm.).

*47·1, 47·2 Shape of 1*m–cu *in fore wing.* In the lower Hymenoptera this vein (which in fact is almost certainly not just *1m–cu* but a composite of this and other vein parts) is angled centrally so the antero-proximal side of the 2nd discal cell is angulate at about 90°. In many ophionines this angulation is present (Fig. 3) and often accompanied by a ramellus (see character 38). This is here tentatively considered to be the plesiomorphic condition (0,0). In many species this vein is evenly curved (1,0), whilst in some it is further modified by being sinuous (1,1). I have certain reservations about the polarity of 47·1 as the evenly curved condition is the widespread condition amongst the out-groups.

*48·1, 48·2 Length of 3*r–m *in the fore wing.* In the majority of more primitive ichneumonids *3r–m* is longer than the abscissa of *M* between *2m–cu* and *3r–m*. In many ophionines this is also the case and it is here considered to be the plesiomorphic state (0,0). In some ophionines *3r–m* is shorter, 0·75–0·50 times as long as *M* (1,0), whilst in a very few it is extremely reduced, 0·35 or less times the length of *M* (1,1).

49 Position of abscissa of Cu_1 *between 1*m–cu *and* Cu_{1a}. This vein is positioned at about 90° to the axis of the fore wing in most ichneumonids and virtually all lower Hymenoptera. In some ophionines it is specialized in being turned so that it is almost parallel to the wing axis (1).

50 Position of cu–a *in fore wing.* The plesiomorphic condition of this vein in ichneumonids is for it to subtend an angle of about 90° to Cu_1. In a few ophionines it is strongly oblique, subtending an angle of 50–60° (1).

51·1, 51·2 Flange on fore tibial spur. The plesiomorphic state for ichneumonids is the possession of a membranous flange on almost the entire length of the fore tibial spur, immediately behind the microtrichial 'comb' (Fig. 48) (0,0). In some ophionines this is reduced to about 0·3 of the length of the spur (1,0), whilst in others it is entirely lost (Fig. 49) (1,1).

52·1, 52·2 Form of hind trochanter. The possession of a simple margin to the trochanter is plesiomorphic for ichneumonids (0,0). In a few ophionines a small marginal tubercle is present (1,0), whilst in some cases this may be long, curved and pointed (1,1).

53 Dorsal margin of hind trochanter. This is also unspecialized in most ichneumonids, but some ophionines are unusual in having a specialization – the margin extended as a flange over the articulation of the trochantellus (1).

54 Hind tibial spurs. In many ophionines and members of the out-groups these spurs are flattened internally and bear a long fringe of close hairs. In some ophionines they are specialized in being cylindrical and bearing only scattered hairs (1).

55 Penultimate distal hamulus. The unspecialized condition in Hymenoptera is for the hamuli to be of similar size and shape. In some ophionines the penultimate hamulus is specialized in being very much longer and more coiled than its fellows (1).

56 Grouping of distal hamuli. The plesiomorphic condition for Hymenoptera is for the row of hamuli to be fairly evenly spaced. In a few ophionines they are arranged in two groups, an apparently specialized condition (1).

57 Number of hamuli distally. Most primitive Hymenoptera have from 9 to about 15 distal hamuli and, as this condition is widespread in primitive ichneumonids and many ophionines, it is considered plesiomorphic in context of this study. Some ophionines have only 4 or 5 distal hamuli and this reduction is considered to be an apomorphic condition (1).

58·1, 58·2 Shape of hind tarsal claw. In most members of the out-groups and many primitive ichneumonids the tarsal claws are fairly evenly curved (Fig. 45) and this condition, where it occurs in ophionines is considered to be plesiomorphic (0,0). In Ophioninae the claw may be modified in one of two ways – either by being longer and straighter (1,0) or by being almost geniculate (0,1).

59 Colour of interocellar area. In most Hymenoptera this area is concolorous with the vertex. In a few ophionines it is sharply chromatically contrasted, and this is tentatively considered an apomorphic feature (1).

60 Distal pectinal tooth of hind tarsal claw. The claws of ophionines possess a sinuous row of pectinal teeth or pectinae (Gauld & Mitchell, 1978) forming a comb-like internal surface. This is apparently an apomorphy of the subfamily, so in the present context such a claw may be considered a plesiomorphy. In some ophionines the claw is specialized in having the distal pectinal tooth on the outer surface of the main tooth (Fig. 46) (1).

61·1, 61·2 Taper of mandibular teeth. In most primitive ichneumonids the mandible is weakly tapered so that the distal apex is more than 0·5 times as broad as the base. This is considered to be the plesiomorphic condition where it occurs in ophionines (0,0). Some species have the mandible more strongly tapered so the apex is 0·4–0·5 times as wide as the base (1,0) whilst a few are exceptional in having the apex <0·3 times as wide as the base (1,1).

62 Thickness of base of Rs+2r. The plesiomorphic condition for Ichneumonidae is for this vein to be slender at its junction with the pterostigma. In some ophionines it is specialized in being broadened so that close to the pterostigma it is more than twice its central thickness (1).

63 Presence of laterotergite 1 of gaster. In primitive ichneumonids a distinct laterotergite is present associated with tergite 1; vestiges of this may be found by partial dissection in many ophionines. Some are specialized in having lost this structure (1).

64 Presence of a pectinal comb on both sides of male claw. The plesiomorphic condition for ophionines is for a single sinuous pectinal comb to be present on the tarsal claws; some males are specialized in having this comb present as a double row of teeth, surrounding a flattened central area (1) (Fig. 47).

Preliminary remarks on the relative values of the characters

For analytical purposes all characters have been treated initially as having equal numerical weight. However, a practising taxonomist does not value characters equally. Intuitively he is more likely to consider some to be more important than others. 'Good' characters are likely to include many of the more bizarre morphological adaptations (Gauld & Mound, 1982). At the other extreme, characters may be considered to have very little value as indicators of phylogenetic affinity. This is often for one of three reasons.

(a) The apomorphic state of the character may involve the disappearance of a structure and, as it is obvious that certain structures are frequently lost in parallel in many distantly related lineages (e.g. the occipital carina has been lost in some taxa independently in virtually all ichneumonid subfamilies), one suspects that an absence in two closely related taxa could also be the result of parallel reduction.

(b) There may be some doubt concerning polarity. This is particularly true in cases where one postulates that a particular state is an apomorphy for the subfamily, but advocates reversal in a few exceptional taxa (e.g. character 12, ocellar size).

(c) Even if the apomorphic condition involves the development of a particular structure, the character may be judged to be unstable, as examination of out-groups suggests it has been derived independently in numerous evolutionary lineages, or is correlated with a particular size range or extreme habitat occupied by a particular species. For example, very large ichneumonids often have similarly coarse reticulate propodeal sculpture, whilst eremic species have short, stout antennae.

The third of these reservations is discussed for individual characters in a subsequent section, but it is appropriate to mention a and b here. Those of the characters used in this study which involve an apomorphic 'loss' are listed below with an asterisk(*), whilst those in which the polarity assignment is suspect are denoted by a prime mark(′). This convention is used extensively in the cladograms presented in the following sections. For comparative purposes a list is given below.

1·1*, 1·2*, 2, 3, 4·1, 4·2*, 5·1, 5·2, 6·1, 6·2, 7·1′, 7·2′, 8·1*, 8·2*, 9, 10, 11, 12*, 13, 14·1′, 14·2′, 15·1, 15·2, 16·1*′, 16·2*′, 17, 18·1, 18·2, 19*, 20·1, 20·2, 21·1, 21·2, 22·1, 22·2, 23, 24·1*, 24·2*, 25·1*, 25·2*, 26, 27·1*, 27·2*, 27·3*, 28·1*, 28·2*, 29·1, 29·2*, 30′, 31, 32, 33*, 34′, 35, 36·1′, 36·2′, 36·3, 37, 38*′, 39, 40, 41, 42·1, 42·2, 43·1′, 43·2′, 44·1, 44·2, 45·1, 45·2, 46, 47·1′, 47·2, 48·1, 48·2, 49, 50, 51·1*, 51·2*, 52·1, 52·2, 53, 54, 55, 56, 57*, 58·1, 58·2, 59′, 60, 61·1, 61·2, 62, 63*, 64.

The phylogenetic analysis

An initial attempt was made to construct a Wagner tree, but with repeated runs it became obvious that there exists a large number of equally or almost equally (less than 1% difference in overall length) short trees, many of which exhibit quite different topologies. As there is no basis on which to prefer one of these, and there is no way of knowing whether all the shortest trees have been computed, Wagner analysis was initially rejected in favour of a more detailed study of characters and taxa using the programs LEQU.BAS and FOURS. From these it was possible to gain some indication of the 'shape' of the primary data set. Tentative groups of taxa recognized initially were reanalysed using Wagner and compatibility methods.

Preliminary analysis of data

Analysis using LeQuesne test program, LEQU.BAS
Using the program LEQU.BAS the primary data matrix (Appendix 2) of 51 selected ophionine taxa was analysed (see Table 6). Of the 95 characters used, six, 8·2, 11, 28·1, 34, 49 and 53,

Table 6 Results of LeQuesne test on the primary data matrix (Appendix 2). Conventions follow table 2. Note that a character with a single incidence of one or other state logically cannot fail the test and is represented by 0 – –.

```
Character number: incompatibilities observed  expected   O/E ratio

 1.1:  71  72.6  0.98      1.2:  54  57.1  0.95      2  :  44  73.2  0.60      3  :  44  71.3  0.62
 4.1:  53  57.5  0.92      4.2:  53  42.4  1.25      5.1:  64  76.5  0.84      5.2:  46  61.6  0.75
 6.1:  60  65.4  0.92      6.2:  31  65.4  0.47      7.1:  63  75.2  0.84      7.2:  60  80.7  0.74
 8.1:  11  28.5  0.39      8.2:   0    -     -       9  :  55  66.1  0.83     10  :  34  28.5  1.19
11  :   0    -     -      12  :  68  74.8  0.91     13  :  52  66.1  0.79     14.1:  65  73.8  0.88
14.2:  66  79.8  0.83     15.1:  73  81.2  0.90     15.2:  62  75.2  0.82     16.1:  73  50.8  0.45
16.2:  77  77.5  0.99     17  :  65  71.3  0.91     18.1:  69  75.2  0.92     18.2:  69  72.3  0.95
19  :  65  66.1  0.98     20.1:  78  79.8  0.98     20.2:  68  80.5  0.84     21.1:  52  65.9  0.79
21.2:  11  28.2  0.39     22.1:  65  80.9  0.80     22.2:  61  76.3  0.80     23  :  57  73.2  0.78
24.1:  72  81.1  0.89     24.2:  76  80.5  0.94     25.1:  15  28.1  0.53     25.2:  72  75.8  0.95
26  :  49  57.8  0.85     27.1:  77  80.7  0.95     27.2:  77  80.0  0.96     27.3:  12  27.5  0.44
28.1:   0    -     -      28.2:  69  73.2  0.94     29.1:  50  50.7  0.99     29.2:  79  81.1  0.97
30  :  68  74.8  0.91     31  :  69  69.0  1.00     32  :  67  71.3  0.94     33  :  69  79.7  0.87
34  :   0    -     -      35  :  55  73.2  0.75     36.1:  71  64.4  1.10     36.2:  76  78.8  0.96
36.3:  58  69.6  0.83     37  :  78  82.2  0.95     38  :  53  62.5  0.85     39  :  78  79.1  0.99
40  :  47  71.3  0.66     41  :  64  62.5  1.02     42.1:  66  72.3  0.91     42.2:  61  77.3  0.79
43.1:  73  73.8  0.99     43.2:  78  81.2  0.96     44.1:  82  81.2  1.01     44.2:  70  68.0  1.03
45.1:  69  76.3  0.90     45.2:  67  80.9  0.83     46  :  56  76.2  0.74     47.1:  46  61.6  0.75
47.2:  74  77.4  0.96     48.1:  73  81.2  0.90     48.2:  61  72.2  0.84     49  :   0    -     -
50  :  31  28.5  1.09     51.1:  61  68.1  0.90     51.2:  62  74.0  0.84     52.1:  51  70.6  0.72
54  :  57  74.8  0.76     55  :  33  57.8  0.57     56  :  30  28.5  1.05     57  :  74  80.8  0.92
58.1:  67  76.9  0.87     58.2:  27  28.1  0.96     59  :  78  81.7  0.95     60  :  19  28.5  0.67
61.1:  70  80.5  0.87     61.2:  72  77.3  0.93     62  :  75  80.3  0.93     63  :  74  81.9  0.90
64  :   5  28.5  0.18

Grand total-    2598 observed,   3007.1 expected. Overall O/E ratio = 0.86

Ranking ratio of scoring characters

64  8.1  21.2  27.3  16.1  6.2  25.1  55  2  3  40  60  52.2  52.1  46  7.2  5.2  47.1  35  54  23
13  42.2  21.1  22.2  22.1  15.2  14.2  45.2  9  36.3  5.1  7.1  51.2  48.2  20.2  26  38  33  61.1
58.1  14.1  24.1  51.1  48.1  15.1  63  45.1  30  12  17  42.1  57  6.1  18.1  4.1  61.2  62  32
28.2  24.2  1.2  37  25.2  27.1  59  18.2  47.2  43.2  58.2  27.2  36.2  29.2  20.1  1.1  19  39
29.1  43.1  16.2  31  44.1  41  44.2  56  50  36.1  10  4.2
```

showed only a single discordant state. In the case of 28·1 and 49 the majority state was the derived condition, whilst in the remainder it was the plesiomorphic condition that predominated. As a minimum of two discordant character-states is logically required for a failure, it follows none of these eight can fail; they are shown as 0 – –.

The remaining 89 characters have two or more discordant states and therefore can potentially fail the test. Each character was paired with every other one (except for the alternatives *n*.1 with *n*.2) and of the 7,855 comparisons made 2,598 resulted in failures. A total of 3,007 failures was expected, so although slightly better than random (O/E value = 0·86), the results suggest a very high incidence of homoplasy. For individual characters a considerable variation in O/E ratio was observed. Characters 6·2, 8·1, 16·1, 21·2, 25·1, 27·3 and 64 all scored better than 0·55, whilst at the other extreme eight characters, 4·2, 10, 36·1, 41, 44·1, 44·2, 50 and 56 all scored worse than 1·00.

Examination of the labels matrix (Appendix 4) showed that two taxa, 909 and 922, had been labelled exceptionally frequently (scoring 89 and 85 labels respectively). Six further species, 906, 908, 921, 923, 942 and 951, were labelled between 45 and 67 times, whilst the rest were labelled less than 42 times. Sixteen taxa were labelled less than ten times and three, 912, 913 and 933 were not labelled at all.

As would be expected, the elimination of bad characters (i.e. those with an exceptionally high O/E score) produced, in general, a progressive improvement in the O/E ratios of the surviving characters. However, the average ratio improved very slowly. With 20 informative characters remaining it was still 0·34. This clearly shows that not all the failures of the 'better' characters were due to clashes with the worst characters; the majority of characters seem to be somewhat homoplastic! Complete elimination of homoplasy (as advocated by LeQuesne, 1972) results in the removal of virtually all characters. The largest cliques contain only ten compatible characters. Several of these have only a very low information value (i.e. have only two or three derived states), but five more informative characters (2, 6·2, 15·1, 15·2 and 22·2) were found to be universal to all the larger cliques. All of these are features that have been used previously in ichneumonid higher classification (Cushman, 1947; Townes, 1971). These characters support the cladogram shown in Fig. 7. Only the group supported by character 2 corresponds with any previously recognized grouping of taxa, the *Thyreodon* group of Cushman (1947).

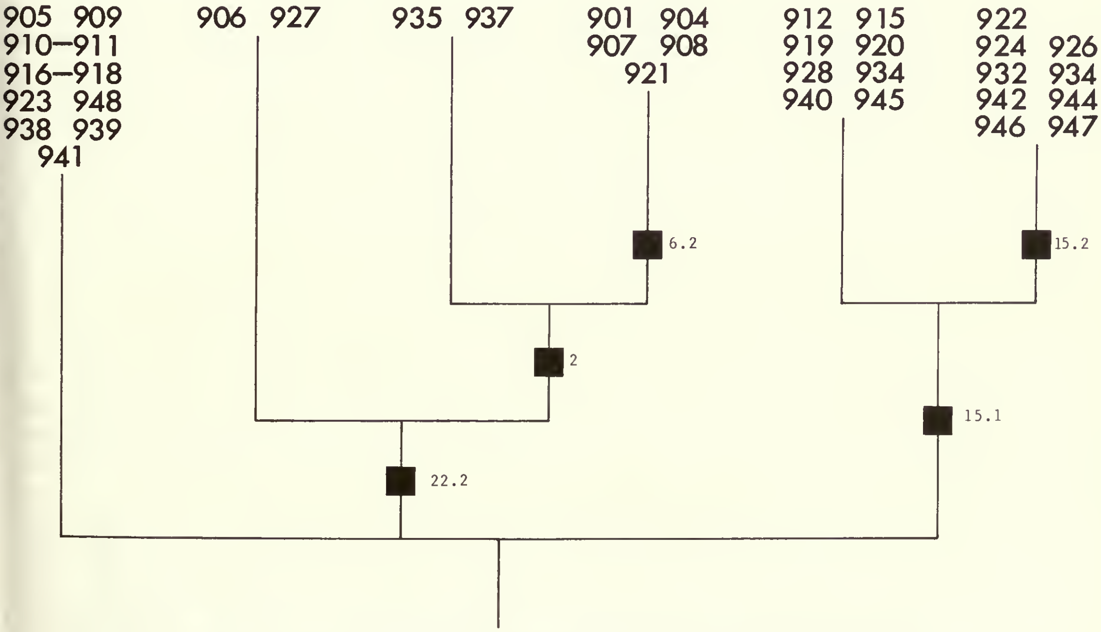


Fig. 7 Cladogram supported by largest clique of compatible characters.

The rate at which the O/E values of individual characters improved (after removal of bad characters) varied tremendously. For example, after removal of the eight worst characters (Table 7), character 29·1, initially the seventy-eighth placed (and the twelfth one scheduled for elimination) progressively improved (with the elimination of each worse character) to sixty-seventh. Character 59, initially placed as sixty-sixth, steadily worsened its position to eighty-third; it would in fact be the tenth character eliminated. If the ten worst characters were removed *en bloc* they would have been 4·2, 10, 36·1, 50, 56, 44·2, 41, 44·1, 31 and 16·2. By stepwise removal of the worst character they would be 4·2, 10, 50, 36·1, 44·1, 41, 39 and 59. All further 'cleaning-up' of data was done by stepwise removal of characters.

Table 7 Results of a LeQuesne test on the primary data matrix after the progressive removal of the highest scoring characters (4·2, 10, 50, 36·1, 44·2, 56, 44·1, 41). Conventions follow table 2; non-informative characters omitted.

```
Character number:  incompatibilities observed  expected  O/E ratio

 1.1:  63  67.7  0.93     1.2:  49  53.8  0.91     2  :  38  68.4  0.56     3  :  40  66.7  0.60
 4.1:  47  54.4  0.86     5.1:  58  71.1  0.82     5.2:  43  57.9  0.74     6.1:  53  61.3  0.86
 6.2:  26  61.3  0.42     7.1:  57  69.9  0.82     7.2:  56  74.6  0.75     8.1:   9  26.9  0.33
 9  :  51  62.0  0.82    12  :  62  69.8  0.89    13  :  48  62.0  0.77    14.1:  60  68.8  0.87
14.2:  59  73.8  0.80    15.1:  66  75.0  0.88    15.2:  56  69.9  0.80    16.1:  20  47.9  0.42
16.2:  71  72.0  0.99    17  :  61  66.7  0.91    18.1:  65  70.0  0.93    18.2:  62  67.4  0.92
19  :  59  62.0  0.95    20.1:  70  73.8  0.95    20.2:  63  74.4  0.85    21.1:  49  61.8  0.79
21.2:   9  26.7  0.34    22.1:  60  74.7  0.80    22.2:  54  70.9  0.76    23  :  51  68.4  0.75
24.1:  68  74.9  0.91    24.2:  69  74.4  0.94    25.1:  15  26.5  0.57    25.2:  66  70.6  0.94
26  :  47  54.4  0.86    27.1:  71  74.5  0.95    27.2:  71  73.9  0.96    27.3:  10  25.9  0.39
28.2:  64  68.4  0.94    29.1:  44  47.7  0.92    29.2:  72  74.9  0.96    30  :  63  70.0  0.90
31  :  63  64.6  0.98    32  :  61  66.7  0.91    33  :  64  73.9  0.87    35  :  52  68.4  0.76
36.2:  71  73.8  0.96    36.3:  54  65.7  0.82    37  :  71  75.9  0.94    38  :  52  58.7  0.89
39  :  72  73.4  0.98    40  :  44  66.7  0.66    42.1:  60  67.4  0.89    42.2:  53  71.7  0.74
43.1:  66  68.8  0.96    43.2:  72  74.9  0.96    45.1:  63  70.9  0.89    45.2:  60  74.7  0.80
46  :  53  70.9  0.75    47.1:  43  57.9  0.74    47.2:  69  71.8  0.96    48.1:  67  75.0  0.89
48.2:  57  67.4  0.85    51.1:  55  63.7  0.86    51.2:  56  68.9  0.81    52.1:  47  66.0  0.71
52.2:  42  58.0  0.72    54  :  51  69.8  0.73    55  :  31  54.4  0.57    57  :  68  74.8  0.91
58.1:  60  71.5  0.84    58.2:  26  26.5  0.98    59  :  73  75.6  0.97    60  :  17  26.9  0.63
61.1:  65  74.4  0.87    61.2:  65  71.7  0.91    62  :  68  74.4  0.91    63  :  68  75.7  0.90
64  :   4  26.9  0.15

Grand total-  2179 observed,  2613.3 expected. Overall O/E ratio = 0.83

Ranking ratios of scoring characters

64  8.1  21.2  27.3  16.1  6.2  2  25.1  55  3  60  40  52.1  52.2  54  42.2  5.2  47.1  23  46  7.2
35  22.2  13  21.1  14.2  15.2  22.1  45.2  51.2  7.1  5.1  36.3  9  58.1  48.2  20.2  51.1  4.1  26
6.1  33  14.1  61.1  15.1  38  12  45.1  42.1  48.1  63  30  61.2  24.1  57  1.2  62  32  17  18.2
29.1  24.1  18.1  1.1  37  25.2  28.2  20.1  19  27.1  43.1  47.2  43.2  27.2  29.2  36.2  59  31
58.2  39  16.2
```

It is apparent from the generally high O/E values that homoplasy is a common feature in the Ophioninae. Any attempt to produce a character set without homoplasy (a clique) necessitates excluding the great majority of characters, including some of the most informative ones. This is unacceptable for two reasons.

(1) A large amount of information would have to be discarded leaving many unresolvable situations. As $2N_t-2$ apomorphies are necessary to fully resolve N_t taxa, a minimum of 100 compatible characters would be needed to fully resolve the ophionine data. Consequently, without homoplasy, even the full set of 95 characters is insufficient for full resolution. Excluding autapomorphies for definition of terminal taxa, a minimum of 49 characters is necessary for

resolution, but in the present case it can be seen that even discarding half the characters, the resultant data set would still be extremely homoplastic.

(2) It is important to realize that just because a character is homoplastic and has been derived independently in two (or more) lineages, this does not mean that it is not of phylogenetic value. Such a character can still be a genuine synapomorphy for species in two different groups of taxa, and many minimally homoplastic characters are still highly regarded by traditional taxonomists. For example, Mason (1981) states that one of the major synapomorphies of the Braconidae (the probable sister-group of the Ichneumonidae) is the fusion of the second and third gastral tergites. Approximately six of the 60,000 species of Ichneumonidae also have tergites 2 and 3 fused. This parallelism in a few specialized ichneumonids does not eliminate the character as a useful apomorphy for defining Braconidae in a phylogenetic sense, it merely reduces the value of the character as an infallible means of identifying braconids. If it were possible to consider all species of the two taxa Ichneumonidae and Braconidae, it is likely that the O/E value of this character would be very low, but if the analysis were of all Parasitica, and a few taxa from each family were selected as examples of the range of morphological variation, it is quite possible that one of the six anomalous ichneumonids would be included, giving the character a much larger O/E value, and consequently risking its exclusion. In the present study certain species of *Enicospilus, Leptophion* and *Laticoleus* were deliberately selected to show the range of morphological variation in the genus, so it is highly likely that these will contribute to the high level of homoplasy in the way outlined above.

In the LeQuesne analysis eight characters were eliminated stepwise until none of the remainder scored worse than 1·00. The particularly high O/E value of these characters strongly suggests they are particularly homoplastic, and consequently of no real value in phylogenetic reconstruction. Considered from a biological point of view it certainly seems these features are homoplastic, but even so several seem to be of use in defining possible holophyletic groups. Considered in order of 'worst' first these characters are as follows.

4·2: reduction of upper tooth of mandible.* The occurrence of the derived state of this feature is limited in the matrix to three species, *Rhynchophion flamipennis* (908), *Sicophion pleuralis* (922) and *Enicospilus unidens* (946). Amongst the Ophioninae in general, this feature is found in the apomorphic state in a group of Madagascan and southern Indian species of *Enicospilus* (Gauld & Mitchell, 1978; 1981) that seem to be related to *E. unidens*, an apparently unrelated Melanesian species (*E. interruptus* Szépligeti) and in an Indian *Ophion* species. Thus although the character has phylogenetic value in some cases (the definition of the *unidens* group) in others it has none. Presumably the apomorphic condition found in three taxa in the matrix is the result of parallel derivation, a conclusion that is strongly suggested by the very high label values (Appendix 4). Amongst out-groups this character is of similar sporadic occurrence (cf. Townes, 1970), sometimes defining an apparent clade and other times being characteristic of a single species. Structurally it is a simple adaptation for biting through fibrous cocoons and as such it is not surprising that it has apparently arisen independently in many different evolutionary lineages.

10: elongation of maxillae. This too is a low information value character as the apomorphic condition occurs in just two taxa in the matrix, *Rhynchophion flamipennis* (908) and *Sicophion pleuralis* (922). Amongst other ophionines it is limited in occurrence to some Neotropical species of *Eremotylus*. All of these taxa are restricted to the drier areas of Central and South America and the structural development seems to be an adaptation to drinking from certain flowers. Similar structural modification can be observed in many other ichneumonids in similar habitats, including many Tersilochinae, Cremastinae and Anomaloninae. In arid areas of south-western Australia species of three closely related cremastine genera, *Trathala, Temelucha* and *Pristomerus*, all have identically modified maxillae. Only familiarity with the world cremastine fauna enables one to recognize this as evolutionary convergence rather than considering it indicative of a holophyletic group. These observations strongly suggest that particularly intense selection pressures in a particular area may elicit the development in parallel, of apparently identical apomorphic features in closely related lineages. This may explain the similarity between the taxa in the matrix.

50: oblique position of cu–a *in fore wing*. Like the preceding two characters this is of low information content as the derived condition occurs in just two taxa in the matrix, *Lepiscelus distans* (909) and *Barytatocephalus mocsaryi* (927). Amongst other ophionines it is limited to occurring in one or two species of *Ophion*. In the sister-group to the Ophioninae, the Campopleginae, the derived condition apparently is useful for defining some genera (e.g. *Cymodusa*, see Townes, 1970) but the character has little apparent phylogenetic significance in the Ophioninae.

*36·1′: vein 1*m–cu *separated from* Cu_{1a} *by less than 0·75, but more than 0·5 of the length of* Cu_{1b}. The majority of taxa have this character present in the presumed derived state. Only *Lepiscelus distans* (909), *Stauropoctonus occipitalis* (917), *Riekophion emandibulator* (920), *Ophionopsis nigrocyaneus* (921), *Sicophion pleuralis* (922), *Rictophion nebulifer* (937) and *Enicospilus nephele* (944) are plesiomorphic for this feature. It is not found in the plesiomorphic state in any other *Stauropoctonus* species, in most other *Enicospilus* species nor any other *Riekophion* species. If the 0 state were a genuine symplesiomorphic feature of these taxa the 1 state must have been derived in parallel in at least species of *Riekophion, Enicospilus* and *Stauropoctonus* (assuming they are natural genera) and therefore the 1 state is not synapomorphic for all species so scored. Alternatively, if the 1 state is a genuine synapomorphy for all ‘other taxa’, the 0 state must represent independent reversals in some taxa. Either way the character is homoplastic. The same argument can be applied even if the polarity is reversed, unless one were to accept the otherwise unsupported clade of 909+917+920+921+922+937+944.

44·2: strongly curved Rs *in hind wing*. In the matrix the apomorphic state of this character is found in *Simophion calvus* (905), *Lepiscelus distans* (909), *Laticoleus curvatus* (915), *Abanchogastra hawaiiensis* (925), *Leptophion maculipennis* (928), *Euryophion adustus* (936), *Rictophion nebulifer* (937) and *Ophion luteus* (939). Elsewhere in the subfamily all species of *Ophion* (*ca* 150 species) have *Rs* strongly curved. The genus *Abanchogastra* is monotypic, but only some species of *Leptophion, Enicospilus, Euryophion* and *Laticoleus* possess the apomorphic state as do some species of *Eremotylus* and *Ophiogastrella*. In both *Leptophion* and *Laticoleus* this feature seems to define holophyletic species-groups, but there is no evidence to support the idea that it could be a synapomorphy of all the taxa listed above. Clearly it must have been derived independently in many ophionine lineages, but although a homoplastic feature, it is interesting to note that it still is quite characteristic of certain species-groups and even genera, suggesting that once the apomorphic state has been derived, it is unlikely to undergo reversal.

56: separation of hamuli into two groups. This feature occurs in the matrix only in two Afrotropical species, *Lepiscelus distans* (909) and *Laticoleus curvatus* (915). The latter is the only species in its genus with this particular modification and *Lepiscelus* is monobasic (Gauld & Mitchell, 1978). The apomorphic condition is also found in some central Asian *Ophion* species. The only feature these taxa seem to have in common is that they inhabit rather dry areas. The character appears to have little phylogenetic value.

41: fore wing with R_1 *not reaching to tip*. The apomorphic condition is found in *Thyreodon atricolor* (901), *Simophion calvus* (905), *Orientospilus melasma* (906), *Ophionopsis nigrocyaneus* (921) and *Sicophion pleuralis* (922). It is not present in many other *Thyreodon* species so it is unlikely that the derived condition in 901 is synapomorphic with that of other species. The exclusion of 901 from the analysis actually resulted in a worsening of the O/E value of this character from 1·02 to 1·12, suggesting it is homoplastic in other taxa. The apomorphic state of this character is found in all species of the genera *Simophion, Orientospilus* and *Ophionopsis*, suggesting this feature, once derived, is not likely to undergo reversal.

44·1: bowed vein Rs *in hind wing*. The apomorphic state of this character is found in all taxa listed under 44·2 above and additionally in 14 other taxa, all from different genera. Elsewhere the feature is of sporadic occurrence in *Ophiogastrella, Aulophion, Leptophion, Laticoleus* and

Enicospilus, as well as being present in all species of *Dictyonotus, Hellwigiella, Sclerophion, Eremotylus, Xylophion* and *Rhopalophion*. This suggests parallel development in many different evolutionary lines.

The high O/E values of several of these characters were surprising as almost all represent structural specializations (not 'loss' apomorphies or dubious polarity assignments). Several (4·2, 41 and 44·2) do apparently have considerable phylogenetic value at certain hierarchical levels and really only two (36·1 and 44·1) are likely to be considered by a traditional taxonomist as category 3 'bad' characters. Character 10 almost certainly would intuitively be regarded as a 'good' character (vide Cushman, 1947). It is interesting to note that two taxa (909 and 922) were cited for at least half of the eight worst characters, as having contributed to the high level of homoplasy. These taxa, also recognizable by their high label scores, were subsequently shown to be amongst the more difficult to place, and small differences in their position in the order of taxa submitted to the WAGNER program, produced large changes in the resulting cladogram.

Another estimate of incidences of homoplasy in the primary data may be obtained from perusal of the labels matrix (Appendix 4). Notably high scores, indicative of homoplastic derivation of the apomorphic state in two or more taxa, can be observed for character 1·2 (taxa 909, 923 and 949), 4·1 (906, 909), 4·2 (908, 922, 946), 10 (908, 922), 26 (906, 923), 29·1 (922, 937), 50 (909, 927), 56 (909, 915), 58·2 (942, 951) and 60 (928, 942). The shared plesiomorphic condition for character 38 in taxa 941 and 943 was also highly labelled, suggesting one or other has undergone reversal. Of these 11 characters, six (4·2, 10, 50, 56, 58·2 and 60) are highly labelled for all apomorphic states (two or three in each case), suggesting these are not useful characters for phylogenetic reconstruction. Rather suprisingly all are 'gain' apomorphies. Four (4·2, 10, 50 and 56) are amongst the eight characters eliminated in cleaning up the LeQuesne matrix; one other (58·2) has a higher than average O/E score, but surprisingly one (60) has a reasonably low O/E value.

Analysis using FOURS program

Using the FOURS program a shared derived character matrix (Appendix 3) was computed. This shows the number of derived characters common to each pair of taxa and has values in the range of 3–37. Multiple linkage clusters drawn for taxa with 29+ shared derived characters are shown in Fig. 8. Four groups are apparent. The largest includes 17 species (912–5, 919, 924, 928–30, 932–4, 942–3, 945–7), the last eight of which form a particularly closely knit group. Taxon 925 and the reciprocal nearest neighbours 911 and 910 are less strongly associated with this group. This complex contains most of the species of *Enicospilus* and *Leptophion*, all *Dicamptus, Laticoleus* and *Pamophion*, together with *Ophiogastrella* and representatives of two of the three endemic Hawaiian genera, *Pycnophion* and *Abanchogastra*. It is noteworthy that *Enicospilus nephele* (944) and *Leptophion tetus* (931) are not associated. Each of these taxa share less derived characters with their supposed congeners than their congeners share with other taxa, although in each case the species' nearest neighbours are its congeners (Table 13).

Taxa 916, 917 and 918 (the *Stauropoctonus* group) form a cluster with 30–34 derived characters in common. This group seems to be associated with the *Enicospilus* group quite closely as 918 shares 28 derived characters with 947, 943, 942 and 919.

Taxa 935, 936 and 937 (the *Euryophion* group) cluster with 30–32 shared derived characters.

Taxa 901–4 (the *Thyreodon* group) form a cluster sharing 28–32 derived characters. Also associated with this cluster are the reciprocal nearest neighbours 907 and 921 (*Dictyonotus/Ophionopsis*).

When linkages of more than 22 shared derived characters are considered (Fig. 9), the majority serve to consolidate the clusters already formed. The *Stauropoctonus* group and *Ophiogastrella* are repeatedly linked to the *Enicospilus* cluster (both having in excess of 60% of possible linkages to the latter) as does taxon 931. Taxa 926 and 944 are less strongly but uniquely associated with this group and taxon 949 also links to this group. The *Thyreodon, Euryophion* and *Dictyonotus/Ophionopsis* groups, together with taxon 908, form a second robust cluster with only *Euryophion* showing any linkage to non-group taxa. Taxon 909 is somewhat

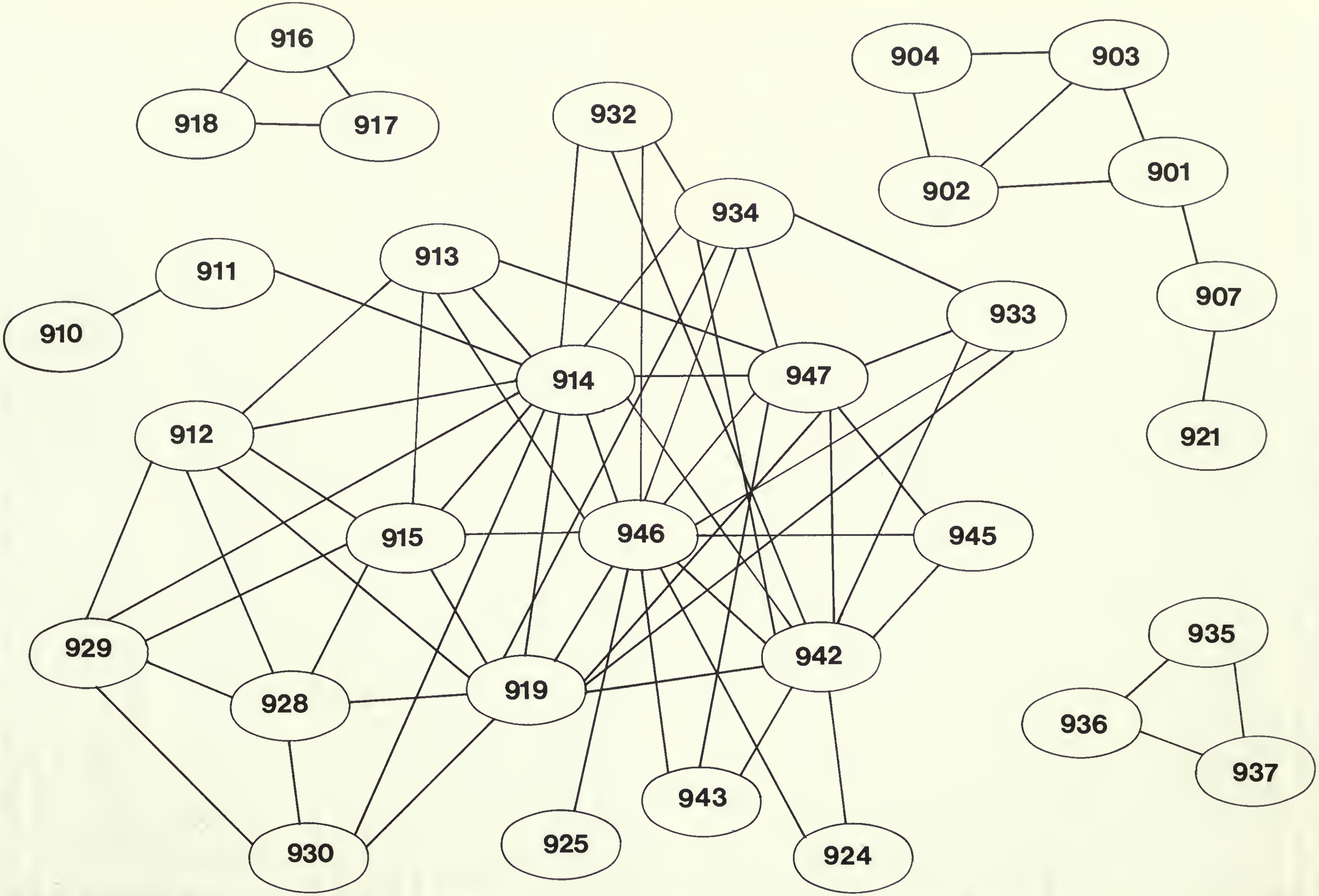


Fig. 8 Multiple linkage clusters drawn for all taxa with 29 or more derived characters in common.

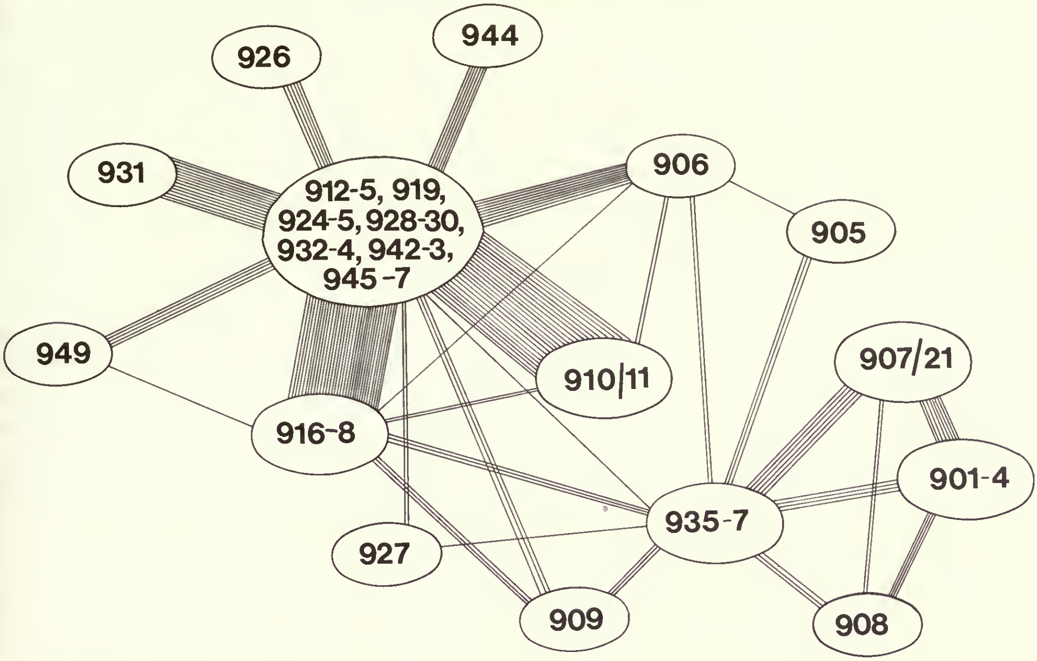


Fig. 9 Multiple linkage clusters drawn for all taxa with 22 or more derived characters in common. As virtually complete linkages occur between taxa enclosed within the boxes, these linkages are not shown so as to avoid confusion.

intermediate linking to both the *Enicospilus* and *Euryophion* groups but shares most derived features with taxa in the *Stauropoctonus* group.

Other taxa occupy a more ambivalent position. Taxon 906 is intermediate between *Enicospilus* and *Euryophion*, whilst 905 appears to be fairly closely associated with *Euryophion* although its nearest neighbour is taxon 906. Taxon 927 is also intermediate. The remaining species, 920, 922, 923, 938–41, 948 and 950–51, are not closely associated with other taxa. To summarize therefore, two major groups are discernible, the *Enicospilus/Stauropoctonus* complex containing taxa 909–919, 924–926, 928–934, 942–947 and 949, and the *Thyreodon/Euryophion* complex with taxa 901–904, 907–908, 921 and 935–937. Taxa 920, 922, 923, 938–941, 948 and 950–951 are not associated at all whilst 905, 906 and 927 are intermediates between the major clusters. It is interesting to note that, excluding the last three taxa, the remainder could be classified phenetically (if one counted shared plesiomorphies of which 920, 922, 938–941, 948 and 950–951 have a considerable number in common) into three groups approximately corresponding to the *Ophion* (plesiomorphic group), *Thyreodon* and *Enicospilus* groups of Cushman (1947).

Phylogenetic analyses of groups of ophionine taxa

The Euryophion group (taxa 935, 936, 937)

It can be seen from Appendix 3 that these taxa form a group with 30+ shared derived characters, and no more than 26 derived characters in common with any other taxon. Using these three as the fixed taxa (3F option) of FOURS, and trying them against all other taxa, nothing broke them up. The three taxa were found to share 29 apomorphies (2, 6·1, 7·1, 16·1, 16·2, 22·2, 24·1, 24·2, 25·1, 25·2, 27·1, 28·1, 28·2, 31, 32, 38, 39, 42·1, 42·2, 43·1, 44·1, 45·1, 47·1, 49, 51·1, 51·2, 58·1, 61·1 and 62). Five of these apomorphies (2, 7·1, 22·2, 42·2 and 58·1) have average or lower O/E values (0·60, 0·84, 0·80, 0·79 and 0·87 respectively) and are shared by relatively few other taxa in the matrix. Of these five apomorphies only one (7·1) has questionable polarity. No character is a unique apomorphy of the group, but the four apomorphies accepted above suggest this group is monophyletic.

There are three possible arrangements of these taxa (Fig. 10). Taxa 935 and 936 have been considered to be congeneric (in *Euryophion*) whilst 937 is usually placed in a separate genus, *Rictophion* (Townes, 1971; Gauld & Mitchell, 1978). *Rictophion* has been separated from *Euryophion* by two unique apomorphies, loss of thyridia and possession of 3-segmented palps. Cladogram A supporting this arrangement is the weakest of the three as it involves only a single informative character, 36·1 which has both a dubious polarity assignment and a very high O/E score. Both B and C also involve some poor scoring characters (19 and 44·2 both have O/E values of more than 0·95). Arrangement B is only supported by 'loss' apomorphies, though one (8·1) has a low O/E value (0·39). However, it has a rather high label score. The characters supporting C are all fairly high scoring (O/E values 0·76+) but do not involve either apomorphic loss or dubious polarity assignment. On balance therefore, C seems to be the preferable arrangement, suggesting that *Euryophion*, as currently recognized, is paraphyletic with respect to *Rictophion*. This conclusion is not surprising as originally *Rictophion* was separated from *Euryophion* on the basis of two autapomorphies. *Rictophion ikuthana* (937), the only species in the genus, can be regarded as a specialized species of *Euryophion*. These species, and all the remainder in the genus, are further analysed below (p. 136).

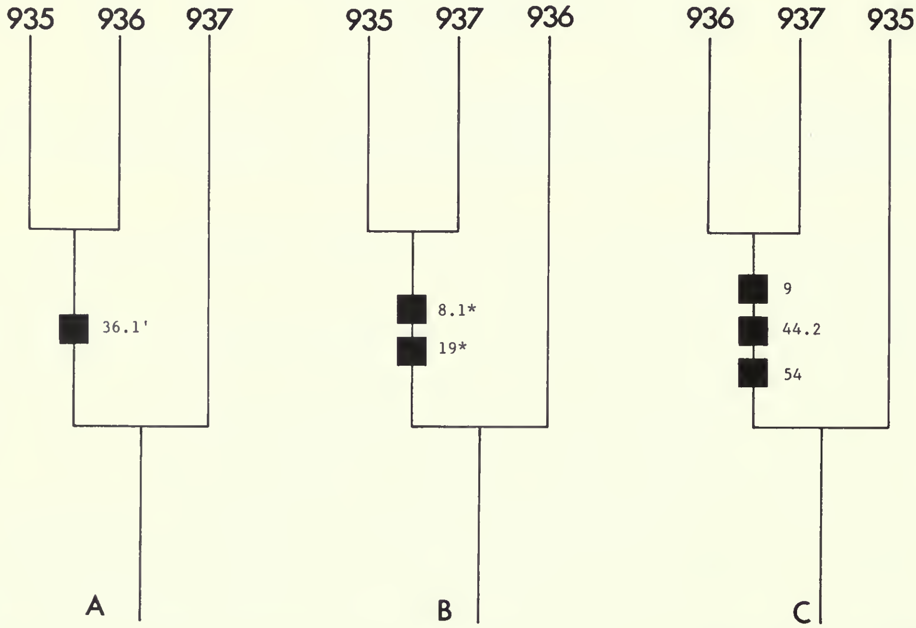


Fig. 10 The three possible dichotomous arrangements of *Euryophion latipennis* (935), *E. adustus* (936) and *Rictophion ikuthana* (937).

The Thyreodon group (taxa 901, 902, 903, 904)

These four taxa, all species currently placed in the genus *Thyreodon* (Townes & Townes, 1966), form a closely knit group. Using the FOURS 3F option any combination of these species remained as a group when tested against any fourth taxon. The *Thyreodon* species share 27 apomorphies (2, 6·2, 7·1, 14·1, 17, 22·2, 23, 24·1, 24·2, 25·1, 25·2, 27·1, 28·1, 28·2, 29·2, 30, 33, 36·1, 38, 42·1, 42·2, 47·1, 49, 51·1, 51·2, 54 and 61·1). Seven of these apomorphies (2, 6·2, 7·1, 22·2, 23, 42·2 and 54) have both lower than average O/E scores (0·60, 0·47, 0·84, 0·80, 0·78, 0·79 and 0·76 respectively) and are shared by relatively few other taxa. Only one, 7·1, involves dubious polarity assignment; the remainder are gain apomorphies suggesting the group is monophyletic. Considering the possible phylogenetic relationships of these taxa to each other, the following result was obtained using the FOURS program (Underwood, 1982).

TAXA NOS. – 901 902 903 904
X 1100: 12* 13
X′ 0011: 36·2′
Y 1010: 21·1
XYZ′ 1110: 26 58·1
XY′Z 1101: 37
X′Y′Z′ 0111: 9

The most favoured arrangement X,XYZ′ is shown in Fig. 11. This involves three forward parallelisms 21·2 (in 901 and 903), 37 (in 901/2 and 904) and 36·2 (in 903 and 904) and one reversal (9 in 901). If the dubious polarity of 36·2 were to be reversed this character would fit the cladogram. It is noteworthy that some authors (e.g. Ashmead, 1900; Cushman, 1947) have placed taxon 904 and its relatives in a separate genus, *Athyreodon*.

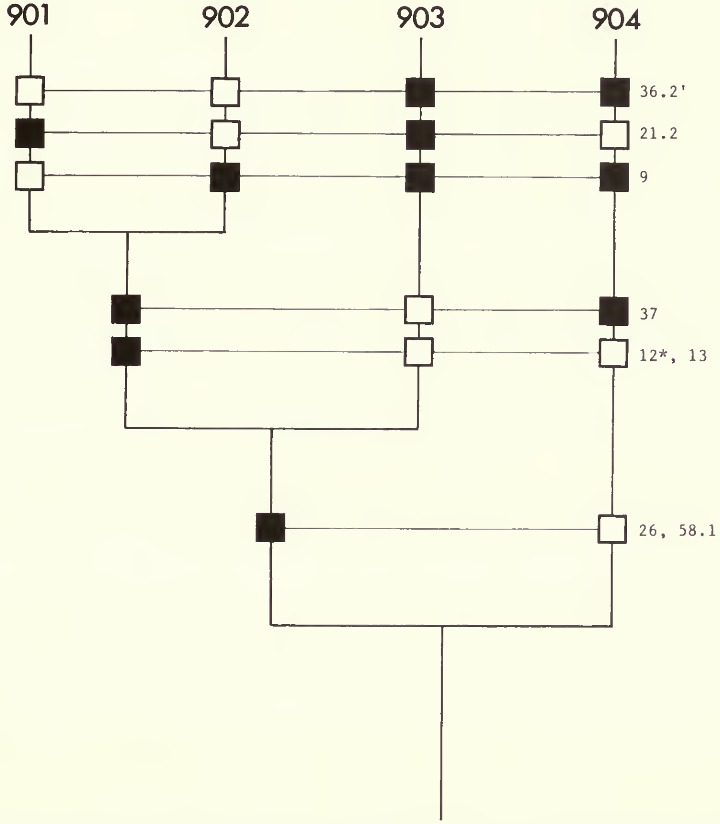


Fig. 11 The arrangement of *Thyreodon* species as supported by the largest number of compatible characters.

The Dictyonotus/Ophionopsis group (taxa 907, 921)
These two taxa are reciprocal nearest neighbours. They share 30 apomorphies (2, 6·2, 7·1, 12, 13, 14·1, 16·2, 18·2, 21·1, 21·2, 22·2, 23, 24·1, 24·2, 25·1, 25·2, 28·1, 28·2, 30, 33, 38, 42·1, 42·2, 44·1, 47·1, 49, 51·1, 51·2, 54 and 58·1). Ten of these (2, 6·2, 7·1, 21·1, 21·2, 22·2, 23, 42·2, 54 and 58·1) have both average or lower O/E values (0·60, 0·47, 0·84, 0·79, 0·39, 0·80, 0·78, 0·79, 0·76 and 0·87 respectively) and are shared by relatively few other taxa in the matrix. One character,

21·2, is a unique apomorphy of this group. The primary label matrix (Appendix 4) suggests characters 16·1, 36·1 and 61·1 (0 scores in taxon 921) may have undergone reversal, whilst character 47·2 (1 score in 921) may have been derived in parallel in 921 and other taxa.

The Thyreodon + Euryophion + Dictyonotus complex (the above three groups)
These three groups of taxa appear to be associated (see shared derived character matrix, Appendix 3). Phylogenetically they also seem to form a distinctive clade, sharing 16 apomorphic features (2, 7·1, 22·2, 24·1, 24·2, 25·1, 25·2, 28·1, 28·2, 38, 42·1, 42·2, 47·1, 49, 51·1 and 51·2). Four of these apomorphies (2, 7·1, 22·2 and 42·2) have both lower than average O/E values (0·60, 0·84, 0·80 and 0·79 respectively) and are shared by very few other taxa. Character 2 is elsewhere only found in the apomorphic state in taxon 908, character 7·1 is apomorphic for taxa 908, 940 and 946, character 22·2 is apomorphic for taxa 906, 908, 927 and 950, whilst character 42·2 is otherwise only apomorphic for taxa 908, 909, 916, 917 and 918. Examination of the labels matrix (Appendix 4) shows that for character 7·1, species 940 and 946 are labelled more than twice as frequently as any other taxon. Similarly for character 22·2, species 906 and 950 are fairly highly labelled. These data suggest parallel derivation of the apomorphic condition of these characters in taxa 906, 940, 946 and 950.

Three other characters are found in the apomorphic condition in all except one taxon in the group. Of these, 61·1 has a high label score for taxon 921, suggesting the apparent plesiomorphic condition in this taxon may be a reversal. Character 54 is present in the apomorphic condition in all taxa in this group except 935; elsewhere it is only found, in the data matrix, in the derived state in three taxa, 908, 941 and 950. The higher values of these last two species suggest the apomorphic state may have been derived in parallel in them. The third of the three characters, 58·1, is usually found in the derived state in *Thyreodon*, so may be presumed to have undergone reversal in 904. Elsewhere it is only found in the apomorphic state in taxa 908, 909, 927, 941 and 950. Taxon 909 has a high label score for this character, suggesting homoplasy. It seems reasonable to treat tentatively all these three characters as apomorphies of the group. This interpretation is certainly the most parsimonious, for in each case the alternative to single postulated reversals must be the advocacy of multiple forward parallelisms.

One other taxon, 908, seems to be consistently associated with this group. Its nearest neighbours all lie within the group (Table 8), and in cluster analysis it readily associated with the group. It shares 18 of the 19 apomorphies of the group and is discordant only in having character

Table 8 The *Thyreodon/Euryophion* complex showing nearest neighbours with numbers of shared derived characters. The rows give the five (or more if several are equal fifth) nearest neighbours of each taxon listed in the left-hand column. The columns show the number of times a species is cited as a near neighbour. It can be seen that taxon 908 occupies an intermediate position between *Thyreodon* (901–4) and *Euryophion* (935–7), having nearest neighbours in both. The *Thyreodon* and *Euryophion* groups have only one near neighbour in common (904–936). Only species in the latter group share large numbers of derived characters in common with non-group taxa (the 'others' column). It is interesting to note that taxon 907, the least autapomorphic in this group (see p. 89), is cited as a near neighbour by all other taxa.

	901	902	903	904	907	921	908	935	936	937	Others
901	+	32	30	28	30	27	--	--	--	--	
902	32	+	30	29	28	26	--	--	--	--	
903	30	30	+	29	27	25	25	--	--	--	
904	28	29	29	+	26	--	--	--	26	--	
907	30	28	27	--	+	30	28	--	--	--	
921	27	26	25	--	30	+	27	--	--	--	
908	25	25	25	--	28	27	+	25	25	27	
935	--	--	--	--	24	--	25	+	30	31	(23- 905, 906, 918)
936	--	--	--	26	26	--	--	30	+	32	(26- 946)
937	--	--	--	--	24	24	27	31	32	+	(25- 905; 24- 906)

28·2 plesiomorphic. However, this character is highly labelled for this taxon suggesting a reversal. In FOURS analyses taxon 908 repeatedly broke into the group. For example –

TAXA NOS. – 901 921 936 908
X 1100: 21·1 30 41
X′ 0011: 16·1
Y′ 0101: 18·2
Y 1010: 29·2 37
Z′ 0110: 9
XYZ′ 1110: 13 28·2
XY′Z 1101: 6·2 12 14·1 23 33
X′YZ 1011: 27·1 36·1 61·1
X′Y′Z′ 0111: 16·2 31 32 44·1

TAXA NOS. – 901 907 936 908
X 1100: 20·1 21·1 30
X′ 0011: 31 32
Y 1010: 37
Y′ 0101: 18·2
Z′ 0110: 43·1
XYZ′ 1110: 13 28·2 29·2
XY′Z 1101: 6·2 12 14·1 23 33
X′YZ 1011: 27·1
X′Y′Z′ 0111: 16·1 16·2 44·1

In both these cases exclusion of taxon 908 from the group, the XYZ′ option, is not the most parsimonious solution. Accordingly, taxon 908, *Rhynchophion flammipennis*, is included for analysis in this group.

Considering only the ten taxa of this group, 35 characters are informative for examining intra-group relationships. A LeQuesne test on this subset of data yielded the results shown in Table 9. Progressive removal of the five worst characters (59, 36·1, 27·2, 9 and 39) markedly altered the ranking of the 'best' scoring characters (i.e. those with an O/E value of 0·6+); the overall O/E ratio improved from 0·69 to 0·52 (Table 10). The data matrix was re-ordered with characters arranged in increasing value of O/E ratio (Tables 11, 12) before and after removal of the worst characters. Considering only the characters with an O/E value greater than 0·55 shows that there are two competing patterns. Characters 16·2, 44·1, 31 and 32 unite the *Euryophion* group (935–7) with the *Dictyonotus* group (907, 921) and 908. This arrangement is contradicted by characters 14·1, 23, 33 and 6·2, which all favour uniting the *Dictyonotus* group with

Table 9 Results of a LeQuesne test on the *Thyreodon*/*Euryophion* data set. Conventions as in Table 2.

```
Character number: incompatibilities observed  expected  O/E ratio

 6.1:  11  22.9  0.48     6.2:  11  22.9  0.48     8.1:   7  16.2  0.42     9  :  30  26.9  1.11

12  :  18  27.9  0.65    13  :  26  27.9  0.93    14.1:  11  23.6  0.47    16.1:  18  26.0  0.69

16.2:  11  26.0  0.42    17  :  12  26.9  0.45    18.2:  24  26.9  0.89    19  :  17  23.6  0.72

20.1:  11  16.2  0.68    21.1:  18  26.4  0.68    21.2:   9  15.6  0.58    23  :  11  23.6  0.47

26  :  10  23.6  0.42    27.1:   9  15.7  0.57    27.2:  28  23.1  1.21    29.2:  22  26.9  0.82

30  :  20  23.6  0.85    31  :  15  27.9  0.54    32  :  15  27.9  0.54    33  :  11  23.6  0.47

36.1:  21  15.7  1.34    36.2:  23  23.1  1.00    37  :  25  26.9  0.93    39  :  17  26.9  0.63

41  :  14  16.2  0.87    43.1:  19  26.9  0.71    44.1:  12  26.4  0.45    44.2:   9  15.6  0.58

45.1:  11  23.6  0.47    59  :  23  16.2  1.42    62  :  11  23.6  0.47

Grand total-    280 observed,   406.3 expected.  Overall O/E ratio = 0.69

Ranking ratio of scoring characters

16.2  26  8.1  17  44.1  62  33  45.1  14.1  23  6.1  6.2  31  32  27.1  21.2  44.2  39  12  20.1

21.1  16.1  43.1  19  29.2  30  41  18.2  37  13  36.2  9  27.2  36.1  59
```

Table 10 Results of a LeQuesne test on the *Thyreodon/Euryophion* data set after progressive removal of five highest scoring characters (59, 36·1, 27·2, 9, 39). Conventions as in Table 2.

```
Character number: incompatibilities observed  expected  O/E ratio

6.1:   6  19.6  0.31     6.2:   6  19.6  0.31     8.1:   3  13.9  0.22     12  :  14  24.1  0.58
13  :  23  24.1  0.96    14.1:   6  20.3  0.30    16.1:  13  22.3  0.58    16.2:   7  22.3  0.31
17  :   8  23.2  0.34    18.2:  22  23.2  0.95    19  :  13  20.3  0.64    20.1:  10  13.9  0.72
21.1:  13  22.7  0.57    21.2:   7  13.4  0.52    23  :   6  20.3  0.30    26  :   6  20.3  0.30
27.1:   7  13.9  0.50    29.2:  19  23.2  0.82    30  :  16  20.3  0.79    31  :  11  24.1  0.46
32  :  11  24.1  0.46    33  :   6  20.3  0.30    36.2:  20  20.3  0.98    39  :  12  23.2  0.52
41  :  11  13.9  0.79    43.1:  14  23.2  0.60    44.1:   8  22.7  0.35    44.2:   6  13.4  0.45
45.1:   6  20.3  0.30    62  :   6  20.3  0.30

Grand total-    158 observed,    303.4 expected. Overall O/E ratio = 0.52

Ranking ratio of scoring characters

8.1  45.1  62  23  26  33  14.1  6.1  6.2  16.2  17  44.1  44.2  31  32  27.1  39  21.2  21.1  12

16.1  43.1  19  20.1  30  41  29.2  18.2  13  36.2
```

Thyreodon (901–4). Characters 6·1, 8·1, 17, 26, 45·1 and 62 clash with neither of these combinations and so, in this context, are uninformative. The very best characters in the original 35 character set (Table 11) favour the former grouping whilst in the 'cleaned-up' 30 character set (Table 12) the best characters favour *Thyreodon* + *Dictyonotus*. Of the eight characters in the two contradictory groups, two, 16·2 and 33, are 'loss' apomorphies and perhaps therefore the apomorphic state is particularly likely to be subject to parallel development. Even disregarding these one is still left with a tie with three characters supporting each arrangement, so it is necessary to consider further characters. Of the characters having an initial O/E value of average or better (16·2–16·1 in Table 11) two, 12 and 21·1, suggest uniting *Thyreodon* with *Dictyonotus* if one postulates minimal reversal in *Thyreodon.* Character 27·1 suggests uniting *Thyreodon* with *Euryophion* and taxon 908, whilst 21·2 is an autapomorphy of taxa 907 and 921. Character 39 suggests linking a single *Thyreodon* species with *Euryophion*. Character 20·1 is apomorphic in only two taxa, 901 and 907.

Considering all characters the most parsimonious arrangement appears to be to treat *Euryophion* as the first branch. By postulating minimal homoplasy (i.e. single reversals or parallelisms) 12 characters can be made to support this arrangement. Only three, 30, 43·1 and 44·2, have an O/E value below average, and only one, 33, is a 'loss' apomorphy. This arrangement involves the following homoplasy (and these are considered to be predictable from the *Thyreodon* labels matrix (Appendix 5) if, for a particular character, the score obtained by the presumed discordant species is higher than that obtained by other species in the group) – 12, reversal in 903/4 (not predictable); 30, reversal in 908, parallelism in 935 (predictable); 39,

Table 11 The *Thyreodon/Euryophion* complex with all 35 informative characters ranked according to their initial O/E value (lowest first). All characters to the left of 27·1 have an O/E value of 0·55 or less.

	16.2	26	8.1	17	44.1	62	33	45.1	14.1	23	6.1	6.2	31	32	27.1	21.2	44.2	39	12	20.1	21.1	16.1	43.1	19	29.2	30	41	18.2	37	13	36.2	9	27.2	36.1	59
901	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	0
902	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	0	1	0
903	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	1	1	1
904	0	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	1	1	0	1	0
908	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0
907	1	0	0	0	1	0	1	0	1	1	0	1	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	1	0
921	1	0	0	0	1	0	1	0	1	1	0	1	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	0	1	0	1	0	0	0
937	1	0	1	0	1	1	0	1	0	0	1	0	1	1	1	0	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0	0
935	1	0	1	0	1	1	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	1
936	1	0	0	0	1	1	0	1	0	0	1	0	1	1	1	0	1	1	0	0	0	1	1	0	1	0	0	0	1	1	1	1	0	1	0

Table 12 The *Thyreodon*/*Euryophion* complex with the 30 'best' informative characters ranked by O/E value computed after progressive removal of five highest scoring characters (see Table 10). All characters to the left of 21·1 have an O/E value of 0·55 or less.

	8.1	45.1	62	23	26	33	14.1	6.1	6.2	16.2	17	44.1	44.2	31	32	27.1	39	21.2	21.1	12	16.1	43.1	19	20.1	30	41	29.2	18.2	13	36.2
901	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	1	0
902	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0
903	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1
904	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	1
908	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0
907	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0
921	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0
937	1	1	1	0	0	0	0	1	0	1	0	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	1	0	0
935	1	1	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0	0
936	0	1	1	0	0	0	0	1	0	1	0	1	1	1	1	1	1	0	0	0	1	1	0	0	0	0	1	0	1	1

parallelism in 904 (predictable); 43·1, parallelism in 907 (predictable); 44·2, parallelism in 921 and reversal in 935 (not predictable).

In attempting to resolve the sister-lineage of *Euryophion*, the *Thyreodon*/*Dictyonotus*/*Rhynchophion* branch, it is apparent that no character is a unique apomorphy of either *Rhynchophion* + *Dictyonotus*, *Rhynchophion* + *Thyreodon* or *Dictyonotus* + *Thyreodon*. Character 30 suggesting the latter is paralleled in taxon 935, 16·2 and 44·1 suggesting *Rhynchophion* + *Dictyonotus* are paralleled in *Euryophion* as is character 27·1 which favours uniting *Rhynchophion* + *Thyreodon*. In any compatibility cladogram (e.g. Fig. 12) these three taxa must remain as an unresolved trichotomy.

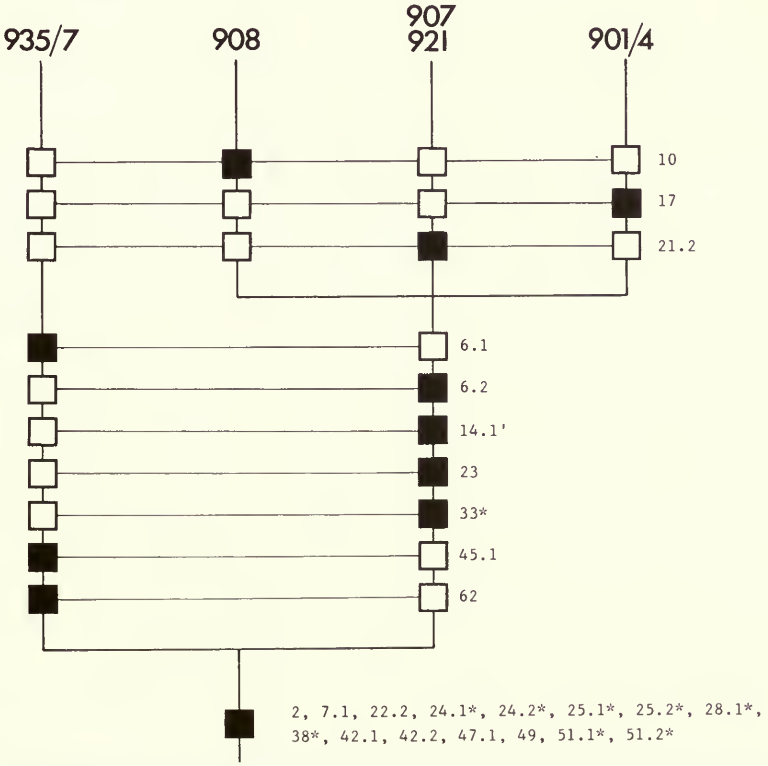


Fig. 12 Cladogram showing inter-relationships of taxa in the *Thyreodon*/*Euryophion* complex as supported by the largest compatible clique.

To resolve these data further it was necessary to use the WAGNER option of PHYLIP. The shortest rooted tree obtained involved 83 transformation steps for the 45 characters showing both 0 and 1 states for this group of taxa (that is the 35 characters shown in the LeQuesne matrix (Table 11) plus 1·1, 4·2, 8·2, 10, 18·1, 29·1, 36·3, 43·2, 47·2 and 57 which are autapomorphies of various individual taxa). To obtain this tree (Fig. 13) 21 characters (1·1, 4·2, 6·1, 6·2, 8·2, 10, 14·1, 17, 18·1, 21·2, 23, 26, 29·1, 33, 36·3, 43·2, 44·2, 45·1, 47·2, 57 and 62) are presumed to have been uniquely derived, 11 characters (8·1, 12, 16·2, 18·2, 20·1, 27·1, 39, 41, 43·1, 44·1 and 59) have undergone two transformations (i.e. have either been derived in parallel or have

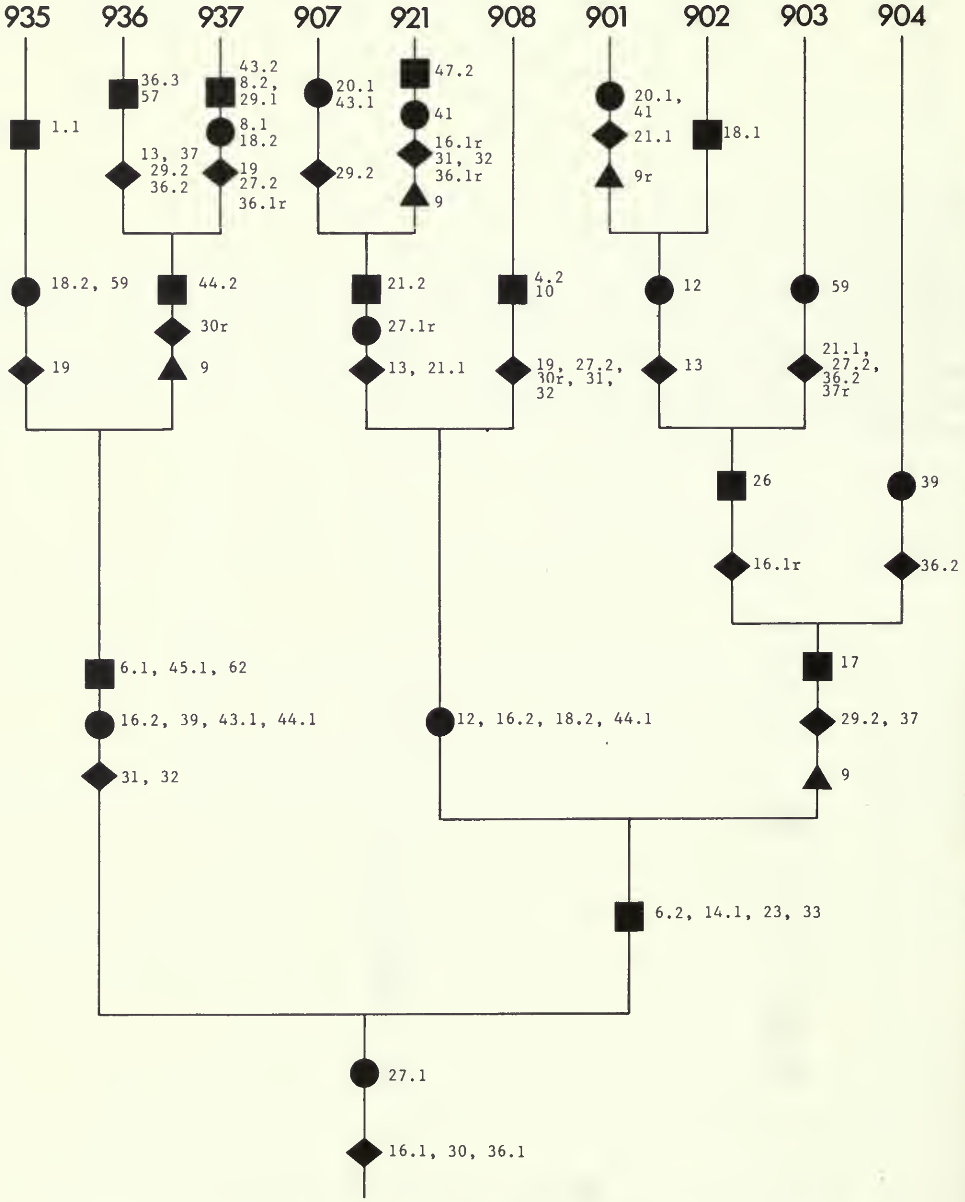


Fig. 13 Most parsimonious cladogram for taxa in the *Thyreodon*/*Euryophion* complex. Black squares represent uniquely derived characters; circles, apomorphic features derived independently in two lineages; diamonds, in three lineages; squares, in four lineages, or involving four transformations.

undergone reversal), 12 characters (13, 16·1, 19, 21·1, 27·2, 29·2, 30, 31, 32, 36·1, 36·2 and 37) have undergone three transformations, whilst one (9) underwent four. It is noteworthy that the cladogram shows only one of a number of competing cladograms with the same arrangement of taxa and the same number of transformation steps, but different positioning of the homoplastic characters. For example, character 30 is shown as a group apomorphy and is postulated as undergoing reversal in the stem 936/7, and in taxon 908, but it would be equally parsimonious to have suggested that 30 was derived in parallel in stems 901/4, 907/21 and taxon 935. Biologically neither is implausible.

The Stauropoctonus group (Taxa 916, 917, 918)
These three taxa share 29 apomorphies (1·1, 5·1, 5·2, 14·2, 16·1, 16·2, 18·2, 21·1, 22·1, 25·1, 28·1, 28·2, 29·2, 33, 37, 38, 39, 42·1, 42·2, 45·1, 47·1, 49, 51·1, 51·2, 52·1, 52·2, 61·1, 61·2 and 62). Six of these apomorphies (5·1, 5·2, 14·2, 21·1, 42·2 and 52·2) have both lower than average O/E values (0·84, 0·75, 0·83, 0·79, 0·79 and 0·71 respectively) and are shared by relatively few other taxa in the matrix.

Within this group all three possible arrangements of taxa are supported: 916 + 917 by 25·2* and 47·2; 916 + 918 by 1·2*, 36·1′, 36·2′, 43·1′ and 63; 917 + 918 by 57*. All of these eight informative characters have high LeQuesne test failure rates (0·9+) and most are either loss characters or have dubiously assigned polarity, making the choice between arrangements difficult. The most parsimonious would obviously be 916 + 918. Currently 916 and 917 are placed together in *Stauropoctonus* whilst 918 is placed in a separate taxon, *Aulophion* (Cushman, 1947; Townes, 1971). *Aulophion* has traditionally been separated from *Stauropoctonus* by the possession of two autapomorphies, loss of the posterior transverse carina of the mesosternum and absence of the epicnemial carina. This suggests *Stauropoctonus* may be a paraphyletic assemblage. For the present these taxa are treated as an unresolved trichotomy, but their inter-relationship is discussed further below (p. 146). It is sufficient now to state that these three taxa seem to form a closely knit and apparently holophyletic group.

The Enicospilus + Stauropoctonus complex (Taxa 909–919, 924–926, 928–934, 942–947)
This, the largest apparent group of ophionine taxa in the matrix, contains 28 species. (N.B. Taxon 949 which associates with this group in the cluster analysis is exceptional in having the plesiomorphic state of a number of characters usually found in the apomorphic condition in this group (e.g. 25·2, 28·2, 42·1, 51·1, 51·2 and 63). For the present this taxon is excluded from the complex and its position discussed later in the work.) Their nearest neighbours are shown in Table 13. These taxa share four apomorphic features (16·1, 25·1, 28·1 and 51·1). A further 13 characters (22·1, 25·2, 28·2, 33, 36·1, 38, 42·1, 43·1, 45·1, 47·1, 49, 51·2 and 63) are present in the apomorphic state in all except one, two or three taxa. Most of these characters are labelled, often highly, for the species in this group that show the plesiomorphic condition (e.g. 38 for taxon 943 and 47·1 for taxa 944 and 945), suggesting a reversal may have occurred. The exceptions are 22·1 and 33 which are plesiomorphic for taxa 910 and 911. Both are unlabelled in the primary label matrix (Appendix 4). Of the 17 characters listed above as possible apomorphies of this complex, all except 22·1, 33 and 63 occur in the apomorphic condition in a large number of other ophionine taxa in the matrix. Individually therefore, they are not good characters for defining the group. Character 49 is plesiomorphic only in the solitary taxon 926, suggesting 49 may be an apomorphy of all ophionines, and 926, an otherwise specialized species, may have undergone a reversal. Character 16·1 is apomorphic for all taxa except 901–3 and 921; character 25·1 for all except 948 and 951; character 25·2 for all except 918, 920, 922, 923, 938–41, 945, 948, 949 and 951; character 28·1 for all except 939; character 28·2 for all except 908, 920, 923, 928, 938–41, 949 and 951; character 36·1 for all except 909, 917, 920, 921, 922, 937 and 944; character 38 for all except 938, 939, 941, 943, 948 and 951; character 42·1 for all except 905, 922, 925, 938–41 and 948–50; character 43·1 for all except 901–4, 908, 909, 917, 921–22, 925 and 941; character 45·1 for all except 901–4, 907–8, 921, 923, 925–26, 931, 941 and 948; character 47·1 for all except 938, 939, 943, 944, 948 and 951; character 51·1 for all except 920, 922, 939–41 and 949–51; and character 51·2 for all except 920, 922, 932, 938–41 and 948–51. Ten of these characters (25·1, 25·2, 28·1, 28·2, 38, 42·1, 47·1, 49, 51·1 and 51·2) have been stated above (p.

Table 13 The *Enicospilus*/*Stauropoctonus* complex showing nearest neighbours with numbers of shared derived characters. Conventions as in Table 8. Particularly striking are taxa 944 (an *Enicospilus* species) and 931 (a *Leptophion* species). Both cite their congeners as nearest neighbours, but neither is cited as near neighbours by its congeners.

	926	925	924	947	946	945	944	943	942	934	933	932	919	915	914	913	912	931	930	929	928	918	917	916	909	910	911	Others
926	+	--	25	25	27	--	--	24	27	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
925	--	+	27	28	30	--	--	--	28	--	--	24	--	--	--	--	--	--	--	--	--	24	--	--	--	--	--	
924	25	27	+	27	29	--	--	--	29	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
947	--	--	--	+	35	31	--	31	34	30	--	--	--	30	30	--	--	--	--	--	--	--	--	--	--	--	--	
946	--	--	--	35	+	--	--	--	37	32	--	32	--	--	32	--	--	--	--	--	--	--	--	--	--	--	--	
945	--	--	--	31	31	+	--	28	31	28	28	--	--	--	28	--	--	--	--	--	--	--	--	--	--	--	--	
944	--	--	--	24	26	24	+	--	26	24	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
943	--	--	--	31	30	28	--	+	31	--	--	--	--	--	--	--	--	--	--	--	--	28	--	--	--	--	--	
942	--	--	--	34	37	31	--	31	+	31	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
934	--	--	--	30	32	--	--	--	31	+	--	30	--	--	30	--	--	--	--	--	--	--	--	--	--	--	--	
933	--	--	--	29	29	--	--	--	29	29	+	--	29	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
932	--	--	--	28	32	--	--	--	30	30	--	+	--	--	29	--	--	--	--	--	--	--	--	--	--	--	--	
919	--	--	--	29	29	--	--	--	29	29	29	--	+	32	33	--	30	--	29	--	30	--	--	--	--	--	--	
915	--	--	--	--	--	--	--	--	--	--	--	--	32	+	36	33	34	--	--	--	31	--	--	--	--	--	--	
914	--	--	--	--	32	--	--	--	--	--	--	--	33	36	+	33	33	--	--	--	--	--	--	--	--	--	--	
913	--	--	--	29	29	--	--	--	--	--	--	--	--	33	33	+	31	--	--	--	--	--	--	--	--	--	--	
912	--	--	--	--	--	--	--	--	--	--	--	--	30	34	33	31	+	--	--	29	--	--	--	--	--	--	--	
931	--	--	--	--	--	--	--	--	--	--	--	--	27	27	27	--	--	+	--	27	27	--	--	--	--	--	--	
930	--	--	--	--	--	--	--	--	28	--	--	--	29	28	29	--	28	--	+	29	30	--	--	--	--	--	--	
929	--	--	--	--	--	--	--	--	--	--	--	--	--	30	29	--	29	--	29	+	29	--	--	--	--	--	--	
928	--	--	--	--	--	--	--	--	--	--	--	--	30	31	29	--	--	--	30	29	+	--	--	--	--	--	--	
918	--	--	--	28	--	--	--	28	28	--	--	--	28	--	--	--	--	--	--	--	--	+	30	34	--	--	--	
917	--	--	--	24	--	--	--	--	24	--	--	--	24	--	--	--	--	--	--	--	--	30	+	31	25	--	--	
916	--	--	--	27	--	--	--	--	--	--	--	--	27	--	--	--	--	--	--	--	--	34	31	+	27	--	--	
909	--	--	--	24	24	--	--	--	--	--	--	--	--	24	--	--	--	--	--	--	--	26	25	27	+	--	--	24-936
910	--	--	--	--	26	--	--	--	--	--	--	--	26	28	28	26	26	--	--	26	--	--	--	--	--	+	30	
911	--	--	--	--	28	--	--	--	--	--	--	--	--	28	30	27	--	--	--	--	--	--	--	--	--	30	+	

90) to be apomorphies of the *Thyreodon*/*Euryophion* complex, suggesting they are characters that unite the *Enicospilus*/*Stauropoctonus* and *Thyreodon*/*Euryophion* generic complexes. Character 16·1 could also be considered an apomorphy of both these major groups if one were to postulate reversal in 901–3 and 921.

Character 22·1 is found in the apomorphic state outside the *Enicospilus*/*Stauropoctonus* complex only in taxa 920, 940, 949 and 951; character 33 in taxa 901–4, 907–8, 920–22 and 949 and character 63 in 905, 906 and 923. Character 33 is a loss apomorphy and has been cited above as an apomorphy of the *Thyreodon*/*Dictyonotus* lineage. It is perhaps not unreasonable to postulate parallel loss in the *Enicospilus*/*Stauropoctonus*, the *Thyreodon*/*Dictyonotus* and the 920, 922 and 949 lineages. However, this feature, the loss of the umbo, is not apomorphic for taxa 910 and 911 included above in the *Enicospilus* group. It is biologically rather unlikely that the umbo would be lost then redeveloped, so this feature favours placing *Ophiogastrella* (910–11) primitive with respect to the rest of the group. Such a position is also favoured by character 22·1. The apomorphic condition, a lengthened anterior part of the propodeum, is rather unlikely to have undergone reversal.

It is interesting to note that character 22 has two alternative derived states, 22·1 or 22·2. The derived state 22·2 is an apomorphic feature of the *Thyreodon*/*Euryophion* complex and is only found elsewhere in taxa 906 and 927. The alternative derived state characteristic of the *Enicospilus*/*Stauropoctonus* group (less *Ophiogastrella*) is also found in very few other taxa (see above). The plesiomorphic condition (0,0) is found in taxa 905, 910, 911, 922, 923, 938, 939, 941 and 948. The character seems to be important in defining two major sister-lineages of the subfamily.

Using the CLIQUE option of PHYLIP eight cliques were found with 12 or more informative characters. These were

A (12) [18·1, 18·2, 21·1, 22·1, 27·3, 33, 35, 36·3, 42·2, 61·1, 61·2, 64] Av. O/E = 0·76
B (12) [15·1, 15·2, 18·1, 18·2, 21·1, 22·1, 27·3, 33, 35, 36·3, 42·2, 64] Av. O/E = 0·75
C (12) [17, 18·1, 18·2, 21·1, 22·1, 27·3, 31, 33, 39, 42·2, 60, 64] Av. O/E = 0·78
D (12) [15·1, 17, 18·1, 18·2, 21·1, 22·1, 27·3, 31, 33, 42·2, 60, 64] Av. O/E = 0·77
E (13) [12, 14·2, 17, 18·2, 21·1, 22·1, 27·3, 31, 33, 39, 42·2, 60, 64] Av. O/E = 0·78
F (12) [12, 15·1, 17, 18·2, 21·1, 22·1, 27·3, 31, 33, 42·2, 55, 64] Av. O/E = 0·76
G (12) [13, 18·1, 18·2, 21·1, 22·1, 33, 35, 36·3, 42·2, 61·1, 61·2, 64] Av. O/E = 0·79
H (12) [13, 15·1, 15·2, 18·1, 18·2, 21·1, 22·1, 33, 35, 36·3, 42·2, 64] Av. O/E = 0·78
A ∩ B ∩ C ∩ D ∩ E ∩ F ∩ G ∩ H = {18·2, 21·1, 22·1, 33, 42·2, 64}

The best clique in the sense of the largest is E but this has a lower average O/E value (0·78) than several others. B has the lowest average O/E value with 0·75, closely followed by A and F with 0·76. The remainder have higher values. The cladograms based on the largest clique (E) and the best O/E scoring clique (B) are shown in Figs 14, 15. The cladogram produced from clique B associated the various taxa fairly well with their congeners. Species of *Enicospilus* (942–47), *Dicamptus* (932–34) and the Hawaiian genera (924–26) (regarded by Townes, 1971, as derived *Enicospilus*) cluster together, except for *E. cionobius* (945) which is excluded by having the plesiomorphic condition of 15·2 (possibly a reversal). *Laticoleus* (912–15) and *Leptophion* (928–30) species form a separate cluster as do the *Stauropoctonus* group (916–18) plus *Lepiscelus* (909). The cladogram derived from clique E has more confusing groupings, uniting some species of *Enicospilus* and *Laticoleus* (character 17) or defining a clade containing *Dicamptus neavei, Leptophion tetus* and *Abanchogastra hawaiiensis* (character 12). The heterogeneous collection of species united by character 14·2 includes representatives of *Dicamptus, Enicospilus, Laticoleus* and *Leptophion*; other species of these genera are excluded. The largest clique, E, is therefore not considered particularly useful in this case; clique B appears to be a better indicator of relationship. It is noteworthy that clique B is more informative ($s = 0{\cdot}681$) than clique E ($s = 0{\cdot}632$).

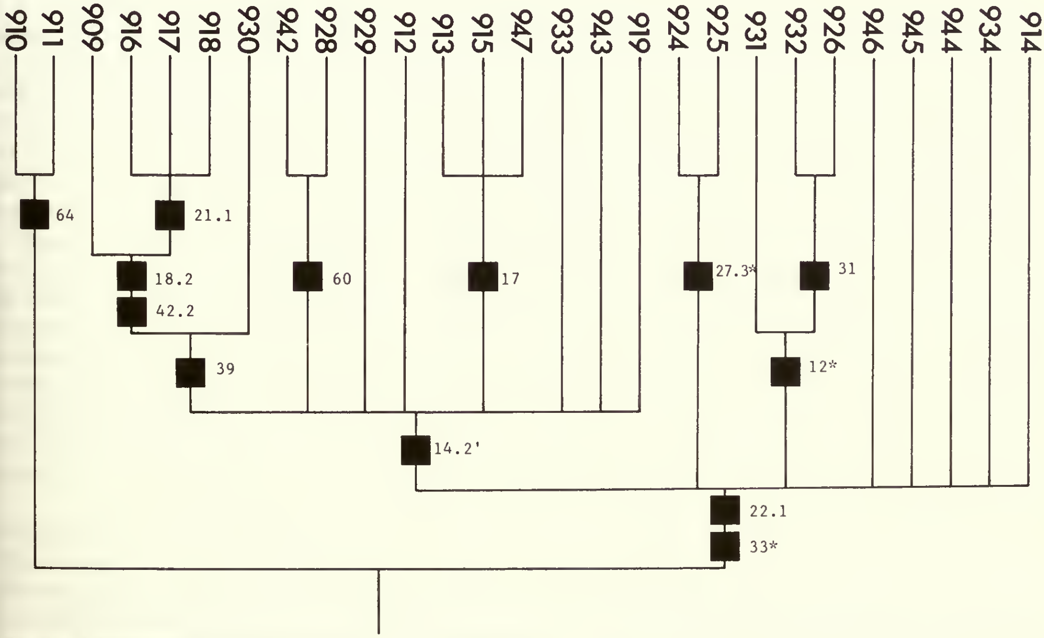


Fig. 14 Cladogram for taxa in the *Enicospilus*/*Stauropoctonus* complex based on the largest clique (E).

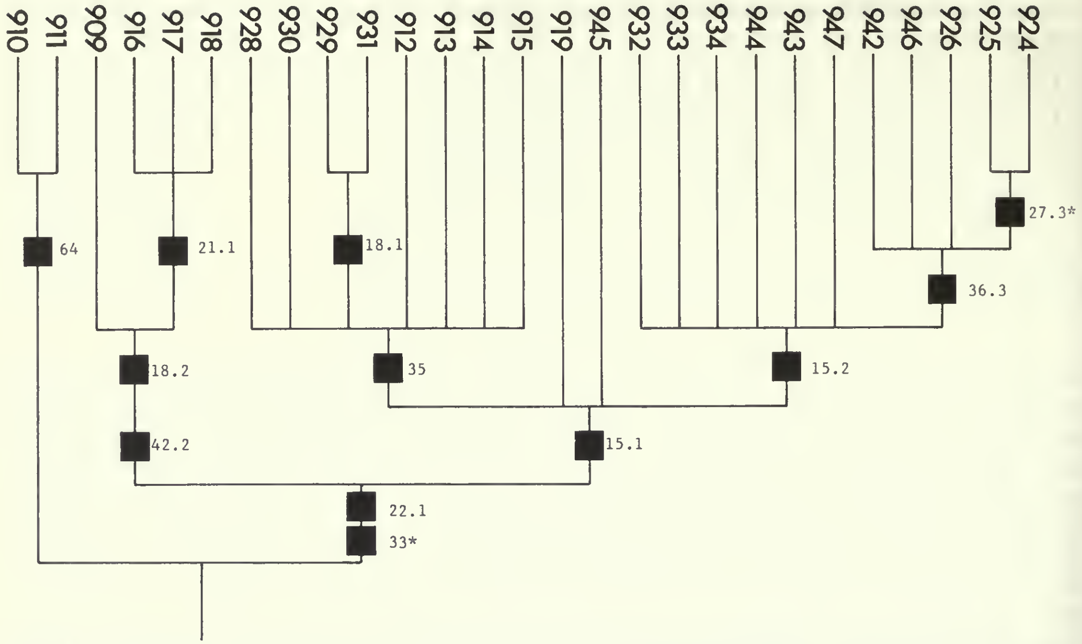


Fig. 15 Cladogram for taxa in the *Enicospilus/Stauropoctonus* complex based on the favoured clique (B).

It is notable that the intersect of these cliques includes several characters previously considered to be good indicators of phylogenetic relationship (Cushman, 1947; Townes, 1971). Three (18·2, 21·1 and 42·2) support the group 909 + 916–18, whilst two others (22·1 and 33) place *Ophiogastrella* (910–11), primitive to the other taxa. Character 64 is an autapomorphy of *Ophiogastrella*.

A LeQuesne test was undertaken on the *Enicospilus/Stauropoctonus* data set and the O/E values are given in Table 14. Stepwise elimination of all characters scoring worse than 1·00 (a total of 15) resulted in considerable cleaning up. The overall ratio improved from 0·89 to 0·74. Amongst the scoring characters the most striking changes in rank occurred to 1·2 which rose from thirty-fifth to eleventh position, and 62 which dropped from thirty-first place to position forty-three. Amongst the best scoring characters 42·2 and 18·2 rose from fourteenth and sixteenth positions to seventh and eighth positions (Table 15). Using the S option of FOURS the data set was reorganized with characters ranked as per O/E value after removal of the 15 most discordant characters (Table 16). It can be seen that the characters with the lowest O/E values, 22·1 and 33, exclude *Ophiogastrella* (910–11) whilst 64 is an autapomorphy of this genus. A number of other characters may be postulated as apomorphies of *Ophiogastrella*, though all apparently have been derived in parallel elsewhere. Characters 18·2 and 42·2 support the *Stauropoctonus* group + 909, whilst 21·1 supports just the former. Character 1·2 is incompatible with 21·1. Initially it had a poor O/E score (0·93 compared with 0·54 for 21·1) but progressive elimination of the poorest characters produced rapid 'clean-up' until with 15 characters eliminated it scored 0·57 compared with 0·34 for 21·1. With only the 18 best characters left in the matrix both taxa scored equally 0·13. A considerable number of slightly homoplastic characters (e.g. 5·1, 5·2, 37, 52·1) support 21·1 but no other character supports 1·2 and it is for this reason that one would prefer the arrangement supported by the former character.

Several other characters support the *Stauropoctonus* + 909 group but necessitate postulating parallel derivation in other places. These include 1·1 (parallelism in 925 and 945), 39 (parallelism in 930), 61·1 (parallelism in 924–26 and 942–47). Many of these parallelisms are also suggested in the reduced labels matrix (Appendix 6), e.g. taxon 930 for character 39 acquires almost half of its total number of labels and taxa 925 and 945 are quite highly labelled for character 1·1.

Table 14 Results of a LeQuesne test on the *Enicospilus*/*Stauropoctonus* data set. Conventions as in Table 2.

Character number: incompatibilities observed expected O/E ratio

1.1:	40	42.7	0.94	1.2:	27	29.2	0.93	3 :	33	47.6	0.69	4.1:	39	35.8	1.09
5.1:	45	50.5	0.89	5.2:	41	42.3	0.97	6.1:	28	19.9	1.40	7.2:	39	51.5	0.76
12 :	27	29.7	0.91	13 :	10	19.9	0.50	14.2:	43	51.5	0.84	15.1:	37	42.3	0.88
15.2:	39	50.0	0.78	16.2:	48	40.1	1.20	17 :	25	29.7	0.84	18.1:	11	19.7	0.56
18.2:	27	35.5	0.76	19 :	27	19.9	1.35	20.1:	38	34.9	1.09	20.2:	46	50.1	0.92
21.1:	16	29.7	0.54	22.1:	5	19.9	0.25	24.1:	49	48.1	1.02	24.2:	50	44.7	1.12
25.2:	26	19.9	1.30	27.1:	41	46.2	0.89	27.2:	41	46.2	0.89	27.3:	11	19.1	0.58
29.2:	34	43.2	0.79	30 :	22	19.9	1.10	31 :	19	19.9	0.95	33 :	5	19.9	0.25
35 :	28	47.6	0.59	36.1:	33	28.6	1.15	36.2:	44	44.3	0.99	36.3:	25	38.8	0.64
37 :	50	49.0	1.02	39 :	36	40.1	0.90	40 :	34	47.6	0.71	42.2:	27	35.8	0.75
43.1:	32	29.0	1.10	43.2:	50	48.3	1.03	44.1:	55	48.2	1.14	44.2:	43	35.0	1.23
45.1:	30	29.0	1.04	45.2:	45	49.4	0.91	46 :	42	50.2	0.84	47.1:	15	19.5	0.77
47.2:	52	50.5	1.03	48.1:	47	50.5	0.93	48.2:	39	46.6	0.84	52.1:	45	48.1	0.94
52.2:	40	42.3	0.95	55 :	25	35.8	0.70	56 :	28	19.9	1.40	57 :	35	35.8	0.98
59 :	48	51.7	0.93	60 :	17	19.9	0.85	61.1:	35	50.7	0.69	61.2:	40	50.5	0.79
62 :	36	40.1	0.90	64 :	5	19.9	0.25								

Grand total- 1035 observed, 1161.2 expected. Overall O/E ratio = 0.89

Ranking ratio of scoring characters

22.1 33 64 13 21.1 18.1 27.3 35 36.3 61.1 3 55 40 42.2 7.2 18.2 47.1 15.2 29.2
61.2 14.2 46 48.2 17 60 15.1 27.1 27.2 5.1 39 62 12 45.2 20.2 1.2 59 48.1 52.1
1.1 52.2 31 5.2 57 36.2 24.1 37 47.2 43.2 45.1 20.1 4.1 43.1 30 24.2 44.1 36.1
16.2 44.2 25.2 19 6.1 56

Table 15 Results of a LeQuesne test on the *Enicospilus*/*Stauropoctonus* data set after progressive removal of 15 highest scoring characters (56, 19, 6·1, 25·2, 44·2, 16·2, 24·2, 44·1, 30, 57, 24·1, 43·2, 36·1, 45·1, 36·2). Conventions as in Table 2.

Character number: incompatibilities observed expected O/E ratio

1.1:	26	33.2	0.78	1.2:	13	23.0	0.57	3 :	23	36.9	0.62	4.1:	27	28.3	0.96
5.1:	33	38.7	0.85	5.2:	29	32.8	0.89	7.2:	27	39.7	0.68	12 :	20	23.5	0.85
13 :	7	15.8	0.44	14.2:	32	39.7	0.81	15.1:	23	32.8	0.70	15.2:	27	38.3	0.70
17 :	18	23.5	0.76	18.1:	9	15.5	0.58	18.2:	13	28.0	0.46	20.1:	24	27.4	0.88
20.2:	32	38.4	0.83	21.1:	8	23.5	0.34	22.1:	1	15.8	0.06	27.1:	30	35.5	0.85
27.2:	30	35.5	0.85	27.3:	6	14.9	0.40	29.2:	25	33.7	0.74	31 :	14	15.8	0.89
33 :	1	15.8	0.06	35 :	20	36.9	0.54	36.3:	17	31.4	0.54	37 :	36	37.9	0.95
39 :	22	31.4	0.70	40 :	25	36.9	0.68	42.2:	13	28.3	0.46	43.1:	22	23.5	0.93
45.2:	34	38.7	0.88	46 :	32	38.7	0.83	47.1:	10	15.3	0.65	47.2:	38	38.8	0.98
48.1:	33	38.7	0.85	48.2:	29	35.9	0.81	52.1:	33	37.0	0.89	52.2:	30	32.8	0.91
55 :	20	28.3	0.71	59 :	36	39.9	0.90	60 :	14	15.8	0.89	61.1:	24	38.9	0.62
61.2:	28	38.7	0.72	62 :	29	31.4	0.92	64 :	1	15.8	0.06				

Grand total- 522 observed 708.4 expected Overall O/E ratio = 0.74

Ranking ratio of scoring characters

22.1 33 64 21.1 27.3 13 42.2 18.2 36.3 35 1.2 18.1 61.1 3 47.1 40 7.2 39 15.1
15.2 55 61.2 29.2 17 1.1 14.2 48.2 46 20.2 27.1 27.2 12 5.1 48.1 20.1 45.2 5.2
31 60 52.1 59 52.2 62 43.1 37 4.1 47.2

Table 16 The *Enicospilus*/*Stauropoctonus* complex data set reordered according to O/E values of the characters given in Table 15. Characters to the left of 17 have an O/E value of average (0·74) or less.

	22.1	33	64	21.1	27.3	13	42.2	18.2	36.3	35	1.2	18.1	61.1	3	47.1	40	7.2	39	15.1	15.2	55	61.2	29.2	17	1.1	14.2	48.2	46	20.2	27.1	27.2	12	5.1	48.1	20.1	45.2	5.2	31	60	52.1	59	52.2	62	43.1	37	4.1	47.2
924	1	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0
925	1	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0
926	1	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0
947	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	1	0	1	1
946	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	1	0	1	1	0	0	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	1	1	1	0	0
945	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	1	1
944	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0
943	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	1	0	1	1	0	0	0	1	0	1	1	1	0	0	1	0	1	1	1	0	1	0
942	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	1	0	1	1	0	0	1	1	1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0	0
934	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	1	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0
933	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	0	0	1
932	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	0	0	1	1	1	0	0
919	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	0	1
931	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1
930	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0
929	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0
928	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1	1	0	1
915	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	1	0	1	0	0	1	1	1	0	0	1	1	1	0	0	0	1	1	0	1	1	1	0	1
914	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1
913	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	0
912	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	1	0	1	1	1	0	0
909	1	1	0	0	0	0	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1
918	1	1	0	1	0	0	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	1	0	1	1	0	0	0	1	1	0	1	0	0	1	1	0	0	1	0	1	1	1	1	0	0
917	1	1	0	1	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	1	0	1
916	1	1	0	1	0	0	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	1	1	0	1
911	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0
910	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1	0	0

Character 15·1 is compatible with those characters that suggest treating 910 + 911 and 909 + 916–18 as the first two branches. This unites all the other taxa to form a residual group that includes *Enicospilus* (942–47), *Dicamptus* (932–34), *Leptophion* (928–31), *Laticoleus* (912–15) and *Pamophion* (919). This is rather a difficult group to resolve. Two of the best characters, 13 and 27·3, are incompatible. Character 35 suggests uniting *Laticoleus* (912–15) with *Leptophion* (928–31), and this is partially supported by character 3. No character unites all the taxa that show the plesiomorphic condition of 35. Three characters, 5·1, 61·1 and 61·2, suggest uniting the Hawaiian genera (924–26) with *Enicospilus* (942–47). Only one taxon, 944, is at variance for a single character, 61·2, and this has a high label value suggesting that a reversal to the plesiomorphic state may have occurred. In several places in the data set it is apparent that similar cases of a single taxon being at variance with its congeners is observable. In the case of 944, it is one of only about ten *Enicospilus* species out of nearly a thousand to have the plesiomorphic condition of character 61·2. Similarly 945 has the plesiomorphic state of 15·2. Both of these taxa do not appear to be primitive in any other features and as they are thus unlikely to be ancestral to all other taxa in the genus it is probable that the apparently unspecialized condition is a reversal.

Character 15·2 favours uniting the Hawaiian genera, *Enicospilus* and *Dicamptus* (932–34) and this is partially supported by character 40 although it is necessary to postulate reversal in the Hawaiian genera. Character 46 is similar. Character 7·2 is contradictory, suggesting a group comprising 912–15, 919 and 928–34. No characters satisfactorily separate *Laticoleus* (912–15) from *Leptophion* (928–31) though 27·1, 27·2 and 55 suggest some separation. Character 3 suggests that *Pamophion* belongs to the *Laticoleus*/*Leptophion* lineage.

Using the CLIQUE option of PHYLIP on the data set with the basal taxa (910–11, 909, 916–18) removed revealed the existence of four cliques with eight or more informative characters. These are

A (8) [4·1, 5·1, 18·1, 27·3, 35, 36·3, 61·1, 61·2]	Av. O/E = 0·81
B (9) [4·1, 5·1, 27·1, 27·2, 27·3, 35, 36·3, 61·1, 61·2]	Av. O/E = 0·83
C (8) [4·1, 5·1, 13, 18·1, 35, 36·3, 61·1, 61·2]	Av. O/E = 0·86
D (9) [4·1, 5·1, 13, 27·1, 27·2, 35, 36·3, 61·1, 61·2]	Av. O/E = 0·87

A ∩ B ∩ C ∩ D = {4·1, 5·1, 35, 36·3, 61·1, 61·2}

These sets support very similar cladograms; the favoured one, with the lowest average O/E, is shown in Fig. 16, but all are similar in showing two large groups (912–15 + 928–31 and 924–26 + 942–47) and leaving taxa 919 and 932–34 unresolved.

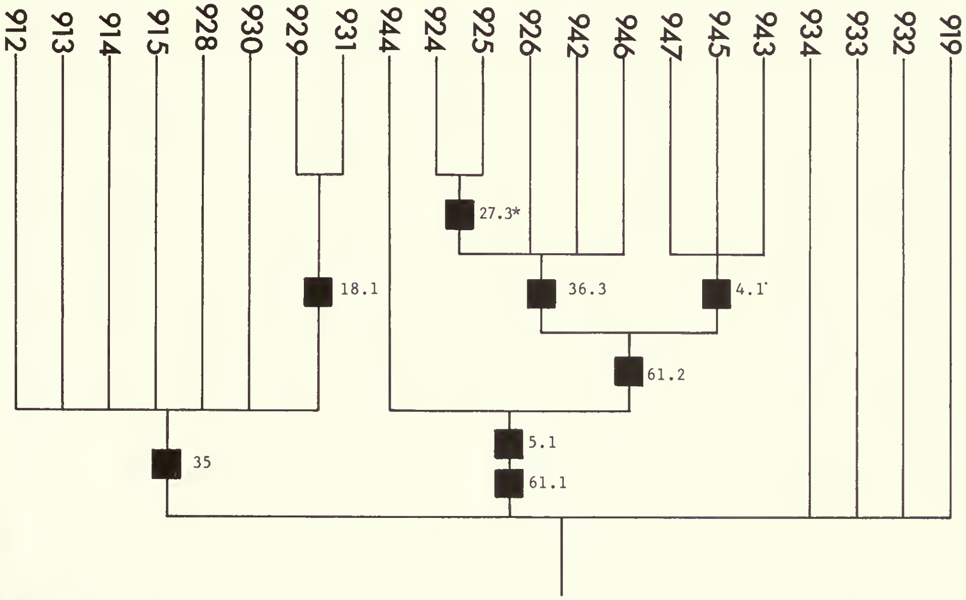


Fig. 16 Cladogram for taxa in the *Enicospilus/Stauropoctonus* complex less taxa 909–911 and 916–8, based on the favoured clique (A).

Using the WAGNER option of PHYLIP several attempts were made to construct the shortest rooted tree possible. The minimum length tree (Fig. 17) necessitated 242 transformation steps.

Both parsimony and compatibility analyses have certain similarities. Both taxa 909 + 916–18 formed a group primitive to most other taxa whilst *Enicospilus* (942–47) and *Dicamptus* (932–34) are amongst the most specialized taxa and separate from *Laticoleus* (912–15) and *Leptophion* (928–31). However, the Wagner parsimony method usually separated the Hawaiian taxa (924–26) as a relatively primitive, discrete group but placed *Ophiogastrella* (910–11) well in the *Enicospilus/Dicamptus/Leptophion/Laticoleus* complex. Compatibility methods suggested the reverse. To assess the relative merits of these alternative arrangements it is necessary to evaluate the characters upon which they are based. As mentioned above, the exclusion of taxa 910 and 911 is based on characters 15·1, 22·1 and 33 which are present in the apomorphic condition in all other taxa. The former two are striking structural modifications and whilst the latter is a loss apomorphy, it is an unusual reduction (when considered for the family as a whole). There is no apparent functional reason why these characters should be linked, so their congruence can be viewed as strong evidence for excluding 910–11 as the first branch. However, 910 and 911 do have a number of apomorphies in common with many other taxa in the group,

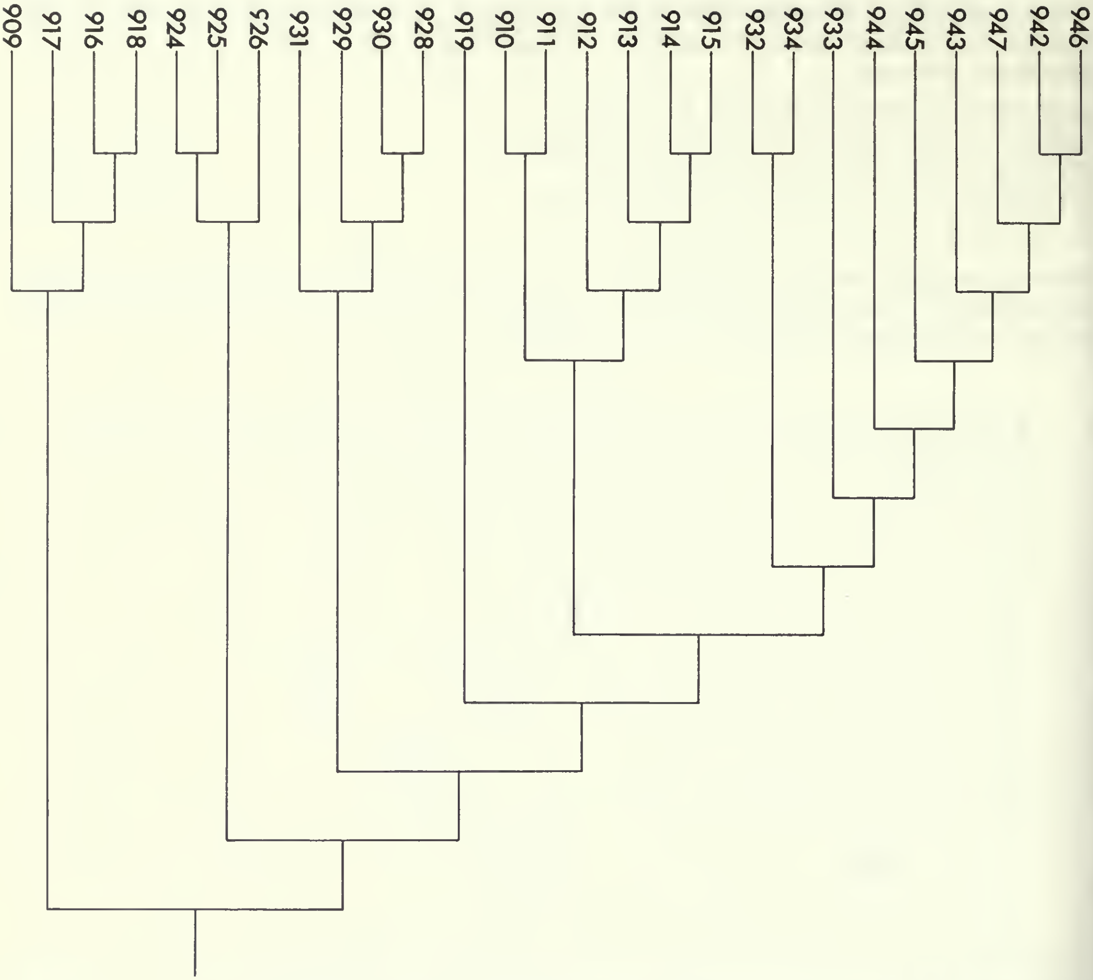


Fig. 17 Minimum length cladogram produced by Wagner parsimony analysis of the *Enicospilus/Stauropoctonus* complex. This tree requires 242 transformation steps.

especially the *Laticoleus/Leptophion* complex (e.g. characters 7·2, 27·1, 27·2, 20·1) which it must be assumed has been derived in parallel if *Ophiogastrella* is indeed the most primitive branch.

The Wagner analysis united all taxa excluding the *Stauropoctonus*/909 complex on the basis of characters 15·1, 36·2 and 43·1. The former has been postulated as having undergone reversal in the stem 910 + 911 so cannot be considered a group apomorphy, whilst 36·2 is highly homoplastic in any favoured arrangement, and in the minimum length tree necessitates six transformations that include being developed, lost and subsequently redeveloped. In fact, this character is also present in the apomorphic condition in some *Stauropoctonus* (916, 918), and it is not stretching credibility to consider it an apomorphy of the entire group here being analysed, and postulate reversal in taxa 909 and 917. This hypothesis involves only a single additional transformation step, and would seem biologically more feasible than the gain-loss-gain scheme favoured by the Wagner analysis. The character itself, relative position of two wing veins, has not been used in higher classification, though it is of considerable use in separating species (Gauld & Mitchell, 1978), and has doubtfully assigned polarity. It is also amongst the very worst characters suggested by the original LeQuesne test (see Table 6). The third character, 43·1, is found widely in the apomorphic condition throughout the Ophioninae. Either it has been derived in parallel in the *Euryophion* group, in most *Ophion* and related taxa and in certain members of the present group, or it is an apomorphy of the Ophioninae and the apparently plesiomorphic state of most *Stauropoctonus* group taxa represents a further apomorphy. Initially the polarity of this character was considered to be tentatively assigned (p. 77). Elsewhere in the Ichneumonidae, although reliance is often placed on character 43·1 in generic keys, it is variable in most higher taxa (cf. Pimplinae in Townes, 1969), suggesting it is a highly homoplastic feature.

Other characters involved in placing *Ophiogastrella* high up the tree are 7·2, 20·2, 27·1, 27·2, 37, 43·2, 45·2, 48·1 and 59. Of these, 7·2 and 59 are highly homoplastic, gain-loss-gain characters which seem biologically implausible, and they also have dubious polarity assignment. Character 45·2 is postulated as having undergone reversal in the stem 910 + 911 so there remains five reasonably robust apomorphies uniting *Ophiogastrella* with the most specialized taxa (20·2, 27·1, 27·2, 43·2 and 48·1). Considered individually, all of these characters are rather 'weak'. The remarks made above about 43·1 can also be applied to 43·2; the loss apomorphies 27·1 and 27·2 have identical state distributions in this group and should perhaps be considered as a single feature, the loss of the posterior mesosternal transverse carina. This carina has been lost, presumably independently, in other ophionine evolutionary lines (e.g. *Ophion*, some *Leptophion*, some of the *Stauropoctonus* group) and has commonly been lost in many ichneumonid evolutionary lineages outside the subfamily under consideration. As a consequence it is not a character which seems to unite convincingly *Laticoleus* (912–5) with *Ophiogastrella*. It is interesting to note that there is at least some degree of correlation between the presence or absence of this carina and the type of habitat occupied. In groups where it is usually absent (e.g. the Phygadeuontinae), species inhabiting very wet areas have the carina complete. In the subfamily mentioned this includes common species of *Paraphylax, Amauromorpha* and *Apsilops* found in Old World rice padi. In the Anomaloninae the two closely related genera *Therion* and *Heteropelma* differ in this feature; the former is characteristically found on dry open areas, whilst most *Heteropelma* species occur in more humid woodlands (Gauld, 1976). In the Ophioninae the carina is always present in those species found in humid rain forests (e.g. most *Enicospilus, Leptophion* and *Dicamptus*) but is incomplete in species favouring drier, more exposed habitats (e.g. some Australian *Leptophion*, most *Ophion*). Both *Ophiogastrella* species and *Laticoleus* seem to favour drier forest habitats than *Leptophion*.

Character 20·2, the development of scutellar carinae, has probably been derived independently in several evolutionary lineages (e.g. some species of *Ophion* and *Leptophion* (Gauld & Mitchell, 1981)), but it also appears to have undergone reversal in other groups (e.g. in taxon 944 and also *Enicospilus arduus* (Gauld & Mitchell, 1978)). It would be only slightly less parsimonious to suggest that the presence of complete scutellar carinae is an apomorphy of the entire *Enicospilus/Stauropoctonus* complex, and to suggest that it has been lost in a few lineages. Certainly the shared presence of these carinae is not a convincing character for uniting *Ophiogastrella* with other genera.

The remaining character, 48·1, is a difference in relative lengths of wing veins and its apomorphic state is found scattered throughout the subfamily.

To summarize therefore, the decision on where to position *Ophiogastrella* hinges on two character sets, one of three unusual and fairly convincing apomorphies (15·1, 22·1 and 33) versus five widely distributed, and thus unconvincing, apomorphies (20·2, 27·1, 27·2, 43·2 and 48·1). The Wagner method, in attempting to minimize tree length, opts for including *Ophiogastrella* amongst the most derived species, whilst the compatibility method favours treating it as the most primitive taxon, thus eliminating homoplasy in three characters (22·1, 33 and 15·1) as the other characters are mutually incompatible.

The position of the Hawaiian genera (924–6) also presents a problem. In the parsimony dendrogram (Fig. 17) the five characters defining the stem 924 + 925 + 926 (5·1, 15·2, 36·3, 61·1 and 61·2) also define at least part of the *Enicospilus* + *Dicamptus* branch (932–4 + 942–7) suggesting the Hawaiian genera could be placed on the larger branch, as in the compatibility dendrogram. The parsimony method has excluded the Hawaiian genera on the basis of characters 7·2, 20·2, 40, 43·2, 45·2, 46, 48·1 and 59. Of these 7·2 and 59 are the biologically implausible gain/loss/gain characters with dubiously assigned polarity, so the real choice has to be made between the two character sets 5·1, 15·2, 36·3, 61·1 and 61·2 versus 20·2, 40, 43·2, 45·2, 46 and 48·1.

Considering the first set first, characters 5·1, 61·1 and 61·2 are all mandible characters. The apomorphic state of all three is elsewhere only found in taxa 916–8 and 942–7 (excluding 944). Although this character set has almost certainly been derived independently in *Stauropoctonus*/*Aulophion* and *Enicospilus* it is not found elsewhere in the Ophioninae. It is of very rare occurrence in other parts of the family, and where it does occur it is usually characteristic of a group of genera e.g. the Orthocentrinae (Townes, 1971) and the *Xanthopimpla*/*Echthromorpha* group of Pimplini (Townes, 1969). Character 15·2, a completely concealed spiracular sclerite, is found in virtually all species of *Enicospilus* and *Dicamptus*. Elsewhere it is found in the derived condition only in the Hawaiian genera, in a few species of *Leptophion* and in the aberrant monotypic genus *Sicophion* (922). The final character in this set, 36·3, an extreme reduction in the length of a wing vein, is only found in a very few taxa, notably (in the matrix) the Hawaiian genera, some *Enicospilus, Euryophion* and *Xylophion*. Elsewhere in the Ophioninae it only occurs in some *Dicamptus* and one aberrant *Laticoleus*.

The second and alternative character set (20·2, 40, 43·2, 45·2, 46 and 48·1) has partially been considered above where characters 20·2, 43·2 and 48·1 have been suggested to be rather poor indicators of phylogenetic affinity. Two of the Hawaiian genera show the derived state of 48·1, so it would be equally parsimonious to postulate that a reversal had occurred in one Hawaiian genus, as opposed to parallel derivation in the subgroup of two Hawaiian taxa and the major line in the larger group. The remaining characters all refer to the fore wing, in particular the antero-distal part of the discosubmarginal cell and the adjacent vein, *Rs+2r*. The apomorphic conditions of characters 40, 45·2 and 46 are the most characteristic features of *Enicospilus*/*Dicamptus*, though the same combination is also found in a very few other taxa (e.g. *Riekophion* species). Several species of *Enicospilus* may have one or more characters in the plesiomorphic state (e.g. the *E. senescens* species-group (Gauld & Mitchell, 1978)), but the trace features found in one or two species suggests this condition represents a reversal. This suite of characters does seem therefore to be good evidence for excluding the Hawaiian taxa from the *Enicospilus* lineage. However, the plesiomorphic condition of all three of these characters occasionally is found in some *Enicospilus* species inhabiting oceanic islands, and in these cases it can be seen that a reversal has occurred as related taxa still have the apomorphic states. For example, the three species *E. vidus, E. ditor* and *E. donor* form a closely interrelated group on the Galapagos Islands (Gauld & Carter, 1983). They belong to the *E. capensis* species-group and probably have evolved from a migrant South American species, all of which have the apomorphic condition for characters 40, 45·2 and 46, as has *E. vidus*. In *E. donor* they all are plesiomorphic, whilst in *E. ditor* intermediate conditions exist. This strongly suggests reversal has occurred. A similar case can be demonstrated for Hawaiian *Enicospilus* (see Cushman, 1944). The majority of *Enicospilus* species are both synchronous and sympatric with numerous congeners. The three characters are developed in such a way as to form a distinctive, species-specific pattern (especially the exact shape of the sclerite, character 46) (see figs 384–641 in Gauld & Mitchell, 1981). In areas where few species occur, such as deserts, there is considerable variation within a species in the exact expression of these characters. Possibly their reversal on oceanic islands is facilitated by a reduction in selection pressure that favours uniformity in areas of high possible interspecific interaction. It is possible that the apparent plesiomorphic condition of these characters in the Hawaiian genera is also a reversal, though in this case no definite close relatives are known.

The remaining character in the second set, 48·1, refers to the relative lengths of veins *3r–m* and *M*. The apomorphic condition has previously been used only to characterize species and both states can be found in most genera, suggesting it is a rather homoplastic feature.

To sum up, once again the Wagner method positioned a group on the basis of the larger set and again biological evidence suggests that perhaps this is incorrect and the position indicated by the compatibility method is more plausible.

The parsimony analysis united all species of *Enicospilus* (942–47) into a single clade but *Dicamptus* was paraphyletic with respect to this. This is not surprising as traditionally *Enico-*

spilus is separated from *Dicamptus* on account of its specialized mandibles; *Dicamptus* is recognized only by the specialized features it has in common with *Enicospilus* plus the possession of unspecialized mandibles, a plesiomorphic feature (Townes, 1971). The compatibility method proved to be less successful at producing groups corresponding with recognized genera, probably because *Enicospilus* and *Leptophion* are polythetic taxa (Gauld & Mound, 1982).

The relative positions of *Leptophion, Laticoleus* and *Pamophion* are less clear. The Wagner method suggested *Leptophion* and *Laticoleus* form separate groups, though both are characterized by the apomorphic condition of 35, and with one exception, 37. The compatibility method suggests *Laticoleus* + *Leptophion* form a group defined by character 35 and these two taxa, plus *Pamophion*, form a group defined by character 3.

To conclude this section, on balance, secondary evidence suggests *Ophiogastrella* and the Hawaiian genera are better placed by the compatibility method whilst *Enicospilus* is most successfully aggregated by parsimony analysis. A 'hybrid' compromise cladogram was postulated that required 249 transformation steps (Fig. 18). This compromise arrangement groups various congeneric species together, thus to some extent corroborating the initial assumption that ophionine genera are not polyphyletic groups.

The relationship of the component genera of the *Enicospilus/Stauropoctonus* complex can be illustrated most clearly if the highly homoplastic characters are omitted, the relative positions of

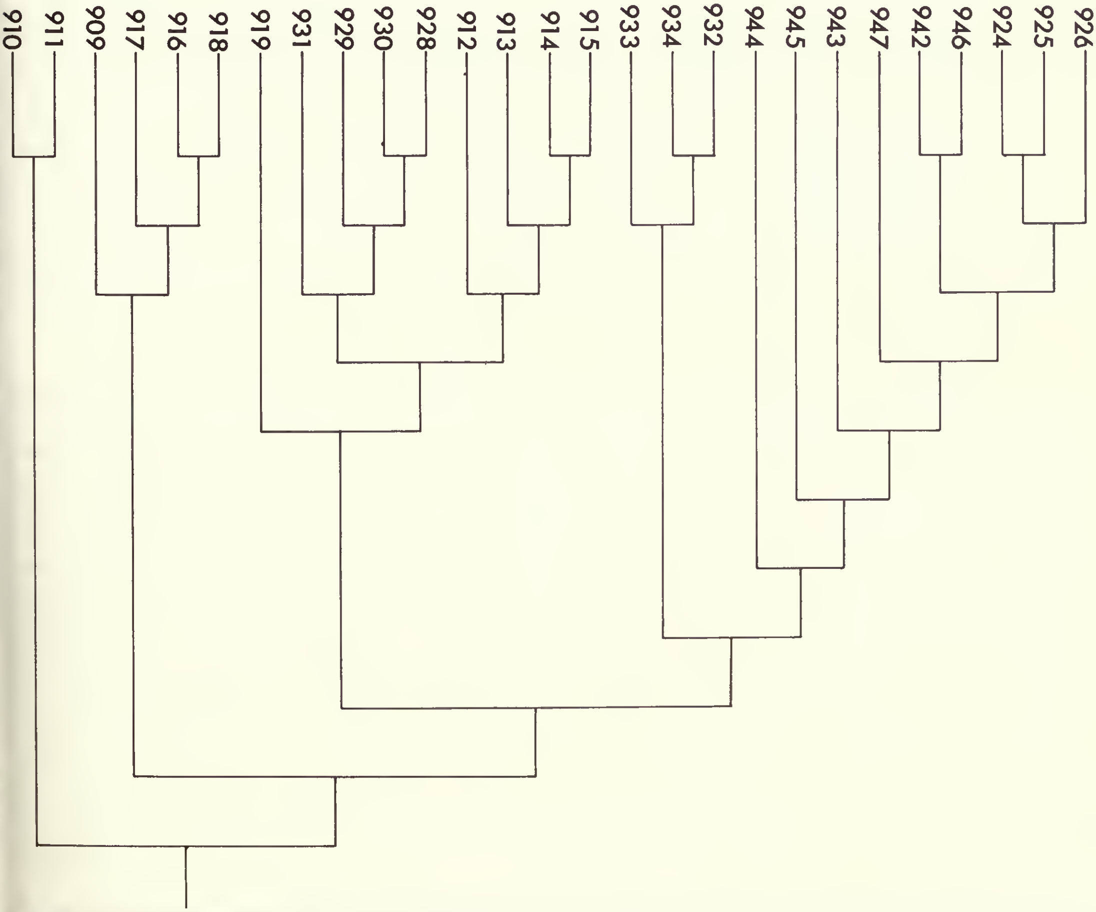


Fig. 18 Hybrid cladogram derived from subjective evaluation of parsimony and compatibility analyses of *Enicospilus/Stauropoctonus* data set. This arrangement requires 249 transformation steps.

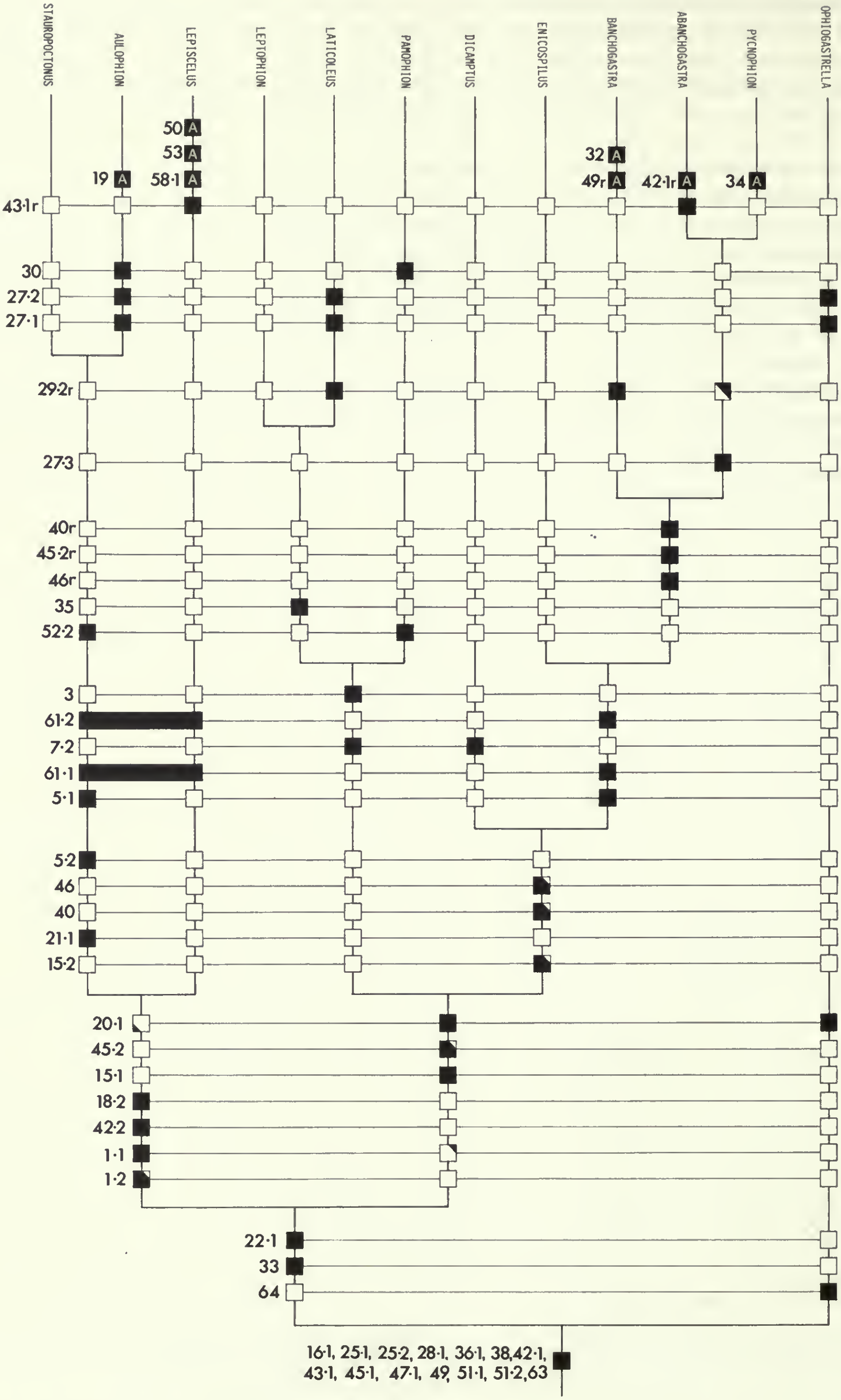


Fig. 19 Cladogram showing putative phylogenetic relationships between the genera of the *Enicospilus/Stauropoctonus* complex as supported by the least homoplastic characters.

species within genera disregarded (and the object of this part of the analysis is to establish the phylogenetic relationships of the genera) and single exceptional character scores, that are almost certainly incidences of homoplasy (e.g. 15·2 in taxon 945; 61·2 in taxon 944), ignored. This simplified cladogram together with supporting characters is illustrated in Fig. 19. Essentially it is the same arrangement as Fig. 18.

This cladogram suggests that *Stauropoctonus* is paraphyletic with respect to *Aulophion, Leptophion* is paraphyletic with respect to *Laticoleus* and *Enicospilus* is paraphyletic with respect to the *Pycnophion/Abanchogastra/Banchogastra* lineage.

The major groups and their relationship with the unassigned taxa

The inter-relationship of the two major generic complexes

The *Enicospilus/Stauropoctonus* complex has been defined above as a holophyletic group on the basis of 17 apomorphies (16·1, 22·1, 25·1, 25·2, 28·1, 28·2, 33, 36·1, 38, 42·1, 43·1, 45·1, 47·1, 49, 51·1, 51·2 and 63) (though *Ophiogastrella* is primitive in respect of two, 22·1 and 33) and the *Thyreodon/Euryophion* complex has similarly been defined by a possible 19 apomorphies (2, 7·1, 22·2, 24·1, 24·2, 25·1, 25·2, 28·1, 28·2, 38, 42·1, 42·2, 47·1, 49, 51·1, 51·2, 54, 58·1 and 61·1). Ten of these apomorphic features (25·1, 25·2, 28·1, 28·2, 38, 42·1, 47·1, 49, 51·1 and 51·2) are common to both sets, suggesting a sister group relationship. Of the apomorphies remaining for defining the *Thyreodon/Euryophion* lineage, three (24·1, 24·2 and 61·1) occur extensively in various species-groups and species in the *Enicospilus/Stauropoctonus* complex, thus weakening their credibility as characters defining the former lineage. Character 42·2 has apparently been derived in parallel in the *Stauropoctonus* line, but the remaining five features (2, 7·1, 22·2, 54 and 58·1) are robust characters that strongly support the monophyly of the *Thyreodon/Euryophion* lineage. Of the six remaining apomorphies defining the *Enicospilus/Stauropoctonus* lineage (16·1, 22·1, 33, 36·1, 45·1 and 63) two (22·1 and 33) exclude *Ophiogastrella*; the apomorphic state of 33 has also been derived in parallel in the *Thyreodon* line. The derived states of characters 16·1 and 36·1 occur in most species of the *Thyreodon/Euryophion* complex, suggesting they are group apomorphies, whilst the derived state of 45·1 also occurs, in parallel, in *Euryophion*. Character 63 is the single convincing apomorphy supporting the monophyly of the *Enicospilus/Stauropoctonus* complex. A cladogram showing the putative phylogeny of these taxa is shown in Fig. 20.

The position of the unassigned taxa

The position of the remaining taxa (905, 906, 920, 922, 923, 927, 938–41 and 948–51) can now be considered in relation to the robust arrangement of the majority of ophionine taxa presented above. To reduce the data matrix to more manageable proportions a number of hypothetical taxonomic units (HTUs) were constructed to represent genera reasonably placed in the earlier part of the work. Scores were assigned to these HTUs by marking each character with the condition found in the majority of species of the genus (including all taxa examined in earlier taxonomic studies (Gauld, 1977; Gauld & Mitchell, 1978, 1981) but not included in the primary data matrix). This method of scoring, rather than deducing a hypothetical ancestor, was adopted because of the high incidence of homoplasy. This idiosyncracy is unlikely to alter any cladistic arrangement significantly, whereas the assumption that the group-ancestor has a particular character present in the plesiomorphic condition, based on occasional incidence of the occurrence of the plesiomorphic (and possibly reversed) condition in some members of the group, could result in considerable alteration to the position assigned to the group. The HTUs utilized are 960 (*Laticoleus*), 961 (*Ophiogastrella*), 962 (*Leptophion*), 963 (*Stauropoctonus*), 964 (*Thyreodon/Dictyonotus*), 965 (*Euryophion*), 967 (*Dicamptus*), 968 (*Enicospilus*). [N.B. There is no 966.] The character scores of these HTUs are given in Appendix 7.

The results of a LeQuesne test on taxa 905, 906, 920, 922, 923, 927, 938–41, 948–51 and 960–68 are given in Table 17. The overall O/E value is strikingly high (0·90), indicating the extremely homoplastic nature of this data set. Perusal of the labels matrix (Appendix 8) shows that a large

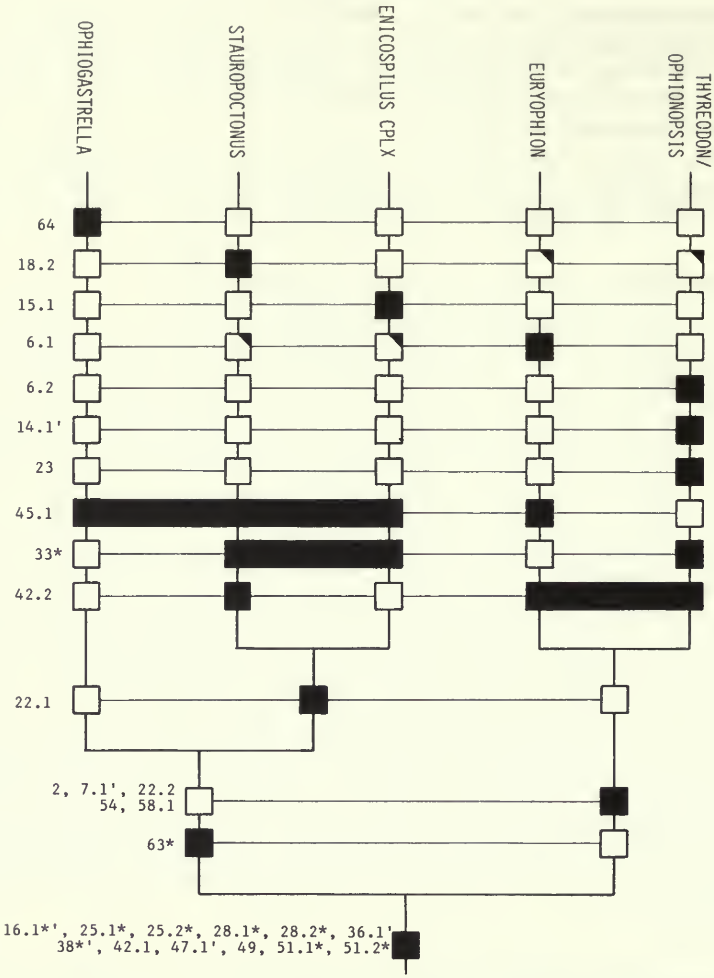


Fig. 20 Putative phylogenetic inter-relationships between groups of taxa in the *Enicospilus/Stauropoctonus* and *Thyreodon/Euryophion* complexes.

number of characters have been labelled highly for certain taxa; this will be discussed below.

Wagner analysis of this data set yielded a number of equally short cladograms with quite different topologies (Figs 21–24). A large number of other trees that were only slightly less parsimonious were also generated (Gauld, unpublished data). Compatibility analysis yielded a single largest clique of 11 informative characters (2, 3, 7·1, 17, 25·1, 26, 38, 40, 41, 47·1 and 52·1) which supports the cladogram shown in Fig. 25. Although differing in many topological details, certain features are common to the dendrograms. In all of the Wagner trees the two major complexes emerged as the most derived groups. Five taxa (938, 939, 941, 948 and 951) occupy the most primitive position in three of the dendrograms and are amongst the eight most primitive taxa in the other two, suggesting these species are amongst the most primitive of all ophionines. This group of species comprises examples of the genera *Xylophion, Ophion, Agathophiona, Rhopalophion* and *Sclerophion*. Gauld (1979) suggested these might represent a holophyletic group, the *Ophion* subgroup, characterized by having a slender *Rs+2r*, which is also straight basally, having an incomplete posterior transverse carina of the mesosternum, having a subapically impressed clypeus, having 1*m–cu* usually with a ramellus, and always angled, and having the anterior area of the propodeum 'occluded'. However, the holophyly of the group is open to question. The shape of *Rs+2r* (corresponding to characters 39, 40 and 62), of 1*m–cu* (38

Table 17 Results of LeQuesne test on data set comprising HTUs and unplaced taxa (905, 906, 920, 922, 923, 927, 938, 939, 940, 941, 948, 949, 950 and 951). Conventions as in Table 2.

```
Character number: incompatibilities observed  expected  O/E ratio

 1.1:. 44  45.4  0.97      1.2:  38  37.7  1.01      2  :  15  25.6  0.59      3  :  26  38.2  0.68
 5.1:  35  38.2  0.92      6.1:  30  38.2  0.79      7.1:  35  37.4  0.94      7.2:  47  61.0  0.77
 9  :  35  38.2  0.92     12  :  36  38.2  0.94     14.1:  50  45.1  1.11     14.2:  46  54.1  0.85
15.1:  53  58.9  0.90     15.2:  30  37.5  0.80     16.2:  56  57.6  0.97     17  :  24  25.6  0.94
18.1:  54  60.2  0.90     18.2:  35  37.4  0.94     19  :  30  38.2  0.79     20.1:  60  60.0  1.00
20.2:  53  58.6  0.90     22.1:  45  60.0  0.75     22.2:  49  50.1  0.98     23  :  43  51.1  0.84
24.1:  54  60.8  0.89     24.2:  44  50.1  0.88     25.1:  14  25.1  0.56     25.2:  58  61.2  0.95
26  :  24  25.6  0.94     27.1:  53  58.6  0.90     27.2:  57  61.0  0.93     28.2:  57  59.6  0.96
29.1:  37  37.5  0.99     29.2:  52  58.9  0.88     30  :  42  38.2  1.10     31  :  28  25.6  1.09
32  :  45  45.9  0.98     33  :  50  60.9  0.82     35  :  47  45.9  1.02     36.1:  25  24.9  1.00
36.2:  59  56.5  1.05     36.3:  28  37.3  0.75     37  :  53  60.9  0.87     38  :  34  51.1  0.67
39  :  61  59.6  1.02     40  :  22  38.2  0.58     41  :  44  45.9  0.96     42.1:  61  60.2  1.01
42.2:  37  37.4  0.99     43.1:  44  37.4  1.18     43.2:  53  60.2  0.88     44.1:  59  61.2  0.96
44.2:  34  37.4  0.91     45.1:  48  45.0  1.07     45.2:  47  58.7  0.80     46  :  33  45.9  0.72
47.1:  22  45.4  0.48     47.2:  34  37.7  0.90     48.1:  59  56.9  1.04     48.2:  32  37.5  0.85
51.1:  57  58.6  0.97     51.2:  55  60.7  0.91     52.1:  22  25.6  0.86     54  :  39  45.9  0.85
55  :  20  25.6  0.78     57  :  56  59.6  0.94     58.1:  42  51.1  0.82     59  :  45  59.6  0.76
61.1:  51  58.7  0.87     61.2:  41  45.0  0.91     62  :  56  57.6  0.97     63  :  52  60.9  0.85

Grand total-  1528 observed,    1705.7 expected.  Overall O/E ratio = 0.90

Ranking ratios of scoring  characters
47.1  25.1  40  2  38  3  46  22.1  36.3  59  7.2  55  6.1  19  45.2  15.2  33  58.1  23  54  14.2
48.2  63  52.1  61.1  37  24.2  43.2  29.2  24.1  18.1  15.1  47.2  20.2  27.1  51.2  44.2  61.2
5.1  9  27.2  18.2  7.1  17  26  57  12  25.2  28.2  41  44.1  1.1  16.2  62  51.1  22.2  32  29.1
42.2  20.1  36.1  1.2  42.1  39  35  48.1  36.2  45.1  31  30  14.1  43.1
```

and 47) and the form of the propodeum (22) are symplesiomorphies and therefore not admissable for defining a holophyletic group. Both the incomplete posterior transverse carina of the mesosternum (equivalent to 1 scores for 27·1 and 27·2) and the impressed clypeus (corresponding to a 1 score for character 7·2) are apomorphic features found in many other taxa. In many of the Wagner trees generated the five taxa formed a clade defined by characters 18·1 and 44·1 in addition to 7·2 and 27·2 (27·1 is most parsimoniously considered an apomorphy of the subfamily). All of these characters are highly homoplastic so it is not surprising that the compatibility cladogram leaves these taxa as an almost unresolved paraphyletic assemblage.

Four further taxa, 920 (*Riekophion emandibulator*), 922 (*Sicophion pleuralis*), 940 (*Eremotylus boguschi*) and 950 (*Hellwigiella nigripennis*) have been placed in the same group as the *Ophion* subgroup (Townes, 1971; Gauld, 1979). The undescribed genus (949) would, on Townes' (1971) criteria, also belong to this group. There is no evidence in any analysis that suggests that these taxa and the *Ophion* subgroup constitute a holophyletic clade. The definition of the group as adopted by previous authors rests on a plesiomorphic feature, possession of a membranous flange on the fore tibial spur, suggesting this 'group' is in fact a paraphyletic assemblage. In Wagner analyses 920, 922, 940, 949 and 950 may be positioned primitively with respect to most other taxa (e.g. Figs 22, 24) but some members may occasionally be united with other taxa. Taxa 949 and 950 are sometimes placed in much more derived positions, the former within the *Enicospilus*/*Stauropoctonus* complex (e.g. Fig. 23) and the latter as the sister-lineage to the *Thyreodon*/*Euryophion* complex (e.g. Fig. 21). *Hellwigiella* (950) is placed as the sister-group to the *Thyreodon*/*Euryophion* complex on the basis of a number of shared, rather striking, derived characters. These characters (which may be shared by several or all species in the complex) are adaptations to a diurnal eremic existence, and include possession of small ocelli (12), a shorter stouter flagellum (14·1), pendant epipleuron 2 (30), cylindrical hind tibial spurs (54) and long weakly curved claws (58·1). Many or all of these features are also found in the

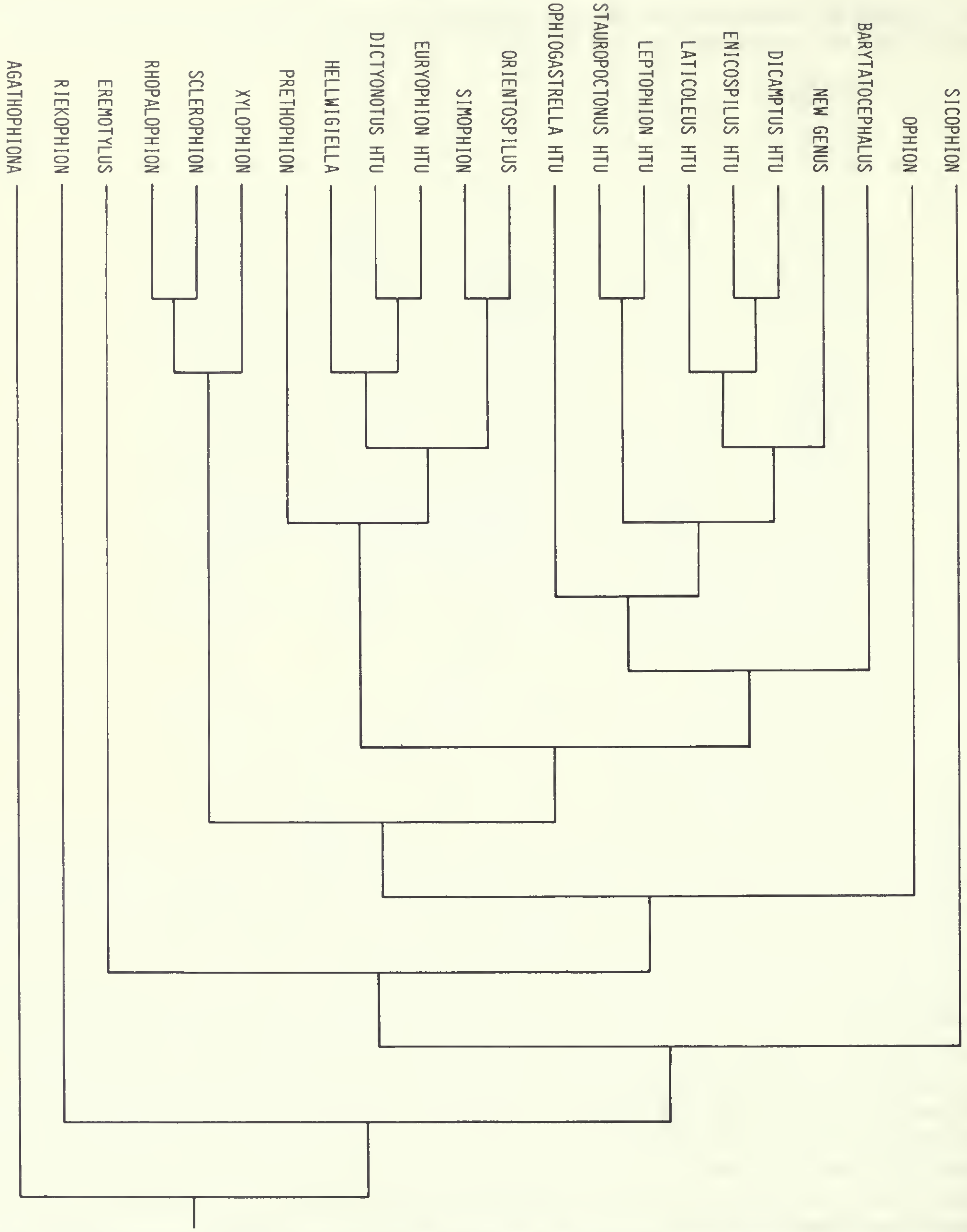


Fig. 21 283 transformation step cladogram derived from Wagner analysis of HTUs plus unplaced taxa.

apomorphic condition in other diurnal eremic ophionines including an undescribed species of *Ophion* from Australia (in ANIC) and *Agathophiona* species from Mexico. In another group of ichneumonids, the Anomaloninae, similar differences occur between closely related eremic and non-eremic organisms (e.g. *Gravenhorstia (Erigorgus)* and *Gravenhorstia (Gravenhorstia)* species (Gauld, 1976)). The occurrence of so many apomorphic states of these characters together in day-flying species strongly suggests the characters should be considered as a character suite and perhaps accorded less taxonomic weight. Unlike members of the *Thyreodon/ Euryophion* complex, *Hellwigiella* shows the plesiomorphic state of important characters used for defining the group (2, 7·1, 44·2). Furthermore, a position near to the base of the common

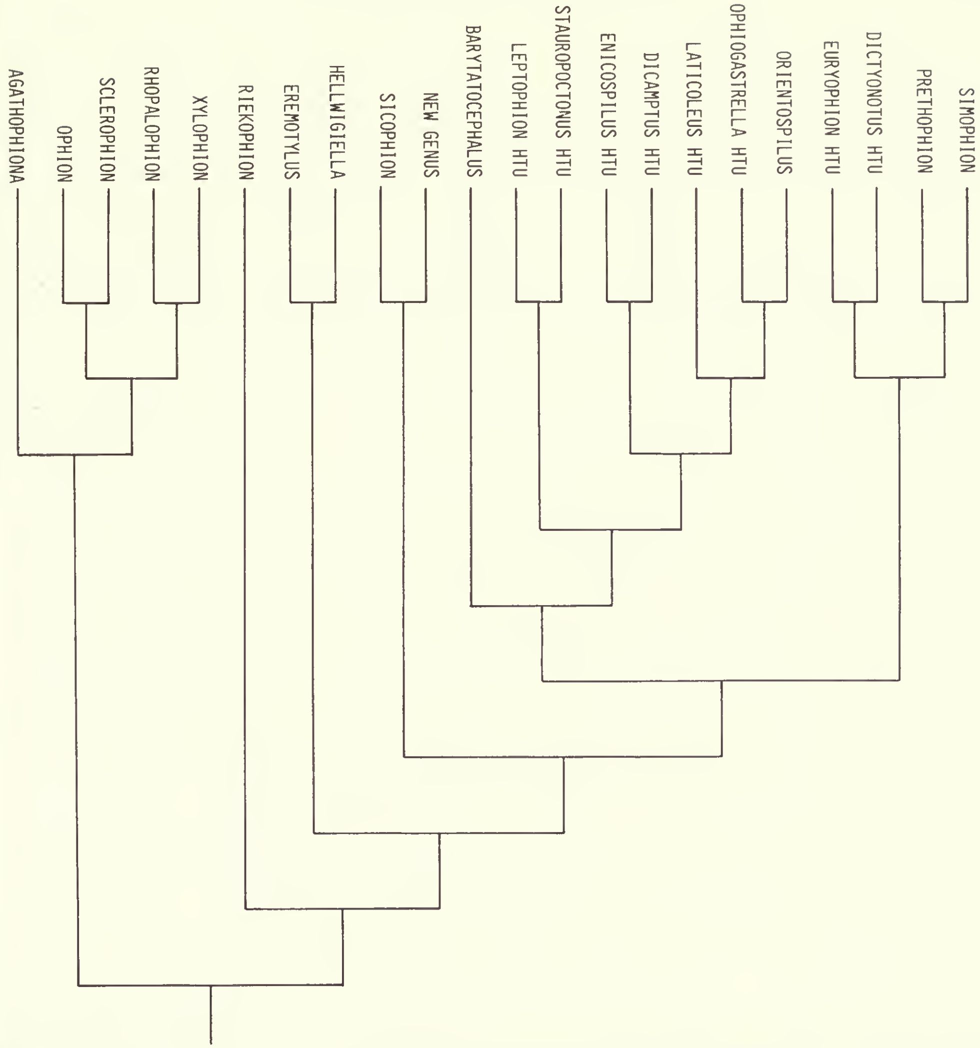


Fig. 22 283 transformation step cladogram derived from Wagner analysis of HTUs plus unplaced taxa.

stem of the two major complexes is suggested by the fact that *Hellwigiella* shows the plesiomorphic states of characters 16·1, 42·1, 52·1 and 52·2.

The position of the new genus (949) is rather perplexing as the taxon exhibits a number of derived features shared with the more specialized taxa, especially those in the *Enicospilus/Stauropoctonus* complex (e.g. 15·1, 16·1, 22·1, 33, 45·1) yet at the same time lacks one major apomorphy of the group (63). Taxon 949 also shows the plesiomorphic state of many of the stem characters, including 25·2, 28·2, 42·1, 51·1 and 52·2. It does, however, share a small number of derived features (including 1·1, 15·1, 16·1, 33 and 45·1) with another enigmatic taxon, *Sicophion pleuralis* (922). *Sicophion*, like taxon 949, is primitive in a surprising array of other features and it seems plausible that these two taxa have a sister-group relationship and represent a primitive group that evolutionarily converged with the *Enicospilus* group, possibly as a result of similar selection pressures. The striking phenetic resemblance between 949 and some species of *Leptophion* is perhaps more understandable when one considers these taxa have apparently evolved in mid altitude tropical cloud forests – 949 in the Neotropics and *Leptophion* in South East Asia.

Taxon 920, *Riekophion emandibulator*, is often placed with 967 and 968 (*Dicamptus* and

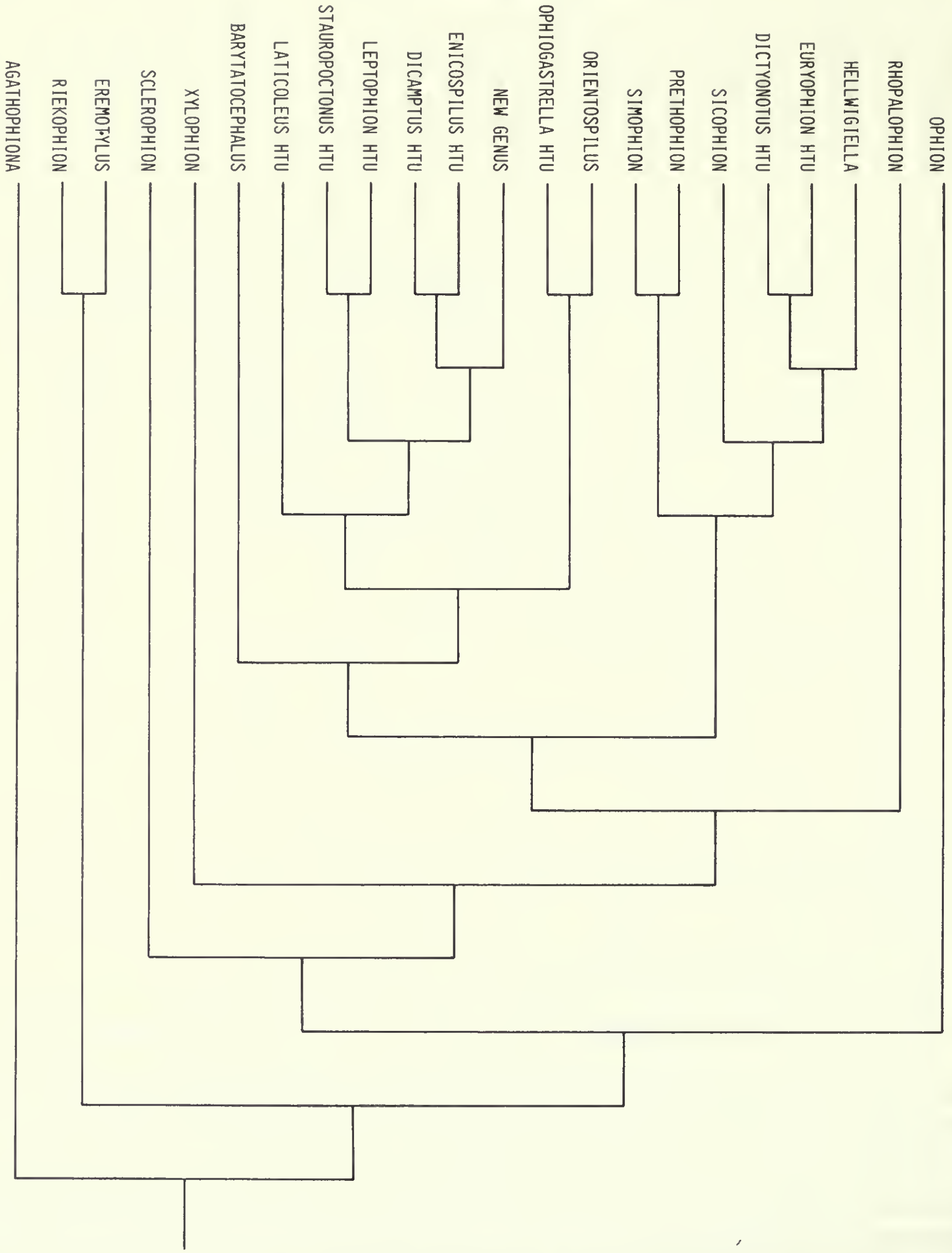


Fig. 23 284 transformation step cladogram derived from Wagner analysis of HTUs plus unplaced taxa.

Enicospilus) in compatibility analyses on the basis of sharing the derived states of characters 40 and 46 (e.g. Fig. 25). In other respects *Riekophion* does not appear to be at all closely related to either *Dicamptus* or *Enicospilus* (Gauld, 1977) and the high label scores obtained by the species for the derived states of these characters (Appendix 8) strongly suggests parallel derivation in two lineages.

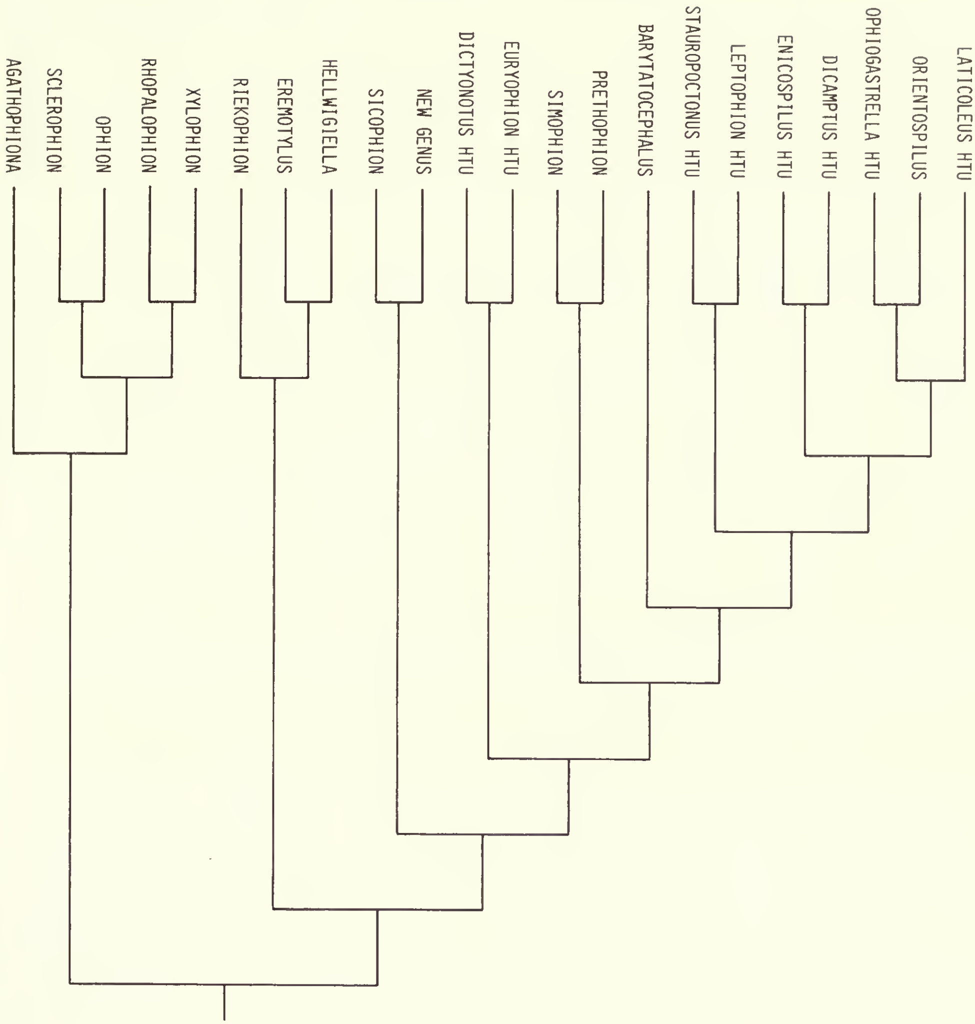


Fig. 24 284 transformation step cladogram derived from Wagner analysis of HTUs plus unplaced taxa.

Accepting that the taxa of the *Ophion* 'genus group' (920, 922, 938–41, 948–51) are the most primitive ophionines, then the most parsimonious arrangement of these taxa with respect to all other groups is that presented in Fig. 26. All other ophionine taxa, 922 + 949 + 920 and 950 + 940 remain as an unresolved trichotomy. The *Ophion* genus-group (i.e. the Ophionini of Townes, 1971) is therefore a paraphyletic grade, an assemblage of less-specialized ophionines. The 'group' possibly comprises three apparently holophyletic clades, the *Ophion*-group (= *Ophion* subgroup of Gauld, 1979), the *Eremotylus* group (940, 950) and the *Sicophion* group (920, 922, 949). The clade, 'all other ophionine taxa', comprises the two groups discussed above (the *Thyreodon*/*Euryophion* complex and the *Enicospilus*/*Stauropoctonus* complex) and four unplaced taxa, 905, 906, 923 and 927. The position of these four taxa can now be considered in relation to the fairly rigid structure derived above.

Taxa 905 and 906 (*Simophion calvus* and *Orientospilus melasma*) share 27 derived characters (Appendix 3); 906 also has a large number in common with other taxa, particularly 947 (28), 946

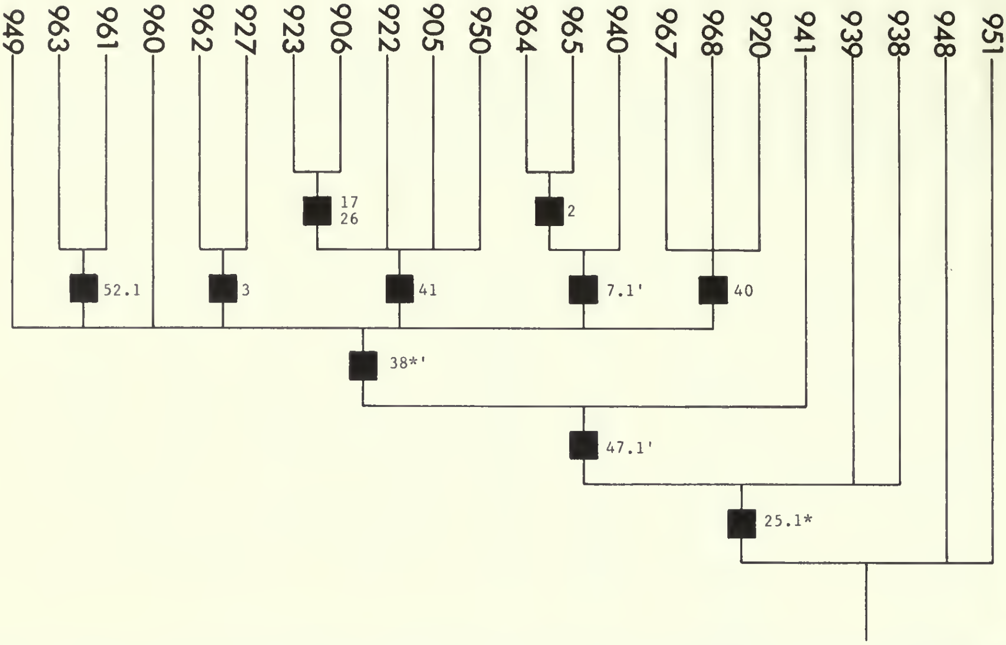


Fig. 25 Cladogram based on largest compatible set of characters obtained from HTUs plus unplaced taxa.

(27), 942 (26), 918, 915, 914, 911 and 910 (25). Taxon 905 is less closely associated with other taxa but shows some affinity with the *Euryophion* group (937 (25), 936 (24) and 935 (23)). Taxa 905 and 906 share several unusual apomorphic features including 6·1 (elsewhere only found in the derived state in 909, 935–37 and 946), 19 (elsewhere only found in 908, 918, 935 and 937), 23 (elsewhere only found in the *Dictyonotus*/*Thyreodon* lineage) and 41 (elsewhere only found in 922 and 923). Taxa 905 and 906 also share all the stem characters of the *Enicospilus*/*Stauropoctonus* + *Thyreodon*/*Euryophion* lineage, except that 905 is plesiomorphic for 42·1. This suggests that they may belong near the other groups, possibly as a sister-species pair. Of the features defining the two major complexes these taxa share only one, an apomorphy of 63, suggesting placement near the base of the *Enicospilus*/*Stauropoctonus* lineage. It is noteworthy that in earlier Wagner analyses (e.g. Figs 22–24) 905 and 906 generally were split up, 905 often grouping with 923, 964 or 965, whilst 906 usually was united with 960 or 961. If the two taxa were entered together first in the data file, then they were not separated , but remained as a distinct clade (Fig. 21).

Taxon 927 (*Barytatocephalus mocsaryi*) shares 24 derived characters with taxon 936, 23 with 914 and 946 and 22 with 913. It shares all the stem features with the major complexes and additionally has the apomorphic condition for 22·2 and 58·1, suggesting it belongs near the base of the *Thyreodon*/*Euryophion* lineage. It does not have the major apomorphies of the *Enicospilus*/*Stauropoctonus* branch (that is 22·1, 33 and 63).

Taxon 923 (*Prethophion latus*) is an enigmatic Neotropical taxon that has relatively few characters in common with any other species. The largest number, 22, are shared with 918 and it has 21 in common with 906. It does have all the 'gain' stem apomorphies in common with other higher taxa, but is plesiomorphic for 25·2, 28·2 and 45. It does not have any of the apomorphies defining the *Thyreodon*/*Euryophion* complex, but is apomorphic for character 63, suggesting it belongs near the base of the *Enicospilus*/*Stauropoctonus* stem. It is most parsimonious to treat *Prethophion latus* as the sister species of the 905 + 906 lineage (on the basis of the derived state of characters 27·1 and 27·2), but this association must be regarded as very tenuous.

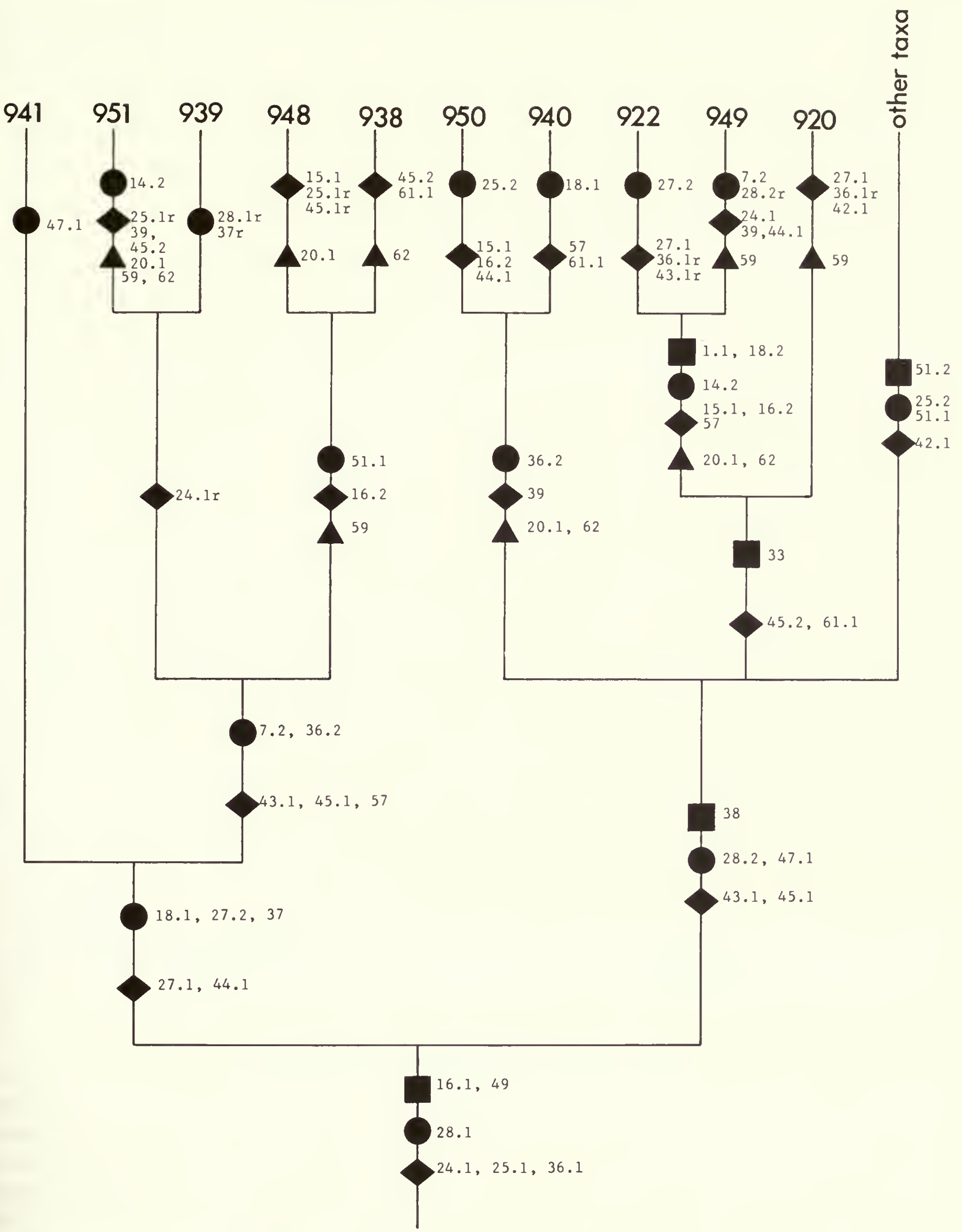


Fig. 26 Most parsimonious arrangement of '*Ophion* genus-group' and all other taxa. Conventions as in Fig. 13.

The cladogram showing the preferred arrangement of taxa as described above is shown in Fig. 27. It is interesting to note that this user defined cladogram is one step more parsimonious than any obtained by Wagner analysis.

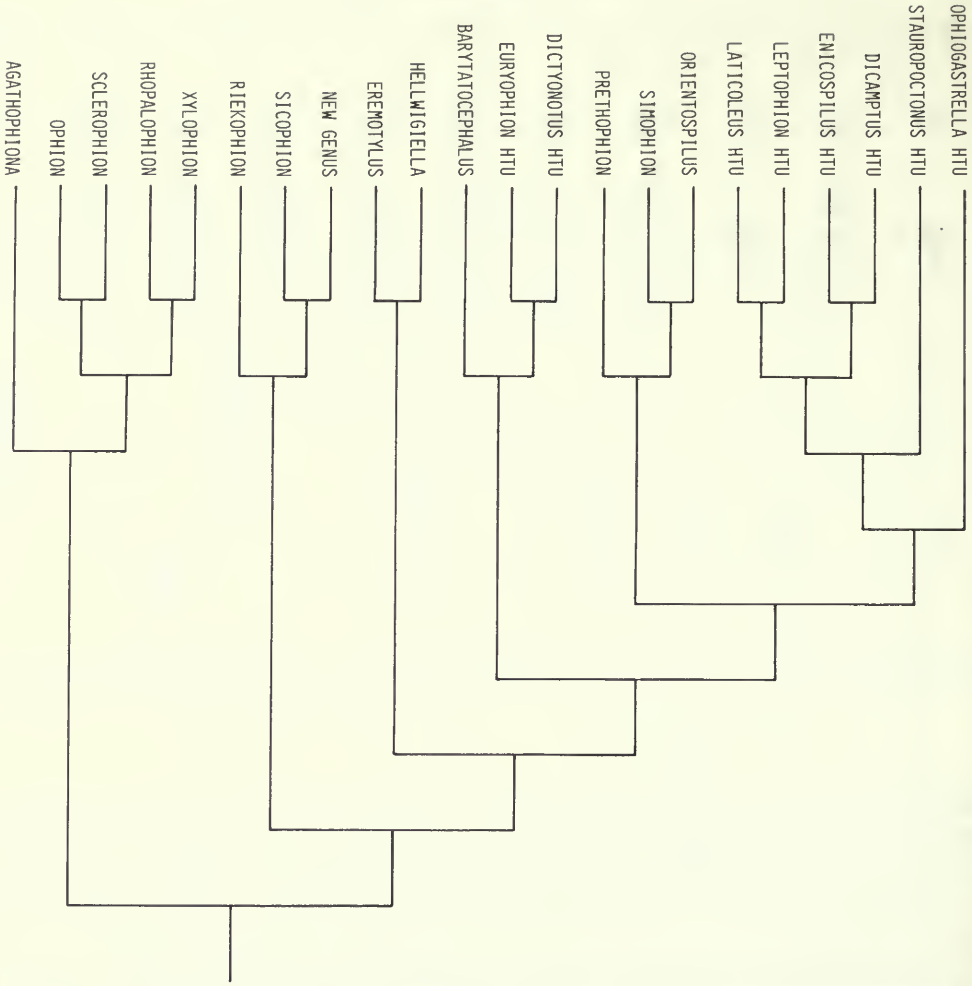


Fig. 27 Cladogram derived from subjective evaluation of character complexes involved in grouping taxa in cladograms presented in Figs 21–25. It is noteworthy that this, at 242 steps, is a more parsimonious arrangement than the best obtained by Wagner analysis, though this is a fortuitous event.

Discussion of suggested phylogeny

A putative phylogeny of the Ophioninae is shown in Fig. 27. Parts of this cladogram seem to be fairly robust, but other groups are only supported by weak homoplastic characters. The overall arrangement, placing the *Ophion* and *Eremotylus* groups in primitive positions and having a bifurcated evolutionary line, does seem reasonably sound. It corresponds with increasing morphological complexity, particularly in the form of the fore tibial spur (character 51), the region of the spiracular sclerite (character 15), the modification of the propodeum (characters 22, 25) and the loss of umbo (character 33). What little is known about the structure of the final instar larvae supports this arrangement. The cephalic capsules of the larvae of *Enicospilus, Dicamptus, Euryophion* and *Thyreodon* are clearly more specialized than those of *Ophion* in having a modified hypostoma (Short, 1978). The larvae of *Euryophion* and *Thyreodon* are similar in having numerous setae (11+) on each part of the maxillary lobe median to the hypostomal spur and adjoining the maxillary palp. *Dicamptus* and *Enicospilus* have eight or less setae in this position. Certain venational characters also support the phylogeny proposed. These include modification of 1*m–cu* and broadening of the base of *Rs*+2*r* (characters 38, 47 and 62).

However, in almost all adult characters it is necessary to postulate parallelism. Reduction of the tibial spur membrane has occurred independently in *Xylophion* and the main evolutionary line, and specialization of the propodeum has occurred in both the main lineage and *Eremotylus*. It is quite disconcerting to see the degree of evolutionary convergence that has occurred in separate lineages (such as the development of alar sclerites and a sinuous *Rs+2r* in *Riekophion* and *Dicamptus*/*Enicospilus* and the general similarity of structure between the undescribed Costa Rican genus and species of *Leptophion*). No amount of rearrangement of lineages could possibly remove any but a small proportion of such homoplasy. Perhaps the development of such similarities is due to some underlying adaptation of the genotype not visually manifested (the underlying synapomorphies of Saether, 1979). It is difficult to explain otherwise (unless one postulates reticulate evolution – 'ancient hybrids' giving introgression) how such an unusual feature as alar sclerites has appeared, apparently independently in at least six evolutionary lineages of Ophioninae (*Afrophion, Sclerophion, Leptophion, Laticoleus, Riekophion* and *Dicamptus*/*Enicospilus*). Similar examples of such unusual parallelisms can be found in the modification of the penultimate distal hamulus, the projecting pecten of the hind tarsal claw and the development of a spine on the hind trochantelli.

The *Ophion* group of genera (*Ophion, Alophophion, Sclerophion, Afrophion, Rhopalophion, Agathophiona, Xylophion*) is defined by the possession of the apomorphic states of four rather homoplastic characters, the loss of the posterior transverse carina of the mesosternum (27·2), the possession of a diagonal mesopleural furrow (18·1), possession of an impressed clypeal margin (7·2) and having *Rs* in the hind wing at least slightly curved (44·1). Not all species of these genera necessarily possess all these apomorphies; *Afrophion* species are exceptional in having both a blunt clypeal margin and a straight *Rs* whilst some *Rhopalophion* species have the mesopleural furrow obsolescent. Although this genus-group is amongst the most primitive of ophionines, its position at the base of the phylogenetic tree rests on the assumptions that characters 38 and 47·1 (shape of 1*m–cu* and presence of a ramellus) are correctly polarized. As mentioned above (pp. 77, 78) the polarity of both features is questionable and if it could be demonstrated that the assigned polarity is incorrect then these two features would become convincing apomorphies supporting the holophyly of the *Ophion* group. This change in polarity would necessitate placing the *Ophion* group a little higher up the evolutionary tree, possibly as the sister lineage to the *Eremotylus* group; these two groups share the apomorphic states of characters 18·1 and 44·1.

The holophyly of the *Eremotylus* group is supported by the angulate base of *Rs+2r* (39), which is somewhat thickened (62), and by the form of the clypeus. In most species it is slightly flared outwards in profile (7·1) and often slightly concave. The mandibles are a subtly different shape to those of virtually all other ophionines but this feature is very difficult to define.

The *Sicophion* group is a rather tenuous association of primitive taxa. The holophyly of the group is supported by the apomorphic states of characters 33 and 45·2. Apart from possession of certain primitive features such as the plesiomorphic state of character 51·2, and more extensive propodeal carination, all of these taxa appear to be highly specialized, sharing a variety of apomorphic features with other taxa placed higher up the phylogenetic tree. More evidence of the holophyly of this group needs to be obtained before it can confidently be accepted.

The holophyly of the *Thyreodon* group is supported by the specialized form of the anterior part of the propodeum (character 22·2) and by the form of the claw (character 58·1). The inclusion of *Barytatocephalus* within this clade does seem reasonable. In addition to the characters used in the analysis, two other features suggest *Barytatocephalus* belongs here. Vein 3*r–m* in the fore wing of species of this genus forms a more obtuse angle with *Rs+2r* than is the case with most other ophionine taxa. Most other members of this clade have a similar specialization. At the base of the hind wing, in the anal cell, a vestige of a vein (? 2*A*) is often discernible. In most ophionines this trace, when observable, can be seen to be fairly near to and parallel with the hind margin of the wing; in both *Barytatocephalus* and other members of the *Thyreodon* complex (but not *Euryophion*) this vein trace is remote from the wing margin and close to and parallel with 1*A*. Townes (1971) considered *Barytatocephalus* to be a derivation of *Enicospilus*, but there is little evidence for this supposition. The exposed spiracular sclerite, the general head shape and form of the propodeum suggest *Barytatocephalus* should not be included in the *Enicospilus* lineage.

The *Enicospilus* group is the largest complex and one of the most difficult to define. Its holophyly is supported by a single apomorphy, loss of vestigial first laterotergites (character 64), but the included taxa do resemble each other in possessing a large number of derived features in common. Within this group five subordinate lineages are recognizable, the *Orientospilus, Ophiogastrella, Stauropoctonus, Leptophion* and *Enicospilus* subgroups. Each of these is apparently a holophyletic group. These are the various groupings recognized in the classification proposed below.

A classification of the Ophioninae

Hennig (1966) pointed out the existence of two sorts of monophyletic taxa – holophyletic and paraphyletic groups. Traditional taxonomists may accord either group the status of a supergeneric rank, though cladists do not recognize paraphyletic taxa (Farris, 1979; Carpenter, 1982). Whilst there are many cases of small paraphyletic taxa that can be satisfactorily amalgamated with a holophyletic taxon to form a slightly larger holophyletic taxon (e.g. *Aulophion* + *Stauropoctonus*), there are other cases where dogmatic adherence to cladistic tenets produces impractical results. For example, if the Hawaiian genera were incorporated into *Enicospilus* to give a single holophyletic taxon, the resultant genus would contain an extraordinary range of morphological and probably biological diversity. I concur with Martin (1981) in believing that a classification, as opposed to a phylogeny, is a compromise between known or hypothesized inter-relationships and nomenclatural convenience. A good classification has at least two important facets: (a) it facilitates generalizations to be made about the component taxa, and (b) it is predictive. Farris (1979) and Mickevich (1978) both contend that a purely phylogenetic classification is an optimum as it is both more predictive and more stable than one that is not entirely phylogenetic. Whilst I agree with these authors that this is *often* the case, I do not think it is always so, especially where there are very unequal rates of evolution in different lineages. Consider, for example, the ichneumonid subfamily Mesochorinae. Five genera, *Cidaphus, Astiphromma, Mesochorus, Stictopisthus* and *Plectochorus* each show progressive morphological complexity. All are quite large genera and are functionally useful, but only *Plectochorus* appears to be holophyletic. Each of the other four taxa is apparently paraphyletic with respect to the genera that are more specialized than it (Townes, 1971; Gauld, 1984*b*). Although not a strict phylogenetic classification, this arrangement of the species (which is based on adult morphological features) was found to have predictive value for larvae (see Short, 1978) which seem to corroborate the idea that these taxa are a nesting paraphyletic series. I personally see no way of establishing a strict phylogenetic classification for such a group, other than by lumping all the genera, an action that would result in a much less informative and less useful classification than the present one.

The existence of such nesting paraphyletic groups would seem to be a corollary of the punctuational model of evolution. Stanley (1979) argues convincingly that many major adaptive changes have occurred very rapidly in isolated populations – thus a new organizational level (higher taxon) may have arisen from a small population of a pre-existing (and, if the rate of phyletic evolution is small, virtually unchanging) species placed in a different higher taxon.

To return to the present example. If the Hawaiian genera have resulted from rapid radiation from an *Enicospilus* ancestor into niches hitherto, for enicospilines, unexploited, it is fairly unlikely that any prediction made from study of the biology of continental *Enicospilus* species will apply to *Pycnophion*. Similarly, any generalizations made about *Enicospilus* are likely to have to be prefaced by 'except in some Hawaiian species'. Consequently the purposes of prediction and generalization would both be better served by recognizing the Hawaiian taxa as distinct genera, even though *Enicospilus* thus becomes a paraphyletic taxon.

A second area of contention relevant to the present work concerns the reality and recognition of polythetic superspecific taxa. The currently recognized ophionine genera have been accepted initially as monophyletic groups, though in several instances it has been mentioned that a number are polythetic (Cushman, 1947). Some authors (e.g. Løvetrup, 1973) tend to dismiss polythetic taxa as the product of unsatisfactory discrimination. Whilst I accept that this is an explanation, I dispute that it is the most obvious one. Most cladistic studies reveal that homoplasy is a common phenomenon. If a data set is highly homoplastic, then logically it follows that some phylogenetically 'real' clades will only be definable in a disjunct (sensu Hull, 1965) way. Imposing a monothetic classification on such groups would result in the erection of a multiplicity of new genera, many of which would be monobasic. The resultant classification will have little predictive value as a high proportion of new taxa are likely to necessitate new genera for their accommodation (Gauld & Mound, 1982).

The following classification is suggested for the subfamily Ophioninae. It is not strictly cladistic, as it recognizes some paraphyletic taxa; however it is a fair approximation of the presumed phylogeny. Formal tribes are not recognized, but these could be used for the various genus-groups. It should be noted that some very small genera were not incorporated in the cladistic analysis (these are denoted by an asterisk), but they were closely studied in an earlier work (Gauld, 1979). This has facilitated their placement in the present system.

Subfamily **OPHIONINAE**
Ophionidae Shuckard, 1840
Enicospilini Townes, 1971

OPHION genus-group
Ophion Fabricius, 1798
Alophophion Cushman, 1947*
Sclerophion Gauld, ~~1979~~ 1980
Afrophion Gauld, ~~1979~~* 1980
Agathophiona Westwood, 1882
Rhopalophion Seyrig, 1935
Xylophion Gauld, ~~1979~~. 1980

SICOPHION genus-group
Riekophion Gauld, 1977
Sicophion Gauld, 1979
***Janzophion* gen. n.**

EREMOTYLUS genus-group
Eremotylus Foerster, 1869
Trophophion Cushman, 1947*
Hellwigiella Szépligeti, 1905

THYREODON genus-group
Barytatocephalus Schulz, 1911
Euryophion Cameron, 1906
Rictophion Townes, 1971 **Syn. n.**
Dictyonotus Kriechbaumer, 1894
Ophionopsis Tosquinet, 1903 **Syn. n.**
Rhynchophion Enderlein, 1912
Thyreodon Brullé, 1846

ENICOSPILUS genus-group
Orientospilus subgroup
Prethophion Townes, 1971
Simophion Cushman, 1947
Orientospilus Morley, 1912
Ophiogastrella subgroup
Ophiogastrella Brues, 1912
Stauropoctonus subgroup
Lepiscelus Townes, 1971
Stauropoctonus Brauns, 1889
Aulophion Cushman, 1947 **Syn. n.**
Leptophion subgroup
Pamophion Gauld, 1977
Laticoleus Townes, *in* Townes & Townes, 1973
Leptophion Cameron, 1901
Enicospilus subgroup
Dicamptus Szépligeti, 1905
Enicospilus Stephens, 1835
Pycnophion Ashmead, 1900
Banchogastra Ashmead, 1900
Abanchogastra Perkins, 1902

Zoogeographic discussion

Present day distribution

The approximate numbers of species per area are given in Table 18. For the purposes of this discussion Melanesia, Australia and New Zealand are considered as a single region, the Australo-Pacific, whilst for purposes of comparison Hawaii, with three endemic and one cosmopolitan genera, is ignored.

Altogether 20 of the 32 ophionine genera (62·5%) are restricted to a single zoogeographic region. This is a surprisingly high proportion compared with many other ichneumonid subfamilies. For example, only about 30% of pimpline genera are endemic to a single region (Townes,

Table 18 Approximate numbers of species of various ophionine genera in each zoogeographic area.

	PALAEARCTIC	AFROTROPICAL	ORIENTAL	MELANESIAN	AUSTRALIAN	NEW ZEALAND	HAWAIIAN	NEOTROPICAL	NEARCTIC
OPHION	50	--	25	1	5	10	--	30	50
ALOPHOPHION	--	--	--	--	--	--	--	25	--
SCLEROPHION	--	--	2	--	--	--	--	--	--
AFROPHION	--	2	--	--	--	--	--	--	--
AGATHOPHIONA	--	--	--	--	--	--	--	1	--
RHOPALOPHION	--	3	--	--	--	--	--	--	--
XYLOPHION	--	--	--	1	3	--	--	--	--
RIEKOPHION	--	--	--	--	3	--	--	--	--
SICOPHION	--	--	--	--	--	--	--	2	--
JANZOPHION	--	--	--	--	--	--	--	1	--
EREMOTYLUS	8	--	1	--	--	--	--	5	20
TROPHOPHION	--	--	--	--	--	--	--	--	1
HELLWIGIELLA	1	--	--	--	--	--	--	--	--
BARYTATOCEPHALUS	2	--	--	--	--	--	--	--	--
EURYOPHION	--	7	1	--	--	--	--	--	--
DICTYONOTUS	1	2	2	--	--	--	--	--	--
RHYNCHOPHION	--	--	--	--	--	--	--	3	1
THYREODON	--	--	--	--	--	--	--	40	3
PRETHOPHION	--	--	--	--	--	--	--	1	--
SIMOPHION	2	--	--	--	--	--	--	--	6
ORIENTOSPILUS	--	2	1	--	--	--	--	--	--
OPHIOGASTRELLA	--	--	--	--	--	--	--	11	--
LEPISCELUS	--	1	--	--	--	--	--	--	--
STAUROPOCTONUS	1	1	2	1	1	--	--	4	--
PAMOPHION	--	--	--	--	1	--	--	--	--
LATICOLEUS	--	10	--	--	--	--	--	--	--
LEPTOPHION	--	--	11	17	7	--	--	--	--
DICAMPTUS	--	13	12	1	5	--	--	--	--
ENICOSPILUS	50	150	180	150	50	2	20	100	25
PYCNOPHION	--	--	--	--	--	--	3	--	--
ABANCHOGASTRA	--	--	--	--	--	--	1	--	--
BANCHOGASTRA	--	--	--	--	--	--	2	--	--

1969) and a similar proportion of genera of other subfamilies are likewise restricted. The majority of the restricted ophionine genera are small taxa with three or fewer species; only *Alophophion, Ophiogastrella* and *Laticoleus* are larger than this and they have ten or more species each.

Six of the more widely distributed genera occur in only two regions: *Rhynchophion* and *Thyreodon* (Neotropical/Nearctic), *Euryophion* and *Orientospilus* (Afrotropical/Oriental), *Leptophion* (Oriental/Australo-Pacific) and *Simophion* (Palaearctic/Nearctic). Two genera occur in just three regions, *Dictyonotus* (Palaearctic/Oriental/Afrotropical) and *Dicamptus* (Afrotropical/Oriental/Australo-Pacific), whilst *Eremotylus* occurs in four regions (Nearctic/Palaearctic/Oriental/Neotropic). *Ophion* occurs in all regions except the Afrotropical and *Stauropoctonus* in all but the Nearctic (though it is absent from the African mainland). Only *Enicospilus* is truly cosmopolitan with quite large numbers of species in all areas.

Considered from a geographical standpoint the Neotropical region contains both the most genera (12) and has the highest degree of generic endemicity (50%). The Afrotropical and Oriental regions both contain ten genera, but the former has a far higher degree of endemicity (40% compared with 10%). The Australo-Pacific region contains eight genera, three of which (37%) are endemic whilst the Palaearctic, with a similar number of genera, has only two endemics (25%). The Nearctic is the most impoverished with seven genera, one of which (14%) is endemic. The faunal similarity (at generic level) between the regions is shown in Table 19.

Table 19 The generic faunal affinities between major zoogeographic regions (Hawaii is excluded). The values at the intersects of rows and columns *V* may be defined as:

$$V = \frac{\text{number of genera common to areas X and Y}}{\text{total number of genera present in areas X and Y}}$$

It is noteworthy that contiguous or recently contiguous areas have a significantly higher value for *V* than do areas that are not contiguous or that have only been contiguous in the distant past (more than 40 million years ago), suggesting that dispersal may be a more important event than vicariance in the biogeographical history of the subfamily.

	NEARCTIC	NEOTROPICAL	AUSTRALO-PACIFIC	ORIENTAL	AFROTROPICAL
PALAEARCTIC	0.36	0.25	0.23	0.38	0.20
AFROTROPICAL	0.06	0.10	0.20	0.43	
ORIENTAL	0.21	0.22	0.38		
AUSTRALO-PACIFIC	0.15	0.18			
NEOTROPICAL	0.36				

Hypothesized evolutionary history of the group: a scenario

Primitive ichneumonids are known from the Upper Cretaceous (80–90mya) (Townes, 1973*b*) and the family may have originated at the beginning of the Cretaceous (Rodendorf & Rasnitsyn, 1980), possibly from a protoichneumonoid ancestor such as the Praeichneumonidae (Rasnitsyn, 1983). The age of the subfamily Ophioninae is not known but it is presumed that it post-dates the primitive Upper Cretaceous groups. A fossil *Ophion* species is known from from the Lower Oligocene (35–40mya) in France and Rodendorf (1962) states that the Ophioninae (?sensu lato, i.e. including the Campopleginae) dates back to the Palaeocene (55–60mya). Possibly the group radiated around the beginning of the Tertiary some 65–70 million years ago.

At this time the continents were still in close proximity to one another (Audley-Charles *et al.*, 1981; Owen, 1981). Australia was connected to Antarctica and an archipelagic connection probably existed between this landmass and South America. Europe and North America were contiguous and South America was not widely separated from Africa. The most primitive lineage of the Ophioninae (the *Ophion* genus-group) may have been widespread at this time, as would have been its sister-group, the stem group of the remaining Ophioninae. The *Sicophion* lineage became isolated in the southern continent of Australia/Antarctica/South America at an early stage whilst its sister-lineage, the ancestor of the *Eremotylus, Enicospilus* and *Thyreodon* lineages, remained in Laurasia or Africa. The ancestor of the *Eremotylus* lineage probably differentiated in Laurasia whilst the ancestor of the *Enicospilus/Thyreodon* radiated in Africa. I suggest that early offshoots of this line must have spread to South America, either by flying across the widening South Atlantic, or by dispersal through Laurasia and across a water gap to South America. Some kind of barrier to the spread of organisms to and from South America is suggested by the high degree of generic endemicity and the fact that the Neotropical species of *Enicospilus* seem to belong to very few species-groups compared with those of other tropical areas. I suggest that the less vagile *Thyreodon* lineage reached South America much later, possibly from Asia via the Bering Straits. Probably the radiation of the *Enicospilus* lineage resulted in widespread extinction of members of the *Ophion* group, thus leaving the isolated specialized groups extant today. *Ophion* almost certainly has undergone secondary radiations giving rise to species complexes in South America (derived from the Nearctic) and Australia (derived initially from the Palaearctic fauna spreading through the Oriental region, where it has subsequently become isolated on mountain tops) (Gauld, 1984*a*). Except for *Xylophion*, a remnant of the early widespread *Ophion* group-distribution, and *Riekophion*, a remnant of the southern radiation of the *Sicophion* lineage, the ophionine fauna of the Australo-Pacific has largely been derived from the Oriental region (as has been observed for other groups, e.g. Wilson, 1959; Gupta, 1962), though New Guinea has served as the epicentre of a considerable radiation, particularly in the case of *Enicospilus*, over 100 endemic species of which occur on the island.

Although the above scenario is largely speculative it is the most parsimonious interpretation of the present distribution in relation to the postulated phylogenetic history of the group. Other scenarios would involve postulation of more widespread extinctions, more transoceanic dispersive events or necessitate postulating a much earlier origin for the subfamily.

The subfamily Ophioninae

In the following section the various genera and new synonymies are discussed in some detail. Keys have not been given here to genera as any attempt to produce a key to world genera would involve the usage of rather difficult couplets to allow for evolutionary parallelism between different species-groups in similar habitats in different zoogeographic regions. Practical keys to genera on a regional basis already exist. The Afrotropical region is covered by Gauld & Mitchell (1978) and the Indo-Australian region by Gauld & Mitchell (1981). This latter key will also suffice for the Palaearctic region. A key to the Neotropical genera is currently in preparation and this will suffice for the Nearctic. Townes (1971) also offers reasonable generic keys, but these are now rather dated, particularly his key to the 'Ophionini' (see Gauld, 1979).

The *OPHION* genus-group

This group contains seven genera, *Afrophion, Agathophiona, Alophophion, Xylophion, Sclerophion, Rhopalophion* and *Ophion*. The first six are holophyletic groups but *Ophion* is probably paraphyletic with respect to them (see p. 125).

The group is characterized by the absence of a posterior mesosternal transverse carina, usually by possession of a diagonal mesopleural furrow, generally by possession of an impressed clypeal apex and by having *Rs* in the hind wing usually at least slightly curved and often very strongly bowed. Virtually all species in this genus-group have 1*m–cu* in the fore wing centrally angled somewhat, and usually have a distinct ramellus present at this point.

As *Ophion* is apparently the paraphyletic stem-group from within which all other genera in this group have arisen, and the genus is primarily a Holarctic taxon, it seems probable that this group originated in the temperate north. It is probable that at some period it was present in most regions and has gradually disappeared from equatorial regions leaving isolated relicts in South Africa (*Afrophion*), Australia (*Xylophion*), Madagascar (*Rhopalophion*) and Patagonia (*Alophophion*). The possibility that there has been repeated expansion into and extinction within the tropics is suggested by the presence of some groups of *Ophion* species on isolated mountains in South East Asia, New Guinea and South America, and by the occurrence of distinctive *Ophion* species-complexes in Australia and New Zealand (Gauld, 1984*a*).

AFROPHION Gauld

Afrophion Gauld, 1979: 79. Type-species: *Ophion nubilicarpus* Tosquinet, by original designation.

Mandibles stout, not twisted, subequally bidentate, barely narrowed apically; outer mandibular surface convex, with strong proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex with apical margin sharp but not clearly impressed; clypeus in anterior aspect weakly convex. Ocelli large, the posterior ones very close to the eyes; frontal carina absent; occipital carina complete, ventrally joining hypostomal carina. Antennae moderately long, 1·3 times length of fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli vestigial; epicnemial carina complete; mesopleural furrow strong, diagonal. Scutellum moderately convex, quite narrow and not carinate laterally; posterior transverse carina of mesosternum absent except laterally. Propodeum with anterior area either occluded or extremly short, the remainder of the propodeum rather abruptly declivous, with irregular vestiges of carinae and rather coarsely microreticulate. Fore wing with pterostigma broad; marginal cell elongate; *Rs+2r* very broad and slightly angled before joining pterostigma; anterior corner of discosubmarginal cell glabrous, in one species extensively so and with a detached alar sclerite (Gauld & Mitchell, 1978); *1m–cu* with small ramellus, centrally angled. Hind wing with *Rs* from straight to weakly curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of close fine hair; hind tarsal claws unspecialized, those of male slightly more closely pectinate than those of the female. Gaster slender; tergite 2 elongate, with thyridia very weak, close to anterior margin; umbo distinct; epipleuron up-turned. Ovipositor sheath slender; male with gonosquamae very large, ploughshare-like.

Afrophion is restricted to the extreme south of Africa. The genus contains two species, the type-species and *A. hynnis* (Gauld & Mitchell). It is distinguished from *Ophion* by the form of the propodeum, the unique structure of the male genitalia and by the basally incrassate *Rs+2r* in the fore wing.

AGATHOPHIONA Westwood

Agathophiona Westwood, 1882: 19. Type-species: *Agathophiona fulvicornis* Westwood, by monotypy.

Mandibles twisted 5–10°, barely tapered, with lower tooth slightly the longer; outer mandibular surface slightly convex, with a strong proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; mouthparts exceptionally specialized in that the distal part of the maxilla projects below the clypeus and the labial glossae project by a distance almost equal to length of hind wing; clypeus in profile rather flat, margin blunt; clypeus in anterior aspect broad, very weakly convex. Ocelli quite small, the posterior ones separated from eye by about their own minimum diameter; frontal carina absent or present but weak; occipital carina dorsally complete or narrowly obsolescent centrally, ventrally obsolescent, not joining the very weak hypostomal carina. Antennae rather short and quite stout, distal segments quadrate. Pronotum unspecialized; spiracular sclerite exposed; notauli short but strongly impressed near anterior margin; epicnemial carina more or less complete; mesopleural furrow virtually absent. Scutellum moderately strongly convex, not laterally carinate; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area occluded, rather deeply impressed; propodeal carinae vestigial; posterior area striate or coriaceous. Fore wing with pterostigma moderately broad; marginal cell slender; *Rs+2r* more or less straight, not thickened before joining pterostigma; discosubmarginal cell without a glabrous anterior area; *1m–cu* generally with only a trace of a ramellus, rather evenly but quite strongly curved. Hind wing with *Rs* quite strongly curved. Fore leg with tibial spur bearing a membranous flange behind the macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur cylindrical, with scattered hairs marginally; hind tarsal claws long and weakly curved. Gaster rather stout; tergite 2 in profile only slightly longer than posteriorly deep; thyridia small and close to anterior margin; epipleuron up-turned. Female with subgenital plate enlarged, as long as tergite 2 and medially notched; ovipositor sheath unspecialized.

Agathophiona is a monobasic genus; the type-species occurs in Mexico. *A. fulvicornis* is diurnally active (Townes, 1971). Structurally this is one of the most specialized of all ophionine genera. The remarkable mouthparts are presumably an adptation to feeding from certain types of flowers but the function of the rather unusually modified female terminalia is not known.

ALOPHOPHION Cushman

Alophophion Cushman, 1947: 439. Type-species: *Ophion chilensis* Spinola, by original designation.

Mandibles not twisted, weakly narrowed apically, subequally bidentate; outer mandibular surface flat, usually punctate and hirsute. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin often impressed, sometimes very narrowly so; clypeus in anterior aspect weakly convex. Ocelli generally large, the posterior ones close to the eyes; frontal carina absent; occipital carina absent. Antennae moderately to very long, at least 1·3 times length of fore wing. Pronotum unspecialized or mediodorsally somewhat flattened and quite long; spiracular sclerite exposed; notauli present on anterior part of mesoscutum; epicnemial carina generally strong; mesopleural furrow distinct, diagonal, extending from episternal scrobe to near subalar prominence. Scutellum very weakly convex, usually narrow and not carinate laterally; posterior transverse carina of mesosternum absent except for lateral vestiges. Propodeum with anterior area occluded, transverse and often lateromedian longitudinal carinae discernible, often almost complete; posterior area smooth or rugulose. Fore wing with pterostigma broad; marginal cell long; *Rs+2r* slender, curved near proximal 0·3 before joining pterostigma near centre; dicosubmarginal cell with glabrous area anterior; *1m–cu* generally centrally angled, sometimes with a short ramellus which is directed more anteriorly than that of *Ophion*. Hind wing with *Rs* curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of long close hairs; hind tarsal claws unspecialized. Gaster moderately slender; tergite 2 in profile elongate, thyridia oval, separated from anterior margin of tergite by its own length or less, umbo distinct; epipleuron up-turned. Ovipositor sheath narrow.

Alophophion is a moderately large genus that is restricted to South America. The majority of species occur in southern Chile and Patagonia. Cushman, when describing *Alophophion* as a distinct genus, commented that it barely warranted generic distinction from *Ophion*. Whilst it is undoubtedly very close to *Ophion*, the combination of characters exhibited by the group clearly separate it as a holophyletic lineage. This lineage is characterized by the following apomorphies: occipital carina entirely absent; *Rs+2r* joining pterostigma near centre; first subdiscal cell stouter than normal; ramellus, when present, directed more anteriorly than that of other ophionines.

OPHION Fabricius

Ophion Fabricius, 1798: 210, 235. Type-species: *Ichneumon luteus* L., by subsequent designation, Curtis, 1836: 600.

Paniscus Schrank, 1802: 316. Type-species: *Ichneumon luteus* L., by monotypy.

Psylonychia Szépligeti, 1905: 21. [Nomen nudum.]

Stenophthalmus Szépligeti, 1905: 23. Type-species: *Stenophthalmus algiricus* Szépligeti, by subsequent designation, Viereck, 1914: 137. [Homonym of *Stenophthalmus* Becker, 1903.]

Pachyprotoma Kohl, 1906: 223. Type-species: *Ophion (Pachyprotoma) capitatus* Kohl, by monotypy.

Australophion Morley, 1912: 4, 30. Type-species: *Ophion peregrinus* Smith, by monotypy.

Neophion Morley, 1912: 4, 30. Type-species: *Neophion crassus* Morley, by subsequent designation, Viereck, 1914: 100.

Apatophion Shestakov, 1926: 262. Type-species: *Apatophion mirsa* Shestakov, by original designation.

Platophion Hellén, 1926: 13. Type-species: *Platophion areolaris* Brauns, by subsequent designation, Cushman, 1947: 475.

Potophion Cushman, 1947: 476. Type-species: *Potophion caudatus* Cushman, by original designation.

Psylonychia Cushman, 1947: 476. [Unavailable name, proposed in synonymy.]

Apomesus Townes, 1971: 54. Type-species: *Apomesus longiceps* Townes, by original designation.

Mecetron Townes, 1971: 60. Type-species: *Stenophthalmus choaspese* Uchida, by original designation.

Mandibles not twisted, from very weakly to moderately narrowed distally, generally subequally bidentate or with upper tooth slightly the longer; outer mandibular surface more or less flat, except for basal concavity, moderately punctate. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly to moderately convex, margin impressed, acute; clypeus in anterior aspect weakly convex, rarely truncate or even slightly concave. Ocelli usually large, the posterior ones separated from eyes by less than their own diameters; frontal carina absent; occipital carina usually complete dorsally, ventrally not reaching the hypostomal carina, rarely with occipital carina mediodorsally obsolescent, or in a few species with it entirely absent. Antennae generally of moderate length, in a few deserticolous species the flagellum short and with central segments quadrate. Pronotum unspecialized; spiracular sclerite usually completely exposed; notauli weak but discernible on anterior 0·2 of mesoscutum; epicnemial carina generally strong and well developed on mesopleuron; mesopleural furrow strongly impressed, extending diagonally from episternal scrobe towards subalar prominence. Scutellum weakly to moderately convex, usually carinate only on anterior 0·2 or less, rarely with lateral longitudinal carinae complete to posterior margin; posterior transverse carina of mesosternum usually present only laterally as vestiges. Propodeum with anterior area occluded except for a small semicircular depression centrally; propodeal carina variously developed, at most with both transverse carinae and the lateromedian longitudinal carinae complete, enclosing an area superomedia, in the most exceptional cases with all carinae only vestigial; posterior area usually rather smooth. Fore wing with pterostigma moderately to very stout; marginal cell very long and slender; *Rs+2r* usually virtually straight, slender, barely broadened before joining pterostigma, in some species evenly broadened to join pterostigma; discosubmarginal cell with glabrous area in anterior corner; 1*m–cu* usually with a well-developed ramellus, rarely with stub-like indication of this vein present; 1*m–cu* centrally strongly geniculate. Hind wing with *Rs* from weakly to very strongly curved. Fore tibial spur with membranous flange behind the macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of close long hairs; hind tarsal claws unspecialized, those of males usually more closely pectinate than those of the female. Gaster moderately slender; tergite 2 in profile moderately to strongly elongate, usually with thyridia large, close to anterior margin; umbo well developed; epipleuron up-turned. Ovipositor sheath usually slender, in one species-group exceptionally stout.

Ophion is a very large genus that is widely distributed throughout the world except for the Afrotropical region. In tropical South America and South East Asia few species occur and these are restricted to high altitudes (Gauld & Mitchell, 1981). *Ophion* as currently defined is almost certainly a paraphyletic assemblage; *Agathophiona, Rhopalophion, Sclerophion, Xylophion, Alophophion* and *Afrophion* are phenetically highly divergent (Gauld, 1979), holophyletic species-groups which have probably arisen from within *Ophion*. A number of other phenetically less divergent species-groups were included by Gauld (1979) within *Ophion*, but as the phylogenetic relationship of the taxa becomes better understood it will be necessary to erect a number of additional genera in order to establish a system of holophyletic taxa. Previous authors (e.g. Morley, 1912; Cushman, 1947; Townes, 1971) have attempted to remove other species-groups from *Ophion* and treat these as separate genera, but in each case the group removed has not been holophyletic as comparatively few of the subtropical and eremic *Ophion* species are known. Recent collecting has greatly increased our knowledge of these insects but more work needs to be undertaken before it is possible to fully resolve this genus. The major species-groups of *Ophion* are outlined below; all except the unsatisfactorily resolved *luteus*-group are holophyletic but I have avoided treating these groups as distinct genera until the *luteus* anathema can be resolved. As each of these groups appears to be defined by a series of unique apomorphies it is not possible to suggest their phylogenetic inter-relationship.

***Ophion peregrinus* species-group.** This species-group contains all the described New Zealand *Ophion* species (Townes *et al.*, 1961). Its monophyly is suggested by the possession of a mediodorsally lengthened pronotum, having *Rs+2r* joining the pterostigma distal to the pterostigma base and having the longitudinal lateral carina of the propodeum with a raised ridge diverging towards the propodeal spiracle. In *O. peregrinus* this is only weakly developed but in other taxa this ridge is frequently very strong and continuous with the carina, and the front part of the carina is absent so the apparent carina curves anteriorly towards the spiracle where it terminates. *O. peregrinus* is apparently the most primitive taxon as it retains most of the propodeal carinae and has a strongly geniculate 1*m–cu*; the other taxa have only a vestige of the anterior carina (the lateromedian and posterior transverse carina are lacking) and frequently have a reduced ramellus and more evenly curved 1*m–cu*. Most also have a fairly straight *Rs* in the hind wing.

***O. bicarinatus* species-group.** This complex contains *O. bicarinatus* Cameron, *O. facetious* Gauld & Mitchell, *O. gerdius* Gauld & Mitchell, *O. horus* Gauld & Mitchell and all of the described Australian species (Gauld, 1977). The group is characterized by possession of a proximally broadened *Rs+2r* which is slightly curved before reaching the pterostigma. The European species, *O. minutus*, may belong to this group. The five Australian species form a monophyletic subgroup characterized by the black interocellar area. In the Oriental region the species of the *bicarinatus* group are restricted to mountains in Sri Lanka, India, Burma, Malaysia, Taiwan and Sumatra. Their present fragmented distribution and their paraphyletic nature with respect to the Australian species-group suggests that this group was more widespread throughout the Indo-Australian region in the past, probably when the climate was cooler (Gauld, 1984*a*).

***O. cronus* species-group.** This monobasic group is restricted to montane New Guinea (Gauld & Mitchell, 1981). The group is characterized by having a very sparsely hirsute discosubmarginal cell and a very short 3*r–m*. It does not appear to be closely related to any other Indo-Australian species.

***O. caudatus* species-group.** This group is characterized by the elongate head shape; the eyes are more oval than normal and the labium is specialized in having the prementum extended far beyond the insertion of the labial palps (Gauld & Mitchell, 1981). This group contains *O. caudatus* (Cushman), *O. silus* Gauld & Mitchell, *O. longiceps* (Townes), *O. ascus* Gauld & Mitchell, *O. sumptious* Gauld & Mitchell, *O. mastrus* Gauld & Mitchell and an undescribed species from Sulawesi (BMNH). All these species occur in mountains in the Oriental region. An undescribed species from high altitude in Peru (TC) has a similarly modified head and like other members of the *O. caudatus* group it has large wings, elongate trochantelli and virtually obscured mesopleural punctures. This Neotropical species clearly seems to belong in this species-group, but it is possible that the apomorphies defining the group are a suite of characters facilitating existence at high altitude and that the Neotropical and Oriental lineages have undergone morphological convergence.

***O. areolaris* species-group.** This group is characterized by the loss of occipital carina, possession of a quadrate scutellum and a somewhat broadened ovipositor sheath, and by having a characteristic pattern of propodeal carina in which the area superomedia is more or less discernible, the posterior transverse carina is often complete and the anterior transverse carina is absent except centrally. This group contains *O. areolaris* Brauns, *O. ocellaris* Ulbricht and *O. fuscomaculatus* Cameron. The first two are western Palaearctic species whilst *O. fuscomaculatus* has an eastern Palaearctic range that extends into the higher mountains of the Oriental region.

***O. similis* species-group.** This group contains the Palaearctic species *O. similis* (Szépligeti), *O. mirsa* (Shestakov), *O. buchariensis* Meyer and two undescribed Nearctic species. All are stout insects with short, compact gasters, rather convex, irregularly sculptured propodea and somewhat shorter antennae than is usual for species of this genus. The ocelli and eyes are moderately small so the orbital-ocellar distance and the malar space are broader than is normal for *Ophion* species. All are apparently diurnally active and most are associated with dry areas.

***O. dentatus* species-group.** This group contains *O. dentatus* Smith, *O. turcomanicus* Szépligeti and *O. virus* Gauld & Mitchell. The group is characterized by possession of unusually long, fairly slender mandibles, having long, weakly curved claws and possessing numerous spines on hind tarsal segments 1–3. Species of this group are widely distributed throughout the eastern Palaearctic region, particularly Central Asia. Several also extend into the drier parts of the Indian subcontinent.

***O. luteus* species-group.** This large group contains all of the other described species of the genus from the Palaearctic, Nearctic and Neotropical regions. It is apparently a paraphyletic group and I can only define it in terms of plesiomorphic features (i.e. absence of apomorphic characters exhibited by other species-groups). With more study it may be possible to subdivide this group into several holophyletic species-complexes but little is yet known about either the eastern Palaearctic or the Nearctic species.

RHOPALOPHION Seyrig

Rhopalophion Seyrig, 1935: 49. Type-species: *Rhopalophion curvus* Seyrig (= *Ophion discinervus* Morley), by original designation.

Mandibles not twisted, weakly narrowed apically, more or less equally bidentate; outer mandibular surface slightly convex with distinct proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin slightly impressed and reflexed or sometimes almost blunt; clypeus in anterior aspect weakly convex or truncate. Ocelli moderately small to large, the posterior ones separated from the eyes by less than 0·8 times their own maximum diameter; frontal carina absent; occipital carina complete, joining hypostomal carina close to base of mandible. Antennae of moderate length, at least 1·2 times as long as fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli virtually absent; epicnemial carina present, extending onto pleuron; mesopleural furrow absent or very indistinct. Scutellum weakly to moderately convex, laterally carinate for its entire length; posterior transverse carina of mesosternum absent except for lateral vestiges. Propodeum with anterior area occluded; anterior and posterior transverse carinae usually complete, rarely with the former vestigial, very rarely all carinae absent; longitudinal carinae not developed; posterior area finely alutaceous to smooth. Fore wing with pterostigma moderately broad; marginal cell long; *Rs+2r* almost straight, not or only very slightly expanded before joining pterostigma; discosubmarginal cell anteriorly broadly glabrous from base of *Rs+2r* to ramellus; *1m–cu* very angulate, with an extremely long ramellus that reaches at least 0·6 of distance to *Rs&M*. Hind wing with *Rs* virtually straight or very weakly curved. Fore tibial spur with membranous flange behind macrotrichial comb reaching 0·5–0·7 of length of spur; mid and hind trochantelli unspecialized; inner hind tibial spur moderately flattened, with a fringe of long close hairs;

hind tarsal claws unspecialized, those of male far more closely and finely pectinate than those of the female. Gaster slender; tergite 2 in profile moderately long with thyridia oval and close to anterior margin; umbo quite well developed; epipleuron up-turned. Ovipositor sheath slender.

Rhopalophion is a small genus with three described species, *discinervus* which is widespread throughout the Afrotropical mainland, and *divergens* and *parallelus* which are restricted to Madagascar (Delobel, 1975). *R. divergens* and *R. parallelus* are apparently sister-species and constitute a clade defined by the following apomorphic features, possession of small ocelli, possession of subquadrate lower face and possession of a relatively long malar space. This clade is the sister-lineage to *R. discinervus* which is defined by possession of a very angulate *1m–cu* and a distally swollen ramellus (Gauld & Mitchell, 1978). The females of *discinervus* are unusual amongst ophionines in that the distal tarsal segment of the female has a lateral projection. This is similar to one found in a species of *Ophiogastrella* (Cushman, 1947). *Rhopalophion* species are easily distinguished from other taxa in the *Ophion* genus-group on account of their unique venation, total lack of propodeal longitudinal carinae and long fore tibial spur.

SCLEROPHION Gauld

Sclerophion Gauld, 1979: 77. Type-species: *Pleuroneurophion longicornis* Uchida, by original designation.

Mandibles stout, not twisted, barely narrowed apically; outer mandibular surface weakly convex. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin not impressed; clypeus in anterior aspect weakly convex. Ocelli large, the posterior ones separated from eyes by less than 0·2 of their minimum diameter; frontal carina absent; occipital carina complete, ventrally reaching hypostomal carina. Antennae very long and slender, more than 1·7 times length of fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli weak but discernible; epicnemial carina complete, strong; mesopleural furrow weak, diagonal, with upper end rather broad and shallow. Scutellum moderately convex, carinate laterally on at least its anterior 0·4; posterior transverse carina of mesosternum absent except as lateral vestige. Propodeum with anterior area occluded except medially where it is semicircular; anterior and posterior transverse carinae usually complete, other carinae weak; posterior area usually rather smooth. Fore wing with pterostigma moderately slender; marginal cell elongate; *Rs+2r* thickened and evenly curved before joining pterostigma; discosubmarginal cell with an extensive glabrous area anteriorly, the distal margin of this area with a thickened corneous mark; *1m–cu* with long ramellus, centrally geniculate. Hind wing with *Rs* very weakly curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with margin of close, long hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 very elongate, with thyridia elliptical, close to anterior margin; umbo well developed; epipleuron up-turned. Ovipositor sheath slender.

Sclerophion species may be recognized by their characteristic fore wing venation, particularly the thickened *Rs+2r* and the corneous mark in the discosubmarginal cell. The genus contains two species, the type-species and *S. uchidai* Gauld & Mitchell. These occur in the mountains at the eastern Palaearctic/Oriental interface (Gauld & Mitchell, 1981).

XYLOPHION Gauld

Xylophion Gauld, 1979: 77. Type-species: *Ophion xylus* Gauld, by original designation.

Mandibles not twisted, weakly to moderately tapered, subequally bidentate; outer mandibular surface flat, punctate, with proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, acute; clypeus in anterior aspect weakly convex. Ocelli large, the posterior ones separated from eyes by their own minimum diameter or less; frontal carina absent; occipital carina strong, ventrally often reaching hypostomal carina, sometimes ventrally obsolescent. Antennae of moderate length or long, usually at least 1·5 times length of fore wing. Pronotum more or less unspecialized, though one species has trace of a median transverse crest; spiracular sclerite exposed; notauli quite weak but usually distinct on anterior 0·2 of segment, rarely absent; epicnemial carina strong, reaching onto pleuron above level of lower corner of pronotum; mesopleural furrow weak, diagonal. Scutellum weakly convex, at most carinate laterally on anterior 0·2; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area more or less occluded except centrally where it is discernible as a semicircular area; anterior transverse carina usually more or less complete, posterior transverse carina from present laterally as vestiges to almost complete; longitudinal carinae vestigial; posterior area rather smooth. Fore wing with pterostigma large and triangular; marginal cell long; *Rs+2r* evenly broadened and curved before joining pterostigma; discosubmarginal cell with a large glabrous area in anterior corner;

1m–cu with a short ramellus, centrally angulate. Hind wing with *Rs* strongly curved. Fore tibia with a membranous flange extending from 0·1–0·3 of its length behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of long, close hairs; hind tarsal claws of female unspecialized, of male unique in having a central gap between an inner and outer row of pectinal teeth. Gaster slender; tergite 2 in profile very elongate with thyridia elliptical, separated from anterior margin by its own length or less; umbo strongly developed; epipleuron up-turned. Ovipositor sheath slender.

Xylophion is a small genus restricted to the Australian tectonic plate. Three species, one of which is undescribed, occur in south-eastern Australia. One of these, *X. xylus*, also occurs more widely throughout Australia and has been found in the New Guinea highlands (Gauld, 1984*a*).

Xylophion is characterized by the venation, particularly the possession of a very short *3r–m*, and the reduced flange on the fore tibial spur. A particularly striking, and hitherto unrecognized, autapomorphy of the genus is the form of the male tarsal claw. Instead of having a sinuous row of pectinal teeth present (as is normal for ophionines), *Xylophion* males have a marked discontinuity in the centre of the row between the teeth on the inner and outer edges of the claw. In its least derived form only the central gap exists (*Xylophion* species 1, BMNH) but the other two species are specialized further in different ways. *X. ketus* has the inner and outer marginal rows extended laterally so that there is a central overlap between the two parallel ends of the rows of teeth. In *X. xylus* there is a less pronounced overlap but the distal portion of the claw is flattened and the terminal tooth reduced so the pectinal row forms a 'fence' around the distal end of the claw.

The *SICOPHION* genus-group

This group comprises three genera, *Sicophion* and *Janzophion* from montane tropical South America and *Riekophion* from Australia. The species in this complex exhibit an unusual combination of plesiomorphic and apomorphic features. All possess a well-developed membranous flange on the fore tibial spur though none has an umbo on tergite 2 and often the upper corner of the pronotum is expanded to partially occlude the spiracular sclerite. It is suggested here that these three genera comprise a distinct lineage which is derived with respect to the *Ophion* group, and that the *Sicophion* group represents a separate southern radiation of the ophionines. However, as mentioned above (see p. 117), if the polarity of characters 38 and 47·1 has been misinterpreted then the *Ophion* lineage may represent a more derived group than the *Sicophion* lineage. If this were the case then it is possible that the *Sicophion* group is a collection of relict genera whose present southern distribution can be explained by Darlington's (1965) 'glove hypothesis'.

JANZOPHION gen. n.

Type-species: *Janzophion nebosus* sp. n.

Mandibles twisted perhaps 5°, slightly tapered distally, with upper tooth slightly the longer; outer mandibular surface with a diagonal line of hair extending from upper proximal corner to near centre. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, in anterior aspect with margin weakly convex. Ocelli very large, the hind ones more or less contiguous with eyes; frontal carina absent; occipital carina absent. Antennae very long and slender, about 1·5 times length of fore wing. Pronotum unspecialized; spiracular sclerite partially concealed; notauli vestigial; epicnemial carina present laterally and ventrally; mesopleural furrow indistinct. Scutellum weakly convex, laterally carinate only on anterior 0·1–0·3; posterior transverse carina of mesosternum complete. Propodeum with anterior area long; anterior transverse carina and usually posterior transverse carina complete, often with a median longitudinal carina present; propodeum otherwise rather smooth. Fore wing with pterostigma moderately broad; marginal cell very long; *Rs+2r* bowed, thickened before joining pterostigma; discosubmarginal cell with glabrous area near anterior corner, but anterior to this is narrow hirsute region; *1m–cu* without a ramellus, proximally fairly straight, distally strongly bowed. Hind wing with *Rs* weakly curved; marginal cell proximally glabrous; penultimate distal hamulus longer than its fellows, the distal one slightly shorter but longer than the proximal ones. Fore tibial spur with a membranous flange behind the macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with margin of close long hairs; hind tarsal claw unspecialized. Gaster slender; tergite 2 in profile very elongate, with thyridia remote from anterior margin; umbo vestigial; epipleuron up-turned. Ovipositor sheath slender.

Janzophion is a distinctive genus which bears a very strong phenetic similarity to the Old World genus *Leptophion*. Unlike *Leptophion*, *Janzophion* species lack the occipital carina, and have a well-developed membranous flange present on the fore tibial spur, behind the macrotrichial comb.

Janzophion nebosus **sp. n.**

Fore wing length 14–16 mm.

Head slightly more elongate than normal for ophionines; lower face polished, 1·4–1·5 times as long as broad; malar space 0·50–0·55 times basal mandibular width; head strongly narrowed behind eyes, occiput mediodorsally slightly concave. Flagellum with 66–68 segments, the tenth segment about 2·0 times as long as wide. Mesoscutum with margin slightly out-turned; scutellum finely shagreened; mesopleuron with upper part highly polished, finely and sparsely punctate, ventrally slightly more coriaceous; metapleuron similar. Propodeum in profile evenly declivous; propodeal spiracle joined to pleural carina by weak ridge; most of alitrunk bearing fine pale pubescence. Fore wing with AI = 1·20–1·25; CI = 0·43–0·47; ICI = 0·61–0·70; SDI = 1·14–1·17; *cu-a* proximal to base of *Rs&M* by about 0·3 times its own length; outer hind corner of 2nd discal cell about 90°. Hind wing with about 8 distal hamuli; NI = 3·70–4·60. Legs unspecialized; hind tarsal claws of male with slightly finer and denser pectinate comb than that of female. Gaster slender, male with subgenital plate bearing long fine pubescence; gonosquamae quite long, dorsally somewhat membranous.

Pale yellowish species, with interocellar area, part of mesoscutum, much of mesopleuron, metapleuron and part of propodeum blackish; gaster with distal part of tergite 5 and tergites 6+ infuscate. Pterostigma and *Rs+2r* blackish, other veins flavous; wing hyaline, proximal angle of marginal cell infumate.

REMARKS. This species has been taken at light in cloud forests between 1500 and 2350 m in Costa Rica. Nothing is known of its biology.

MATERIAL EXAMINED

Holotype ♂, **Costa Rica**: Alajuela Prov; Volcan Poas N. P., xii.1982 (*Janzen & Hallwachs*) (BMNH).

Paratypes. **Costa Rica**: 1 ♂, same data as holotype (BMNH); 1 ♂, same locality as holotype, xii.1981 (*Janzen & Hallwachs*) (BMNH); 1 ♀, Monte Verde Reserve, 1500 m, ii.1980 (*Mason*) (TC).

RIEKOPHION Gauld

Riekophion Gauld, 1977: 21. Type-species: *Allocamptus emandibulator* Morley, by original designation.

Mandibles not twisted, weakly evenly tapered or distally parallel-sided, subequally bidentate; outer mandibular surface flat, punctate. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin usually blunt, in one species, impressed; clypeus in anterior aspect from weakly convex to slightly concave. Ocelli from large, the hind ones contiguous with eyes, to rather small, the hind ones separated from eyes by 0·5 times their minimum diameter; frontal carina absent, or weakly present in one species; occipital carina usually complete, in one species ventrally obsolescent, not reaching hypostomal carina. Antennae moderately long and relatively slender, at least 1·3 times length of fore wing. Pronotum either unspecialized, or in two species mediodorsally long and flat; spiracular sclerite exposed, or in one species with slight expansion of dorsal lobe of pronotum; notauli vestigial or absent; epicnemial carina complete, generally curved to meet anterior margin of pleuron; mesopleural furrow very weak to quite distinct diagonally. Scutellum weakly convex, very characteristic in being fairly narrow and barely tapered, and medially longitudinally higher than laterally; carinae if present only on anterior 0·3 or less; posterior transverse carina of mesosternum complete. Propodeum with anterior area moderately to very long, often irregularly striate; propodeum usually with anterior and posterior transverse carinae complete, lateromedian ones weaker but often complete behind anterior transverse carina and usually enclosing a long narrow area superomedia. Fore wing with pterostigma moderately to very slender; marginal cell usually long; *Rs+2r* proximally sinuous, only weakly broadened and not curved abruptly to join the pterostigma, unusual in joining stigma distal to proximal end; discosubmarginal cell anteriorly glabrous, often with group of isolated hairs near base of *Rs+2r*, always bearing a detached corneous or sclerotized patch in membrane. *1m–cu* weakly sinuous or fairly evenly curved. Hind wing with *Rs* straight or very weakly curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, the margin with close long hairs; hind tarsal claws elongate, with thyridia small, widely separated from anterior margin to which it is joined by a groove; umbo absent; epipleuron up-turned. Ovipositor sheath slender; unusual in having male subgenital plate ornamented with projections.

Riekophion is a very distinctive genus, characterized by the quadrate scutellum, unusual venation and ornamented subgenital plate (Gauld, 1977). It contains three species which occur in southern and western Australia. The phylogenetic inter-relationships of these species are suggested in Fig. 28. Nothing is known of the biology of these insects.

SICOPHION Gauld

Sicophion Gauld, 1979: 71. Type-species: *Sicophion pleuralis* Gauld, by original designation.

Mandibles stout, twisted about 25–35° and with lower tooth slightly the longer; outer mandibular surface more or less flat, sparsely punctate. Maxillary palp 5-segmented, labial palp 4-segmented; maxillae elongate; clypeus in profile convex, apical margin not impressed, in anterior aspect truncate. Ocelli very large, the posterior ones close to margin of eye; frontal carina absent; occipital carina mediodorsally incomplete, ventrally obsolescent, not reaching hypostomal carina. Antennae very long and slender, at least 1·4 times length of fore wing. Pronotum unspecialized; spiracular sclerite virtually completely occluded by enlarged flap formed from hind corner of pronotum; notauli absent; epicnemial carina strong, extending onto mesopleural furrow; mesopleural furrow strong, extending from episternal scrobe forward. Scutellum quite convex, narrow, carinate only on anterior 0·2–0·3; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area occluded; anterior transverse carina present centrally, laterally obsolescent; posterior transverse carina present as lateral vestiges; propodeum otherwise rather smooth, posterior area not differently sculptured from spiracular area. Fore wing with pterostigma broad, distally abruptly narrowed; marginal cell moderately long and slender, unique amongst ophionines in being broadest distad of centre at sinuation in distal abscissa of *Rs*; *Rs+2r* not angled near junction with pterostigma, but somewhat broadened, somewhat angled slightly proximal to centre; discosubmarginal cell very extensively glabrous anteriorly, the glabrous area bearing indistinct corneous areas; 1*m–cu* without a ramellus, rather abruptly curved. Hind wing with *Rs* unique in the Ophioninae in being slightly convex. Fore tibial spur with membranous flange behind macrotrichial comb; mid and hind trochantelli very elongate, but unspecialized; inner hind tibial spur strongly flattened with a fringe of long, close hairs; hind tarsal claws unspecialized, markedly sexually dimorphic, those of male being far more closely pectinate than those of the female. Gaster exceptionally slender; tergite 2 elongate, thyridia absent; umbo absent; epipleuron very narrow, pendant. Ovipositor sheath slender, ovipositor unique in being proximally angled and without a subapical notch.

Sicophion is a small Neotropical genus with a single described Bolivian species (Gauld, 1979). In the BMNH is a short series of a putative second species collected in Costa Rica by Janzen & Hallwachs. These differ from *S. pleuralis* in having a more extensive glabrous area in the discosubmarginal cell and a less obviously 'bent' *Rs+2r*. There are subtle differences in colour and head shape also.

Sicophion is one of the most distinctive of ophionine genera. The sinuous *Rs* in the fore wing, the slightly convex *Rs* in the hind wing and the basally angulate, acutely pointed ovipositor with no subapical notch are, amongst ophionines, unique autapomorphies of the genus. Their very slender form with extensive semi-matt black coloration is a typical feature of ophionines from higher elevations (e.g. *Enicospilus ruwenzorius* Gauld & Mitchell) and the rather elongate head shape is also found in some upper montane species (e.g. *Ophion longiceps* (Townes), Gauld & Mitchell, 1981). The presumed loss of the dorsal notch is a feature that occurs in several genera of ichneumonids with more slender ovipositors (e.g. *Parania* in the Anomaloninae, Gauld, 1976).

Sicophion species are only known to occur at mid and high elevation in the Neotropical region. Specimens have been taken between 1600 and 3000 m. Nothing is known of their host ranges.

The *EREMOTYLUS* genus-group

This group contains three genera, *Eremotylus, Trophophion* and *Hellwigiella*. The last two are monobasic and probably really represent single phenetically highly divergent species of *Eremotylus*. The majority of species of all genera are eremic organisms.

The *Eremotylus* genus-group is characterized by the fore wing venation; *Rs+2r* is strongly geniculate and thickened before joining the pterostigma whilst 1*m–cu* is usually fairly evenly arcuate. The clypeus is usually flat or out-flared and the margin is not subapically impressed.

EREMOTYLUS Foerster

Eremotylus Foerster, 1869: 150. Type-species: *Ophion marginatus* Gravenhorst (= *Anomalon marginatum* Jurine), by subsequent monotypy, Thomson, 1888: 1193.

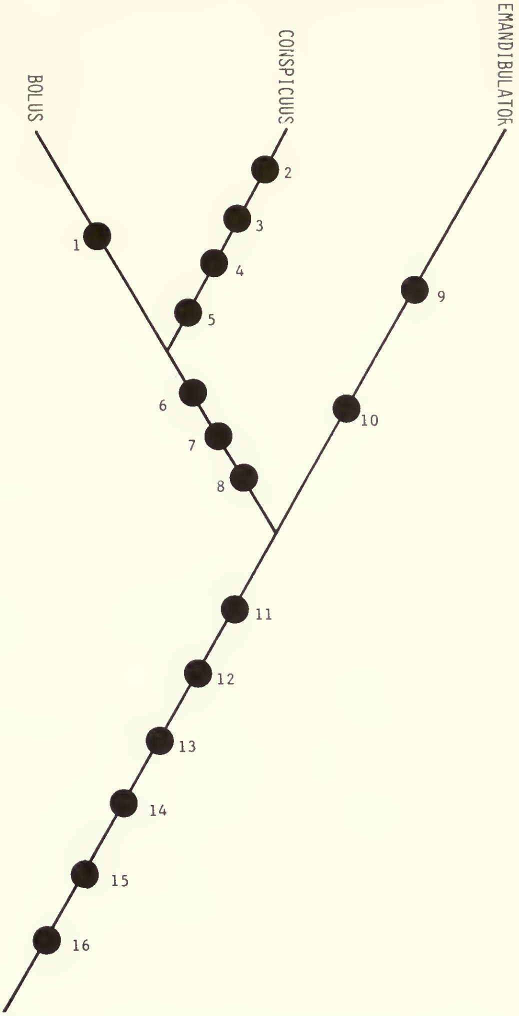


Fig. 28 Suggested phylogenetic inter-relationships of species of *Riekophion*. The apomorphic characters supporting this arrangement are: 1, mandible slender; 2, ocelli small; 3, occipital carina mediodorsally broadened; 4, body extensively black; 5, pronotal lobe expanded; 6, pronotum medio-dorsally flat and lengthened; 7, presence of hair patch in fenestra; 8, cubital index small; 9, distal sclerite lost; 10, ocelli grossly enlarged; 11, scutellum quadrate; 12, possession of alar sclerites; 13, metapleuron inflated; 14, *Rs+2r* sinuous; 15, *Rs+2r* joining pterostigma near centre; 16, male subgenital plate ornamented.

Camptoneura Kriechbaumer, 1901: 23. Type-species: *Ophion marginatus* Gravenhorst (= *Anomalon marginatum* Jurine), by subsequent designation, Viereck, 1914: 27. [Junior homonym of *Camptoneura* Agassiz, 1846.]

Genophion Felt, 1904: 123. Type-species: *Genophion gilletti* Felt (= *Ophion costale* Cresson), by original designation.

Camptoneuroides Strand, 1928: 52. [Replacement name for *Camptoneura* Kriechbaumer.]

Clistorapha Cushman, 1947: 450. Type-species: *Ophion subfuliginosus* Ashmead, by original designation.

Boethoneura Cushman, 1947: 450. Type-species: *Boethoneura arida* Cushman, by original designation.

Chilophion Cushman, 1947: 450. Type-species: *Ophion abnormum* Felt, by original designation.

Chlorophion Townes, 1971: 55. Type-species: *Chlorophion vitripennis* Townes, by original designation.

Mandibles not twisted, usually quite long, moderately strongly narrowed, usually subequally bidentate or with upper tooth slightly the longer; outer mandibular surface flat or slightly convex, punctate. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile more or less flat or even slightly out-flared, margin never impressed; clypeus in anterior aspect truncate or slightly concave. Ocelli usually moderately large to large, the posterior ones separated from the eyes by less than 0·5 their own maximum diameter, or in a few species with the ocelli small and the posterior ones separated from the eyes by more than their own maximum diameter; frontal carina absent or rarely very faintly indicated; occipital carina complete, rarely ventrally somewhat obsolescent. Antennae moderately long, at least 1·2 times length of the fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli vestigial or absent; epicnemial carina usually complete; mesopleural furrow usually rather weak but discernible, faintly indicated between episternal scrobe and subalar prominence. Scutellum weakly convex, usually carinate 0·3 to 0·8 of its length, rarely without carinae; posterior transverse carina of mesosternum from complete to present only laterally as vestiges. Propodeum generally with anterior area short but not occluded, in some species moderately long; anterior transverse carina usually distinct, at least centrally, sometimes complete, rarely absent; posterior transverse carina present laterally as vestiges or absent, other carinae generally absent; posterior area from smooth and polished to rugulose. Fore wing with pterostigma moderately slender; marginal cell long and slender, rarely rather short; *Rs+2r* abruptly geniculate and thickened near pterostigma; discosubmarginal cell with a small glabrous area in anterior corner; *1m–cu* without a ramellus, arcuate or very weakly sinuous. Hind wing with *Rs* from almost straight to strongly curved. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur generally flattened with a marginal fringe of close hairs; hind tarsal claws usually unspecialized, sometimes slightly longer and less evenly curved than normal. Gaster slender; tergite 2 in profile elongate with thyridia separated from fore margin by its own length or a little more, characteristically at the posterior end of a weak trough; umbo usually distinct, rarely weak; epipleuron up-turned. Ovipositor sheath slender.

Eremotylus is a moderately large genus containing about 35 species, most of which occur in the drier regions around the Mediterranean, the Middle East, Central Asia, the south-western United States and northern Mexico. Isolated species have a wider distribution; *E. subfuliginosus* occurs in the north-eastern part of the U.S.A., whilst the morphologically very specialized species *E. marginatus* is not uncommon throughout much of western Europe. *E. vitripennis* occurs in the drier parts of southern South America, whilst *E. perdix* occurs in the Indian subcontinent (Gauld & Mitchell, 1981). The Palaearctic species were monographed recently by Horstmann (1981) who recognized eight species. The New World species are extremely poorly known. Virtually nothing is known about the host ranges of species of *Eremotylus*. The only reliable host record to hand is of one European species (*E. curvinervis* Kriechbaumer) which has been reared from a species of *Dryobota* Lederer (Lepidoptera: Noctuidae) (Seyrig, 1926).

Some authors (e.g. Cushman, 1947; Townes, 1971) divided the species of *Eremotylus* between a number of small genera characterized mostly by differences in the development of carinae, particularly the transverse mesosternal carina. Gauld (1979) pointed out that despite these differences, all species share a large number of features and seem to comprise a natural group. Horstmann (1981) accepted this treatment. The present study has reinforced the author's opinion that this is a natural group; it is definable on the basis of several apomorphies including the characteristically modified *Rs+2r*, the arcuate or slightly sinuous *1m–cu* and the unoccluded anterior propodeal area. The characteristic clypeus and rather slender, longish mandibles are useful confirmatory characters.

The present disjunct distribution of the genus suggests that at one time the range of the genus must have been wider. Further discussion of zoogeography is best left until the New World species are better known.

HELLWIGIELLA Szépligeti

Hellwigiella Szépligeti, 1905: 23. Type-species: *Hellwigiella nigripennis* Szépligeti, by subsequent designation, Viereck, 1914: 67.

Mandible twisted about 15°, not appreciably narrowed, with upper tooth slightly shorter than the lower and bearing a pronounced very sharp ventral flange; outer mandibular surface punctate, with a strong proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile quite convex centrally, with margin reflexed, quite thin; clypeus in anterior aspect almost truncate. Ocelli small, the posterior ones separated from eye margin by more than their own maximum diameter; frontal carina absent; occipital carina strong, ventrally joining hypostomal carina. Antennae short and stout, central segments transverse, the flagellum barely longer than the fore wing. Pronotum mediodorsally quite long, otherwise unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina strong, complete; mesopleural furrow vestigial. Scutellum quite convex, laterally carinate about 0·8 of its length; posterior transverse carina of mesosternum complete or obsolescent centrally. Propodeum with anterior area quite short, impressed as a deep U-shaped groove; anterior transverse carina more or less complete, other carinae indistinct, posterior area reticulate. Fore wing with pterostigma moderately stout; marginal cell quite long and slender; *Rs+2r* abruptly geniculate and slightly broadened before joining pterostigma; discosubmarginal cell with a very small glabrous area anteriorly; *1m–cu* evenly curved, usually without a ramellus. Hind wing with *Rs* evenly bowed. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur almost cylindrical, with a fringe of sparse hairs; hind tarsal claw quite long and weakly curved. Gaster moderately slender, tergite 2 about twice as long as deep with thyridia separated from anterior margin by about their own length; umbo distinct; epipleuron membranous, pendant in most individuals. Ovipositor sheath slender.

Hellwigiella contains what is, I believe, a single Mediterranean species, though it is sculpturally and chromatically rather variable and has been divided into two (Szépligeti, 1905). *Hellwigiella* is morphologically extremely distinctive on account of the characteristic clypeus and mandible, and the form of the propodeum. The majority of apomorphic features characterizing the genus are obviously adaptations to a diurnal existence and most are paralleled in other genera with similar habits. It is possible that *Hellwigiella* is merely a specialized diurnal offshoot of *Eremotylus*, but if this were so then it is necessary to postulate that the specialized invaginated condition of the anterior area of the propodeum (character 22·2) has been derived from the partially elongated condition of *Eremotylus* (character 22·1). In the preceding phylogenetic analysis it has been suggested that the apomorphic states of these characters represent alternative specializations, so it is possible that *Eremotylus* and *Hellwigiella* have a sister-group relationship. Nothing is known of the biology of *Hellwigiella*.

TROPHOPHION Cushman

Trophophion Cushman, 1947: 447. Type-species: *Trophophion tenuiceps* Cushman, by original designation.

Mandibles barely twisted, quite stout, weakly narrowed, subequally bidentate; outer mandibular surface weakly convex. Maxillary palp 5-segmented, labial palp 4-segmented; maxilla and labium elongate, projecting below mandibles; clypeus in profile flat, in anterior aspect almost truncate. Ocelli small, the posterior ones separated from the eye by more than their own maximum diameter; frontal carina absent; occipital carina complete dorsally, ventrally incomplete. Antennae short, slightly clavate, barely longer than fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina complete; mesopleural furrow indistinct. Scutellum weakly convex, without lateral carinae; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area short but not occluded; anterior transverse carina present medially, posterior one present laterally as vestiges, other carinae obsolescent; posterior area polished, punctate. Fore wing with pterostigma moderately slender; marginal cell moderately short; *Rs+2r* thickened and curved to join pterostigma; discosubmarginal cell with glabrous area anteriorly; *1m–cu* evenly curved, without a ramellus. Hind wing with *Rs* bowed. Fore tibial spur with a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur weakly flattened, fringed with long fine hairs; tarsal claws rather long and weakly curved. Gaster moderately stout and rather more cylindrical than that of most ophionines; tergite 2 in profile less than twice as long as posteriorly deep, with thyridia separated from anterior margin by about its own length; umbo rather weak; epipleuron up-turned. Female with tergites 3–7 shallowly notched medially, with subgenital plate large, strongly sclerotized and centrally notched; ovipositor and sheath rather stout.

Only a single species of *Trophophion* is known. This occurs in the drier south-west of the U.S.A. Its host is unknown. *Trophophion* is recognizable on account of the specializations of the head and mouthparts and the female gaster. In other respects it is very similar to some *Eremotylus* species, and it is almost certainly a specialized offshoot of this genus. However, I have hesitated to synonymize *Trophophion* until some details of its biology and host relationship are known. If these are very different from those of *Eremotylus* then I suggest if be left as a separate genus even though this leaves *Eremotylus* as a paraphyletic taxon. Additional material from the dry parts of the U.S.A. and northern Mexico might help in elucidating the phylogenetic position of this bizarre species.

The *THYREODON* genus-group

This group contains five genera, *Barytatocephalus, Euryophion, Thyreodon, Rhynchophion* and *Dictyonotus*. The first of these is included in the complex on the basis of three apomorphies, the possession of an impressed anterior propodeal area (22·2), long, weakly curved tarsal claws, and absence of any transverse carinae on the propodeum. *Barytatocephalus* lacks the tilted mandibular axis, slender pterostigma and cylindrical hind tibial spurs of other genera, and thus seems to constitute the most primitive branch of the lineage. The remaining genera form a holophyletic group, and this may be divided into two holophyletic subgroups, one comprising *Thyreodon*, *Dictyonotus* and *Rhynchophion*, the other containing just *Euryophion*. The former subgroup is defined by the possession of a pointed clypeus, a very short and stout flagellum and an exceptionally elongate propodeal spiracle. A further possible apomorphy of this lineage is the possession of an evenly hirsute anterior part of the discosubmarginal cell (assuming that presence of a small glabrous area is an apomorphy of the subfamily). *Euryophion* has a slightly concave clypeus and a somewhat thickened and usually proximally curved *Rs+2r*. These two lineages seem to be biologically distinct; species of the *Thyreodon* subgroup have only been recorded as parasites of Sphingidae (Gauld & Mitchell, 1978; 1981; Carlson, 1979), whilst *Euryophion* species attack Eupterotidae and Saturniidae.

The close relationship between *Dictyonotus*, an Old World genus, and *Rhynchophion* and *Thyreodon*, primarily Neotropical genera, suggests they may have had a common ancestor that was widely distributed throughout the Nearctic and eastern Palaearctic regions. *D. purpurascens*, which could well be rather similar to the group ancestor, is currently widely distributed in the eastern Palaearctic, occurring as far north as 50° (Townes *et al.*, 1965), so a slight extension of its range northwards would have permitted migration across the Bering Strait. Movement from Asia to America is postulated on the belief the group has had an Old World origin, a suggestion favoured by the present distribution of the most primitive member of the group (*Barytatocephalus*) and the sister-lineage of the *Thyreodon* subgroup (*Euryophion*).

The exact relationship between the genera *Thyreodon, Rhynchophion* and *Dictyonotus* is unclear, as slight evidence in the form of a very few highly homoplastic characters can be marshalled for placing *Thyreodon* as the sister-group of either *Rhynchophion* or *Dictyonotus*, or

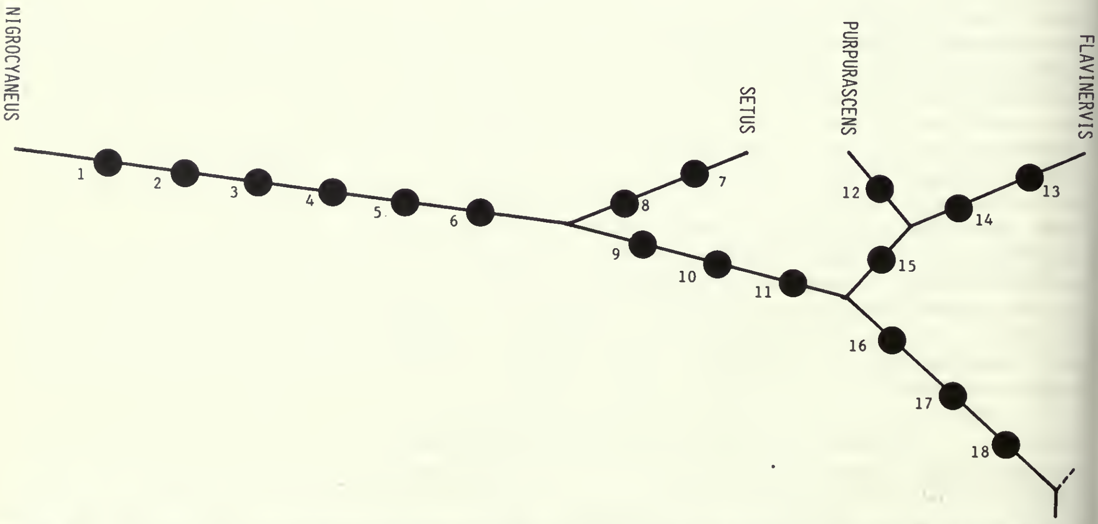


Fig. 29 Suggested phylogenetic inter-relationships of *Dictyonotus* species. The length of the lines is proportional to the number of apomorphies characterizing it. The apomorphic characters supporting this arrangement are: 1, presence of a metapleural tubercle; 2, striation present on gena; 3, hind tarsus flattened; 4, *1m–cu* sinuous; 5, body densely pubescent; 6, tergite 2 posteriorly deeper than long; 7, malar space longer than basal mandibular width; 8, occipital carina mediodorsally broadened; 9, petiole depressed; 10, tergite 2 posteriorly at least as deep as long; 11, petiolar spiracles anterior to margin of sternite; 12, presence of metanotal swelling; 13, reduction in number of hamuli; 14, development of strongly punctate scutellum; 15, thyridia remote from anterior margin of tergite; 16, complete posterior transverse carina of mesosternum (? a reversal); 17, presence of tubercle on metanotal margin; 18, epipleuron 2 pendant.

even *Rhynchophion* + *Dictyonotus* (see p. 93). What is clear is that both *Rhynchophion* and, more particularly, *Thyreodon*, are characterized by a string of apomorphies (as is *nigrocyaneus*), whilst *purpurascens* may well have changed very little from the form of the group ancestor (Fig. 29). One wonders what adaptation acquired by the *Thyreodon* lineage has allowed it to radiate so markedly in the Neotropics and give rise to a complex of 30 or more quite closely related species attacking sphingids, whilst in Asia, *Dictyonotus*, although presented with a very similar diversity of potential hosts (Rothschild & Jordan, 1903), has apparently failed to radiate appreciably.

BARYTATOCEPHALUS Schulz

Barycephalus Brauns, 1895: 43. Type-species: *Barycephalus mocsaryi* Brauns, by subsequent designation, Viereck, 1914: 19. [Homonym of *Barycephalus* Guenther, 1860.]
Barytatocephalus Schulz, 1911: 23. [Replacement name for *Barycephalus* Brauns.]

Mandible not twisted, very weakly narrowed, with upper tooth a little stouter but no longer than the lower; outer mandibular surface with a strong proximal concavity, and with a weak trace of a diagonal groove. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, acute; clypeus in anterior aspect weakly convex. Ocelli small, the posterior ones remote from the eyes; frontal carina absent, though a small trace may be discernible in some specimens; occipital carina complete, ventrally reaching to hypostomal carina. Antennae quite short, about 1·3 times as long as fore wing, central segments slightly elongate. Pronotum unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina complete, present on mesopleuron; mesopleural furrow weak but discernible as a short diagonal impression extending from episternal scrobe towards subalar prominence. Scutellum convex, carinate laterally only on anterior 0·4; posterior transverse carina of mesosternum complete. Propodeum convex, with anterior area impressed as a deep groove; propodeal carinae absent; posterior area coarsely punctate. Fore wing with pterostigma moderately slender; marginal cell moderately long; *Rs*+*2r* slender, proximally almost straight; discosubmarginal cell with a small glabrous area at anterior corner, remainder of cell sparsely hirsute; 1*m–cu* somewhat irregularly convex, without a ramellus. Hind wing with *Rs* virtually straight; genus unusual in having distal abscissa of Cu_1 very weak and the first abscissa of Cu_1 and *cu–a* forming an almost straight line, oblique, so anterior corner of first submarginal cell is about 50°. Fore tibial spur without membranous flange behind macrotrichial comb; mid and hind trochantelli simple; inner hind tibial spur somewhat flattened (though less so than in most taxa in this subfamily), with a fringe of moderately long hairs; hind tarsal claws long, weakly curved. Gaster moderately slender; tergite 2 in profile with thyridia close to anterior margin, elongate, umbo vestigial; epipleuron up-turned. Ovipositor slender.

Barytatocephalus is a small genus containing a single species that is widely distributed throughout the eastern Mediterranean region and the southern U.S.S.R. Nothing is known of its biology.

DICTYONOTUS Kriechbaumer

Dictyonotus Kriechbaumer, 1894*a*: 198. Type-species: *Dictyonotus melanarius* Kriechbaumer (= *Thyreodon purpurascens* Smith), by monotypy.
Aglaophion Cameron, 1903: 131. Type-species: *Aglaophion flavinervis* Cameron, by monotypy.
Ophionopsis Tosquinet, 1903: 389. Type-species: *Ophionopsis fulvipes* Tosquinet (= *Ophionopsis nigrocyaneus* Tosquinet), by subsequent designation, Viereck, 1914: 106. **Syn. n.**
Hybopleurax Enderlein, 1912: 624. Type-species: *Hybopleurax sumatranum* Enderlein (= *Thyreodon purpurascens* Smith), by monotypy.
Hypselogastrina Enderlein, 1918: 217. Type-species: *Hypselogastrina saliina* Enderlein (= *Ophionopsis nigrocyaneus* Tosquinet), by original designation. **Syn. n.**
Coracophion Shestakov, 1926: 260. Type-species: *Coracophion manganicolor* Shestakov (= *Thyreodon purpurascens* Smith), by monotypy.

Mandibles stout, not twisted, barely narrowed distally, equally bidentate or with lower tooth slightly the longer; outer mandibular surface more or less flat, with scattered hairs. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile flat, with margin often slightly out-flared, in anterior aspect convex with a median obtuse point. Ocelli small, the hind ones separated from the eye margins by at least their own minimum diameter; frontal carina present; occipital carina complete, ventrally usually not joining the hypostomal carina. Pronotum unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina more or less complete, always present on mesopleuron; mesopleural furrow weakly impressed, horizontal, extending from episternal scrobe to near upper end of epicnemial carina. Scutellum moderately convex, with longitudinal lateral carinae present only on anterior end; posterior transverse carina of mesosternum complete; metanotum exceptional in being produced into a blunt prominence above upper end of spiracle. Propodeum with anterior area short, impressed as a deep groove; propodeal carinae absent or with vestiges of lateromedian ones discernible; posterior area convex, rugose-reticulate. Fore wing with pterostigma slender; marginal cell of moderate length; *Rs+2r* very slightly bowed proximally, not appreciably broadened; *1m–cu* evenly curved to somewhat sinuous, without a ramellus; discosubmarginal cell evenly hirsute anteriorly. Hind wing with *Rs* weakly curved or almost straight. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur cylindrical, without a row of long marginal hairs; hind tarsal claws long and weakly curved. Gaster stout to very stout; tergite 2 in profile from about 1·5 times as long as posteriorly deep to less than 1·0 times as long as deep, with thyridia oval, separated from anterior margin by about its own diameter or more; umbo absent; epipleuron pendant. Ovipositor sheath slender.

This genus contains four species, *D. purpurascens* (Smith), *D. flavinervis* (Cameron) from the Oriental and eastern Palaearctic regions and *D. nigrocyaneus* (Tosquinet) **comb. n.** and *D. setus* (Gauld & Mitchell) **comb. n.** from the Afrotropical region. The last two were formerly placed in *Ophionopsis*, a genus originally proposed to accommodate the morphologically aberrant *nigrocyaneus. D. setus* is much more similar to the main *Dictyonotus* line than is *nigrocyaneus*, suggesting the two genera should be united (Gauld & Mitchell, 1978). The *Dictyonotus* lineage is distinguished only by one weak apomorphy (Fig. 29), and *purpurascens* in turn by a further one, suggesting this species may resemble the ancestor of this genus, and also the ancestors of *Rhynchophion* and *Thyreodon*.

The hosts of *Dictyonotus* are apparently the larvae of Sphingidae (Townes *et al.*, 1965; Gauld & Mitchell, 1978; 1981).

EURYOPHION Cameron

Euryophion Cameron, 1906: 83. Type-species: *Euryophion nigripennis* Cameron, by monotypy.

Eurycamptus Morley, 1912: 27. Type-species: *Ophion latipenne* Kirby, by subsequent designation, Viereck, 1914: 57.

Thoracophion Roman, 1943: 22. Type-species: *Thoracophion ventrator* Roman (= *Ophion latipenne* Kirby), by monotypy.

Primophion Townes, 1971: 65. Type-species: *Primophion adustus* Townes, by original designation.

Rictophion Townes, 1971: 66. Type-species: *Euryophion nebulifer* Morley (= *Cymatoneura ikuthana* Kriechbaumer), by original designation. **Syn. n.**

Mandibles large, not twisted, weakly narrowed apically, subequally bidentate. Maxillary palp 3–5 segmented, labial palp 3–4 segmented; clypeus in profile flat or with apex out-turned, in anterior aspect usually with margin slightly concave. Ocelli small to large; frontal carina present or absent; occipital carina usually complete, rarely dorsally incomplete. Antennae rather stout, not longer than fore wing. Pronotum unspecialized, spiracular sclerite exposed; notauli weak or vestigial; epicnemial carina present ventrally, sometimes laterally absent; mesopleural furrow usually vestigial. Scutellum without lateral carinae; hind margin of metanotum at the most only weakly swollen before propodeal spiracle; posterior transverse carina of mesosternum absent except for lateral and rarely central vestiges. Propodeum with anterior area short, impressed as a deep trough; carinae virtually absent though their former position may be indicated by rugosities; posterior area from punctate to finely wrinkled to coriaceous. Fore wing with pterostigma slender; marginal cell moderately long; *Rs+2r* abruptly curved and thickened basally; discosubmarginal cell without a distinct fenestra, but usually with a small glabrous area in anterior corner; *1m–cu* fairly evenly curved, without a distinct ramellus. Hind wing with *Rs* from weakly to strongly curved. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli simple; inner hind tibial spur subcylindrical or slightly flattened, often with a reduced fringe of hairs; hind tarsal claws long and weakly curved, rarely with a small apical flange. Gaster stout, tergite 2 in profile short and deep, generally less than 3 times as long as deep posteriorly; thyridia present or absent; umbo vestigial; epipleuron pendant or up-turned. Ovipositor sheath slender, often concealed.

Although no character is a unique autapomorphy of this genus, the species share a large number of apomorphic features (p. 87). They resemble each other greatly in venation, shape of the gaster and form of the head. No other ophionines have reduced palpar segments nor do any have the claw flange found in some more specialized *Euryophion*. The initial analysis suggested that *Euryophion* is paraphyletic with respect to *Rictophion*. In order to resolve this matter further a more detailed analysis was undertaken using all species in the two genera, and this confirmed the paraphyletic nature of *Euryophion*. The sole representative of *Rictophion, R. ikuthana,* can be considered a specialized species of *Euryophion*, and it is on this basis that *Rictophion* is here treated as a synonym.

The more detailed analysis involved eight species, *E. latipennis* (201), *E. adustus* (202), *E. ikuthana* (203), *E. nigripennis* (204), *E. meridionalis* (205), *E. variegatus* (206), *E. vexatious* (207) and *E. pisinnus* (208). Eighteen characters from the original set (1·1, 8·1, 8·2, 9, 13, 18·2, 19, 27·2, 29·1, 29·2, 30, 36·1, 36·2, 37, 43·2, 54, 57 and 59) were used together with the following eight characters.

70 Labrum shape. In most ichneumonids the labrum is either semicircular or triangular, but broader basally than medially long; some *Euryophion* are specialized in having the labrum longer than broad (1).

71 Hind tarsal claw. In some *Euryophion* the hind claw is specialized in having a small flange near the apex (1).

72 *Rs* in hind wing. The moderately curved condition is considered plesiomorphic for *Euryophion*; in some taxa it is strongly curved (1).

73 Wing patterning. The plesiomorphic condition for ophionines (and members of out-groups) is unpatterned wings. In some *Euryophion* species the fore wings are distinctly patterned (1).

74 Wing ground colour. Transparent, virtually colourless wings are plesiomorphic for ophionines. The strongly infumate condition found in some *Euryophion* species is considered to be a derived feature (1).

75 *Rs* in fore wing. The plesiomorphic condition is for this vein to be simply arcuate. The sinuous condition of a few species of *Euryophion* is considered to be derived (1).

76 Rugosity of propodeum. The plesiomorphic condition for *Euryophion* species and related genera appears to be possession of at least some rugae close to the position of the vestigial carinae; the smooth, punctate propodeum of one *Euryophion* species is considered to be derived (1).

77 Hairiness of ovipositor sheath. The plesiomorphic condition for most ophionines, and other ichneumonids, is for the sheath to bear close, moderately long pubescence. The short sparse pubescence of one species is considered to be a derived characteristic (1).

The primary data matrix obtained (Table 20) was analysed using the methods outlined in the generic analysis. Characters 8·1, 18·2, 29·1, 29·2, 76 and 77 each have only a single derived state and therefore make no contribution to resolving phylogenetic relationships. A LeQuesne test on the remaining data set (Table 21) showed three characters (9, 59, 74) to be particularly homoplastic. Removal of these caused an improvement in the overall O/E ratio from 0·62 to 0·45. The high values evident in the labels matrix

Table 20 Primary data matrix for genus *Euryophion*. The taxa corresponding to the numbers are given in the text (p. 137).

	1.1	8.1	8.2	9	13	18.2	19	27.2	29.1	29.2	30	36.1	36.2	37	43.2	54	57	59	70	71	72	73	74	75	76	77
201	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
202	0	0	0	1	1	0	0	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	1	0	0	0
203	0	1	1	1	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
204	1	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0
205	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0
206	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	1	1	0	0	1	0	1	0	1	0	0
207	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	1	0	0	1	1	1	0	1	1	1
208	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	1	0	1	1	1	0	1	0	0

Table 21 Results of LeQuesne test on *Euryophion* data matrix. Conventions as in Table 2.

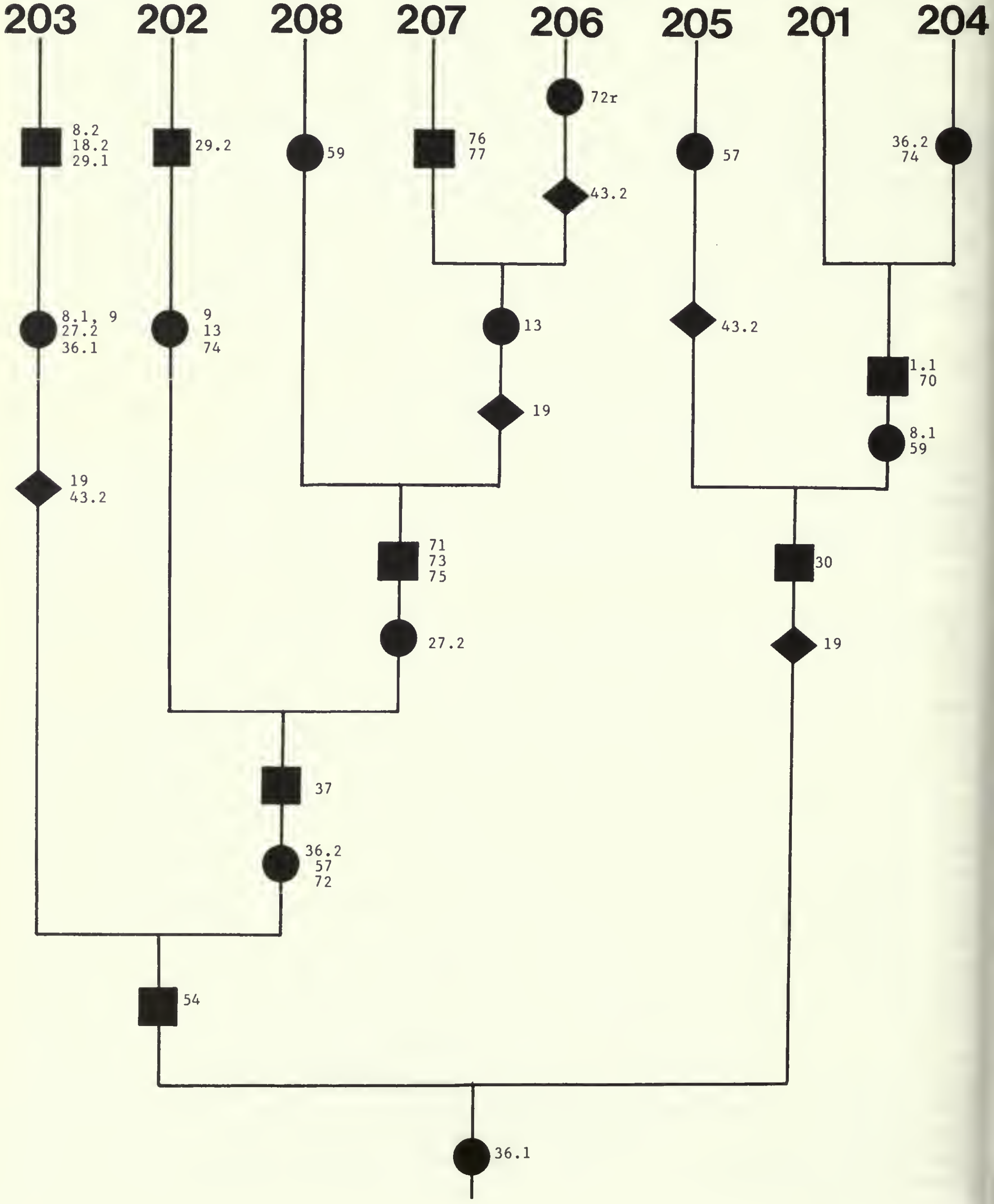
Character number:	Failures observed	expected	O/E ratio												
1.1:	2	9.3	0.22	8.1:	8	13.2	0.60	9 :	10	9.3	1.08	13 :	9	13.2	0.68
19 :	8	9.3	0.86	27.2:	10	14.1	0.71	30 :	6	13.2	0.45	36.2:	10	13.2	0.76
37 :	5	14.1	0.35	43.2:	12	13.2	0.91	54 :	6	13.2	0.45	57 :	8	13.2	0.60
59 :	13	13.2	0.98	70 :	2	9.3	0.22	71 :	5	13.2	0.38	72 :	8	13.2	0.60
73 :	5	13.2	0.38	74 :	12	9.3	1.29	75 :	5	13.2	0.38				

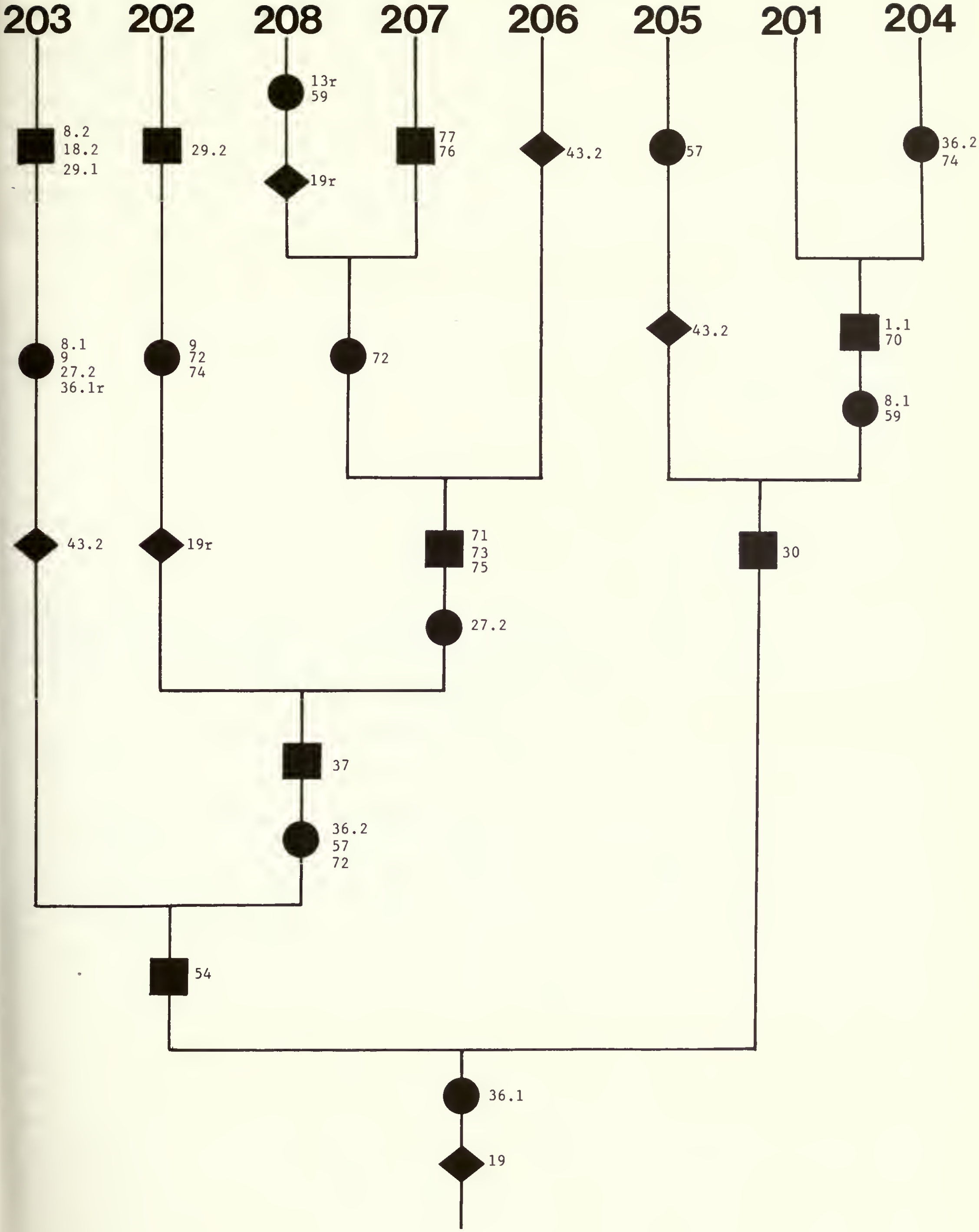
Grand totals-	failures observed	expected	O/E ratio
	72	116.7	0.62

Ranking ratios

1.1 70 37 71 73 75 30 54 8.1 57 72 13 27.2 36.2 19 43.2 59 9 74

(Appendix 9) strongly suggest parallelism for the derived state of character 9 (in taxa 202 and 203), of character 59 (in taxon 208 with respect to other taxa) and character 74 (in taxa 202 and 204). The single largest compatible clique comprises nine informative characters, 1·1, 8·2, 30, 37, 54, 70, 71, 73 and 75. These support a cladogram that resolves all taxa except 206–8 which remain as a trichotomy. Parsimony analysis yields two equally long minimum length trees which differ in their arrangement of taxa 206–8. There is little biological justification for preferring one or other of these two arrangements (Figs 30, 31) but the larger number of reversals involved in Fig. 31 mitigate marginally in favour of treating taxa 206 and 207 as sister-species.





Figs 30, 31 Alternative cladograms showing most parsimonious arrangement of species of *Euryophion*. Squares indicate autapomorphic developments; circles that an apomorphic feature has been derived in parallel in two separate lineages; diamonds that a feature has undergone three transformations.

All methods of analysis yielded similar results in suggesting that *E. latipennis* and *E. nigripennis* are very closely related, with the former possibly the ancestor of the latter. *E. meridionalis* was always placed on the sister-species to the clade *latipennis* + *nigripennis*, and these three taxa formed a rather distinct species-group. The three taxa whose interrelationship is difficult to resolve, *E. variegatus, E. vexatious* and *E. pisinnus*, form a very distinct clade whilst *E. ikuthana* and *E. adustus* are less closely related. Clearly it would be unsatisfactory to place *ikuthana* in a separate genus without at least creating separate genera for the *variegatus* species-group and the *latipennis* species-group. *E. adustus* could be incorporated into the former or also treated as a separate genus. As these insects are essentially similar animals that form a distinct group with respect to other ophionines, it is suggested that they be placed in a single genus, *Euryophion*, but to represent the phylogeny of the group four species-groups may be recognized. The formal classification may thus be summarized as follows.

EURYOPHION Cameron
        Rictophion Townes
  latipennis species-group
    latipennis (Kirby)
    nigripennis Cameron
    meridionalis (Morley)
  ikuthana species-group
    ikuthana (Kriechbaumer)
  adustus species-group
    adustus (Townes)
  variegatus species-group
    variegatus Gauld & Mitchell
    pisinnus Gauld & Mitchell
    vexatious Gauld & Mitchell

Euryophion is primarily an Afrotropical genus with one species, *E. vexatious*, inhabiting southern India (Gauld & Mitchell, 1978; 1981). This taxon is one of the most derived in the genus, and it is very closely related to two African species. This suggests that *Euryophion* may only have recently become established in the Oriental region. The data strongly suggest an African origin for the genus.

RHYNCHOPHION Enderlein

Rhynchophion Enderlein, 1912: 630. Type-species: *Rhynchophion odontandroplax* Enderlein, by original designation.

Mandibles stout, not twisted, barely narrowed distally, with lower tooth somewhat longer than the upper; outer mandibular surface more or less flat, with scattered hairs. Maxillary palp 5-segmented, labial palp 4-segmented; maxilla and labium elongate, projecting below apex of clypeus by about a distance equal to half the length of the head; clypeus in profile flat, with margin often slightly out-flared, in anterior aspect with median obtuse point. Ocelli small, the hind ones separated from the eye by at least their own diameter; frontal carina absent or present but weak; occipital carina complete, ventrally not joining hypostomal carina. Antennae short and stout, not as long as fore wing, and centrally with segments transverse. Pronotum unspecialized; spiracular sclerite exposed; notauli obsolescent; epicnemial carina present only ventrally, not extending onto mesopleuron; mesopleural furrow weakly impressed, horizontal. Scutellum convex, laterally carinate only at extreme anterior end; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area short, present as a deep transverse groove; propodeal carinae absent or with lateral longitudinal ones present as vestiges posteriorly; posterior area convex, rugose-reticulate grading to punctate. Fore wing with pterostigma very slender; marginal cell quite short; *Rs+2r* slightly bowed proximally, barely widened near pterostigma; discosubmarginal cell uniformly hirsute; *1m–cu* fairly evenly curved, without a ramellus. Hind wing with *Rs* very weakly bowed. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli simple; inner hind tibial spur cylindrical, without a fringe of long close hairs; hind tarsal claw long, weakly curved. Gaster stout; tergite 2 in profile about as deep posteriorly as long, sometimes deeper, with thyridia close to anterior margin; umbo absent; epipleuron up-turned. Ovipositor sheath slender.

Rhynchophion is a small genus restricted to the southern part of the U.S.A. and the Neotropical region. Three species have been described, but these may be variants of a single species. They differ principally in the colour of the wings and antennae.

THYREODON Brullé

Thyreodon Brullé, 1846: 150. Type-species: *Thyreodon cyaneus* Brullé, by subsequent designation, Hooker, 1912: 107.

Athyreodon Ashmead, 1900: 87. Type-species: *Athyreodon thoracicus* Ashmead (= *Ophion atriventris* Cresson), by original designation.

Tipulophion Kriechbaumer, 1901*b*: 75. Type-species: *Tipulophion gigas* Kriechbaumer (= *Ophion atriventris* Cresson), by monotypy.

Macrophion Szépligeti, 1905: 32. Type-species: *Macrophion ornatus* Szépligeti (= *Ophion atriventris* Cresson), by subsequent designation, Viereck, 1912: 640.

Oleter Shestakov, 1926: 259. Type-species: *Oleter selenaction* Shestakov (= *Thyreodon laticinctus* Cresson), by original designation.

Mandibles not twisted, massive, weakly to moderately narrowed distally, usually fairly evenly bidentate, or with lower tooth slightly the longer; outer mandibular surface flat except for a deep proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile from flat to slightly out-flared ventrally, generally with margin sharp; clypeus in anterior aspect with a median apical tooth. Ocelli usually small, the posterior ones widely separated from the eyes, or in a few species with ocelli very large, almost contiguous with eyes; frontal carina present, often very strong; frons medially unusual in many species in being quite strongly raised between the antennal bases; occipital carina present, usually complete, sometimes not reaching hypostomal carina ventrally. Antennae short and stout, central flagellar segments transverse. Pronotum mediodorsally specialized in having anterior and posterior margins raised to form flanges or transverse crests; spiracular sclerite exposed; notauli often strong, generally extending the entire length of the mesoscutum, frequently with crests across anterior ends; epicnemial carina complete, present on mesopleuron; mesopleural furrow absent. Scutellum rather small, moderately convex, either without lateral carinae, or, at most, with carinae present on anterior 0·4; posterior transverse carina of mesosternum present as lateral and central vestiges. Propodeum highly modified, with central part strongly swollen so anterior part is in a very deep groove, as is the spiracle, and with the metapleuron appearing unusually small; propodeal carinae absent, but usually with postero-dorsal surface of propodeum bearing a deep longitudinal concavity; posterior area otherwise from almost smooth to very strongly reticulate. Fore wing with pterostigma slender; marginal cell from short to moderately long; *Rs+2r* usually only slightly curved and weakly broadened before joining pterostigma; discosubmarginal cell without a glabrous area anteriorly; 1*m–cu* usually evenly curved, without a ramellus. Hind wing with *Rs* more or less straight. Fore tibial spur without a membranous flange behind the macrotrichial comb; mid and hind trochantelli simple; inner hind tibial spur cylindrical, without a pronounced marginal fringe of long close hairs; hind tarsal claws long and weakly curved. Gaster from moderately stout to long and slender; tergite 2 in profile from slightly to very elongate, with thyridia widely separated from anterior margin; umbo absent; epipleuron pendant, but often creased anteriorly. Ovipositor sheath slender.

Thyreodon is a New World genus with about 25 described species. The majority are diurnally active, and frequently seen feeding from flowers. These species are generally black or brightly coloured, and have small ocelli whereas a few nocturnal species are predominantly brown and have large ocelli. It is perhaps an interesting behavioural 'hangover' from their nocturnal ancestry, that predominantly diurnal species are quite frequently nocturnally active as well and are taken at light.

The centre of diversity of the genus appears to be in northern South America. One species extends as far north as Canada.

The *ENICOSPILUS* genus-group

This is the largest genus-group in the subfamily, containing both the greatest number of genera and species; it also contains some of the most morphologically specialized of all ophionines. The 14 genera in this group can be divided into five subgroups (the *Orientospilus, Ophiogastrella, Stauropoctonus, Leptophion* and *Enicospilus* subgroups) which correspond with the main evolutionary lineages apparent in the group. The holophyly of this group is supported by a single apomorphy, the loss of the vestigial first laterotergites, which is not a particularly convincing reason for uniting the component genera. However, all share a number of other features, including the complete atrophy of the flange on the fore tibial spur, though this feature is shared with the *Thyreodon* genus-group. It is possible that the *Enicospilus* group may be paraphyletic with respect to the *Thyreodon* group but this relationship could not be resolved further with the characters and material at hand. The majority of genera in this group (that is the *Stauropoctonus, Leptophion* and *Enicospilus* subgroups) clearly constitute a holophyletic group (see Fig. 19); the *Ophiogastrella* subgroup would seem to be the sister-lineage to these. The position of the *Orientospilus* subgroup is less clear, but it seems reasonably placed as the most primitive extant lineage of the group.

This genus-group is primarily a Pan-tropical complex of genera. Only isolated species of *Simophion, Stauropoctonus, Dicamptus* and *Enicospilus* occur in the Holarctic region. The hosts of the majority of species appear to be tree- and shrub-feeding lepidopterous larvae, though only a small percentage of all the species has been reared.

The *ORIENTOSPILUS* subgroup

This group contains three genera, *Orientospilus, Simophion* and *Prethophion.* The systematic position of the latter genus is far from clear as it is united with *Orientospilus* and *Simophion* solely on the basis of a weak character – an incomplete posterior transverse carina of the mesosternum – and its present position is really only the most parsimonious possible. *Prethophion* does share certain features with *Thyreodon* – it has a slightly twisted mandibular axis, though not as pronounced as that of species in the *Thyreodon* lineage, and a similarly stout gaster; like species of the *Thyreodon* lineage the anterior margin of the tegula is not reflexed (possibly a derived feature). However, the plesiomorphic form of the anterior part of the propodeum and tarsal claws seem to exclude *Prethophion* from the *Thyreodon* group as here defined. Furthermore, the first laterotergite is lost and the mandibles are specialized in a quite different way, and much more closely resemble the derived form found in *Orientospilus.*

Simophion and *Orientospilus* are more convincingly related; both have a similarly modified clypeus, have a basally angulate *Rs+2r* in the fore wing, have lost the epicnemial carina laterally and have a short marginal cell.

ORIENTOSPILUS Morley

Orientospilus Morley, 1912: 6. Type-species: *Orientospilus individuus* Morley, by subsequent designation, Morley, 1913: 378.

Mandibles not twisted, long, strongly and evenly tapered, with upper tooth much longer than the lower; outer mandibular surface flat, sparsely hirsute. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile flat with margin out-flared; in anterior aspect concave. Ocelli moderately large, the posterior ones separated from the eyes by 0·3–1·3 times their minimum diameter; frontal carina absent; occipital carina complete, though ventrally not reaching hypostomal carina. Antennae moderately stout, the distal segments quadrate, the flagellum barely longer than the fore wing. Pronotum mediodorsally with anterior and posterior margins reflexed, raised as keels; spiracular sclerite exposed; notauli absent; epicnemial carina present ventrally, not reaching above level of lower corner of pronotum; mesopleural furrow vestigial or absent. Scutellum quadrate, weakly to moderately convex, with lateral longitudinal carinae complete; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area short, deeply impressed as groove; anterior transverse carina from complete to obsolescent, other carinae absent; posterior area coarsely reticulate, usually medially concave. Fore wing with pterostigma of moderate breadth, evenly narrowed distally; marginal cell short; *Rs+2r* curved and broadened before joining pterostigma; discosubmarginal cell with a glabrous area anteriorly; 1*m–cu* evenly arcuate without a ramellus. Hind wing with *Rs* from virtually straight to curved abruptly proximally. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; hind inner tibial spur more or less flattened, with margin of long close hairs; hind tarsal claw unspecialized. Gaster slender; tergite 2 in profile elongate, with thyridia obsolescent, or if discernible, small and quite close to anterior margin; umbo present; epipleuron usually up-turned, rarely, in some individuals, the posterior part is pendant. Ovipositor sheath slender.

This small genus contains three described species, *capitatus* Gauld & Mitchell from southern and west Africa, *melasma* Townes from Madagascar and *individuus* Morley from eastern peninsular India. Structurally these are very similar insects. The Madagascan species is the least specialized; both the Indian and African species have lost the anterior transverse carina of the propodeum and have a shorter, stouter and apically more setaceous flagellum and have a broader malar space suggesting they are sister-species (Fig. 32). The Madagascan species may well be the ancestor of the other two.

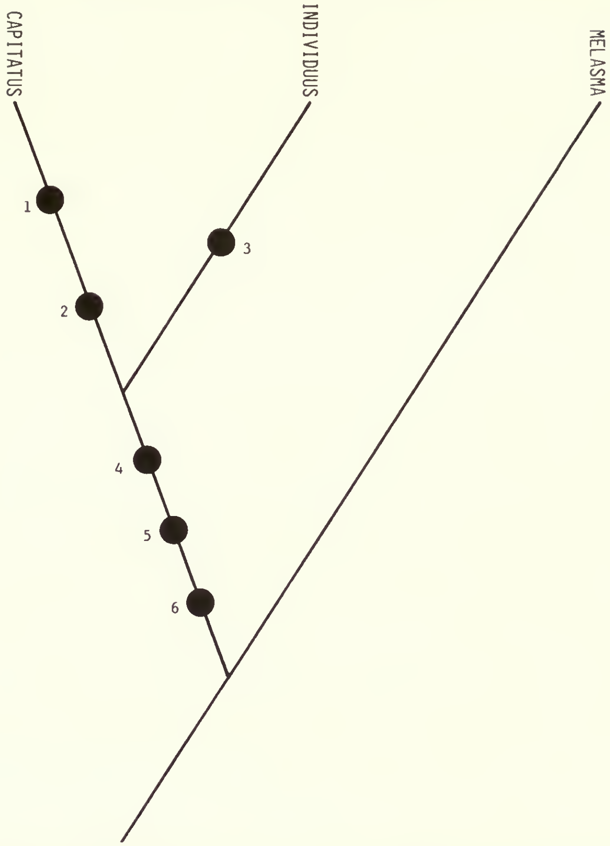


Fig. 32 Putative phylogenetic arrangement of species of *Orientospilus*. This cladogram is supported by the following apomorphic features: 1, malar space very wide; 2, ocelli widely separated from eyes; 3, *Rs* in hind wing curved proximally; 4, flagellum with proximal segments almost quadrate; 5, anterior transverse carina of propodeum absent; 6, malar space moderately wide, at least 0·4 times basal mandibular width.

PRETHOPHION Townes

Prethophion Townes, 1971: 74. Type-species: *Prethophion latus* Townes, by original designation.

Mandibles very slightly twisted, very strongly narrowed, subequally bidentate; outer mandibular surface slightly convex, with a proximal concavity. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile almost flat, margin centrally blunt, clypeus in anterior aspect virtually almost truncate. Ocelli large, the posterior ones more or less touching eyes; frontal carina absent; occipital carina entirely absent. Antennae moderately slender, barely longer than fore wing but with central segments clearly elongate. Pronotum unspecialized; spiracular sclerite exposed; notauli vestigial; epicnemial carina present on mesosternum, present but very weak on mesopleuron; mesopleural furrow very distinct, oblique, extending from episternal scrobe to subalar prominence, the speculum posterodorsal to this carina strongly inflated. Scutellum convex, laterally carinate only on extreme anterior end; posterior transverse carina of mesosternum absent except for lateral vestiges. Propodeum short and abruptly declivous posteriorly; anterior area unspecialized; anterior transverse carina complete; blunt tubercles (which are possibly vestiges of posterior transverse carina) discernible; posterior area concave, very finely alutaceous. Fore wing with pterostigma moderately slender; marginal cell slender; *Rs+2r* proximally not broadened, almost straight; discosubmarginal cell without a glabrous area anteriorly; *1m–cu* fairly evenly curved, without a ramellus. Hind wing with *Rs* strongly curved. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli not specialized; inner hind tibial spur flattened, with a margin of long close hairs; hind tarsal claw unspecialized. Gaster quite stout, centrally almost cylindrical;

tergite 2 in profile elongate, with thyridia close to anterior margin; umbo low but distinct; epipleuron up-turned. Ovipositor sheath stout.

This enigmatic genus contains a single species which occurs at low altitudes in Peru and Bolivia. Nothing is known of its biology.

SIMOPHION Cushman

Simophion Cushman, 1947: 446. Type-species: *Simophion excarinatus* Cushman, by original designation.

Mandibles fairly evenly tapered, not or barely twisted, subequally bidentate or with lower tooth slightly the shorter; outer mandibular surface punctate, proximally concave. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile flat, apically sometimes slightly out-flared, in anterior aspect concave. Ocelli moderately large, the posterior ones separated from eye by 0·2–0·7 times their maximum diameter; frontal carina absent; occipital carina complete, though generally not reaching hypostomal carina ventrally. Antennae moderately long and slender, about 1·4–1·6 times length of fore wing. Pronotum unspecialized; spiracular sclerite exposed; notauli vestigial; epicnemial carina present ventrally, not reaching onto mesopleuron laterally; mesopleural furrow weak, diagonal, extending from episternal scrobe to near subalar prominence. Scutellum moderately convex, narrow, without lateral carinae; posterior transverse carina of mesosternum present only laterally as vestiges. Propodeum with anterior area short, striate slightly centrally; anterior transverse carina absent as are other propodeal carinae, the propodeum being narrowed distally; marginal cell short; *Rs+2r* very abruptly angled before joining pterostigma, its extreme end abruptly broadened; discosubmarginal cell very sparsely hirsute, with a glabrous area anteriorly; 1*m–cu* curved or sinuous, without a ramellus. Hind wing with *Rs* very strongly bowed. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of long hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 in profile elongate, with thyridia obsolescent, or if present quite large and relatively close to anterior margin of tergite; umbo distinct; epipleuron up-turned. Ovipositor sheath slender.

This moderately small genus is restricted to the 'Mediterranean' type biomes of the northern hemisphere. Two species occur in the Middle East and Central Asia (Horstmann, 1981), whilst five or six occur in the south-west of the United States (Townes, 1971). Similar disjunct distributions occur in several genera of lower Aculeata (M. C. Day, pers. comm.) and in the myrmicine ant genus *Messor* (Bolton, 1982). Amongst ophionines *Eremotylus* has a similar, though slightly more extensive distribution.

The *OPHIOGASTRELLA* subgroup

This group comprises a single Neotropical genus, *Ophiogastrella*, which was treated as a member of the *Ophion* genus-group by Cushman (1947), but as a member of the Enicospilini by Townes (1971). Townes & Townes (1973) considered it to be closely related to *Laticoleus*.

Structurally *Ophiogastrella* shows a remarkable combination of primitive and derived features. The specialized fore tibial spur and first laterotergite suggest it belongs close to the base of the *Enicospilus* lineage, but the well-developed umbo, exposed spiracular sclerite and unspecialized anterior part of the propodeum suggest it is more primitive than many other genera. These features, together with the lack of an impressed clypeal apex, externally flat mandible and slender ovipositor sheath suggest it is not at all closely related to *Laticoleus*. The peculiar male claws are an autapomorphy of this taxon.

Ophiogastrella is confined to the southern part of Central America and northern South America. There is no evidence to suggest the group has ever occurred elsewhere.

OPHIOGASTRELLA Brues

Ophiogastrella Brues, 1912: 201. Type-species: *Ophiogastrella maculithorax* Brues, by original designation.

Brachyscenia Enderlein, 1921: 36. Type-species: *Brachyscenia nigriventris* Enderlein, by original designation.

Mandibles not twisted, evenly but only moderately narrowed apically, subequally bidentate; outer mandibular surface flat except for small proximal concavity, centrally with scattered hairs. Maxillary palp 5-segmented; labial palp 4-segmented; clypeus in profile flat or weakly convex, margin blunt or sharp, never impressed; clypeus in anterior aspect weakly convex, straight or very slightly concave. Ocelli large, the posterior ones generally very close to the eyes; frontal carina absent; occipital carina complete, ventrally (as genal carina) usually sharply angled and complete to hypostomal carina. Antennae of moderate length, 1·2–1·5 times the length of the fore wing, rarely slightly longer. Pronotum unspecialized; spiracular sclerite exposed; notauli absent; epicnemial carina complete; mesopleural furrow absent or weakly impressed, diagonal, extending from episternal scrobe to near subalar prominence. Scutellum weakly to moderately convex, with lateral longitudinal carina extending about 0·8 of its length; posterior transverse carina of the mesosternum vestigial. Propodeum with anterior area short, unspecialized; anterior transverse carina from complete to absent, other carinae at most present only as vestiges; posterior part of propodeum generally rather smooth. Fore wing with pterostigma quite large and broad; marginal cell long; *Rs+2r* curved or slightly angled proximally, from slender to moderately broadened; discosubmarginal cell with a small glabrous area anteriorly; *1m–cu* very strongly and evenly curved, without a ramellus. Hind wing with *Rs* from almost straight to strongly bowed. Fore tibial spur without a membranous flange behind the macrotrichial comb; mid and hind trochantelli simple or with a blunt tooth near distal margin; inner hind tibial spur flattened, with a fringe of close hairs; hind tarsal claws of female unspecialized, of male flattened with pectinal comb present on both sides (Fig. 47). Gaster moderately slender; tergite 2 in profile elongate, with thyridia remote from anterior margin; umbo quite well developed; epipleuron generally upturned. Ovipositor sheath slender.

Ophiogastrella is a small genus containing about 10 species, of which only three are described (Townes & Townes, 1966). They are restricted to the Neotropical region from Costa Rica to about 10°S in Brazil, and seem to be associated with areas which have a pronounced dry season.

The species are rather similar to each other, and best separated by differences in the length of *3r–m*, shape of *Rs* in the hind wing and sculpture of the propodeum. There are also more subtle differences in the shape of the clypeus, and the head.

The *STAUROPOCTONUS* subgroup

This subgroup contains two genera, *Stauropoctonus* (including as a synonym *Aulophion*) and *Lepiscelus*. The exposed spiracular sclerites of species in this complex suggest it is one of the more primitive of enicospiline lineages. It is also one of the taxonomically most distinctive as its members are characterized by an incomplete occipital carina, a transverse mesopleural furrow, slender pterostigma, basally thickened and bent *Rs+2r* and a very sinuous *1m–cu*. Most species have *1m–cu* and Cu_{1a} basally widely separated, and all have the mid and hind trochantelli specialized.

The group contains few species. The most primitive *Stauropoctonus* species and the solitary *Lepiscelus* occur in the Old World, suggesting an Old World origin for the group.

LEPISCELUS Townes

Lepiscelus Townes, 1971: 73. Type-species: *Lepiscelus gracile* Townes (= *Eremotylus distans* Seyrig), by original designation.

Mandibles twisted about 5°, proximally strongly narrowed, distally parallel-sided with upper tooth about twice as long as the lower; outer mandibular surface more or less flat. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin narrowly acute, laterally blunted, short, exposing labrum; clypeus in anterior aspect truncate or even slightly concave. Ocelli large, the hind ones very close to the eyes; frontal carina absent; occipital carina entirely absent. Antennae very long and slender, about 1·7 times length of the fore wing. Pronotum mediodorsally rather long, flat; spiracular sclerite exposed; notauli very short but often strongly impressed in part; epicnemial carina weak, laterally becoming obsolescent at level of lower corner of pronotum; mesopleural furrow very weakly impressed, transverse. Scutellum almost rectangular, carinate laterally only at extreme anterior end; posterior transverse carina of mesosternum complete. Propodeum with anterior area moderately long, dorsally without carinae, with posterior area finely wrinkled to rugulose. Fore wing with pterostigma slender; marginal cell long; *Rs+2r* abruptly curved and broadened before joining pterostigma; discosubmarginal cell anteriorly glabrous; *1m–cu* very strongly sinuate. Hind wing with *Rs* strongly curved; hamuli arranged in two groups, the proximal group comprising two which are longer and flatter than those in the distal group of three. Fore tibial spur without a membranous flange behind the macrotrichial comb; mid and hind trochantelli extended apically as a broad flange over the proximal end of the femur; inner hind tibial spur flattened, with a margin of long, close hairs; hind tarsal claws quite long, those of male more closely pectinate than those of the female. Gaster slender; tergite 2 in profile elongate, with thyridia remote from anterior end; umbo vestigial; epipleuron up-turned. Ovipositor sheath slender; male with gonosquama unusually long.

Lepiscelus contains a single species which is widespread, but apparently rather uncommon, throughout the Afrotropical region between latitude 10°N and 20°S. The most distinctive feature of this genus is the flanged mid and hind trochantelli which are, amongst the Ichneumonidae, a unique feature of *Lepiscelus distans*. Nothing is known of the biology of this insect, but the form of the mandibles and head shape are reminiscent of some species of *Enicospilus* that either inhabit arid areas or are active in the dry season.

STAUROPOCTONUS Braun

Stauropoctonus Brauns, 1889: 75. Type-species: *Ophion bombycivorus* Gravenhorst, by monotypy.
Stauropodoctonus Morley, 1913: 375. [Unjustified emendation.]
Nipponophion Uchida, 1928: 201. Type-species: *Nipponophion variegatus* Uchida (= *Ophion bombycivorus* Gravenhorst), by monotypy.
Aulophion Cushman, 1947: 458. Type-species: *Aulophion bicarinatus* Cushman, by original designation. **Syn. n.**

Mandibles twisted about 85°, evenly, but quite strongly narrowed apically, subequally bidentate. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, in anterior aspect with margin slightly convex. Ocelli large, the posterior ones close to eye margins; frontal carina absent; occipital carina usually absent, partially present in one species. Antennae very long and slender, sometimes up to 2 times length of fore wing. Pronotum unspecialized, spiracular sclerite exposed; notauli vestigial or absent; epicnemial carina from present and complete to absent; mesopleural furrow strong, extending from episternal scrobe to upper end of prepectal carina (or the corresponding position if this carina is absent), in some species impressed as a deep groove. Scutellum moderately convex to convex, either without lateral carinae or with carina incomplete; posterior transverse carina of mesosternum from complete to reduced to lateral vestiges. Propodeum with anterior area long; anterior transverse carina usually complete, the posterior one sometimes discernible; posterior area from weakly rugulose to reticulate. Fore wing with pterostigma moderately slender; marginal cell long; *Rs+2r* abruptly curved and slightly thickened basally; discosubmarginal cell with a glabrous area anteriorly, which may be expanded along *Rs+2r*; *1m–cu* without a ramellus, either evenly bowed or sinuous. Hind wing with *Rs* from almost straight to weakly bowed. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli specialized in having the outer distal margin produced into a strongly decurved sharp spine; inner hind tibial spur flattened, with a marginal fringe of long hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 in profile very elongate, with the thyridia remote from anterior margin; umbo vestigial; epipleuron pendant or up-turned. Ovipositor sheath slender.

In the analysis of the genera *Stauropoctonus* appeared to be paraphyletic with respect to *Aulophion*. The latter genus has been separated from *Stauropoctonus* by possession of two apomorphic features (Cushman, 1947; Townes, 1971). No apomorphies have ever been suggested for *Stauropoctonus*, though the clade *Stauropoctonus* + *Aulophion* is one of the most clearly defined in the subfamily. It is characterized by the following combination of apomorphies (though none is actually unique to the clade) – at least partial loss of occipital carina; presence of projections on mid and hind trochantelli; presence of impressed transverse furrow on mesopleuron; presence of strongly twisted mandibles; having *Rs+2r* in the fore wing basally angled. In addition to these features the head and mesoscutal profile of species of this clade are characteristic, though these 'apomorphies' are so subtle I have not been able to code them. To further resolve the relationship between *Aulophion* and *Stauropoctonus* more data were analysed.

The following taxa were included – *Aulophion* sp. 1 (? *bicarinatus*) (301), *Aulophion* sp. 2 (302), *Stauropoctonus bombycivorus* (303), *S. torresi* (304), *S. townesorum* (305) and *S. occipitalis* (306). This is all the species in the group except for one (or possibly two) *Aulophion* species which are very closely related to taxon 302. To represent the range of interspecific variation in the group the following characters from the primary set were utilized – 1·2, 19, 20·1, 24·1, 25·2, 27, 30, 36, 43·1, 43·2, 44·1, 45·2, 47·2, 57 and 59. (It is noteworthy that 27 and 36 are composites of 27·1 and 27·2 and 36·1 and 36·2 respectively; these characters showed identical state distribution over the data and therefore were treated as single characters to avoid excess weighting.) In addition to these fifteen, three further characters were used.

80 Median carina of propodeum. This apomorphic feature (1) is found only in a few isolated Neotropical ophionines. The plesiomorphic condition, no median carina, is found in virtually all ophionines and members of the various out-groups.

81 Metapleural sculpture. In most out-group taxa, most ophionines and several species of this group the metapleuron is smooth and finely punctate. Some *Stauropoctonus* species are specialized in having this region coarsely rugose (1).

82 Position of *cu–a* with respect to *Rs&M* in fore wing. The plesiomorphic condition for ophionines apparently is for *cu–a* to be proximal to the base of *Rs&M*. A few *Stauropoctonus* are specialized in having these veins opposite (1).

Table 22 Primary data matrix for genus *Stauropoctonus*. The taxa corresponding to the numbers are given in the text (p. 146).

	1.2	19	20.1	24.1	25.2	27	30	36	43.1	43.2	44.1	45.2	47.2	57	59	80	81	82
301	1	1	0	0	0	1	1	1	1	1	1	1	0	1	0	1	0	0
302	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0
303	1	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0
304	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1
305	1	0	0	0	1	0	0	1	0	1	0	1	0	1	1	0	1	1
306	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0

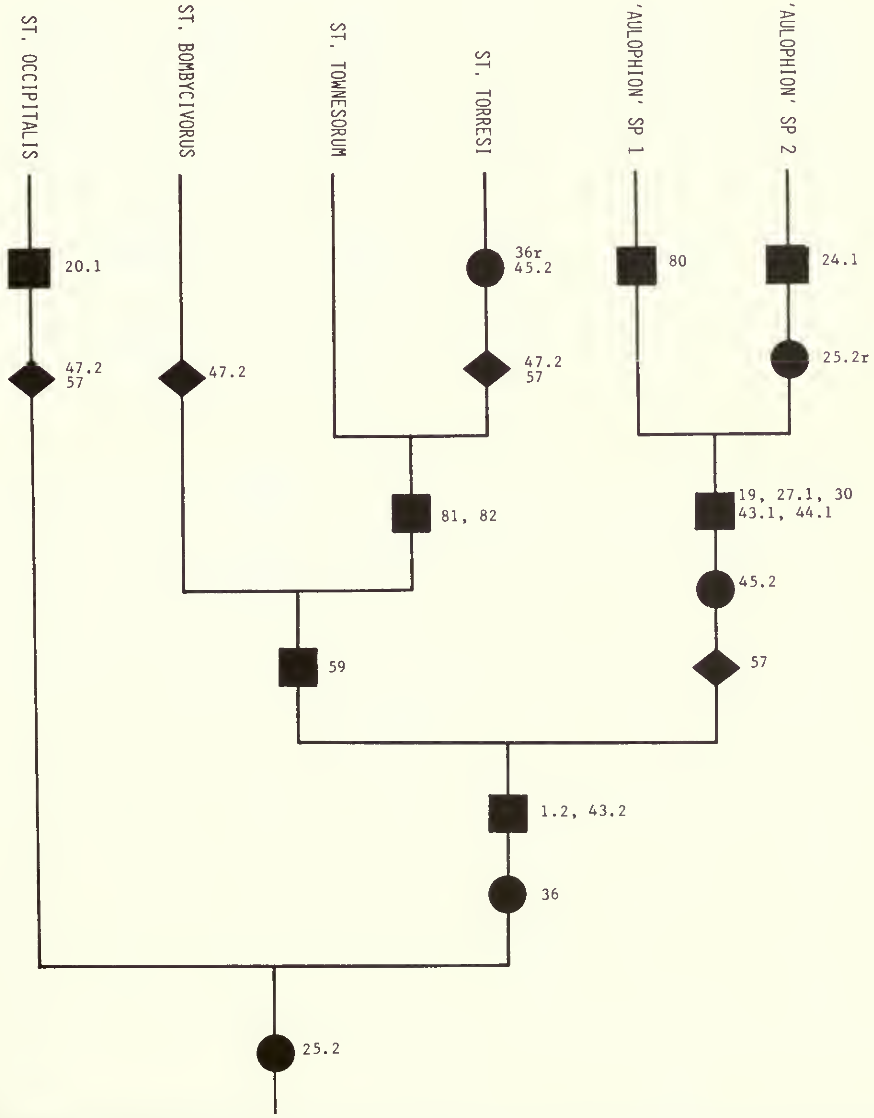


Fig. 33 Favoured cladogram showing putative phylogenetic arrangement of species of *Stauropoctonus*. This is based on the largest compatible set of ten informative characters and requires 25 transformation steps.

The primary data matrix for taxa 301–6 is shown in Table 22. Parsimony and compatibility analyses, using techniques outlined above, yielded two 'best' alternative hypotheses of phylogenetic relationship (Figs 33, 34). The cladograms have a large number of features in common. Firstly, both suggest *Stauropoctonus* is paraphyletic with respect to *Aulophion*, and this in turn suggests that *Aulophion* can be treated as a synonym of *Stauropoctonus*, as has been formally proposed above. Secondly, both suggest that

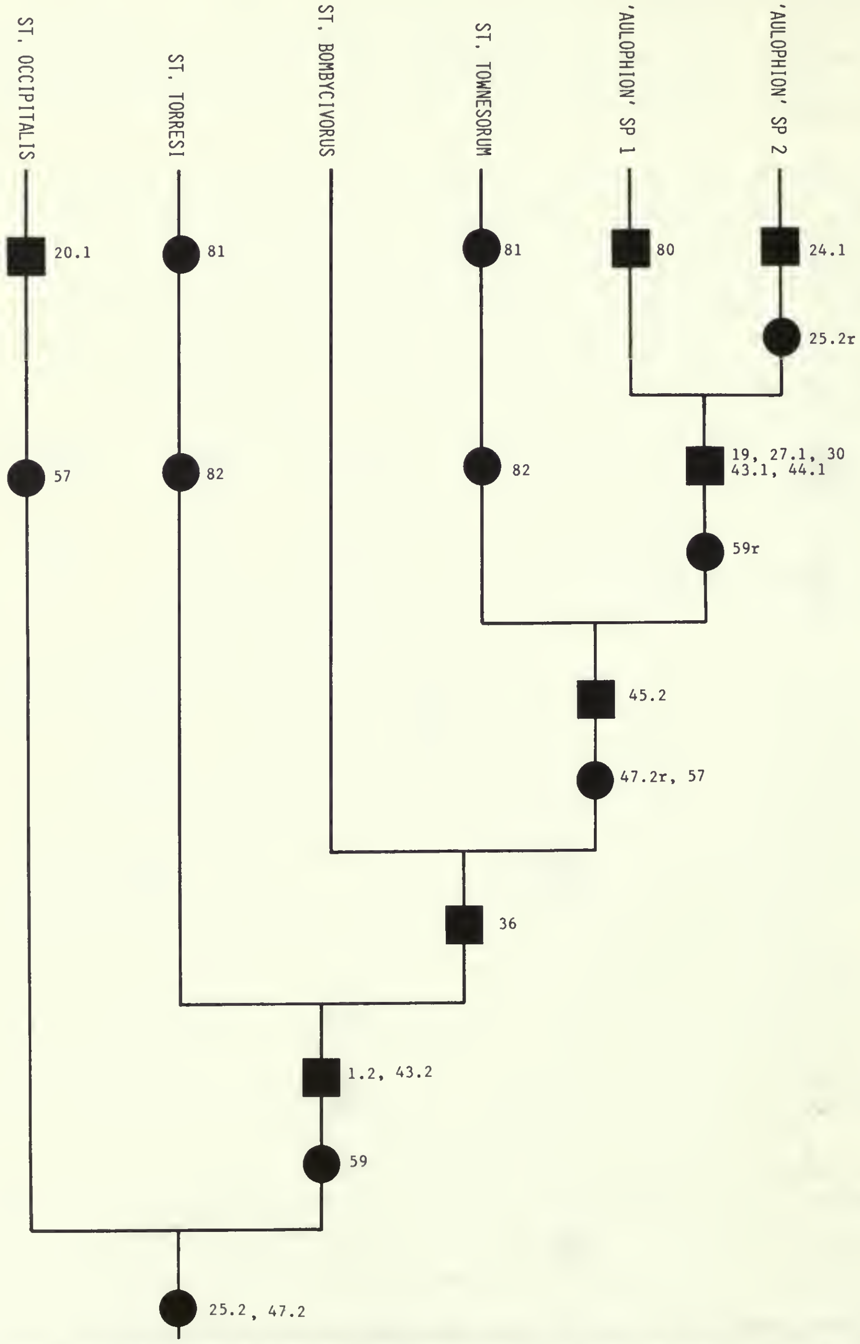


Fig. 34 Alternative cladogram for species of *Stauropoctonus*. This is the most parsimonious arrangement of taxa discovered and requires 24 transformation steps. (Symbols as for Figs 30–31.)

Aulophion is both a holophyletic clade and the most derived lineage in the group. Thirdly, both place *S. occipitalis* as the most primitive taxon in the group. The two cladograms differ in their arrangement of *S. bombycivorus, S. torresi* and *S. townesorum* and these different arrangements depend on the alternative compatible sets of characters 36 and 45·2 versus 59, 81 and 82. Character 36 has been demonstrated to be both unreliable and of dubious polarity, whilst 45·2 can be regarded as a loss apomorphy (loss of hairs on wing membrane). Character 59 (colour of interocellar area) is also far from a convincing apomorphy, but 81 and 82 strongly suggest that *torresi* and *townesorum* are sister-species. *S. bombycivorus* is rather difficult to place, but could be either the ancestor of, or a close relative of the ancestor of both the '*Aulophion*' species-group and *torresi*/*townesorum*.

The more primitive species of this genus (*occipitalis* and *bombycivorus*) are restricted to the Old World, the former to the mountains of Madagascar and the latter to the southern part of the Palaearctic, except in Asia where it extends north into Kamchatka and the Kurile Islands (Townes, Momoi & Townes, 1965). Possibly the ancestor of these taxa was widely distributed in the Old World at one time, and the Madagascan survivor is a relict of this. There are clear indications in the Madagascan fauna of an ancient Palaearctic affinity amongst the Hymenoptera. The symphytan taxon Cephidae is represented on the island and in the Holarctic only (Benson, 1935), and a number of ichneumonid genera have rather similar distributions, e.g. *Neliopisthus, Euceros* (Townes, 1969: Barron, 1978). As the widespread Palaearctic species *bombycivorus* may be almost directly ancestral to the two other species-groups, it may at one time have also occurred in the Nearctic region. The *torresi*/*townesorum* group is Malesian/Melanesian, with the former species constituting part of the characteristically intrusive, Indo-Papuan faunal element in northern Australia (Gauld, 1984*a*). The distribution of *torresi*, in transcending both Wallace's and Weber's lines, suggests its current range is the result of a dispersive rather than a vicariance event. The Neotropical species form a rather distinctive clade. The most northerly extent of their distribution seems to be Costa Rica where one species occurs in lower montane (1000–1500 m) forest, whilst none has been found south of 25°S. Perhaps the ancestor of this group reached South America from the north during the Miocene when an archipelagic connection existed between the two continents (Rich & Rich, 1983). This evolutionary 'scenario' is based on the supposition that a *Stauropoctonus* occurred in the United States. At present there is no evidence for this; the scenario presented is merely the most parsimonious interpretation of data. Other scenarios would necessitate advocating much more widespread extinction.

The *LEPTOPHION* subgroup

This complex of genera is characterized by the form of the mandibles, which have a more or less discernible impressed groove extending diagonally, the convex clypeus with an impressed acute margin, the very long slender antennae and, for most species, a somewhat broadened ovipositor sheath. The venation of all species is rather similar in having *Rs+2r* basally broadened, and often angulate before joining the pterostigma; *1m–cu* is either sinuate or evenly curved.

This subgroup contains three genera, *Leptophion, Laticoleus* and *Pamophion* which are difficult to resolve as the holophyly of *Leptophion* cannot convincingly be demonstrated. *Pamophion*, a monobasic taxon, is holophyletic and is apparently the sister-lineage of *Leptophion* + *Laticoleus*. The latter is a holophyletic group, but it may have arisen from within the former. The only apomorphy that can be postulated for *Leptophion* is the presence of a specialized penultimate hamulus. (The apomorphies shown in Fig. 19 are subject to much exception and parallelism in some species of *Laticoleus*, and reference to the overall classification suggests that presence of a complete posterior transverse carina of the mesosternum is plesiomorphic for this complex – though some taxa have partially lost this carina.) The assumption that the specialized hamulus is a group apomorphy necessitates speculating that reversal has occurred in several taxa, but there is some evidence that this has happened. For example, *L. tetus* has a slight indication of some enlargement of the hamulus and its sister-species, *L. yampus*, has it clearly specialized, though not as large as that of *L. iochus*, the sister-species of *yampus* + *tetus*. *L. ankylosus* and *L. eithos* are highly specialized species (without a modified hamulus) which are closely related to *L. vernalis* which has a long penultimate hamulus, and *Leptophion* species 1 (BMNH) which has it only slightly modified. These four species apparently belong to the *maculipennis* lineage, the remainder of which all have a highly specialized hamulus. A tentative phylogeny for this subgroup is proposed in Fig. 35. *Laticoleus* is retained as a separate genus, but its validity needs to be reassessed as more material becomes available for study and the phylogeny of the species of *Leptophion* is better understood.

Judging from the present distribution of this group (Fig. 36) it is most parsimonious to postulate an Old World origin for this complex of genera. The more primitive taxa are restricted to Melanesia or Australia which suggests an Australo-Melanesian origin for this group. However, if *Laticoleus* is truly primitive with respect to *Leptophion*, then an alternative hypothesis is that this group was once widely spread in the Old

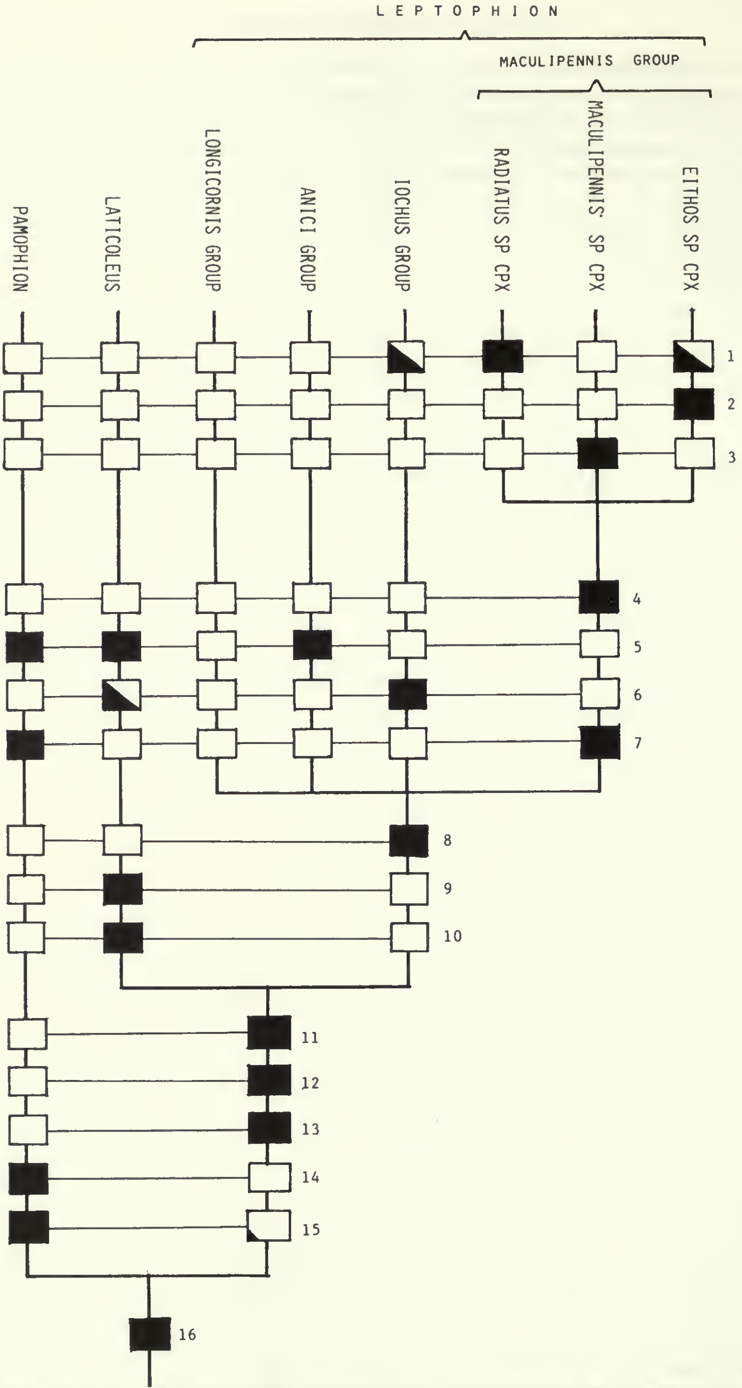


Fig. 35 Cladogram showing putative phylogeny of groups of species in the *Leptophion* subgroup. Black squares represent apomorphic features, white plesiomorphic; diagonally divided squares indicate a mixture of the two states in the component species of a particular lineage. The characters that support this arrangement are: 1, loss of specialized hamulus; 2, *Rs*+*2r* emitted from centre of pterostigma; 3, 1*m–cu* very sinuous; 4, specialized hind tarsal claws; 5, loss of posterior transverse carina of mesosternum; 6, presence of a 'hair brush' on mandible; 7, genal carina evanescent before joining hypostomal carina; 8, lengthened penultimate distal hamulus; 9, exceptional broad ovipositor sheath that in profile is almost quadrate; 10, long malar space; 11, ovipositor sheath at least moderately broad, in profile more than 0·4 times as deep as long; 12, marginal cell of hind wing at least partially glabrous; 13, anterior area of propodeum elongate; 14, epipleuron 2 pendant; 15, hind trochantellus marginally produced into blunt tooth; 16, posterior transverse carina of mesosternum present.

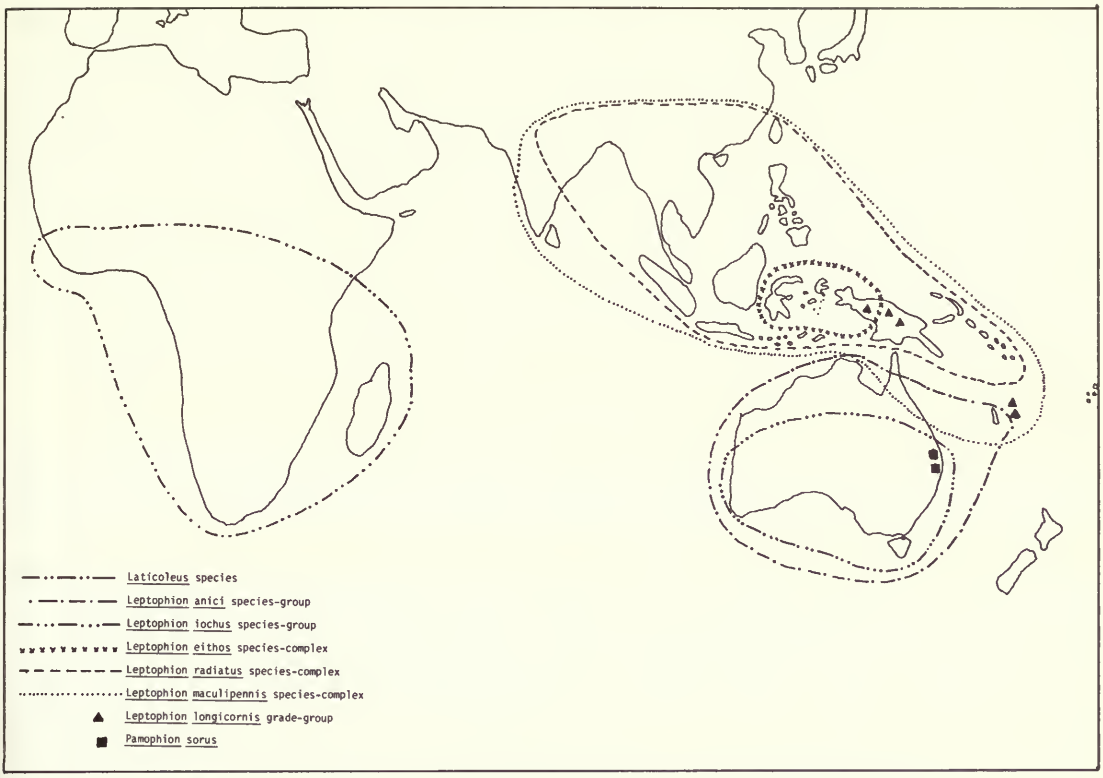


Fig. 36 The geographical distribution of taxa of the *Leptophion* subgroup.

World tropics and has suffered considerable extinction, leaving only a rather specialized primitive lineage in the Afrotropical region and a few relicts east of Wallace's line. Gauld (1984*a*) suggested that the *anici* and *iochus* groups of *Leptophion*, in Australia, have had a northern origin, and that once their ancestors had adapted sufficiently to cross the rain forest/savannah interface (Taylor, 1972) then they had ample opportunity to give rise to radiations in species-poor Australia (Gauld, 1984*a*). The most specialized group of *Leptophion*, the *maculipennis* group, is best represented in the more easterly parts of Indonesia and Melanesia. It is probable that this species-group arose in this area and a few species have spread west to the Asian mainland.

LATICOLEUS Townes

Laticoleus Townes, *in* Townes & Townes, 1973: 358. Type-species: *Coiloneura unicolor* Szépligeti, by original designation.

Mandibles not twisted, weakly narrowed apically, generally subequally bidentate; outer mandibular surface with subbasal swelling weak or well developed, with a diagonal groove extending from the upper proximal corner to between bases of teeth. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, in anterior aspect with margin weakly convex. Ocelli generally moderately large, the posterior ones separated from the eyes by 0·2–1·0 times their minimum diameter; frontal carina absent; occipital carina complete, the lower part (genal carina) reaching to hypostomal carina. Antennae very long and slender, at least 1·5 times length of fore wing. Pronotum usually unspecialized, or in one Madagascan species with anterior margin mediodorsally expanded and curved back; spiracular sclerite partially concealed; notauli vestigial or absent; epicnemial carina complete, weak or even absent on mesopleuron; mesopleural furrow undeveloped. Scutellum weakly convex, with lateral longitudinal carinae present, more or less complete; posterior transverse carina of the mesosternum incomplete, present as lateral or rarely central vestiges. Propodeum with anterior area moderately long, striate or smooth; anterior transverse carina present or absent, other carinae usually absent; posterior area from rugose to virtually smooth. Fore wing with pterostigma moderately stout; marginal cell long; *Rs+2r* conspicuously thickened near pterostigma, often abruptly curved in proximal part; discosubmarginal cell with a glabrous area in anterior corner, this area generally quite large, and in one species, bearing a weak sclerite; 1*m–cu* without a ramellus, usually fairly evenly bowed, in a few species slightly sinuous. Hind wing with *Rs* from almost straight to strongly curved, with marginal cell proximally, at least narrowly glabrous; distal hamuli unspecialized, or with proximal three enlarged. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized or with a weak tooth projecting distally; inner hind tibial spur flattened with a margin of close long hairs; hind tarsal claws usually unspecialized, rarely with very coarse pectinae. Gaster slender; tergite 2 in profile very elongate, with thyridia well removed from anterior margin; umbo absent; epipleuron up-turned. Ovipositor sheath exceptionally broad.

Laticoleus is a moderately small Afrotropical genus containing 11 described species (Gauld & Mitchell, 1978). The majority occur in Madagascar and east Africa. Nothing is known of the biology of species of this genus.

LEPTOPHION Cameron

Leptophion Cameron, 1901: 227. Type-species: *Leptophion longiventris* Cameron, by monotypy.
Spilophion Cameron, 1905: 124. Type-species: *Spilophion maculipennis* Cameron, by monotypy.
Coiloneura Szépligeti, 1905: 35. Type-species: *Coiloneura melanostigma* Szépligeti (= *Leptophion longiventris* Cameron), by subsequent designation, Viereck, 1914: 35.

Mandibles not twisted, weakly narrowed apically, generally subequally bidentate; outer mandibular surface often with a basal swelling, and with a diagonal groove extending from near upper corner to between bases of teeth, sometimes with this groove bearing a brush of long hairs, other times with the groove very weak. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed acute, in anterior aspect usually with margin weakly convex, rarely slightly concave. Ocelli generally large, the posterior ones close to the margins of the eyes, or rarely in some Australian examples, with ocelli smaller; frontal carina absent; occipital carina either complete or obsolescent at extreme ventral end so the carina fails to join the hypostomal carina. Antennae in most species very long and slender, at least 1·5 times the length of the fore wing, in some Australian species shorter, barely longer than the fore wing. Pronotum unspecialized; spiracular sclerite partially concealed, in a few Malesian taxa almost completely covered; notauli vestigial or absent; epicnemial carina complete; mesopleural furrow usually undeveloped. Scutellum moderately convex, from without lateral carinae to with these carinae complete; posterior transverse carina of mesosternum complete, interrupted before mid coxae, or rarely absent. Propodeum with anterior area long and usually striate; anterior transverse carina usually complete, rarely absent, the other carinae usually not discernible; posterior area from strongly rugose to smooth and shining. Fore wing with pterostigma moderately broad; marginal cell long; *Rs*+2*r* conspicuously thickened near pterostigma, usually abruptly curved or angled near base; discosubmarginal cell usually with a glabrous area in anterior corner, this area usually large and extending 0·2 of the way down *Rs*+2*r*, rarely with a weak alar sclerite, sometimes secondarily with microtrichia obscuring part of glabrous area; 1*m–cu* usually without a ramellus, either evenly bowed or, more usually, sinuous. Hind wing with *Rs* from almost straight to very strongly bowed, with marginal cell adjacent to this vein at least narrowly glabrous; distal hamuli unspecialized or with penultimate hamulus long and coiled. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a fringe of long close hairs; hind tarsal claws unspecialized or with distal pectinal tooth projecting beyond the apex of the claw. Gaster usually slender, tergite 2 in profile from moderately to very elongate, with thyridia remote from anterior margin; umbo absent; epipleuron up-turned. Ovipositor sheath moderate, broad.

Leptophion is a moderately large Indo-Pacific genus containing 30 described species (Gauld, 1977; Gauld & Mitchell, 1981). The majority are restricted to lower montane forests on the islands to the east of the Sunda Shelf. Many are endemic to a particular island and recent collecting has yielded an undescribed species from Sulawesi (BMNH). Most species are only known from relatively few individuals.

The genus is divisible into four species-groups, the largest of which, the *maculipennis* species-group, may be subdivided into three species-complexes.

Key to species-groups and complexes of *Leptophion*

1 Anterior transverse carina of mesosternum incomplete; propodeum often with anterior transverse carina absent .... ***anici*** species-group

– Anterior transverse carina of mesosternum complete; propodeum almost always with anterior transverse carina complete 2
2 Hind tarsal claw simple; genal carina usually joining hypostomal carina 3
– Hind tarsal claw with distal pectinal tooth projecting apically; genal carina usually not reaching hypostomal carina (***maculipennis*** species-group) 4
3 Mandible with a dense brush of long stout hair on outer surface .... ***iochus*** species-group
– Mandible with scattered hairs on outer surface .... ***longicornis*** grade-group
4 Fore wing with *Rs+2r* emitted from near centre of pterostigma; anterior corner of discosubmarginal cell partially hirsute .... ***eithos*** species-complex
– Fore wing with *Rs+2r* emitted from proximal end of pterostigma; anterior corner of discosubmarginal cell glabrous 5
5 Penultimate distal hamulus unspecialized; fore wing with 1*m–cu* from evenly curved to weakly sinuous .... ***radiatus*** species-complex
– Penultimate distal hamulus long and coiled; fore wing with 1*m–cu* moderately to strongly sinuous .... ***maculipennis*** species-complex

***longicornis* grade-group**

This paraphyletic assemblage contains two species, *L. longicornis* (Szépligeti) and *L. bakeri* (Cheesman). The group can only be characterized by symplesiomorphies. It is restricted to New Guinea and the New Hebrides.

***anici* species-group**

This holophyletic group contains three species, *L. anici* Gauld, *L. antennatus* (Morley) and *L. unicalcaratus* Gauld. The group is characterized by the loss of the posterior transverse carina of the mesosternum; species tend to have less propodeal sculpture than most *Leptophion* species, and usually the transverse carina is lost. The *anici* species-group is restricted to Australia and New Caledonia where species occur in drier habitats than most *Leptophion*.

***iochus* species-group**

This holophyletic group contains three Australian species, *L. iochus* Gauld, *L. yampus* Gauld and the aberrant *L. tetus* Gauld. The group is characterized by possession of a brush of hair on the outer surface of the mandible; they are generally more robust species with more densely pubescent wings than most *Leptophion* species.

***maculipennis* species-group**

This holophyletic group is characterized by the presence of a modified hind tarsal claw; the majority of species have infumate marks in the proximal corner of the marginal cells and in most the genal carina does not join the hypostomal carina. This is the largest species-group and may be subdivided into three apparently holophyletic species-complexes.

***eithos* species-complex.** This group contains four species, *L. eithos* Gauld & Mitchell, *L. ankylosus* Gauld & Mitchell, *L. vernalis* Gauld & Mitchell and *Leptophion* species 1 (BMNH). It is characterized by the highly modified fore wing venation in which *Rs+2r* is emitted near the centre of the pterostigma. This complex is restricted to Western New Guinea, Sulawesi and the intervening islands.

***radiatus* species-complex.** This group contains six species, *L. radiatus* (Uchida), *L. pterospilus* Gauld & Mitchell, *L. vechti* Gauld & Mitchell, *L. lavellai* Gauld & Mitchell, *L. cheesmanae* Gauld & Mitchell and *L. illustrious* Gauld & Mitchell. It is characterized by the possession of unspecialized hamuli; most species have a rather evenly curved 1*m–cu* and very few have *Rs* in the hind wing appreciably curved. This group is widely distributed from the Solomon Islands to the Continental Asian mainland.

***maculipennis* species-complex.** This group contains 13 species, *L. maculipennis* (Cameron), *L. pubescens* Gauld & Mitchell, *L. gobius* Gauld & Mitchell, *L. kus* Gauld & Mitchell, *L. juxtus* Gauld & Mitchell, *L. magus* Gauld & Mitchell, *L. townesi* Gauld & Mitchell, *L. alleni* Gauld & Mitchell, *L. nodus* Gauld & Mitchell, *L. samari* Gauld & Mitchell, *L. samuelsoni* Gauld & Mitchell, *L. quorus* Gauld & Mitchell and *L. longiventris* Cameron. These are the characteristic *Leptophion* species of Cushman (1947) and Townes (1971) in that they possess both a specialized hind tarsal claw and modified penultimate hamulus. Most species have 1*m–cu* very strongly sinuous and *Rs* in the hind wing strongly bowed. This is the most widespread of all groups with species throughout the Indo-Pacific region. One species has colonized tropical Australia (Gauld, 1984*a*).

PAMOPHION Gauld

Pamophion Gauld, 1977: 28. Type-species: *Pamophion sorus* Gauld, by original designation.

Mandibles not twisted, weakly narrowed apically, subequally bidentate; outer mandibular surface with subbasal swelling, and with a diagonal groove. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile convex, margin impressed, acute, in anterior aspect weakly convex. Ocelli large, the posterior ones close to the eye margins; frontal carina absent; occipital carina complete except at extreme ventral end. Antennae long and slender. Pronotum unspecialized; spiracular sclerite partially concealed; notauli vestigial; epicnemial carina quite strong, present on mesopleuron; mesopleural furrow undeveloped. Scutellum weakly convex, carinate laterally most of its length; posterior transverse carina of mesosternum incomplete, usually discernible as a discontinuous ridge. Propodeum with anterior area rather short, striate; anterior transcarina complete, other carinae absent, posterior area rugose-reticulate. Fore wing with pterostigma moderately broad; marginal cell long; *Rs+2r* conspicuously thickened near pterostigma, proximally curved; discosubmarginal cell broadly glabrous anteriorly; *1m–cu* without a ramellus, moderately sinuous. Hind wing with *Rs* straight; marginal cell evenly hirsute; hamuli unspecialized. Fore tibial spur without a membranous flange behind the macro-trichial comb; mid and hind trochantelli with a distinct blunt distal tooth; inner hind tibial spur flattened, with a fringe of long, close hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 in profile very elongate, with thyridia moderately close to anterior margin; umbo absent; epipleuron pendant, narrow. Ovipositor sheath slender, unspecialized.

A single species, *P. sorus*, is known to occur in Queensland. It is apparently the most primitive species in this genus-group. Nothing is known of its biology.

The *ENICOSPILUS* subgroup

This group contains five genera, *Dicamptus, Enicospilus, Pycnophion, Banchogastra* and *Abanchogastra*. The last three are endemic Hawaiian taxa and probably constitute a monophyletic clade which almost certainly arose from within *Enicospilus*. They are so phenetically divergent, however, that it would be quite impractical to include them within *Enicospilus*, an otherwise structurally uniform genus of over 700 species.

The relationship of *Enicospilus* to *Dicamptus* is not clear; the latter may be paraphyletic with respect to the former though subtle differences in venation, alar sclerite form, sculpture and body shape suggest that *Dicamptus* is actually holophyletic.

The *Enicospilus* group is characterized by a number of apomorphic features including having the spiracular sclerite concealed, having an elongate anterior propodeal area, having a rather sinuous *Rs+2r* and generally having alar sclerites. Individual species may be exceptional in one or two of these features.

Dicamptus, clearly the least specialized genus in this complex, is restricted to the Old World, and *Enicospilus* is apparently most diverse in the Old World tropics, suggesting a palaeotropical origin for the group. Preliminary study of Neotropical species of *Enicospilus* suggests that very few large species-groups occur in South America; several of these also occur in the Nearctic region. The Australian *Dicamptus* and *Enicospilus* have apparently been derived from immigration from South East Asia (Gauld, 1984*a*).

The Hawaiian genera seem to be a holophyletic group. This is attested by the total lack of alar sclerites, possession of a straight, rather slender *Rs+2r* and loss of the last 0·3 or so of the lateral scutellar carinae. There are a number of other similarities in sculpture and exact position of wing veins that further supports this clade.

The inter-relationship of these three genera may be misrepresented in the cladogram (Fig. 37). Considering only the characters in the primary data matrix five (16·2, 27·3, 37, 48·1 and 49) support *Pycnophion* + *Abanchogastra* whilst three (13, 42·2, 43·1) support the group *Pycnophion* + *Banchogastra*. None supports the third combination. Of the first five characters 16·2 has almost certainly undergone reversal in *Banchogastra* as the character is apomorphic in the greater part of the presumed ancestral lineage of the species. The plesiomorphic state is otherwise generally only found in primitive ophionines and (again as a reversal) in a few diurnal specialized species (*Banchogastra* has not been taken at light and thus may well be diurnally active). Character 27·3, a centrally interrupted posterior mesosternal carina, is only found in the primary data set in *Pycnophion* and *Abanchogastra*, but this carina is weak centrally in *Banchogastra* and may even be absent narrowly in some specimens. A medioventrally evanescent mesosternal carina can therefore be considered an apomorphy of the Hawaiian genera. Character 49, position of Cu_1 in the fore wing, is plesiomorphic only for *Banchogastra*. The derived condition must therefore be considered to be an apomorphy of the subfamily and the anomalous inclination of this vein in *Banchogastra* is presumably a further specialization, perhaps resulting from the very close proximity of the

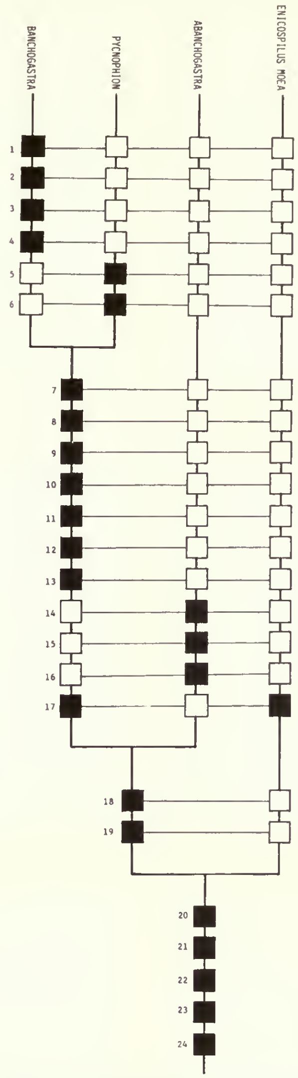


Fig. 37 Putative phylogenetic arrangement of Hawaiian genera in relation to *Enicospilus moea* Cheesman. This cladogram is supported by the following apomorphic features: 1, petiolar spiracles anterior to margin of sternite 1; 2, tergite 2 depressed; 3, epipleuron 2 pendant; 4, further reduction in ocellar size; 5, possession of an elongate ovipositor; 6, loss of hair in discosubmarginal cell centrally; 7, development of a stout gaster; 8, possession of large thyridia close to anterior margin of tergite; 9, metapleuron inflated; 10, epicnemial carina medioventrally incomplete; 11, possession of a short, rounded propodeum; 12, presence of incipient frontal carinae; 13, possession of inflated hind trochanters; 14, loss of occipital carina mediodorsally; 15, upper tooth of mandible compressed; 16, increase in torsion of mandible; 17, reduction in size of ocelli; 18, loss of fenestra; 19, development of fine, granulate thoracic sculpture; 20, loss of alar sclerites; 21, reduction in length of second abscissa of Cu_1 in fore wing; 22, medially evanescent posterior transverse carina of mesosternum; 23, straight and slender *Rs*+*2r*; 24, loss of posterior part of lateral carina of scutellum.

bases of 1*m–cu* and Cu_{1a}. In some individuals this abscissa of Cu_1 is occluded. The remaining two apomorphies (37 and 48·1) are venational features which are usually rather variable. The three apomorphies uniting *Pycnophion* with *Banchogastra* are slightly more convincing, particularly 42·2, the pterostigma shape. Furthermore, *Pycnophion* and *Banchogastra* resemble each other in many other specialized features. Both have smaller ocelli than normal, have a medioventrally interrupted epicnemial carina, have a strongly inflated metapleuron and a rather short anterior propodeal area and possess rather inflated trochanters. The thyridia of tergite 2 are large and close to the anterior margin (? a reversal) and the gaster is stouter than most other ophionines. The first segment of the gaster is very much broader and shorter than the corresponding segment in other enicospilines. In view of these marked similarities it would seem that *Pycnophion* + *Banchogastra* constitute a distinct clade.

A Marquesan species, *Enicospilus moea* Cheesman, shares a number of apomorphies with the Hawaiian genera, including possession of a straight, rather slender *Rs*+*2r*, having a medioventrally obsolescent posterior mesosternal carina and having only the anterior 0·7 of the scutellum carinate. Like the Hawaiian genera the abscissa of Cu_1 between 1*m–cu* and Cu_{1a} is very short and *cu–a* is well proximal to the base of *Rs&M*. This species does, however, possess fenestra but this, rather than any of the extant Hawaiian species, may be closest to the base of the *Pycnophion*/*Banchogastra*/*Abanchogastra* evolutionary line (Fig. 37).

ABANCHOGASTRA Perkins

Abanchogastra Perkins, 1902: 141. Type-species: *Abanchogastra debilis* Perkins, by monotypy.

Mandibles twisted about 45°, strongly and evenly narrowed with teeth subequal, slightly depressed; outer mandibular surface almost flat. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin blunt; clypeus in anterior aspect weakly convex. Ocelli large, the posterior ones separated from eye by 0·1–0·2 times their own diameter; frontal carina absent; occipital carina present, mediodorsally interrupted, ventrally weak but joining hypostomal carina. Antennae incomplete. Pronotum unspecialized; spiracular sclerite concealed by pronotal flange; notauli absent; epicnemial carina weak but present on mesopleuron; mesopleural furrow absent. Scutellum weakly convex, carinate laterally about 0·7 of its length; posterior transverse carina of mesosternum centrally obsolescent. Propodeum with anterior area long, striate, carinae absent, posterior area coriaceous. Fore wing with pterostigma of moderate width; marginal cell long; *Rs*+*2r* straight and slender; discosubmarginal cell uniformly hirsute; 1*m–cu* evenly curved, without a ramellus. Hind wing with *Rs* weakly curved. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, hind tarsal claws unspecialized. Gaster slender; tergite 2 very elongate, thyridia elliptical, remote from anterior margin, umbo absent; epipleuron up-turned. Ovipositor sheath slender.

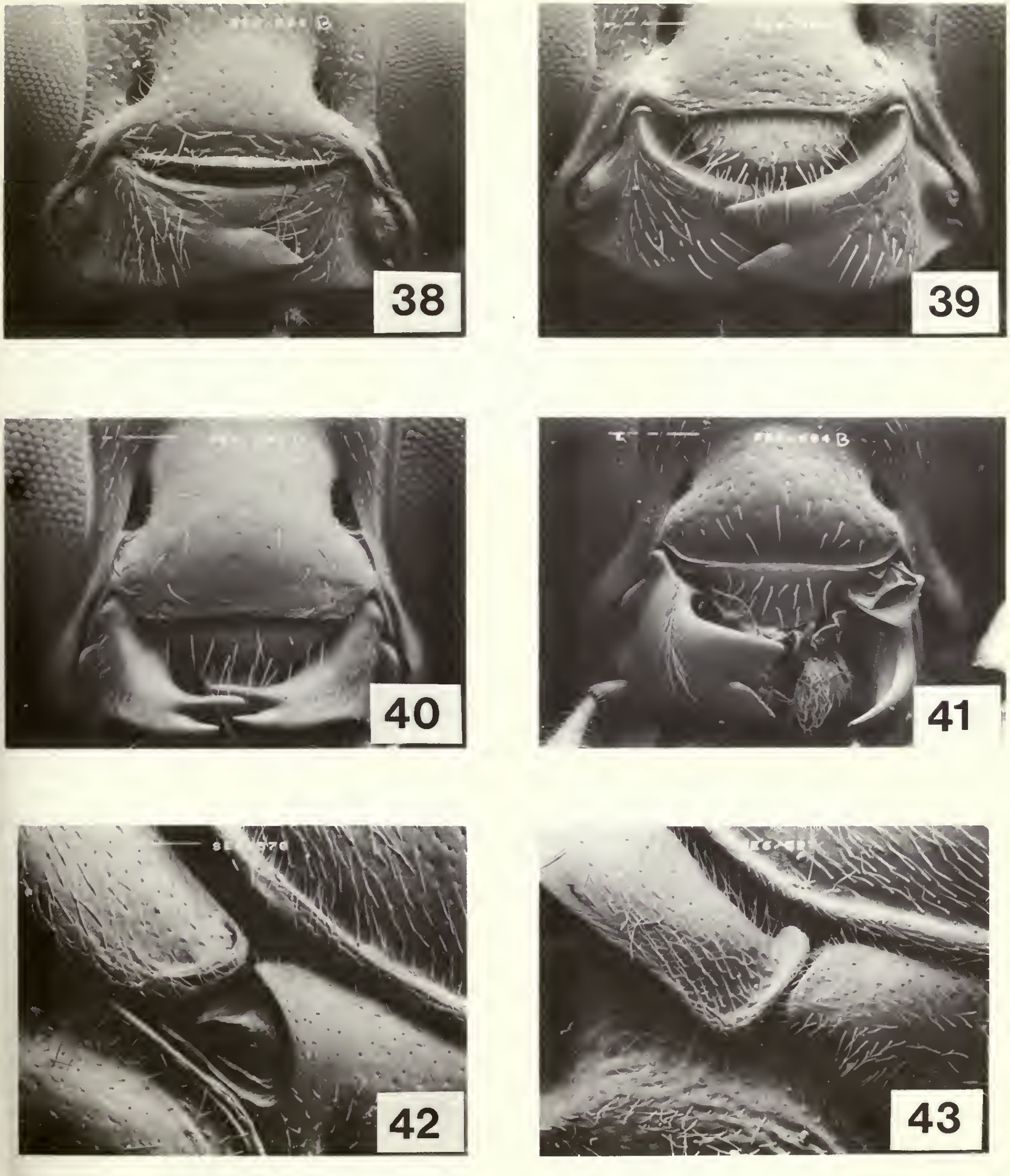
This genus contains a single Hawaiian species which differs strikingly from any *Enicospilus* in the fore wing venation. Nothing is known of its biology.

BANCHOGASTRA Ashmead

Banchogastra Ashmead, 1900: 87. Type-species: *Banchogastra nigra* Ashmead, by original designation.

Mandibles twisted about 25°, strongly and evenly narrowed apically with upper tooth a little longer than the lower; outer mandibular surface with strong proximal concavity, remainder of surface virtually flat but with diagonal tract of dense hair. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile weakly convex, margin sharp, not impressed at all; clypeus in anterior aspect with margin very weakly convex. Ocelli small, the posterior ones separated from eyes by more than their own minimum diameter; frontal carina very weak but discernible; occipital carina complete, ventrally not quite reaching hypostomal carina. Antennae moderately slender, about 1·2 times length of fore wing. Pronotum unspecialized; spiracular sclerite completely occluded by pronotal flange; notauli weak; epicnemial carina strong, present on mesopleuron but medioventrally interrupted; mesopleural groove virtually absent. Scutellum convex, carinate laterally about 0·8 of its length; posterior transverse carina of mesosternum complete, or slightly weak medioventrally. Propodeum with anterior area moderately short but clearly discernible; anterior transverse carina complete; posterior transverse carina vestigial, others absent; posterior area rugose. Fore wing with pterostigma moderately slender; marginal cell long; discosubmarginal cell evenly hirsute; *Rs*+*2r* straight, expanded slightly immediately before joining pterostigma; 1*m–cu* evenly arcuate, ramellus absent; unusual in having 1*m–cu* and Cu_{1a} basally contiguous or united. Hind wing with *Rs* almost straight. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli short and stout, otherwise unspecialized; inner hind tibial spur slightly flattened, with a fringe of fine hairs; hind tarsal claws long but closely pectinate. Gaster stout; tergite 2 depressed, barely longer than deep, not longer than broad; thyridia large, oval, close to anterior margin; umbo absent; laterotergite narrow, pendant. Ovipositor sheath short, slender.

Banchogastra is a small genus containing two Hawaiian species (Townes, 1971). Nothing is known of their biology.



Figs 38–43 Stereoscan photographs of ophionines: 38–41, mandibles of (38) *Ophion* sp.; (39) *Ophiogastrella* sp.; (40) *Enicospilus* sp.; (41) *Leptophion alleni* Gauld & Mitchell. 42, 43, hind corner of pronotum and spiracular sclerite of (42) *Ophion* sp.; (43) *Enicospilus* sp.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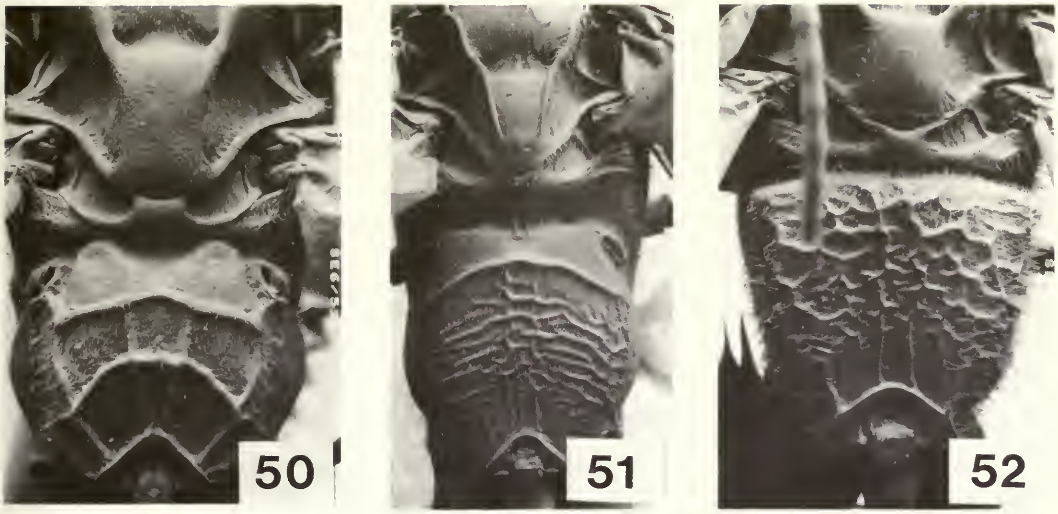
Figs 44–49 Stereoscan photographs of Ophioninae: 44, mandibles of *Thyreodon* sp. 45–47, hind tarsal claws of (45) *Ophion* sp. ♀; (46) *Leptophion* sp. ♀; (47) *Ophiogastrella* sp. ♂. 48, 49, fore tibial spurs of (48) *Ophion* sp.; (49) *Enicospilus* sp.



Figs 50–52 Stereoscan photographs of dorsal region of posterior part of alitrunk of: 50, *Ophion* sp.; 51, *Enicospilus* sp.; 52, *Thyreodon* sp.

DICAMPTUS Szépligeti

Dicamptus Szépligeti, 1905: 21. Type-species: *Dicamptus giganteus* Szépligeti, by monotypy.

Mandibles not twisted, generally very weakly narrowed, almost equally bidentate; outer mandibular surface weakly convex with proximal concavity, sometimes with pronounced proximal swelling and diagonal hirsute groove. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile from flat to convex or even pyramidal, usually with margin impressed and acute; clypeus in anterior aspect truncate or weakly convex. Ocelli generally large, the posterior ones usually virtually contiguous with eyes except in a few Afrotropical species; frontal carina absent; occipital carina usually complete, ventrally joining hypostomal carina. Antennae moderately to extremely elongate, from slightly longer than fore wing to 2·0 times fore wing length and with upwards of 90 flagellar segments. Pronotum unspecialized; spiracular sclerite virtually completely concealed by pronotal lobe; notauli vestigial or absent; epicnemial carina usually complete, often strong; mesopleural furrow generally absent. Scutellum weakly to moderately convex, with lateral longitudinal carinae strong, usually complete; posterior transverse carina of mesosternum complete. Propodeum with anterior area long, striate; anterior transverse carina usually complete and other carinae obsolescent or absent; posterior area usually coarsely reticulate. Fore wing with pterostigma fairly slender; marginal cell very long; *Rs+2r* broadened and variously sinuate before joining pterostigma; discosubmarginal cell with a large glabrous fenestra near anterior corner, this fenestra bearing at least one sclerite (proximal one); *1m–cu* from arcuate to sinuous, usually without a ramellus. Hind wing with *Rs* virtually straight. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur flattened, with a margin of long close hairs; hind tarsal claws unspecialized. Gaster slender; tergite 2 very elongate, with thyridia remote from anterior margin; umbo absent; epipleuron up-turned. Ovipositor sheath slender.

Dicamptus is a moderate-sized genus with 27 described species and two undescribed species (ANIC; BMNH) in the Palaeotropical region. A few species extend into temperate areas, *D. fuscicornis* (Erichson) reaches Tasmania and *D. nigropictus* (Matsumura) occurs northwards as far as Japan and Korea.

Two quite distinct species-groups are recognizable. The *pulchellus* group comprises gracile species with a very small cubital index (0·55 or less), a short vein *3r–m* (less than 0·5 of the length of *M* between *2m–cu* and *3r–m*) and a fairly well-developed mandibular groove. This group contains *D. collessi* Gauld, *D. uptoni* Gauld and *Dicamptus* species 1 (ANIC) which are Australian endemics, *D. indicus* Nikam and *D. fuscicornis* which are widespread Indo-Australian species, *D. isshikii*, an Oriental species and the Afrotropical species *D. crassellus* (Morley), *D. xhosa* Delobel, *D. betsileo* Delobel, *D. pellucidus* (Kriechbaumer), *D. seyrigi* Delobel, *D. townesi* Delobel and *D. pulchellus* (Morley).

The remaining species (the *giganteus* group) are in general very much larger insects with a larger cubital index, a longer *3r–m* and stouter mandibles. This may well be a paraphyletic grade-group, as almost certainly the characters defining it are plesiomorphic for the genus. The majority of species in this group occur in areas with a pronounced dry season, particularly parts of Africa and India. Some of the very largest species (*reticulatus* (Cameron), *nigropictus* (Matsumura) and *giganteus* Szépligeti) occur in montane forest, a very wet habitat. None of the species in the *giganteus* group occur east of Weber's line. In New Guinea they seem to have been replaced by some exceptionally large species of *Enicospilus* (*E. enormous* Gauld & Mitchell species complex).

ENICOSPILUS Stephens

Enicospilus Stephens, 1835: 126. Type-species: *Ophion merdarius* Gravenhorst sensu Stephens (= *Ichneumon ramidulus* L.), by subsequent monotypy, Stephens, 1845.

Henicospilus Agassiz, 1846: 138. [Unjustified emendation.]

Allocamptus Foerster, 1869: 150. Type-species: *Ophion undulatus* Gravenhorst, by subsequent designation, Thomson, 1888: 1189.

Dispilus Kriechbaumer, 1894*b*: 309. Type-species: *Ophion (Dispilus) natalensis* Kriechbaumer, by monotypy.

Pleuroneurophion Ashmead, 1900: 86. Type-species: *Pleuroneurophion hawaiiensis* Ashmead, by original designation.

Cymatoneura Kriechbaumer, 1901*a*: 22. Type-species: *Ophion undulatus* Gravenhorst, by subsequent designation, Viereck, 1914: 8.

Pterospilus Kriechbaumer, 1901*c*: 156. Type-species: *Ophion (Enicospilus) dubius* Tosquinet, by subsequent designation, Viereck, 1914: 126. [Junior homonym of *Pterospilus* Rondani, 1856.]

Trispilus Kriechbaumer, 1901*c*: 156. Type-species: *Ophion (Enicospilus) trimaculatus* Tosquinet (= *Henicospilus seminiger* Szépligeti), by monotypy.

Metophion Szépligeti, 1905: 28. Type-species: *Metophion bicolor* Szépligeti, by subsequent designation, Viereck, 1914: 94.

Ceratospilus Szépligeti, 1905: 28. Type-species: *Ceratospilus biroi* Szépligeti, by monotypy.

Atoponeura Szépligeti, 1905: 34. Type-species: *Atoponeura concolor* Szépligeti (= *Enicospilus atoponeurus* Cushman), by monotypy.

Ophiomorpha Szépligeti, 1905: 34. Type-species: *Ophion curvinervis* Cameron (= *Enicospilus cameronii* Dalla Torre), by subsequent designation, Hooker, 1912: 134. [Junior homonym of *Ophiomorpha* Nilsson, 1836.]

Cryptocamptus Brèthes, 1909: 230. [Unnecessary replacement name for *Allocamptus* Foerster.]

Eremotyloides Perkins, 1915: 530. Type-species: *Eremotyloides orbitalis* Ashmead, by monotypy.

Amesospilus Enderlein, 1918: 222. Type-species: *Ophion unicallosus* Snellen, by original designation.

Schizospilus Seyrig, 1935: 79. Type-species: *Schizospilus divisus* Seyrig, by original designation.

Mandibles twisted from 10 to 90°, weakly to very strongly narrowed, from equally bidentate to with upper tooth conspicuously the longer, rarely with lower tooth the longer; outer mandibular surface usually with a proximal concavity, the remainder either almost flat or with a diagonal hirsute groove. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile from flat to nasute, with margin blunt or acute or acute and subapically impressed; clypeus in anterior aspect usually weakly convex, rarely truncate or concave, in one Neotropical species with an indication of a median tooth. Ocelli usually large, generally with the posterior ones very close to or contiguous with the eyes, in a few species with the ocelli smaller; frontal carina absent; occipital carina usually complete, sometimes mediodorsally obsolescent or interrupted. Antennae usually more than 1·5 times as long as the fore wing. Pronotum usually unspecialized, in some Madagascan species with median transverse crests; spiracular sclerite almost always completely occluded by flange of pronotum; notauli vestigial or absent; epicnemial carina usually well developed, present on mesopleuron, usually reaching to level of lower corner of pronotum; mesopleural furrow usually absent. Scutellum from almost flat to strongly convex, almost always with strong lateral carinae virtually entire, rarely with these carinae short; posterior transverse carina of mesosternum usually complete. Propodeum with anterior area moderately long to long, generally striate; anterior transverse carina of propodeum usually present, almost always complete; posterior transverse carina usually absent, rarely present laterally; posterior area usually reticulate or rugose, sometimes finely irregularly wrinkled, in a few species concentrically striate, very rarely the posterior area almost smooth or punctate. Fore wing with pterostigma moderately broad to quite slender; marginal cell long; *Rs+2r* almost always broadened and variously sinuate before joining the pterostigma; discosubmarginal cell usually with a glabrous fenestra adjacent to the vein *Rs+2r*, this fenestra often bearing one or more detached sclerites; *1m–cu* usually arcuate or sinuous, rarely somewhat angulate; ramellus usually absent, rarely in one or two species well-developed. Hind wing with *Rs* straight or weakly bowed. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli usually simple, rarely with a marginal tooth; inner hind tibial spur flattened, with margin of close long hairs; hind tarsal claws various, most usually unspecialized and slightly sexually dimorphic, sometimes extremely sexually dimorphic, the male having a very fine pectinal comb, in a few taxa with the claws strongly geniculate, occasionally with the claws asymmetrical, in other taxa with the distal pectina projecting beyond the apex of the true claw, and very rarely, in a few eremic species, with the pectina reduced. Gaster from moderately stout to very slender; tergite 2 usually very long and slender, rarely posteriorly almost as deep as long, almost always with thyridia remote from anterior margin; umbo vestigial or absent; epipleuron usually up-turned, pendant in a few (or one) Neotropical species. Ovipositor sheath slender; ovipositor usually short, straight, in isolated taxa it may be upcurved or decurved, and very rarely it may be straight but project well beyond the apex of the gaster.

Enicospilus is an extremely large genus, most species of which occur in the tropics. The major centres of radiation appear to be New Guinea, where there are about 200 endemic species, and Madagascar, which has about half that number. The Philippines, Hawaii and Zaire river basin are other areas of pronounced endemicity. In the tropics, the greatest diversity of species seems to occur at mid-elevation in the cloud forests (moss forests) between 1200 and 2000 m. A number of species are restricted to areas that have a pronounced dry season (e.g. *Enicospilus capensis*), and a few species seem to inhabit deserts (e.g. *E. psammus*). Many species are capable of sustained flight over great distances (e.g. across the Tasman Sea from Australia to New Zealand) and several occur on almost all South Pacific archipelagos as far east as the Tuamotus. Most small oceanic islands apparently have several species of *Enicospilus* present, and on the Micronesian islands six of the 33 recorded ichneumonids are *Enicospilus* (Townes, 1958). Outside the tropics there are notably fewer species. Scaramozzino (1983) records only ten from Italy whilst Viktorov (1957) knew of only 15 species from the Soviet Union. Five nominal species are recorded from Britain, but probably only four species occur there (Fitton *et al.*, 1978).

Certain generalized distribution patterns can be observed in the genus. New Guinea and Madagascar have large numbers of endemic species in endemic species-groups; for example eight of the 24 species-groups recognized as occurring in the Afrotropical region are restricted to Madagascar, and these eight groups contain 35 species (Gauld & Mitchell, 1978). The Philippines, Hawaii and South America each contain very few species-groups, but these may be very large. Relatively few of the numerous other species-groups are endemic to a single zoogeographic area. Several of the species-groups that are widespread in South East Asia have their greatest diversity in New Guinea (e.g. the *xanthocephalus* and *tremulus* species-groups, Gauld & Mitchell, 1981). Virtually no widespread South East Asian groups have a localized centre of diversity outside Melanesia; most species seem to be widespread with isolated local endemics (e.g. the *flavicaput* species-group, Gauld & Mitchell, 1981). Many widespread South East Asian groups are also represented in mainland Africa (e.g. the *capensis* and *antefurcalis* species-groups). A number of species-groups are either endemic to mainland Africa (e.g. the *babaultii*, *biimpressus* and *rubens* species-groups) or are most diverse in Africa (e.g. the *dolosus* species-group). Most species occurring in the Palaearctic region belong to species-groups that are well-represented in the Nearctic region, but neither region appears to have any endemic species-groups, nor is any species-group endemic to the Holarctic region. The *Enicospilus* species of Australia are virtually all either widespread South East Asian species or are endemics derived from South East Asia (Gauld, 1984*a*). New Zealand has no endemic species, but shares two with Australia. A distinct faunal region is apparent which comprises part of the Mediterranean basin, most of the Middle East and extends eastwards into Central Asia and south-eastwards into north-west India. Although the fauna of this area is poorly known, it seems that at least one species-group may be endemic to the region (the *przewalskii* species-group).

Gauld & Mitchell (1978; 1981) outline a very large number of species-groups and several of these are refined by Gauld (1984*a*). Large numbers of other species are currently unplaced; these may belong to less clearly definable groups, or they may be aberrant members of existing groups, or they may represent numerous monobasic species-groups. The phylogenetic inter-relationships of most of these species-groups are very difficult to assess as most are definable on the basis of a number of autapomorphies. Few share obvious specializations with other species-groups.

Repeated attempts have been made to subdivide *Enicospilus* into a number of smaller genera (Kriechbaumer, 1901*c*; Szépligeti, 1905; Seyrig, 1935) but none of these subdivisions has endured, largely for two reasons – the authors proposing the separation have very limited experience of the range of morphological diversity afforded by the genus, and the characters used to effect separation are superficial differences, usually in the number of alar sclerites. The clearest demonstration of the great variability of alar sclerite form and number can be seen between the closely related species of the *unidens* species-group, a group definable by several autapomorphies. The proximal sclerite is present in all species but only *E. unidens* has a central sclerite; the distal sclerite is present in *E. unidens, E. akainus* and *E. mirax* but absent in *E. gonidius* and *E. amygdalis*. The most important features for recognizing apparently 'natural' groupings seem to be the form of the tarsal claws (including the degree of sexual dimorphism), the structure of the mandibles and clypeus, the presence or absence of the proximal sclerite and the structure of the male genitalia.

Little is known of the biology of species of *Enicospilus*. The majority of host records refer to species parasitizing larvae of Noctuidae, Geometridae, Lymantriidae or Saturniidae. A few species attack pyralids. Many of the larger species that attack saturniid larvae spin their cocoon within the host cocoon, but other species spin a cocoon that is not enclosed by that of the host. Most species seem to attack larvae that are free-living, tree-leaf-feeding caterpillars, but the few with longer ovipositors seem to attack larvae mining stems (e.g. *E. terebrus*). It must be stressed that the hosts of the majority of tropical species are not known.

PYCNOPHION Ashmead

Pycnophion Ashmead, 1900: 87. Type-species: *Pycnophion molokaiensis* Ashmead, by monotypy.

Mandibles twisted about 20°, evenly tapered, with upper tooth broader but of about equal length to the lower tooth; outer mandibular surface slightly concave, sparsely pubescent. Maxillary palp 5-segmented, labial palp 4-segmented; clypeus in profile moderately convex, margin blunt; clypeus in anterior aspect weakly convex. Ocelli moderately large, the posterior ones separated from the eye by about 0·5 times their own diameter; frontal carina very weak; occipital carina complete, mediodorsally with a depression. Antennae moderately long, about 1·3 times the length of the fore wing. Pronotum slightly flattened mediodorsally; spiracular sclerite covered by pronotal flange; notauli vestigial; epicnemial carina strong, curved to nearly reach the anterior margin of the pleuron above the level of the lower corner of the pronotum; mesopleural furrow absent. Scutellum convex, laterally carinate at least 0·6 of its length; posterior transverse carina of the mesosternum centrally obsolescent. Propodeum with anterior area moderately short but clearly discernible; anterior transverse carina complete, at least centrally, the posterior one vestigial, the other absent; posterior area finely coriaceous. Pterostigma moderately slender; marginal cell long; *Rs+2r* virtually straight, evenly but abruptly widened before joining pterostigma; discosubmarginal cell with an ill-defined glabrous area anteriorly, the entire cell very sparsely hirsute; 1*m–cu* fairly evenly arcuate, ramellus absent. Hind wing with *Rs* straight. Fore tibial spur without a membranous flange behind macrotrichial comb; mid and hind trochantelli unspecialized; inner hind tibial spur somewhat flattened, with a fringe of long hairs; tarsal claws unspecialized. Gaster moderately stout; tergite 2 in profile, slightly longer than posteriorly deep, with thyridia large, oval and close to anterior margin; umbo vestigial; epipleuron up-turned. Ovipositor exceptional in being very long and up-curved, reaching beyond apex of gaster by at least length of tergites 2–5.

Pycnophion is a small genus containing three Hawaiian species (Townes *et al.*, 1961). It is one of the most atypical of ophionine genera and females superficially resemble campoplegines or phygadeuontines. One species, *P. fuscipennis* Perkins, has been reared as a parasite of the larvae of *Hyposmocoma chilonella* (Lepidoptera: Cosmopterygidae) (Swezey, 1931) which are borers in the pith of stems of *Rubus, Acacia* and a variety of other woody plants.

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Appendix 1 The ophionine taxa used in the cladistic study.

901	*Thyreodon atricolor* (Olivier)	Nearctic
902	*Thyreodon laticinctus* Cresson	Neotropical
903	*Thyreodon fulvescens* Cresson	Neotropical
904	*Thyreodon flamminiger* (Morley)	Neotropical
905	*Simophion calvus* Viktorov	Palaearctic
906	*Orientospilus melasma* Townes	Afrotropical
907	*Dictyonotus purpurascens* (Smith)	Oriental/Eastern Palaearctic
908	*Rhynchophion flammipennis* (Ashmead)	Neotropical
909	*Lepiscelus distans* (Seyrig)	Afrotropical
910	*Ophiogastrella* sp. 1 (BMNH)	Neotropical
911	*Ophiogastrella* sp. 2 (BMNH)	Neotropical
912	*Laticoleus unicolor* (Szépligeti)	Afrotropical
913	*Laticoleus pronotalis* Gauld & Mitchell	Afrotropical (Madagascar)
914	*Laticoleus spilus* Gauld & Mitchell	Afrotropical
915	*Laticoleus curvatus* Delobel	Afrotropical
916	*Stauropoctonus bombycivorus* (Gravenhorst)	Palaearctic
917	*Stauropoctonus occipitalis* Gauld & Mitchell	Afrotropical (Madagascar)
918	*Aulophion* sp. 1 (BMNH)	Neotropical
919	*Pamophion sorus* Gauld	Australian
920	*Riekophion emandibulator* (Morley)	Australian
921	*Ophionopsis nigrocyaneus* Tosquinet	Afrotropical
922	*Sicophion pleuralis* Gauld	Neotropical
923	*Prethophion latus* Townes	Neotropical
924	*Pycnophion molokaiensis* Ashmead	Hawaiian
925	*Abanchogastra hawaiiensis* (Ashmead)	Hawaiian
926	*Banchogastra nigra* Ashmead	Hawaiian
927	*Barytatocephalus mocsaryi* (Brauns)	Palaearctic
928	*Leptophion maculipennis* (Cameron)	Oriental
929	*Leptophion anici* Gauld	Australian/New Caledonian
930	*Leptophion pterospilus* Gauld & Mitchell	Oriental
931	*Leptophion tetus* Gauld	Australian
932	*Dicamptus neavei* Gauld & Mitchell	Afrotropical
933	*Dicamptus giganteus* Szépligeti	Oriental
934	*Dicamptus fuscicornis* (Erichson)	Oriental/Australian
935	*Euryophion latipennis* (Kirby)	Afrotropical
936	*Euryophion adustus* (Townes)	Afrotropical
937	*Rictophion ikuthana* (Kriechbaumer)	Afrotropical
938	*Xylophion xylus* (Gauld)	Australian/Papuan
939	*Ophion luteus* (L.)	Palaearctic
940	*Eremotylus boguschi* (Meyer)	Palaearctic
941	*Agathophiona fulvicornis* Westwood	Neotropical
942	*Enicospilus tremulus* Gauld & Mitchell	Oriental
943	*Enicospilus spathius* Gauld & Mitchell	Oriental
944	*Enicospilus nephele* Gauld & Mitchell	Oriental
945	*Enicospilus cionobius* Gauld & Mitchell	Oriental
946	*Enicospilus unidens* Seyrig	Afrotropical
947	*Enicospilus mahalonius* Gauld & Mitchell	Afrotropical (Madagascar)
948	*Rhopalophion discinervis* (Morley)	Afrotropical
949	*Janzophion nebosus* sp. n.	Neotropical
950	*Hellwigiella nigripennis* Szépligeti	Palaearctic
951	*Sclerophion uchidai* Gauld & Mitchell	Oriental/Eastern Palaearctic

Hypothetical taxa

960 *Laticoleus* ancestor
961 *Ophiogastrella* ancestor
962 *Leptophion* ancestor
963 *Stauropoctonus* ancestor
964 *Thyreodon/Dictyonotus* ancestor
965 *Euryophion* ancestor
966 *Dicamptus* ancestor
967 *Enicospilus* ancestor

Appendix 2 Primary data matrix of 51 selected ophionines and 95 characters. 0 indicates a presumed plesiomorphic condition, 1 a presumed apomorphic state.

	1.1	1.2	2	3	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2	8.1	8.2	9	10	11	12	13	14.1	14.2	15.1	15.2	16.1
901	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0
902	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0
903	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0
904	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1
905	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
906	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
907	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1
908	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	0	1
909	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
910	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
911	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
912	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
913	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
914	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
915	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
916	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
917	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
918	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
919	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
920	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
921	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0
922	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1
923	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
924	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1
925	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
926	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1
927	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
928	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
929	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
930	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
931	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1
932	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1
933	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1
934	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1
935	1	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1
936	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1
937	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1
938	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
939	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
940	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
941	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
942	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
943	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
944	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
945	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
946	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1
947	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
948	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
949	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
950	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
951	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1

Appendix 2 – *cont.*

	16.2	17	18.1	18.2	19	20.1	20.2	21.1	21.2	22.1	22.2	23	24.1	24.2	25.1	25.2	26	27.1	27.2	27.3	28.1	28.2	29.1	29.2
901	0	1	0	0	0	1	0	1	0	0	1	1	1	1	1	1	1	1	0	0	1	1	0	1
902	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	1	0	1
903	0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0	1
904	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	1	1	0	1
905	1	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0
906	1	1	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	1	0
907	1	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1	1	0	1
908	1	0	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0	0	0
909	0	0	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	0	1
910	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	1	1	0	1
911	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	1	1	0	1
912	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	0	0
913	1	1	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	1	1	0	1	1	0	0
914	1	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	1	1	0	1	1	0	0
915	1	1	0	0	0	1	1	0	0	1	0	0	1	0	1	1	0	1	1	0	1	1	0	0
916	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
917	1	0	0	1	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
918	1	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	1	0	1
919	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
920	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	1
921	1	0	0	1	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1	1	0	0
922	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	1	1	0
923	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0
924	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0	0
925	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	1	1	1	0	1
926	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0
927	1	0	1	0	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	0
928	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1
929	1	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1
930	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
931	1	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
932	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	0	1
933	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
934	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
935	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	0	0
936	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	0	1
937	1	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	1	1	0
938	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0
939	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0
940	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0
941	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1	0	0	0
942	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
943	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
944	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
945	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1
946	1	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	0	1
947	1	1	0	0	1	1	1	0	0	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1
948	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0
949	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1
950	1	0	0	0	0	1	1	0	0	0	1	1	1	0	1	1	0	0	0	0	1	1	0	0
951	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0

Appendix 2 – *cont.*

	30	31	32	33	34	35	36.1	36.2	36.3	37	38	39	40	41	42.1	42.2	43.1	43.2	44.1	44.2	45.1	45.2	46	47.1	47.2
901	1	0	0	1	0	0	1	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0
902	1	0	0	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
903	1	0	0	1	0	0	1	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
904	1	0	0	1	0	0	1	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0
905	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	1	1	1	0	0	1	0
906	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	0	1	0	0	1	0
907	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	1	0
908	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	0
909	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	1	1	0	0	1	1
910	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	0
911	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0	0	1	0	0	1	0
912	0	0	0	1	0	1	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1	0	1	0
913	0	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	0	0	0	1	1	0	1	0
914	0	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0	0	1	1	1	1	1
915	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	0	1	1
916	0	0	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	0	0	0	1	0	0	1	1
917	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	1	0	0	1	1
918	1	0	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	0
919	1	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0	0	1	1	0	1	1
920	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	1	1	1
921	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	1	1
922	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0
923	0	0	1	0	0	1	1	1	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0
924	0	0	0	1	1	0	1	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
925	0	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0
926	0	1	1	1	0	0	1	1	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0
927	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
928	0	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	1	1
929	0	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	0
930	0	0	0	1	0	1	1	1	0	1	1	1	0	0	1	0	1	0	0	0	1	1	1	1	0
931	0	0	0	1	0	1	1	1	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1
932	0	1	0	1	0	0	1	1	0	1	1	0	1	0	1	0	1	1	0	0	1	1	1	1	0
933	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	1	1	1
934	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	0	1	1	0	0	1	1	1	1	0
935	1	1	1	0	0	0	1	0	0	0	1	1	0	0	1	1	1	0	1	0	1	0	0	1	0
936	0	1	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1	0	1	1	1	0	0	1	0
937	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	0	0	1	0
938	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0
939	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0
940	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0
941	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
942	0	0	0	1	0	0	1	1	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	1	0
943	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	0	1	1	1	0	1	1	1	0	0
944	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0
945	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	1	1	1
946	0	0	0	1	0	0	1	1	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	1	0
947	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	1	0	0	1	1	1	1	1
948	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
949	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	1	1	0	1	1	0	1	1
950	1	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	1	0	1	0	0	1	0
951	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	1	0	1	1	1	0	0

Appendix 2 – *cont.*

	48.1	48.2	49	50	51.1	51.2	52.1	52.2	53	54	55	56	57	58.1	58.2	59	60	61.1	61.2	62	63	64
901	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0
902	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0
903	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0
904	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
905	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
906	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0
907	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0
908	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0
909	0	0	1	1	1	1	0	0	1	0	0	1	1	1	0	1	0	1	1	1	1	0
910	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1
911	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1
912	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0
913	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0
914	1	0	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0
915	1	0	1	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	1	1	0
916	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0
917	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0
918	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0
919	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0
920	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
921	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
922	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0
923	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
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925	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0
926	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0
927	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
928	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	0
929	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0
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936	0	0	1	0	1	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0
937	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0
938	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0
939	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
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941	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
942	1	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	0
943	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0
944	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
945	1	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0
946	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	0
947	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0
948	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
949	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	0	0
950	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
951	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0

Appendix 3 Shared derived character matrix for the 51 selected ophionines.

	901	902	903	904	905	906	907	908	909	910	911	912	913	914	915	916	917	918	919	920	921	922	923
951	7	7	8	9	14	17	8	8	12	19	19	21	20	22	22	14	12	19	19	13	4	11	12
950	18	16	16	17	20	22	21	18	14	17	17	17	18	19	19	15	13	16	18	10	19	15	13
949	10	9	10	11	15	17	15	12	21	18	17	22	20	22	24	22	20	24	23	17	10	18	14
948	9	9	10	10	15	15	11	10	9	19	18	18	20	20	20	11	9	14	16	8	7	11	12
947	17	16	18	18	20	28	19	16	24	25	25	27	29	30	30	27	24	28	29	20	14	19	17
946	19	18	19	20	22	27	21	18	24	26	28	28	29	32	29	26	23	27	29	20	15	20	17
945	14	13	13	14	17	24	17	13	22	22	22	26	24	28	27	24	23	26	27	19	12	18	17
944	12	12	12	13	16	18	15	12	17	17	17	21	19	21	21	20	18	21	21	16	11	15	13
943	13	12	13	14	16	22	16	12	21	21	21	23	22	26	25	25	23	28	27	15	10	16	15
942	16	15	15	17	19	26	18	14	21	25	25	28	27	29	28	26	24	28	29	18	12	19	17
941	13	14	12	12	13	10	13	17	9	11	12	11	13	13	13	7	6	10	7	8	13	8	12
940	10	10	10	12	16	16	12	10	13	13	15	14	15	16	15	14	13	15	14	12	7	12	12
939	4	5	6	6	13	11	6	7	7	13	12	11	12	12	13	7	5	11	9	7	3	7	10
938	9	10	11	11	18	18	11	12	12	20	20	19	19	21	21	14	11	19	17	13	7	13	15
937	20	21	22	22	25	24	24	27	23	18	19	18	18	20	21	19	18	23	16	13	24	16	18
936	24	25	24	26	24	23	26	25	24	21	22	19	21	22	22	22	20	24	20	13	24	14	19
935	21	21	22	22	23	22	24	25	23	18	19	18	19	20	20	21	18	23	18	13	22	15	18
934	14	13	15	15	18	23	17	13	18	25	25	28	26	30	28	22	18	22	29	18	12	15	15
933	14	13	14	14	15	20	16	12	21	22	23	27	25	28	28	22	20	22	29	18	12	16	13
932	18	17	16	18	19	22	20	17	18	23	25	25	26	29	26	21	18	22	26	18	16	16	14
931	15	15	15	15	18	19	19	15	20	22	21	25	24	27	27	22	19	21	27	13	15	13	18
930	15	14	14	17	18	21	17	13	20	22	22	28	27	29	28	24	22	25	29	14	12	16	16
929	16	16	16	17	21	23	18	16	20	26	25	29	28	29	30	23	21	27	28	14	13	17	20
928	14	13	13	15	18	20	17	14	21	23	22	28	27	29	31	23	21	24	30	14	13	15	17
927	19	19	17	18	19	20	21	18	18	20	21	20	22	23	21	18	17	18	21	11	16	13	15
926	15	14	13	14	15	21	17	15	17	18	19	21	20	22	21	20	18	21	22	11	14	14	16
925	17	16	16	18	20	20	19	16	22	21	21	20	23	23	23	23	22	24	21	12	14	17	16
924	16	15	14	16	18	22	18	14	18	21	20	23	24	24	23	23	21	23	23	13	13	16	16
923	13	15	16	15	19	21	14	16	16	17	16	17	18	18	19	19	14	22	15	10	12	12	
922	13	11	12	12	16	17	14	15	16	13	14	18	18	18	19	16	18	21	17	12	12		
921	27	26	25	23	15	15	30	27	18	12	12	12	14	15	15	16	16	16	14	9			
920	11	11	12	12	12	13	12	11	15	14	15	16	16	19	18	15	13	16	16				
919	16	15	16	17	17	22	18	13	21	26	26	30	28	33	32	27	24	28					
918	18	17	19	29	22	25	21	19	26	24	23	25	24	27	27	34	30						
917	17	15	15	17	15	19	19	15	25	18	18	20	19	22	22	31							
916	17	16	18	19	19	21	20	16	27	21	21	22	22	25	24								
915	17	16	17	17	22	25	18	17	24	28	28	34	33	36									
914	17	16	18	18	22	25	18	17	21	28	30	33	33										
913	18	17	19	19	21	24	18	17	20	26	27	31											
912	15	14	15	15	19	24	16	15	19	26	26												
911	17	16	18	18	21	25	17	15	19	30													
910	15	14	16	16	20	25	17	15	17														
909	17	17	18	18	20	20	20	18															
908	25	25	25	24	19	19	28																
907	30	28	27	26	18	19																	
906	20	18	20	20	27																		
905	16	16	17	18																			
904	28	29	29																				
903	30	30																					
902	32																						

Appendix 3 – *cont.*

	924	925	926	927	928	929	930	931	932	933	934	935	936	937	938	939	940	941	942	943	944	945	946	947
951	13	11	12	13	18	20	18	15	17	18	18	12	14	12	19	13	14	10	20	18	11	17	19	18
950	16	16	16	18	17	17	17	17	20	15	18	20	21	19	13	9	15	14	18	15	13	16	19	18
949	17	18	15	14	23	22	22	20	20	22	21	16	16	15	17	10	16	8	22	19	17	25	22	23
948	14	15	11	15	15	18	14	16	15	13	15	12	14	11	18	12	11	11	15	13	9	14	17	16
947	27	28	25	20	26	25	26	24	28	29	30	19	20	18	18	9	16	8	34	31	24	31	35	
946	29	30	27	23	26	26	27	24	32	29	32	22	26	21	21	9	19	10	37	30	26	31		
945	24	23	23	18	26	25	26	23	26	28	28	17	18	16	16	9	15	7	31	28	24			
944	21	19	19	14	19	20	20	18	23	22	24	15	16	16	13	6	11	5	26	23				
943	23	23	24	16	24	24	24	21	24	27	26	15	18	15	15	9	13	6	31					
942	29	28	27	21	28	27	28	23	30	29	31	17	22	17	19	9	17	8						
941	8	11	8	12	9	12	8	10	13	6	7	13	15	14	12	9	9							
940	16	15	14	16	14	15	15	14	15	13	14	14	17	13	15	10								
939	9	9	6	10	11	13	9	10	9	8	9	8	11	9	14									
938	15	16	12	17	16	19	15	15	18	14	17	15	18	15										
937	15	16	16	19	16	19	16	15	18	15	16	31	32											
936	21	22	20	24	21	22	21	19	21	17	18	30												
935	16	17	16	20	16	18	17	17	18	16	17													
934	23	22	22	19	26	25	27	25	30	29														
933	21	19	22	17	26	25	26	24	26															
932	23	24	22	21	24	25	26	23																
931	21	21	21	21	27	27	26																	
930	23	21	20	21	30	29																		
929	23	22	21	21	29																			
928	22	22	20	20																				
927	21	20	18																					
926	25	22																						
925	27																							

	948	949	950
951	17	18	13
950	14	16	
949	13		

Appendix 4 Primary labels matrix derived from analysis of 51 selected ophionines. The figure in brackets to the immediate right of the taxon number indicates the number of times that taxon alone is responsible for the failure of a character in the LeQuesne test. Notably high values in any column suggest that a particular character state shared by the respective characters is likely to be the result of parallel development or reversal. For example, character 1·2 has high values for taxa 909 and 923; as both taxa share an apomorphic 1 state, the labels matrix suggests this condition has been independently derived in the two taxa, and thus should not be considered a synapomorphy uniting 909 + 923.

	1.1	1.2	2	3	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2	8.1	9	10	12	13	14.1	14.2	15.1	15.2	16.1	16.2
901 (5)	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	2	--
902 (7)	--	--	1	--	--	--	--	--	--	1	--	--	--	--	--	--	1	--	--	--	--	2	--
903 (11)	--	--	--	--	--	--	--	--	--	1	--	--	--	1	--	1	1	1	--	--	--	5	--
904 (6)	--	--	1	--	--	--	--	--	--	2	--	--	--	--	--	--	--	--	--	--	--	--	--
905 (10)	--	--	--	--	--	--	--	--	2	--	--	--	--	--	--	--	--	1	--	--	--	--	--
906 (48)	--	--	--	--	11	--	--	--	5	--	--	--	--	--	--	--	--	6	--	--	--	--	--
907 (12)	--	--	--	--	--	--	--	--	--	1	--	--	--	1	--	--	--	--	--	--	--	1	--
908 (67)	1	--	3	--	--	22	2	--	--	5	1	--	--	--	34	3	--	2	1	2	2	--	--
909 (89)	3	11	--	2	13	--	--	--	7	--	--	2	--	--	--	1	--	--	3	1	--	--	6
910 (6)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1
911 (6)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2
914 (6)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--
915 (34)	1	1	--	2	1	--	--	--	1	--	--	1	--	--	--	--	--	--	--	1	--	--	1
916 (5)	--	1	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--
917 (13)	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
918 (19)	--	2	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
919 (2)	--	--	--	1	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--
920 (9)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--
921 (56)	--	--	2	--	--	--	--	--	--	3	2	--	--	5	--	1	3	2	--	--	--	12	--
922 (85)	4	--	1	--	--	12	6	--	1	1	2	--	--	--	34	1	--	1	5	2	11	--	--
923 (45)	5	13	1	--	--	--	--	--	--	--	1	--	--	14	--	--	--	1	1	--	--	--	--
924 (13)	1	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	2	--	--	--	--	--	--
925 (30)	4	--	--	--	--	--	1	7	--	--	--	--	--	--	--	--	1	--	1	--	1	--	--
926 (14)	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	2	2	--	--	--	1	--	--
927 (42)	1	1	--	10	1	--	--	--	1	--	--	3	--	--	--	1	--	--	1	1	--	--	1
928 (21)	--	--	--	2	--	--	1	--	--	--	--	1	--	--	--	--	--	--	--	--	1	--	--
929 (4)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
930 (3)	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
931 (3)	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--
932 (17)	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--	4	--	6	--	--	1	--	--
934 (4)	--	--	--	4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--
935 (19)	5	--	2	--	--	--	--	--	1	--	1	--	11	1	--	--	--	--	--	--	--	--	--
936 (12)	--	--	2	--	--	--	--	--	1	--	--	--	--	2	--	--	4	--	--	--	--	--	--
937 (28)	1	--	2	--	--	--	--	--	--	--	1	--	11	4	--	--	--	--	--	--	--	--	--
938 (10)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
939 (5)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
940 (6)	--	--	--	--	--	--	--	--	--	--	5	--	--	--	--	--	--	--	--	--	--	--	--
941 (35)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	3	--	--	--	--	1
942 (46)	--	--	--	1	--	--	2	--	--	--	--	2	--	--	--	--	--	--	1	1	2	--	1
943 (35)	--	--	--	--	4	--	1	4	--	--	--	--	--	--	--	--	--	--	--	--	3	--	2
944 (8)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--
945 (12)	3	--	--	--	3	--	2	--	--	--	--	3	--	--	--	--	--	--	1	--	--	--	--
946 (36)	--	--	--	--	--	19	2	--	8	--	10	--	--	--	--	--	--	--	--	2	2	--	--
947 (12)	--	--	--	--	1	--	1	1	--	--	--	--	--	--	--	--	--	--	--	1	2	--	--
948 (16)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--	1
949 (19)	--	10	--	--	--	--	--	--	--	--	--	2	--	--	--	--	--	--	--	1	--	--	--
950 (16)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	4	--	--	--
951 (46)	--	--	--	--	--	--	1	--	--	--	--	1	--	--	--	--	--	--	2	2	1	--	2

UNLABELLED TAXA: 912, 913, 933

Appendix 4 – *cont.*

	17	18.1	18.2	19	20.1	20.2	21.1	21.2	22.1	22.2	23	24.1	24.2	25.1	25.2	26	27.1	27.2	27.3	28.2	29.1	29.2	30	31
901	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--
902	--	6	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--
903	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	1	--	1	--	--	--	--	--	--
904	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
905	--	4	--	2	--	--	--	--	--	1	3	--	--	--	--	--	--	--	--	--	1	--	--	--
906	2	--	--	1	--	2	--	--	1	5	6	6	1	--	--	11	1	1	--	--	8	1	--	--
907	--	--	--	--	1	--	--	11	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	1
908	--	--	--	7	2	--	--	--	--	3	3	--	1	--	1	--	--	--	--	8	1	--	2	2
909	1	1	4	--	3	2	--	--	2	1	--	1	3	--	--	--	1	1	--	--	--	2	--	--
910	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--
911	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--
914	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--	--	--	--	--	1	--	--
915	4	--	1	--	1	1	--	--	--	--	--	--	1	--	--	--	1	1	--	--	--	1	--	--
916	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
917	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--
918	--	--	--	6	--	--	4	--	--	--	--	--	--	--	6	--	1	1	--	--	--	--	3	--
919	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--
920	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	1	--	--	2	--	--	--	--
921	1	--	2	--	1	--	4	11	1	1	2	--	--	--	--	1	2	--	--	--	--	3	--	5
922	--	--	1	2	1	--	--	--	3	1	2	--	2	--	5	--	1	1	--	1	17	--	4	1
923	5	3	1	--	--	--	--	--	1	2	1	1	1	--	3	10	--	--	--	4	--	1	--	--
924	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--	--	12	--	--	1	--	--
925	--	--	--	--	--	--	--	--	--	--	--	1	2	--	--	--	--	--	12	--	--	1	--	--
926	--	--	--	--	--	2	--	--	1	--	--	1	1	--	--	--	--	--	--	--	--	--	--	5
927	--	1	1	--	1	--	--	--	2	3	--	--	--	--	--	--	--	--	--	--	--	1	--	--
928	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--	--
929	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--	--	--
930	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
931	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
932	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	6
934	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
935	--	--	1	--	--	--	--	--	--	1	--	--	--	--	--	--	--	1	--	--	1	--	2	2
936	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--
937	--	--	2	2	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	10	--	1	1
938	--	1	--	--	1	--	--	--	--	--	--	--	--	--	1	--	--	1	--	1	--	--	--	--
939	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--
940	--	--	--	--	--	--	--	--	--	--	--	--	1	--	1	--	--	--	--	--	--	--	--	--
941	--	1	--	--	--	--	--	--	--	1	--	--	3	--	6	--	--	--	--	--	--	--	--	6
942	--	1	--	--	--	--	--	--	--	--	--	--	--	1	1	--	1	1	--	2	--	1	--	--
943	--	1	--	--	--	--	--	--	--	--	--	--	--	--	1	--	1	1	--	--	--	1	--	--
944	--	--	--	--	2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
945	--	--	--	--	--	1	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--
946	--	--	1	--	--	2	--	--	1	--	--	--	--	--	--	--	1	1	--	--	--	1	--	--
947	5	--	--	5	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--	--	--	--	--
948	--	--	--	--	--	--	--	--	1	--	--	1	--	15	--	--	--	--	--	1	--	--	--	--
949	--	--	3	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
950	--	--	--	--	--	2	--	--	--	4	3	--	2	--	1	--	--	--	--	--	--	--	1	--
951	--	2	--	--	--	--	--	--	1	--	--	1	--	15	1	--	1	1	--	2	--	1	--	--

Appendix 4 – *cont.*

	32	33	35	36.1	36.2	36.3	37.	38	39	40	41	42.1	42.2	43.1	43.2	44.1	44.2	45.1	45.2	46	47.1	47.2	48.1
901	--	--	--	--	--	--	1	--	--	--	3	--	--	--	--	--	--	--	--	--	--	--	--
902	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--
903	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
904	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	1	--	--	--	--	--
905	--	--	--	--	--	--	--	--	--	--	2	2	--	--	--	--	2	--	--	--	--	--	--
906	--	1	--	--	--	--	--	--	2	--	5	--	--	--	3	--	--	1	--	--	--	--	1
907	1	--	--	1	--	--	--	--	--	--	1	--	--	2	--	--	--	--	--	--	--	1	--
908	2	--	--	1	--	--	--	--	--	--	1	1	3	1	--	2	--	3	2	--	--	--	--
909	--	1	1	4	1	1	2	--	2	--	--	--	3	5	2	1	3	--	1	--	--	2	1
910	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--
911	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--
914	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1
915	--	--	1	1	--	--	1	--	1	--	--	--	1	1	1	--	2	--	1	--	--	--	1
916	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--
917	--	--	--	4	2	--	1	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--
918	--	--	--	--	--	--	1	--	--	--	--	--	2	--	1	--	--	--	2	--	--	--	--
919	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
920	--	--	--	2	--	--	--	--	--	6	--	--	--	--	--	--	--	--	--	2	--	--	--
921	4	--	9	--	--	--	--	--	--	--	4	--	1	1	--	1	--	1	--	--	--	15	--
922	1	1	--	3	--	--	--	--	1	--	9	4	1	2	--	1	--	1	4	--	--	--	3
923	3	1	6	--	--	--	--	--	1	--	--	--	1	--	--	1	--	1	--	--	--	--	--
924	--	--	--	--	--	--	--	--	--	--	--	1	--	1	--	1	1	1	--	--	--	--	1
925	--	--	--	--	--	3	--	--	--	--	--	3	--	3	1	1	6	4	--	--	--	--	--
926	4	--	--	--	--	--	--	--	--	--	--	--	--	--	2	1	--	1	--	--	--	--	--
927	--	2	--	1	1	2	1	--	1	--	--	--	1	1	--	1	1	--	--	--	--	1	--
928	--	--	1	--	--	1	--	--	--	1	--	--	--	--	1	1	2	--	--	1	--	1	1
929	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--
930	--	--	1	--	--	--	--	--	2	--	--	--	--	--	1	--	--	--	--	1	--	--	--
931	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	1	--
932	1	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	3	3	--	--	--
934	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--
935	1	--	--	1	--	--	--	--	--	--	--	--	--	--	1	--	1	--	--	--	--	--	--
936	1	1	--	--	--	4	--	--	1	--	--	--	1	--	--	--	1	--	--	--	--	--	--
937	1	2	--	3	--	--	--	--	--	--	1	--	1	--	5	--	1	--	--	--	--	--	--
938	--	--	--	--	--	3	--	2	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--
939	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	5	--	--	--	1	--	--
940	--	--	--	--	--	1	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--
941	1	1	11	--	1	--	--	12	--	--	--	2	--	3	--	--	--	1	--	--	1	--	--
942	--	1	1	--	--	3	--	1	1	2	--	--	--	--	1	2	1	--	--	1	1	1	1
943	--	1	--	--	--	--	2	17	--	5	--	--	--	--	--	1	--	--	--	--	6	--	2
944	--	--	--	1	1	--	--	1	--	1	--	--	--	--	--	1	--	--	--	1	5	--	--
945	--	--	--	--	--	--	--	--	--	2	--	--	--	--	--	--	--	--	--	1	--	--	--
946	--	--	--	--	1	1	1	--	1	3	--	--	--	1	1	--	--	--	2	3	--	--	1
947	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	2	--
948	--	--	--	--	--	--	--	--	1	--	--	1	--	--	1	--	--	2	1	1	1	--	--
949	--	--	--	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	1	2
950	--	--	--	--	--	--	--	--	1	--	--	1	--	--	--	--	--	--	--	--	--	--	1
951	--	3	--	--	--	1	--	2	4	1	--	1	--	--	1	1	--	1	1	3	2	--	--

Appendix 4 – *cont.*

	48.2	50	51.1	51.2	52.1	52.2	54	55	56	57	58.1	58.2	59	60	61.1	61.2	62	63	64
901	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
902	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
903	--	--	--	--	--	--	1	--	--	--	--	--	7	--	--	--	--	--	--
904	--	--	--	--	--	--	1	--	--	--	3	--	--	--	--	--	1	--	--
905	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
906	6	--	--	--	--	--	--	--	--	3	--	--	--	--	--	5	--	1	--
907	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--
908	--	--	1	1	--	--	2	--	--	2	2	--	--	--	--	--	2	--	--
909	--	31	--	--	1	--	--	--	30	--	7	--	1	--	1	3	1	2	--
910	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	2	--	5
911	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	5
914	--	--	--	--	--	6	--	--	--	--	--	--	--	--	--	--	--	--	--
915	--	1	--	--	3	--	--	--	30	--	1	--	--	--	1	1	--	--	--
916	--	--	--	--	1	1	--	--	--	4	--	--	--	--	--	--	--	--	--
917	--	--	--	--	3	4	--	--	--	--	--	--	--	--	--	1	--	4	--
918	--	--	--	--	2	2	--	--	--	--	--	--	--	--	--	1	--	--	--
919	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
920	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--
921	--	--	--	--	--	--	1	--	--	--	--	--	--	--	11	--	--	--	--
922	--	--	6	5	--	--	1	--	--	1	1	--	--	--	--	--	1	1	--
923	--	--	--	--	--	--	1	--	--	--	--	--	--	--	1	4	--	1	--
924	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
925	6	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--
926	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--
927	--	31	--	--	--	--	--	--	1	--	2	--	1	--	1	1	2	2	--
928	1	--	--	--	--	--	--	2	--	--	--	1	--	19	1	1	--	--	--
929	--	--	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	--	--
930	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
931	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--
932	2	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--
934	1	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--
935	--	--	--	--	--	--	2	--	--	--	--	--	3	--	--	--	--	--	--
936	--	--	--	--	--	--	2	--	--	3	--	--	--	--	--	--	--	--	--
937	--	--	--	--	--	--	3	--	--	--	2	--	1	--	--	--	--	--	--
938	7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--
939	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
940	--	--	2	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
941	--	--	4	1	--	--	4	--	--	1	3	--	--	--	--	--	--	1	--
942	2	--	1	1	--	--	--	1	--	--	--	27	1	19	2	2	--	1	--
943	--	--	--	1	6	7	--	--	--	--	--	--	--	--	--	2	--	1	--
944	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--
945	--	--	--	--	--	--	--	5	--	--	--	--	--	--	--	2	--	--	--
946	2	--	--	--	--	--	--	--	--	--	--	--	1	--	--	2	--	2	--
947	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--
948	--	--	1	--	--	--	--	--	--	--	--	1	--	--	--	--	1	--	--
949	--	--	2	2	--	--	--	7	--	--	--	--	1	--	--	1	--	2	--
950	--	--	3	2	--	--	3	--	--	--	3	--	--	--	--	--	--	--	--
951	1	--	2	1	--	--	--	--	--	--	--	27	1	1	1	1	1	1	--

Appendix 5 Labels matrix derived from the reduced *Thyreodon*/*Euryophion* data set.

		6.1	6.2	8.1	9	12	13	14.1	16.1	16.2	17	18.2	19	20.1	21.1	21.2	23	26	27.1	27.2	29.2	30	31	32	33	36.1	36.2	37	39	41	43.1	44.1	44.2	45.1	59	62
901	(31)	--	--	--	7	--	--	--	2	3	3	2	--	11	1	2	--	3	2	--	1	--	1	1	--	1	--	4	--	14	1	3	--	--	--	--
902	(2)	--	--	--	--	--	--	--	1	--	--	--	--	--	2	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
903	(51)	1	1	1	1	3	3	1	5	3	3	1	2	--	5	--	1	6	--	14	2	1	2	2	1	--	7	5	2	--	1	3	--	1	23	1
904	(9)	--	--	--	--	--	1	--	2	1	2	--	--	--	--	--	--	--	--	--	--	--	1	1	--	--	--	1	6	--	1	2	--	--	--	--
907	(36)	--	--	--	2	1	--	--	4	1	1	4	--	11	2	9	--	1	9	--	3	--	4	4	--	2	--	1	1	3	8	1	--	--	--	--
908	(24)	2	2	--	2	4	1	2	--	--	--	--	10	--	--	--	2	--	--	2	--	11	--	--	2	--	--	--	2	--	2	--	--	2	--	2
921	(58)	1	1	1	3	1	2	1	9	1	2	2	1	3	4	9	1	1	9	1	6	1	5	5	1	21	--	1	1	14	3	2	1	1	--	1
935	(49)	3	3	7	11	1	--	3	1	1	1	3	4	--	1	--	3	1	--	3	2	9	1	1	3	1	1	--	2	--	1	1	1	3	23	3
936	(66)	5	5	1	--	1	12	5	--	2	2	2	9	--	--	--	5	--	--	2	9	7	2	2	5	1	16	15	1	--	2	2	9	5	--	5
937	(53)	3	3	7	2	2	2	3	1	--	--	11	3	--	1	1	3	--	1	12	1	2	--	--	3	21	1	1	3	1	2	--	9	3	1	3

Appendix 6 Labels matrix derived from the reduced *Enicospilus*/*Stauropoctonus* data set.

		1.1	1.2	3	4.1	5.1	5.2	6.1	7.2	12	13	14.2	15.1	15.2	16.2	17	18.1	18.2	19	20.1	20.2	21.1	22.1	24.1	24.2	25.2	27.1	27.2	27.3	29.2	30	31	33	35	36.1	36.2	36.3	37	39
909	(139)	4	16	1	17	11	4	28	2	--	--	1	6	1	13	1	--	12	--	9	4	1	--	7	11	--	1	1	--	1	--	--	--	1	11	3	1	10	8
910	(17)	--	--	--	--	--	--	--	--	--	--	--	1	--	3	--	--	--	--	--	--	--	5	3	3	--	--	--	--	--	--	--	5	--	--	--	--	--	--
911	(20)	--	--	--	--	--	--	--	--	--	--	--	--	--	8	--	--	--	--	--	--	--	5	3	3	--	1	1	--	--	--	--	5	--	--	--	--	1	--
913	(6)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	1	--	1	1	--	--	--	--	--	1	--	--	--	--	--
914	(10)	--	--	1	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	1	2	--	1	1	--	2	--	--	--	1	--	--	--	--	--
915	(40)	1	1	2	1	--	--	1	1	--	--	--	1	--	1	7	--	1	--	1	1	--	--	--	1	--	2	2	--	3	--	--	--	1	1	1	--	1	1
916	(20)	1	2	--	--	--	1	--	--	--	--	1	1	1	--	--	--	1	--	--	--	2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1
917	(20)	--	1	--	--	--	2	--	--	--	--	--	--	--	--	--	--	1	--	4	--	5	--	1	1	--	--	--	--	--	--	--	--	--	6	3	--	1	--
918	(112)	4	9	1	2	3	4	--	4	--	--	1	4	1	--	1	--	8	27	5	3	9	--	1	--	26	15	15	--	--	22	--	--	--	--	1	--	2	6
919	(22)	1	1	1	--	1	1	--	1	--	--	--	1	--	--	--	--	1	1	1	1	1	--	--	--	1	1	1	--	--	22	--	--	--	--	--	--	--	1
924	(21)	1	--	--	--	--	1	--	--	1	10	--	--	--	1	--	--	--	--	--	2	--	--	1	1	--	--	--	11	2	--	1	--	--	--	--	--	1	--
925	(52)	6	--	--	--	1	6	--	--	1	1	3	1	3	--	--	--	1	--	--	--	--	--	2	3	--	--	--	11	1	--	--	--	--	1	1	5	1	1
926	(47)	--	--	--	--	2	--	--	2	9	10	--	--	--	6	--	--	--	--	--	4	--	--	1	1	--	--	--	1	6	--	19	--	--	--	--	5	4	--
928	(19)	--	--	1	--	1	--	--	1	--	--	--	--	1	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	1	--	--	1	--	--
929	(14)	--	--	1	--	--	--	--	--	1	--	1	--	--	--	--	11	--	--	--	--	--	--	--	--	--	2	2	--	--	--	--	--	--	--	--	--	1	--
930	(10)	1	--	1	--	--	--	--	1	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	9
931	(30)	--	--	4	--	1	--	--	1	8	--	1	--	2	--	--	11	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--	--	3	--	--	1	2	--
932	(31)	--	--	--	--	1	--	--	1	10	1	--	--	--	1	--	--	--	--	--	1	--	--	3	3	--	--	--	--	1	--	19	--	--	--	--	1	2	--
934	(5)	--	--	4	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
942	(18)	--	--	1	--	1	--	--	1	--	--	1	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	2	--	--
943	(29)	--	--	--	4	--	3	--	--	--	--	1	--	2	3	--	--	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	--	2	--
944	(44)	2	--	--	1	1	1	--	1	--	--	3	2	2	1	--	--	2	--	11	1	--	--	--	--	--	--	--	--	--	--	--	--	--	16	2	--	--	2
945	(46)	5	1	--	4	2	1	--	5	--	--	3	1	1	--	--	--	1	1	1	2	1	--	--	--	26	1	1	--	--	1	--	--	1	--	2	--	2	1
946	(29)	1	1	--	1	1	--	28	--	--	--	1	1	1	1	--	--	1	--	1	1	--	--	--	--	--	--	--	--	--	--	--	--	--	1	1	2	1	1
947	(47)	1	1	--	4	1	1	--	1	--	--	--	1	2	--	15	--	1	27	1	1	1	--	1	--	1	2	2	--	1	1	--	--	1	--	--	--	3	1

Appendix 6 – *cont.*

	40	42.2	43.1	43.2	44.1	44.2	45.1	45.2	46	47.1	47.2	48.1	48.2	52.1	52.2	55	56	57	59	60	61.1	61.2	62	64
909	1	12	10	4	2	11	--	3	2	--	1	4	1	5	3	--	28	--	2	--	1	2	--	--
910	--	--	--	--	3	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	5	5
911	--	--	--	--	3	--	--	--	--	--	--	1	1	--	--	--	--	--	--	--	--	--	3	5
913	--	--	--	3	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	1	--
914	--	--	--	--	--	--	--	--	3	--	--	1	--	--	6	--	--	--	--	--	--	--	--	--
915	--	1	1	2	2	6	--	1	--	--	--	1	--	3	--	--	28	--	--	--	1	1	1	--
916	1	1	--	1	1	--	--	1	--	--	1	1	--	1	1	--	--	18	1	--	--	1	--	--
917	--	1	7	--	1	1	--	--	--	--	--	--	--	2	3	--	--	--	--	--	--	--	--	--
918	1	8	--	5	4	--	--	5	2	--	7	2	1	2	2	1	--	--	3	--	3	3	1	--
919	--	1	--	--	1	--	--	--	--	--	1	--	--	--	--	--	--	--	1	--	1	1	--	--
924	--	--	1	1	1	1	2	--	--	--	--	1	1	--	--	--	--	--	--	--	--	--	1	--
925	--	1	15	1	2	10	12	--	--	--	2	2	6	--	--	--	--	--	--	--	--	--	4	--
926	1	--	--	2	1	--	7	1	1	--	--	4	1	--	--	--	--	1	--	--	2	2	1	--
928	1	--	--	1	1	3	--	--	1	--	1	1	1	--	--	2	--	--	--	17	1	1	--	--
929	--	--	--	1	--	--	1	1	--	--	1	--	--	--	--	4	--	--	1	--	--	--	--	--
930	--	--	--	1	--	--	--	--	2	--	--	--	--	--	--	1	--	--	--	--	1	1	--	--
931	--	--	--	2	1	--	11	1	--	--	3	--	--	--	--	1	--	--	3	--	1	1	--	--
932	2	--	--	--	--	--	2	2	2	--	--	2	2	--	--	--	--	4	--	--	1	1	--	--
934	1	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	2	--	--	--	--	--	--
942	1	--	--	1	1	1	--	--	1	--	1	1	1	--	--	1	--	--	--	17	1	1	--	--
943	4	--	--	--	3	--	--	--	2	15	1	1	--	5	6	--	--	1	--	--	--	1	--	--
944	3	2	1	1	1	--	--	1	2	15	1	3	--	1	1	--	--	3	--	--	--	5	--	--
945	4	1	--	--	1	--	--	--	2	--	1	2	--	1	1	12	--	--	--	--	1	2	--	--
946	1	1	1	1	1	1	--	1	1	--	1	1	1	--	--	--	1	1	--	--	--	--	--	--
947	--	1	--	--	1	--	--	--	3	--	3	1	4	1	1	--	--	--	1	--	1	1	5	--

Appendix 7 Character matrix for the HTUs.

	1.1	1.2	2	3	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2	8.1	8.2	9	10	11	12	13	14.1	14.2	15.1	15.2	16.1	16.2	17	18.1	18.2	19	20.1	20.2	21.1	21.2	22.1
960	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	0	0	1
961	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
962	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	0	0	1
963	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1
964	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
965	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
967	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	1
968	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	1

	22.2	23	24.1	24.2	25.1	25.2	26	27.1	27.2	27.3	28.1	28.2	29.1	29.2	30	31	32	33	34	35	36.1	36.2	36.3	37	38	39	40	41	42.1	42.2	43.1	43.2	44.1	44.2
960	0	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	1	0	1	1	0	0
961	0	0	0	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0	0
962	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	1	0	1	0
963	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	0	0	0
964	1	1	1	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0
965	1	0	1	1	1	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	1	1	1	0	1	1
967	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	0	1	1	0	0
968	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	0	1	1	0	0

	45.1	45.2	46	47.1	47.2	48.1	48.2	49	50	51.1	51.2	52.1	52.2	53	54	55	56	57	58.1	58.2	59	60	61.1	61.2	62	63	64
960	1	1	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0
961	1	0	0	1	0	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	1
962	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0
963	1	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0
964	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0
965	1	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0
967	1	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
968	1	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0

Appendix 8 Labels matrix derived from the HTUs plus the unplaced taxa (905, 906, 920, 922, 923, 927, 938, 939, 940, 941, 948, 949, 950 and 951).

		1.1	1.2	2	3	5.1	6.1	7.1	7.2	9	12	14.1	14.2	15.1	15.2	16.2	17	18.1	18.2	19	20.1	20.2	22.1	22.2	23	24.1	24.2	25.1	25.2	26	27.1	27.2	28.2	29.1	29.2	30	31	32	33
905	(23)	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	--	5	--	3	2	--	--	3	2	--	4	--	--	--	--	--	--	6	--	--	--	--	--
906	(108)	2	2	--	--	--	13	--	1	2	--	13	--	--	--	--	24	2	--	13	4	5	--	10	7	7	2	--	2	24	--	1	2	10	--	--	--	2	--
920	(59)	2	1	--	--	1	--	--	1	--	--	--	2	2	2	2	--	--	2	--	3	2	2	--	--	3	--	--	1	--	2	1	2	1	1	1	--	--	--
922	(134)	7	1	--	--	17	1	--	--	--	--	2	7	3	24	2	--	--	14	1	2	1	5	1	3	4	1	--	5	--	3	5	1	21	4	16	--	--	2
923	(109)	10	17	--	--	--	2	1	--	20	--	2	2	--	--	--	24	6	1	2	2	2	1	3	3	3	1	--	6	24	1	2	7	2	1	--	--	9	2
927	(46)	--	--	--	14	--	--	--	4	--	13	1	1	1	--	--	--	2	--	--	1	--	1	6	1	--	6	--	1	--	2	--	1	--	--	--	--	1	1
938	(25)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	2	1	--	--	--	1	--	--	1	--	1	1	1	--	--	--	--	--	--
939	(20)	--	--	--	--	--	1	--	1	--	--	--	--	--	--	1	--	--	--	1	--	--	--	--	1	1	1	--	1	--	--	--	1	--	--	--	--	--	--
940	(27)	--	--	--	--	--	--	20	1	1	--	--	--	--	--	2	--	1	--	--	1	--	2	1	1	--	1	--	1	--	2	--	1	--	--	--	--	--	--
941	(98)	--	--	1	--	--	1	1	1	1	13	9	--	--	--	4	--	5	--	1	1	--	--	5	3	--	7	--	6	--	1	4	7	--	--	1	28	5	1
948	(28)	--	--	--	--	--	--	--	1	--	--	--	1	6	--	1	--	1	--	--	1	1	1	--	--	1	--	14	--	--	--	--	3	--	--	--	--	--	--
949	(53)	5	14	--	1	1	--	--	4	--	--	--	--	3	--	--	--	--	8	--	2	--	--	--	--	1	--	--	1	--	1	--	3	--	1	--	--	--	--
950	(53)	--	--	--	--	--	--	--	--	--	10	2	--	7	--	--	--	1	--	--	2	5	--	5	6	--	3	--	2	--	6	1	--	--	--	11	--	6	1
951	(36)	--	--	--	--	--	--	--	--	--	--	--	7	1	--	2	--	2	--	--	--	1	3	--	--	1	--	14	--	--	--	1	2	--	1	--	--	--	2
960	(15)	--	--	--	8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	1	1	--	--	--	--	--	--	--
961	(29)	1	1	--	--	1	--	--	1	--	--	--	1	--	--	3	--	--	1	--	1	1	1	--	--	--	--	--	--	--	1	2	--	--	3	--	--	--	2
962	(27)	1	1	--	4	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	1	--	--	1	--	1	1	1	--	2	--	--	--	--
963	(84)	4	7	--	--	10	--	1	1	1	--	--	4	2	1	1	--	--	13	--	5	1	2	1	1	1	1	--	4	--	3	1	2	--	--	--	--	--	1
964	(86)	--	--	15	--	--	1	8	--	9	--	7	--	1	--	7	--	1	--	1	1	--	--	5	7	--	3	--	2	--	--	2	-2	--	12	15	1	3	10
965	(88)	--	--	15	--	--	14	7	--	6	1	3	--	--	--	3	--	2	--	14	--	--	--	2	1	--	--	--	1	--	--	4	1	2	2	1	28	6	2
967	(8)	--	--	--	--	1	--	--	3	--	--	--	--	--	5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
968	(16)	1	--	--	--	8	--	--	--	--	--	--	1	1	1	--	--	--	1	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

Appendix 8 – *cont.*

	35	36.1	36.2	36.3	37	38	39	40	41	42.1	42.2	43.1	43.2	44.1	44.2	45.1	45.2	46	47.1	47.2	48.1	48.2	51.1	51.2	52.1	54	55	57	58.1	59	61.1	61.2	62	63
905	--	--	--	--	--	--	--	--	4	4	--	--	--	1	3	--	--	--	--	--	--	--	--	1	--	--	--	1	1	--	--	--	--	3
906	2	--	--	--	1	--	3	--	7	2	--	--	9	4	2	2	--	--	--	--	2	14	--	--	--	1	--	6	2	1	--	8	--	2
920	--	25	2	--	--	--	1	16	1	1	--	1	1	--	--	--	1	7	--	13	1	--	1	1	--	--	--	2	--	2	--	--	6	1
922	--	25	4	--	--	--	3	2	14	4	--	19	3	--	--	1	6	2	--	2	8	--	4	4	--	2	--	3	2	1	--	1	2	3
923	8	--	1	--	1	--	3	--	2	--	1	--	2	3	--	8	--	--	--	1	3	2	--	2	--	2	--	5	2	--	1	9	1	5
927	1	--	--	11	1	--	--	--	--	2	--	--	--	1	--	--	--	--	--	--	2	--	1	2	--	1	--	3	4	--	2	--	3	1
938	--	--	--	10	--	3	--	--	--	1	--	--	1	2	--	--	2	--	3	--	--	14	--	1	--	--	--	--	--	1	2	--	--	1
939	--	--	--	--	2	2	1	--	--	--	--	--	--	--	17	--	--	--	3	--	--	--	1	1	--	--	--	1	--	1	1	--	1	--
940	--	--	1	7	1	--	1	--	--	1	1	--	--	--	--	--	--	--	--	--	1	--	2	1	--	1	--	1	1	--	--	--	--	--
941	14	--	3	--	6	12	1	--	--	2	1	13	--	1	1	3	--	--	--	--	2	--	4	3	--	9	--	2	6	--	3	--	3	1
948	--	--	--	--	--	2	1	--	--	1	--	--	2	--	--	8	1	1	3	--	--	--	1	--	--	--	--	1	--	2	--	--	2	--
949	1	--	4	--	1	--	1	--	--	4	--	--	4	2	--	--	2	--	--	6	4	--	2	2	--	--	20	--	--	4	1	1	--	2
950	--	--	2	--	1	--	2	--	7	1	--	1	--	1	--	--	--	--	--	--	1	--	3	3	--	7	--	--	4	--	4	--	1	--
951	--	--	--	--	1	5	4	--	--	3	--	--	1	1	--	1	1	11	5	--	--	--	1	--	--	--	--	--	--	--	--	--	1	--
960	5	--	3	--	--	--	--	--	--	--	--	--	2	1	--	--	2	--	--	--	1	--	--	--	--	--	--	--	--	2	--	--	--	1
961	--	--	--	--	--	--	1	--	--	--	1	--	1	--	--	--	--	--	--	1	1	4	--	--	22	--	--	--	--	1	--	1	3	2
962	4	--	1	--	1	--	1	--	--	1	--	--	1	1	--	--	1	--	--	1	2	--	1	1	--	--	20	--	--	1	2	--	--	1
963	--	--	3	--	7	--	2	--	--	1	22	--	2	1	--	--	3	--	--	15	2	1	2	2	22	1	--	1	1	2	--	6	1	3
964	--	--	--	--	--	--	4	--	1	2	7	12	--	4	1	12	--	--	--	--	2	--	2	2	--	4	--	--	2	--	--	--	6	--
965	1	--	3	--	1	1	3	--	2	2	8	2	--	3	14	3	--	--	--	--	4	--	1	1	--	4	--	--	2	--	--	--	2	2
967	--	--	--	--	--	--	--	2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	1	2	--	--	--
968	--	--	--	--	--	--	--	4	--	--	--	--	1	--	--	--	1	3	--	--	1	--	--	--	--	--	--	1	--	2	--	5	--	--

Appendix 9 Labels matrix derived from the *Euryophion* primary data matrix (Table 20).

		1.1	8.1	9	13	19	27.2	30	36.2	37	43.2	54	57	59	70	71	72	73	74	75
201	(6)	2	--	--	--	--	--	--	4	--	1	--	--	1	2	--	--	--	2	--
202	(36)	1	2	10	7	8	5	1	1	3	1	1	2	2	1	2	6	3	12	3
203	(24)	--	6	10	1	1	5	3	4	2	3	3	6	2	--	--	1	--	1	--
204	(18)	2	2	1	1	1	--	2	6	1	--	2	2	1	2	--	1	--	12	--
205	(11)	--	3	--	--	--	1	4	2	--	3	4	3	2	--	--	--	--	--	--
206	(10)	--	--	--	2	--	--	--	1	1	6	--	--	--	--	2	4	2	--	2
207	(0)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
208	(22)	--	1	1	5	8	2	1	--	1	--	1	1	11	--	3	2	3	1	3

Index to generic names

Synonyms are in *italics*.

British Museum (Natural History)

An introduction to the Ichneumonidae of Australia

I. D. Gauld

In the important field of biological and integrated control of pests the parasitic Hymenoptera are of particular significance, and this work considers one of the largest families of Parasitica, the Ichneumonidae. The group has received little attention in Australia – though it has already been utilized successfully in curtailing the ravages caused by accidentally introduced pests. For selective control programmes to be effective, however, a sound knowledge of the biology of both the pest and its parasites is essential – and a sound taxonomic base is vital for the development of such knowledge.

Ironically, considering the group's economic importance, the parasitic Hymenoptera is amongst the least studied of any group of living organisms, and taxonomic difficulties have presented major problems to many entomologists working with the Parasitica. **An Introduction to the Ichneumonidae of Australia** will go a long way towards rectifying this situation, being a taxonomic treatment, by genus, of the Australian ichneumonids, a comprehensive illustrated identification guide, and a summary of all available information on the group. It will also serve as an introduction to the biology and distribution of Australian ichneumonids, and provide a check-list of the described species and an index to their known hosts. It provides an important revision of ichneumonid nomenclature in order to bring the group into line with the generally accepted principles of zoological nomenclature.

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Department of Entomology, British Museum (Natural History), Cromwell Road, London
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Contents

Synopsis

Observations on phthirapteran morphology are analysed with particular reference to the Trichodectidae. Problems of structure, homology and nomenclature associated with major morphological features are briefly reviewed and solutions suggested where possible; where appropriate, the morphological terminology is clarified. A cladistic analysis of the 351 species and subspecies of Trichodectidae is carried out using the states of 187 characters, and the taxa are re-classified in accordance with the results and the principles of phyletic sequencing. Twenty genera are accepted in five subfamilies. Ten of the genera are divided into 27 subgenera. This necessitates the description of one new subfamily, three new genera and four new subgenera. Three genera are newly synonymised, eight genera and subgenera are recalled from synonomy, and four genera are reduced to subgenera. The generic placements of 106 species and subspecies are changed. Keys to the subfamilies, genera and subgenera are provided, and the genera and subgenera are described.

Introduction

The Trichodectidae is a family of ischnoceran chewing lice parasitic on mammals. There are 351 described species and subspecies grouped into between 13 and 39 genera, various workers having widely differing views on generic limits. The classification of the Trichodectidae at the generic level is perhaps more confused than that of any other group of lice (Hopkins, 1949, 1960; Emerson & Price, 1981) and no workable keys to genera are available. The confusion and

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disagreement surrounding the classification of the family persists despite a sound basis of taxonomic knowledge at the species level, derived largely from the works of Werneck (1948, 1950), although this author did not attempt to produce any keys.

The purpose of this study is to present a classification of the species of Trichodectidae and to describe and provide a key to the recognised genera and subgenera. The foundation of the classification proposed below is a cladistic analysis, and for the purpose of determining character polarity in that analysis a suitable out-group had to be identified first. Ideally this out-group should be the sister-group of the taxon studied, and in this case would be expected to be a group in the same suborder, the Ischnocera. However, the holophyly of the Ischnocera has not been demonstrated (Lyal, 1985), although there is evidence that indicates the holophyly of a group comprising most of the Ischnocera (including the Trichodectidae). The classification of the Ischnocera is unsettled, and the sister-group of the Trichodectidae has not been identified. A single teneral male specimen of a possible sister-group has been seen, purportedly collected from a corvid in Austria. The specimen has the single tarsal claws of a mammal parasite, but no other apomorphies of the Trichodectidae, although it has the same general facies as members of the family. As out-group, therefore, the Ischnocera s.l. is used, reference being made where appropriate to the other three suborders of Phthiraptera (Lyal, 1985).

The term 'holophyletic' is used below to refer to groups of taxa comprising a single ancestral species (known or inferred) and all of its descendants. The more familiar term 'monophyletic' is avoided because ambiguities in its use have caused misunderstandings in the resolution of systematic problems.

Scale lines equivalent to 50 μm are given in most figures.

This study formed part of the results of a research project submitted to the University of London for the degree of Doctor of Philosophy.

Acknowledgements

I am very grateful to all those who have given advice and read parts of this paper whilst in preparation, particularly Dr R. G. Davies, University of London; Dr L. A. Mound, Dr T. Clay, Mr W. R. Dolling, Mr D. Hollis and Mrs J. M. Palmer, British Museum (Natural History); and Dr B. Heming, University of Alberta. I also thank the following people who were of great assistance during part of this study which was carried out in the United States: Dr K. C. Emerson, Florida; Dr K. C. Kim, Pennsylvania State University; Dr R. D. Price, University of Minnesota; Dr O. Flint, United States National Museum; Dr R. Traub and Miss H. Starke, University of Maryland School of Medicine; and Dr W. A. Drew and Dr D. Peters, Oklahoma State University.

Method of systematic analysis

Systematic analysis is carried out in order to determine 'relationships' between different taxa, the relationships discovered being employed to study some aspect of the biology or evolution of the taxa and/or to provide a framework for their classification. Taxa may be deemed to be 'related' according to a number of different criteria, so the type of analysis performed is dictated by the requirements of other studies to be undertaken. In this case the systematic analysis is preliminary to an examination of the phylogenetic linkages between Trichodectidae and their hosts (Lyal, in prep., *a*). The relationships required from the analysis are therefore phylogenetic in nature. Although it has been suggested that phylogenetic relationships can be determined by phenetic analysis (Sneath & Sokal, 1973), this is generally believed not to be the case, and a phyletic analysis is required (Wiley, 1981). In this study a manual cladistic analysis was deemed most suitable as computerized methods of sufficient power and capacity were unavailable when the study was initiated (Lyal, 1983).

The first stage in the analysis was a character survey of all species of the family, with the aim of discovering suitable apomorphies. As analysis proceeded some characters initially selected were rejected, if the polarity of their states could not be determined, or if their apomorphic states were restricted to single species.

The observations were recorded in a data matrix, but it rapidly became apparent that this matrix was too large to be manipulated conveniently. Preliminary inspection of the taxa had led to the recognition of sufficient apomorphies to divide the family into five or six plausible holophyletic groups, so secondary data matrices were compiled for each of these. The smaller number of species and apomorphies then necessary on each of these matrices enabled manual analysis to proceed. These matrices were inclusive rather than exclusive, and taxa with low probabilities of membership were included; as a consequence some taxa were included in more than one matrix. The matrices were examined and taxa or holophyletic groups sharing the greatest number of synapomorphies were united as sister-groups. This process was continued until the cladistic relationships within each matrix were resolved as fully as possible. The full matrix was then compiled using the largest holophyletic groups identified in the analysis of the secondary matrices. This matrix was then analysed using the same technique and the full cladogram drawn. The cladogram, which gave the full distribution of apomorphies, was examined to ensure that the most parsimonious distribution of apomorphies had been achieved.

Character states were weighted by a simple 'gain' or 'loss' criterion. 'Loss' states were only used in the analysis where 'gain' states were not available, and after 'gain' states had been used to resolve the cladogram as fully as possible. It follows that, whereas the distribution of 'gain' states should be maximally parsimonious over the cladogram, this is unlikely to be the case for 'loss' states.

Relationship of systematic analysis and classification

Biological classifications are designed not only to enable the taxa classified to be located in the literature and in collections, but also to store information about those taxa. In many cases the nature of this information is not clear from the classification, and taxa are grouped together on the basis of some ill-defined combination of phenetic and phyletic relationships. The type of information stored in the classification (i.e. the type of relationship used in its construction) may, however, be indicated precisely, and the classification used as an efficient data-retrieval system. This can only be done by utilisation of cladistic information alone; attempts to incorporate phenetic or anagenetic information lower the retrieval facility (Cracraft, 1974).

The method whereby the classification was constructed from the results of the cladistic analysis in this study was by using both rank and sequence in which taxa of equal rank are listed (G. Nelson, 1972, 1974; Cracraft, 1974; Wiley, 1979, 1981). This process has been termed phyletic sequencing (Cracraft, 1974). The convention employed is that within a classification holophyletic taxa of equal rank are listed ('sequenced') so that each taxon is the sister-group of all those taxa of the same rank (and within the same taxon of immediately higher rank) listed below it in the classification (modified from Cracraft, 1974). Use of this criterion allows recovery of a dichotomously-branching cladogram from the classification. However, holophyletic groups with a trichotomous or polychotomous interrelationship must also be accommodated. Wiley (1979) recommends that these be placed in the classification with equal rank and be noted as 'sedis mutabilis' to indicate that their order is unknown or interchangeable. It must be remembered that this convention is for a formal classification, not for regular use in discussion.

All hierarchical groups may be sequenced, but it is probably more efficient to employ informal groups below the subgenus level, especially with larger genera.

Morphology

The discussion below is intended to clarify morphological terms used in this study, to point out structures of taxonomic or systematic interest, and to describe briefly the morphology of the insects.

Head

Figures 1 and 2 depict the dorsal and ventral aspects of a generalised trichodectid head with the regions and major features labelled with the terms used in this study.

The internal carinae of the head are strongly developed in many species, and differences in the

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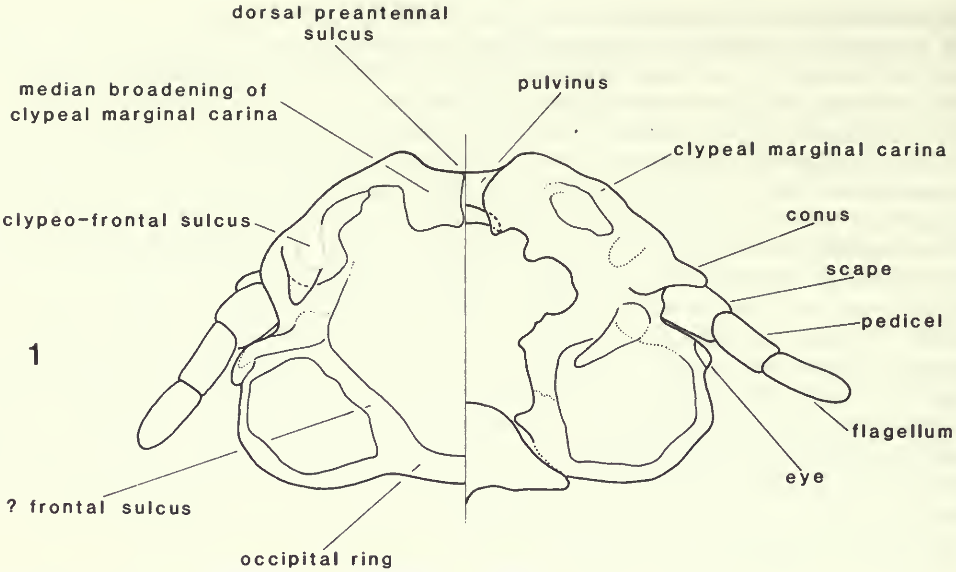

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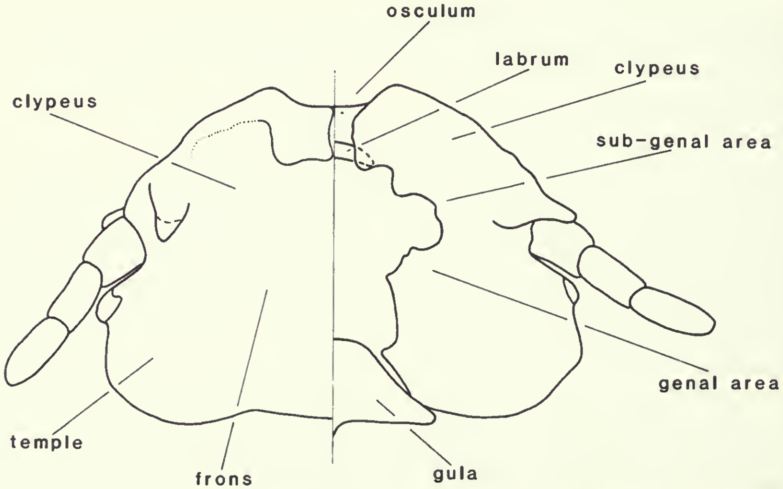


Figs 1, 2 Terminology applied to trichodectid head, modified slightly from Symmons (1952). Mandible, maxilla, hypopharynx and labium omitted. 1, structures of head (♀); 2, regions of head (♀).

degree of sclerotisation and position are useful taxonomically, particularly at the species level. The postoccipital sulcus is marked by a greatly-developed internal carina ('occipital ring') projecting posteriorly into the thorax; this structure is present in many other lice, but rarely so well developed.

The postero-lateral margins of the head ('temple margins') are more or less rounded and may be produced at the postero-lateral angles in some species. The lengths of the setae on the postero-lateral angles may provide characters of taxonomic value. The eyes are positioned adjacent to the antennae or more posteriorly; in some species (e.g. those in the genus *Cebidicola*) the eyes occupy lateral projections.

Anterior to the antennal socket the margin of the head is produced into a variable sclerotised conus (Fig. 1), but the trabecula (Clay, 1946) is absent. A sclerotised conical projection from the dorsal nodus of the clypeo-frontal sulcus may be present projecting parallel to the margin of the antennal socket. This projection is frequently present in only one sex of a species.

The anterior margin of the head may, in plan, form an unbroken arc ('circumfasciate head'), but in most Trichodectidae it is interrupted medially by the pulvinus or the osculum (Symmons, 1952). The pulvinus is a thick bilobed pad of unsclerotised tissue developed from the clypeolabral suture, and is found in all Ischnocera (Fig. 1). The osculum is a median indentation of the anterior margin of the head (Fig. 2). When the insect is at rest the pulvinus and osculum have been observed to be applied to the hair of the host (see discussion of mandibular morphology below). The width of the osculum is therefore probably influenced by the diameter of the hair in the region of the host's body inhabited by the louse. In cases where the pulvinus fails to reach the anterior margin of the head a small ventral sulcus ('ventral preantennal sulcus' of Clay, 1951) may connect it to the margin or osculum. Many species have a small dorsal preantennal sulcus (Clay, 1951) also interrupting the anterior margin medially.

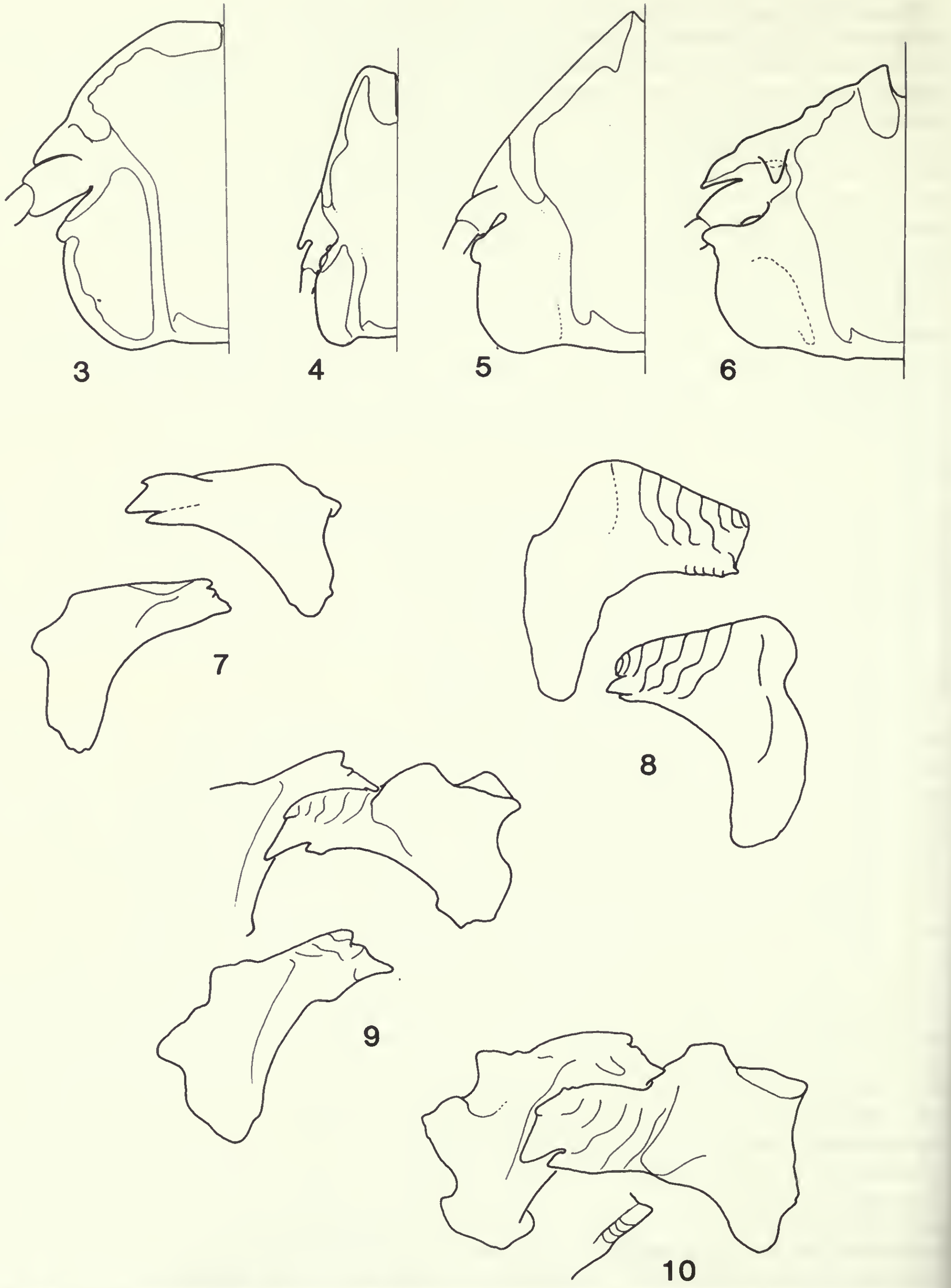
Between the antennae and the osculum the margin of the head may, in plan, be shallowly or broadly convex, sinuate or straight (Figs 3–6); sclerotisation along the margin (forming the 'clypeal marginal carina') may be minimal or heavy, but is usually pronounced in the median dorsal region (Fig. 1). Much of the variation is possibly influenced by the density and texture of the hair of the host.

Only two structures of the mouthparts need be mentioned, the mandibles and the cibarial sclerite.

The mandibles of Trichodectidae, like those of many other Amblycera and Ischnocera, are asymmetric. There are three apical teeth on the right mandible and two on the left; on the right the centre tooth is generally longest, whilst on the left the posterior tooth is normally the better developed (Figs 7–10). Mandibular asymmetry is considered by Snodgrass (1935) to be a feature of insects that masticate their food, and the lack of asymmetry in the mandibles of some species of *Ricinus* (Amblycera) is associated by B. Nelson (1972) with blood-feeding in those species. *Trichodectes canis*, the only trichodectid known to take blood meals (Bouvier, 1945), has dimorphic mandibles, as do all other Trichodectidae.

In addition to the collection and preparation of food the mandibles of Trichodectidae are employed in anchoring the insect. When at rest, *Trichodectes canis* and *T. melis* have been observed to enclose a hair in the pulvinus with the mandibles and whilst in this position may completely release the grip of the tarsal claws and straighten the legs laterally from the body. The insect is then held on only by the mandibles. In addition to the species above, specimens of *Felicola* sp. collected from dried museum skins have been found in this position, and specimens of most genera have been found preserved in alcohol clinging to single hairs by their mandibles alone. The selective pressures on the mandibles of Trichodectidae are different, therefore, from those operating on lice that do not have a mandibular anchoring mechanism, and possibly precludes the assumption of monomorphy in blood-feeding species. The 'interior' face of the right or of both mandibles may be ridged, so that when the mandibles are folded closed, the ridges on one mandible are not covered by the other, and all or most of the exposed mandibular area is ridged. The ridges are therefore not positioned in such a way that they can act against one another, and it is suggested that they are developed to prevent the mandibles slipping on a hair when clasping it (Figs 8–10). When the mandibles are closed, the right is always interior to the left, which may have a concavity to receive it (Figs 7, 9, 10); the left mandible is not then kept by the right from contact with the hair, and the greatest possible mandibular area is utilised. In some species the right mandible has a basal notch on the anterior margin, which receives the tip of the left mandible (Figs 7, 10); this feature may act in concert with the restraint of the right mandible to 'lock' the mandibles closed about a hair. Although, as said above, none of the Trichodectidae have monomorphic mandibles, the mandibles of *Damalinia (T.) conectens* (Fig. 7) are very slender and pointed, and the centre tooth of the right mandible of *Dasyonyx* spp. and *Eurytrichodectes* spp. (Fig. 9) is long and pointed, suggesting in each case a piercing function and thus possible haemophagy. In contrast, the mandibles of *Damalinia (T.) indica* (Fig. 8) are blunt and broad, suggesting an adaptation to grinding and chewing.

The sitophore sclerite (Figs 11, 12) varies considerably in the Psocodea (Cummings, 1913; Haub, 1967, 1972, 1973, 1977). The form of the sclerite, particularly of its posterior border, is obscured in slide-mounted specimens, and differential inclination of the specimens may change



Figs 3–10 Variation in trichodectid head and mouthpart structure. 3–6, ♀ head, dorsal aspect, of (3) *Bovicola caprae*; (4) *Damalinia lineata*; (5) *Felicola subrostratus*; (6) *Trichodectes zorillae*. 7–10, mandibles, dorsal aspect, of (7) *Damalinia conectens*; (8) *Damalinia indica*; (9) *Eurytrichodectes paradoxus*, showing mandibles interlocking; (10) *Trichodectes canis*, with detail of postero-dorsal margin of left mandible.

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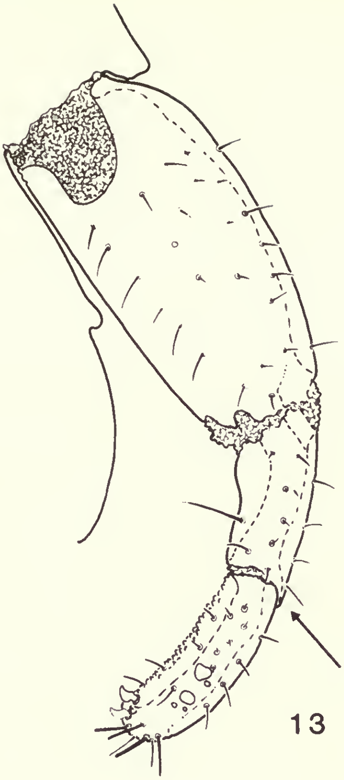

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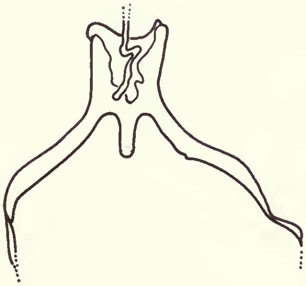

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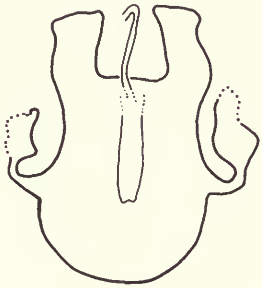

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Figs 11–16 Trichodectid morphology. 11, *Damalinia neotheileri*, sitophore sclerite. 12, *Bovicola hemitragi*, sitophore sclerite. 13, *Damalinia indica*, right antenna of ♂, dorsal, arrow indicating prolongation of antero-ventral pedicel margin. 14–16, lateral aspect of metatarsal claws of (14) *Dasyonyx (D.) smallwoodae*; (15) *Dasyonyx (N.) diacanthus*; (16) *Eurytrichodectes paradoxus*.

the apparent dimensions (Haub, 1977). Trichodectidae differ from other Psocodea in having an open posterior border to the sclerite, a character state identified by Haub (1973) as plesiomorphic, but which is almost certainly apomorphic. Within the family the sclerite is present in all species and the form is fairly constant (Fig. 11), although in two species groups the posterior arms are extended laterally (Fig. 12) and the sclerite is difficult to see. The minor variation in the form of the sclerite at the species level is so far unexploited in taxonomic study.

The sitophore sclerite is cup-shaped, and is opposed on the dorsal surface of the sitophore by a closely-fitting projection, the epipharyngeal crest. These two structures have been identified as a 'mortar and pestle' for grinding food (Weber, 1936) and as components of a salivary pump

(Buckup, 1959; Kéler, 1966). Rudolph (1982*a*, 1982*b*, 1983) demonstrates that it is a pump, sucking water absorbed from the atmosphere onto the lingual sclerites through the Y-shaped duct linking these and the sitophore sclerite.

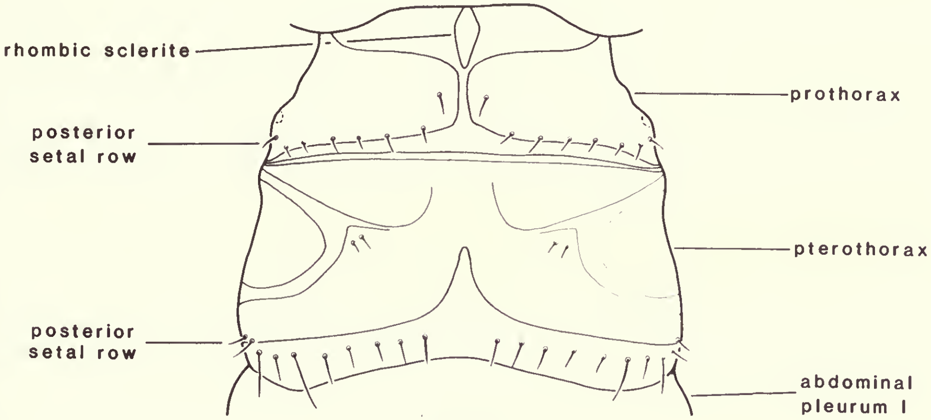
The antennae are made up of a scape, pedicel and flagellum. In common with other Thysanura-Pterygota the pedicel and flagellum are annulations formed by subdivision of a single segment (Imms, 1939; Matsuda, 1965). Consequently, the only intrinsic muscles of the antennae are in the scape and insert on the pedicel, moving the pedicel and flagellum as a unit; the scape itself is moved by muscles inserted on its basal margin and arising on the anterior arms of the tentorium. The positions of the muscle insertions on the scape and pedicel are such that the antenna can be moved through 360 degrees, but there is no muscular mechanism for flexing the flagellum. Whilst the prime function of the antenna is sensory, secondary modification in the male has taken place in some Ischnocera (including almost all Trichodectidae) and some Anoplura, the antennae being used to clasp the female round the abdomen during copulation (Kéler, 1938*a*; Sikora & Eichler, 1941; Lyal, in prep., *b*). This development has led to an increase in length and degree of sclerotisation of the pedicel and flagellomeres and an increase in strength of the antennal muscles. The intrinsic muscles of the scape are enlarged and the scape expanded; the extrinsic muscles are also enlarged and the head concomitantly broader in the male than in the female. To facilitate free movement of the flagellum the joint between the scape and the pedicel is broad and membranous (other than at the two articulatory points). However, because there is no direct muscular control of the flagellum, the degree of free movement relative to the pedicel must be limited, so that control may be effected by the intrinsic muscles of the scape. Observations made in this study reveal that the apex of the pedicel is angled relative to the long axis of the annulation, the longest margin of the pedicel being the antero-ventral (Fig. 13). There is very little membrane between the pedicel and the flagellum on the antero-ventral margin, but more on the postero-dorsal, so some flexibility between the pedicel and flagellum is possible, although limited in the anterior direction by the prolongation of the pedicel. During copulation the male clasps the female around the top of the abdomen from underneath (Werneck, 1936; Sikora & Eichler, 1941), the pedicel and flagellum being curved to match the curvature of the abdomen. The antennae are raised above the head of the male and the intrinsic adductor muscles contracted. The pedicel and flagellum are thus brought down over the abdomen of the female, the flagellum being constrained by the form of its junction with the pedicel. The form of the pedicel-flagellum joint is such that, should the haemolymph pressure be reduced, the joint membrane would collapse and further contract the flagellum against the female. However, lice are not known to have control over haemolymph pressure in their antennae, although larvae of Lepidoptera are known to control their antennal movement partially by this means (Matsuda, 1965). The mechanical strength and degree of possible control of a system involving joints as described above is likely to be inversely proportional to the number of joints in succession, with a single joint being the most efficient. The degree of curvature attainable using three segments is sufficient to grasp the female. For these reasons only the first flagellomere is required to take on a clasping function; the apical two flagellomeres may be retained in a sensory capacity (most Ischnocera) or lost (Trichodectidae). In Trichodectidae the last two flagellomeres have contracted and fused to the first flagellomere in all males (although a small semicircular sclerotisation, probably representing the apical flagellomere, is present in the male of *Eurytrichodectes paradoxus*) and in females of the Neotrichodectinae, Trichodectinae, Bovicolinae and most Eutrichophilinae. The sensilla of the two apical flagellomeres are retained on the remaining flagellomere.

The firmness with which the female is held may be increased by projections in the form of spikes or denticles on the antennae, particularly on the flagellum. Trichodectidae are characterised by the possession of two modified setae apically on the male flagellum, which take the form of sharp, stout teeth (Fig. 13).

Trichodectidae have two sensilla coeloconica and three sensilla placodea on the terminal flagellomere, sometimes closely associated (Clay, 1970; Kim & Ludwig, 1978). In *Lorisicola malaysianus* and *L. mjoebergi* the sensilla are in pits with tongue-like projections around them.

Thorax

Figures 17 and 18 depict a generalised trichodectid thorax, labelled with the terms used in this study. In all Trichodectidae the rhombic sclerite anterior to the pronotum is present; the pronotum itself generally bears two lateral sclerites, sometimes narrowly joined medially. The mesonotum and metanotum are fused, with prominent pleural ridges extending onto them; there may, as with the pronotum, be a medial zone of desclerotisation. Contrary to the assertion of Mayer (1954), the lateral cervical sclerite is always present and bears two anterior setae. The pronotum is fused to the propleuron, which in turn is fused to the prosternum. The prosternum may extend anteriorly between the fore-coxae and be unsclerotised medially. The mesosternite, fused to the prosternite, may also be medially divided. The mesepisternum is difficult to delimit, but rarely extends unbroken between the metasternite and the metanotum. The metasternite, if present, is only rarely fused to the mesosternite, and is never sclerotised medially. Posterior to



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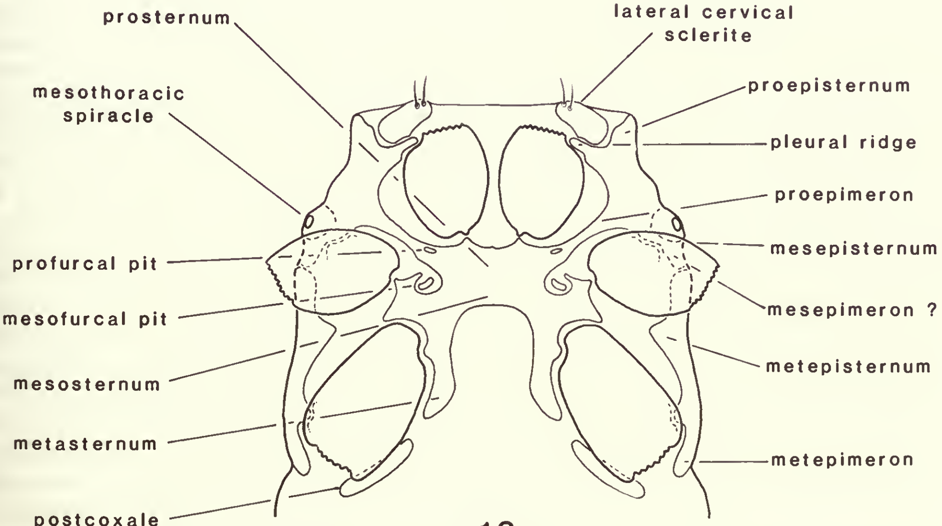

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Figs 17, 18 Diagrammatic representations of generalised trichodectid thorax, with terms used in this study. 17, dorsal. 18, ventral.

the metacoxa may be a semicircular sclerite ('postcoxale' of Matsuda, 1970). In *Procavicola (Meganarionoides)* this is very heavily sclerotised and fused to abdominal pleurum II; the two postcoxales may also fuse medially.

One, two or three setae are always present medially on the anterior margin of the thorax posterior to the temple margin of the head. The lateral margins of the thorax also bear setae, which may be more or less abundant. A row of setae is generally present across the posterior dorsal margin of the prothorax and pterothorax, sometimes interrupted medially ('median gap'). Setae are sometimes present on the dorsal disc of the prothorax and pterothorax ('anterior setae'), and medially on the mesosternum.

The legs of Trichodectidae, in common with those of most other mammal lice, terminate in a single tarsal claw. In most species this claw is smooth ventrally, but it is toothed ventrally in *Dasyonyx* (Figs 14, 15) and ridged in *Eurytrichodectes* (Fig. 16). In many species a small hyaline projection, which may be pointed or blunt (Figs 14, 15), is present at the base of the claw. Mayer (1954), in her study of *Bovicola caprae*, terms this structure a 'pulvillus' but, as a true pulvillus is generally paired (Richards & Davies, 1977; Chapman, 1982), this term is inappropriate. The projection is more probably an empodium or arolium, or even a simple basal tooth of no wider homology. Kim & Ludwig (1978, 1982) maintain that the pulvillus and empodium do not occur in the Phthiraptera, but Clay (1969) demonstrates the presence of an empodium in Menoponidae (Amblycera), and Clay (1970) figures structures in *Boopia* (Amblycera) that almost certainly are pulvilli, although she follows Kéler (no reference given) in terming them euplantulae (plantulae) of the second tarsomere.

Abdomen

In this study the 'true' segment number is referred to by roman numerals to distinguish it from the apparent number. The terms 'sternite', 'pleurite' and 'tergite' are used for the sclerites of the sternum, pleurum and tergum respectively of each segment.

Segment I is represented in Trichodectidae by the reduced tergum I only. In this respect the family is similar to the Trichophilopteridae, but differs from all other Ischnocera, in which segment I is absent.

Segments III–VIII bear the spiracles, if these are present; spiracles are never present on segments I and II. Within the Trichodectidae many species have fewer than the plesiomorphic number of six pairs of abdominal spiracles (Table 1). Loss has apparently taken place sequentially from the posterior, so that if any spiracles are present one pair is on segment III, and if more than one pair is present there are no intercalating segments which lack spiracles between those segments with spiracles. There is, however, no evidence that spiracles have necessarily been lost one pair at a time. Whilst in *Procaviphilus (Meganarionoides) angolensis, P. (M.) colobi* and *P. (M.) baculatus* the posterior pair of spiracles only is very small and apparently in process of being lost, in *Lorisicola (L.) hercynianus* and *L. (L.) siamensis* the posterior two pairs are extremely small, probably non-functional, and apparently in process of being lost. In a number of clades, sister-groups exhibit multiple discontinuities in spiracle number. The sister-species *Lorisicola (L.) mjoebergi* and *L. (L.) malaysianus* have six and zero pairs respectively; *Felicola viverriculae* and an undescribed sister-species have three and zero pairs respectively; the *Lorisicola (P.) lenicornis – wernecki* clade and the sister *L. (P.) acuticeps – neoafricanus* clade have four and zero pairs respectively. Variation within species can occur, although it is generally erratic. *Felicola subrostratus* normally has three pairs of abdominal spiracles; the species is widespread and found on many hosts, but on Madagascar, where the host is *Eupleres goudoti*, there may be three or two pairs, and specimens exhibiting asymmetry are present in the British Museum (Natural History) collection. Asymmetry has also been noted in *Trichodectes emeryi*, one paratype of which has six spiracles on one side of the abdomen and five on the other. *Trichodectes (S.) potus* is unusual in that the female has three pairs of abdominal spiracles and the male only two, the only known example in the lice of sexual dimorphism in spiracle number.

Most Trichodectidae have either six, three or no pairs of abdominal spiracles, other numbers

TAXA	NUMBER OF PAIRS OF SPIRACLES
Geomydoecus, *Neotrichodectes*, *Felicola* (*F.*) *helogale*, *F.* (*F.*) *hopkinsi*, *F.* (*S.*) *fahrenholzi*, *F.* (*S.*) *guinlei*, *Lorisicola* (*L.*) *malaysianus*, *L.* (*P.*) *paralaticeps* - *mungos* clade, *L.* (*P.*) *acuticeps* - *neoafricanus* clade	0
Felicola (*S.*) *bedfordi*	1
Felicola (*F.*) *subrostratus* from *Eupleres*, *Trichodectes* (*S.*) *potus* ♂	2
Felicola (*F.*) all species except *helogale* and *hopkinsi*, *F.* (*S.*) all species except *bedfordi*, *fahrenholzi* and *guinlei*, *Trichodectes* (*S.*) *fallax*, *T.* (*S.*) *octomaculatus*, *T.* (*S.*) *potus* ♀	3
Lorisicola (*P.*) *bengalensis* - *juccii* clade, *L.* (*P.*) *aspidorhynchus*, *L.* (*P.*) *sumatrensis*, *L.* (*P.*) *lenicornis*, *L.* (*P.*) *wernecki*	4
Trichodectes (*Paratrichodectes*)	5
Trichodectes (*T.*), *T.* (*S.*) all species except *fallax* - *potus* clade, *Werneckodectes*, *Neolutridia*, *Lutridia*, *Protelicola*, *Lorisicola* (*L.*) all species except *malaysianus*, Dasyonyginae, Eutrichophilinae, Bovicolinae	6

Table 1 Distribution of number of pairs of abdominal spiracles in the Trichodectidae.

being less common (Table 1). From the cladogram, reduction to five, four and one pair can be seen to have occurred once, reduction to two and three pairs twice, and reduction to none eight times. The loss of abdominal spiracles plainly cannot be used *a priori* as a taxonomic character defining (holophyletic) genera, as proposed by Ewing (1936), but neither is it as variable as suggested by Kéler (1938*a*) and Hopkins (1941), who treat it as a character of specific value only. The selective advantage of this reduction is not known, but it may be an adaptation to exclude dust from the tracheal system, or to reduce water loss.

A posterior commissure joining the two main abdominal tracheal trunks is present in Anoplura, Rhyncophthirina, Boopiidae and Trimenoponidae (Amblycera), Philopteridae (Ischnocera) and 'some Trichodectidae' (Harrison, 1915; Ferris, 1931). All species of Trichodectidae examined in this study possess a posterior commissure, which is consequently assumed to have a universal distribution throughout the family. The presence of the posterior commissure is assumed to be plesiomorphic for the Phthiraptera (Clay, 1970).

In all lice segment IX is the genital segment, and the male genitalia open to its posterior and the female genitalia to its anterior. Modifications of this segment are discussed in detail below.

In both sexes of Trichodectidae segments X and XI are fused. In females segment XI lies caudally, posterior to X, but in males the modifications of segment IX have led to the displacement of both X and XI onto the dorsal surface of the abdomen. Most male Trichodectidae have the genital opening posterior or postero-dorsal. The postgenital segments are reduced to form a small anal cone arising from the dorsal (anterior) wall of the genital chamber (Kéler, 1957) (Fig. 19).

Conical projections are present either dorsoposteriorly or ventroposteriorly on the first three

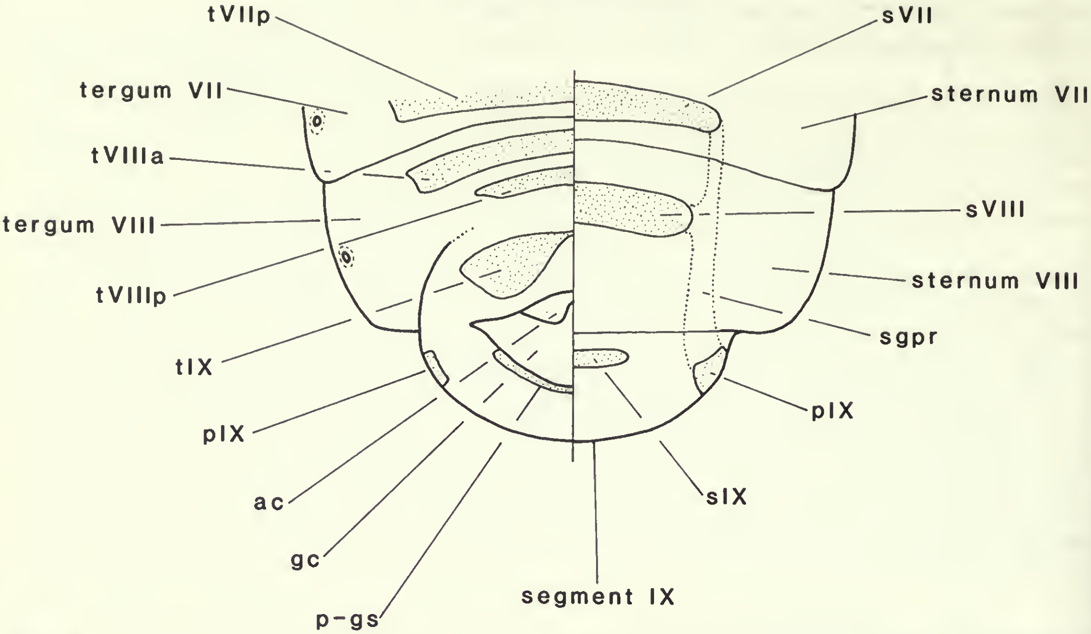

Fig. 19 Diagrammatic representation of terminal segments of trichodectid male abdomen, with terms used in this study. t – tergite; s – sternite; p – pleurite; ac – anal cone; gc – genital chamber; p-gs – post-genital sclerite; sgpr – lateral rods of subgenital plate.

pleura (II, III and IV) in many Trichodectidae. The distribution of the pleural projections is summarised in Table 2.

Male Trichodectidae, alone among Phthiraptera, possess 'lateral abdominal flecks', first noted in *Werneckiella* by Moreby (1978). The flecks are small pits positioned on the anterodorsal angles of pleura III–VII, occasionally on II and VIII, and anterolaterally on terga III–V in many species (Fig. 218). In *Werneckiella* there are small sclerites situated anteriorly and posteriorly of the pit; in *Trichodectes canis* there are no sclerites bordering the pit but a small sclerite is present at its base; in *Neotrichodectes* there are no sclerites associated with the pit at all. The function of these structures is unknown.

In some species of Phthiraptera terga II and/or III of the males are ornamented with large setae or projections. Such developments are numerous in the Trichodectidae. Many species of *Felicola* have a pair of long setae medially on male tergum II (Figs 180, 187, 188), whilst *Geomydoecus (Thomomydoecus)* spp., *Trichodectes ovalis, T. ugandensis* and an undescribed subspecies of *T. galictidis* have paired 'combs' of long setae on male terga II and III (Fig. 161), and *Bovicola multispinosa* and *B. hemitragi* have paired semicircular 'brushes' of setae on male tergum II (Fig. 41). *Damalinia ornata* has sclerotised blunt projections on male terga II and III. These specialised setae and projections may in some way assist the male to hold the female during copulation, although in no case have the setae or projections been observed to be damaged, as they might be expected to be should they operate against the female abdomen, and there is no observational evidence to support the hypothesis.

Males of *Neotrichodectes* species have a pair of small median setae on terga II–VII, sometimes separated by a seta of normal length (Fig. 229). This feature, not found in females or males of any other group, is of unknown function.

Female genitalia

The female subgenital plate of Trichodectidae comprises either sternite VIII or sternites VIII and VII fused. The posterior margin of sternum VIII forms the ventral margin of the vulva. In many species the margin is expanded posteriad and slightly laterad (Fig. 94), and in others the

TAXA	SEX	PLEURUM II			PLEURUM III			PLEURUM IV		
		D	V	S	D	V	S	D	V	S
Neotrichodectes mephitidis	♀							+		
Cebidicola	♂ ♀								+	+
Procavicola - *Eurytrichodectes* clade, *Lorisicola mjoebergi*, *Felicola zeylonicus* - *viverriculae* clade	♂ ♀							+	+	+
Felicola bedfordi, *F. congoensis*, *F. cooleyi*, *F. cynictis*, *F. decipiens*, *F. helogale*, *F. minimus*, *F. liberiae* - *subrostratus* clade, *Lorisicola aspidorhynchus*, *L. caffra*, *L. felis*, *L. hercynianus*, *L. malaysianus*, *L. mungos*, *L. spenceri*, *L. sumatrensis*, *L. wernecki*, *L. bengalensis* - *juccii* clade	♂ ♀							+		+
Lorisicola acuticeps, *L. africanus*, *L. lenicornis*, *L. neoafricanus*	♂ ♀							+		?
Felicola occidentalis, *F. quadraticeps*, *F. vulpis*	♂ ♀				+			+		
Felicola calogaleus, *F. setosus*	♂ ♀					+	+		+	+
Trichodectes zorillae	♂	+		+	+		+	+		
	♀	+		+	+		+	+		?
Geomydoecus (*G.*) most species	♂ ♀	+			+			+	+	
Geomydoecus (*G.*) *thomomyus* - *dakotensis* clade	♂	+		+	+		+		+	+
Geomydoecus (*Thomomydoecus*)	♀	+		+	+		+	+	+	+

Table 2 Distribution of abdominal pleural projections in the Trichodectidae. For pleura II, III and IV an indication is given whether a dorsal ('D') or ventral ('V') projection is present, and whether those projections are sclerotised ('S'). In each case the presence state is indicated by '+'. Very light sclerotisations are indicated by '?'.

centre of the margin is greatly expanded into a flat lobe termed the 'subgenital lobe' (Figs 149, 153, 175). The subgenital lobe appears to have evolved at least three times in the Trichodectidae, and its form is of taxonomic and systematic value. Its function, however, is not known.

To each side of the vulva is a projection from sternum VIII, the gonapophysis of segment VIII (Lyal, in prep., *b*). The structure of this is variable. In all cases a basal internal apophysis is produced, presumably as a muscle attachment (Kéler, 1938*a*). The gonapophysis lies longitudinally, parallel to the abdomen; it may curve onto the dorsal surface apically. It may be long, slender and apically acute (Fig. 235), long and apically rectangular (Fig. 154), broad and membranous (Fig. 243), produced into a rounded, toothed or rectangular medial lobe with an apical 'spur' (Figs 175, 233, 236), with the spur reduced (Fig. 237) or absent (Fig. 211), sometimes with serrations laterally (Fig. 211). Setae may be present on the gonapophyses and the ventral vulval margin in various configurations, occasionally arising from sclerotised tubercles. In some cases a sclerotised band links the gonapophyses and the vulval margin, but in most cases this is not present and the connection is membranous.

The curvature of the gonapophyses about both longitudinal and lateral axes produces a complex three-dimensional structure difficult to interpret on slide-mounted specimens. The orientation of the gonapophysis may be altered by pressure of the coverslip during mounting, especially if it has a membranous base. In addition, differences in orientation, either natural or caused by the mounting process, may give the impression of very different shapes.

Observations by Ferris (1951) and Murray (1957*a*, 1957*b*) indicate that the gonapophyses are used, at least in some species, to trap the hair on which the egg is to be laid, guide the egg onto it, and mould the attaching cement. For *Bovicola ovis* the diameter of the hair is of importance in determining whether the egg will be laid (Murray, 1957*b*) and this is almost certainly detected by the gonapophysis. There is thus selection pressure on the form of the gonapophysis relating to the structure of the host hair.

Posterior to the vulva and sometimes covered by the subgenital lobe is the 'sub-vulval area', which sometimes bears characteristic spines or scales.

Also posterior to the vulva is a single sclerite which, as it cannot be homologised with either the gonangulum or sternite IX + X (Lyal, in prep., *b*), is termed the 'post-vulval sclerite' (Moreby, 1978). This sclerite may be single, medially divided, narrow and strip-like, broad and triangular, fused to the postgenital pleurite, or absent (Figs 154, 175, 236, 237, 243).

The female genital chamber, opening at the vulva, is oval, dorso-ventrally compressed, and lightly-sclerotised. The dorsal wall of the chamber may be heavily sculptured and bear sclerotised spicules, ridges or spines; this sculpturing may extend on to the postgenital sterna. The ventral wall may be similarly sculptured, although usually to a lesser extent; where the subgenital lobe is present the sculpturing of the genital chamber may extend onto its dorsal surface. The sculpturing of the walls of the chamber probably provides a highly frictional surface against which the spicular surface of the endophallus acts to provide a firm union during copulation. The nature of the sculpturing and the distributions of spicules or spines may be taxonomically useful at the specific or subspecific level. The common oviduct opens into the anterior end of the genital chamber and curves sharply posteriad to lie dorsally to the chamber. Dorsal to the vulva the common oviduct curves sharply anteriad and divides into the two paired oviducts (Fig. 20). The genital chamber, although assuming a more or less circular cross-section during the passage of an egg and perhaps during copulation, is, when at rest, a dorso-ventrally

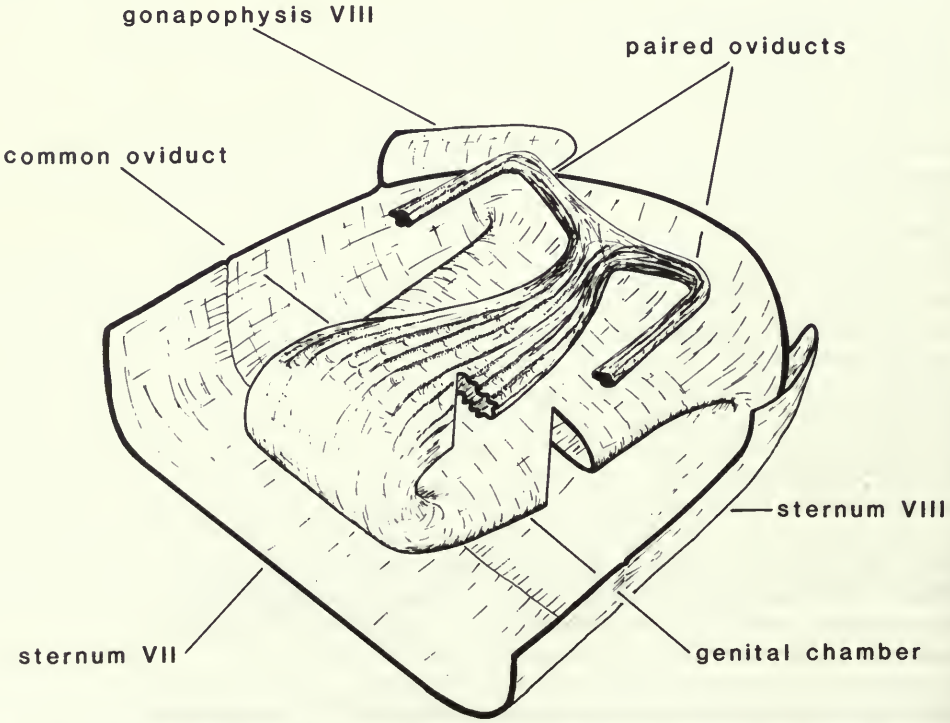

Fig. 20 Diagrammatic three-dimensional representation of trichodectid female genital chamber and oviducts (internal), with terms used in this study.

flattened, fairly rigid structure, the minimum width of which is governed by the diameter of the egg. The oviduct, however, is an elastic, folded membranous tube, compressed and folded to reduce volume, and expanding only to allow passage of the egg. The common oviduct must, at the junction with the genital chamber, be the same diameter as the chamber. At its division into the paired oviducts, however, it is narrow and greatly folded when at rest. Between these two points it narrows more or less abruptly, and folds may be apparent in its walls. Price & Emerson (1971) interpret these folds in *Geomydoecus* as striations of the dorsal wall of the genital chamber, and term this apparently membranous structure the 'genital sac'. The true dorsal wall is interpreted as the ventral wall and the true ventral wall is apparently not observed. The form of the folds of the 'genital sac' (common oviduct), as well as its length and the width of its junction with the genital chamber, have been utilised by Price and his co-workers as specific and subspecific characters in their revisionary work on *Geomydoecus* (e.g. Price, 1974; Price & Emerson, 1971; Price & Hellenthal, 1976; Timm & Price, 1980). The apparent constancy of the dimensions of the oviduct is related to the size of the egg and perhaps to the restrictions in variability of size of the genital chamber imposed by selection. The apparent constancy of the folds is more puzzling although it is possible that tubes of identical length and diameter have an optimum folding pattern if compressed in the same way. The wall of the common oviduct may also be lightly sclerotised, at least near to the junction with the genital chamber. The folds of the common oviduct have not been utilised as a taxonomic character elsewhere in the Phthiraptera.

Blagoveshtchenski (1956) examines several species of Trichodectidae but fails to find evidence of a spermatheca in the family. In this study examination of slide-mounted specimens of most species has failed to reveal a spermatheca in any genus apart from problematically in *Dasyonyx*, where a lightly-sclerotised sac, differing in form between species, is developed from the wall of the common oviduct. The relatively anterior position of this sac in comparison to the spermatheca of other Phthiraptera suggests that the two structures are not homologous. No histological or anatomical studies have been carried out on the sac.

The male abdomen and copulation

The opening of the male genital chamber ('genital opening') is always posterior to sternum IX, and primitively in the lice is ventrally positioned and distant from the anus, which is terminal. During copulation the male and female are usually oriented the same way, with male ventral to female. The tip of the male's abdomen is curved dorsally and anteriorly so that the genital openings of the male and female meet. The male genitalia consequently enter the female genital chamber 'upside-down', with the ventral side of the former coming into contact with the dorsal wall of the latter. Should sclerotised tergites be absent (as in *Neotrichodectes* and *Geomydoecus*) or greatly reduced (as in *Trichodectes galictidis* and *Felicola*) flexion of the male abdomen during copulation is evenly distributed along the membranous dorsal surface. If sclerotised tergites are present and fully-developed, however, flexion must be about the sclerite-membrane-sclerite joints of the dorsal surface, these thus functioning as 'hinges'. At each such hinge, there will be considerable deformation of the internal structures during flexion, whilst between the hinges there will be no deformation. Increasing the number of hinges on the dorsal surface permits smoother curvature of the abdomen and reduces the internal deformation at each hinge. Many male Trichodectidae have tergal sclerites divided into an anterior and a posterior plate on at least some segments (Figs 103, 105, 136), possibly for this reason. The degree of internal deformation may be further reduced by modification of the shape of the plates. The form of plate which, when placed in series, causes maximum internal deformation and requires maximum membrane area: sclerite area ratio for flexion is a simple rectangle, with anterior and posterior margins at right angles to the long axis of the abdomen. These factors can be diminished by introducing curvature in the anterior and posterior margins of the plates, either with both margins parallel or opposite, producing a series of alternating biconvex and biconcave plates (Lyal, 1983). Both these patterns are approached in the Trichodectidae (Figs 68, 103, 105). The flexibility required of the ventral surface of the abdomen is developed, should the sterna be sclerotised, by increasing the lengths of the sclerites and allowing them to overlap when the abdomen is at rest (Figs 103, 105).

Despite the increased flexibility of the abdomen achievable by modifications of the tergal and sternal plates, the position taken by the male during copulation is compatible with a ventral genital opening only if the abdomen is long and slender. A short, broad abdomen will not deform sufficiently to turn back on itself and bring the male genital opening into contact with the vulva. Such a short, broad abdominal form has been developed several times in the Phthiraptera, however, including at least once in the Trichodectidae. In most cases the limitation imposed on the degree of curvature of the abdomen has been met by a posterior or even dorsal migration of the genital opening, thus reducing the degree of curvature necessary. This displacement has been effected by an increase in length of sterna VII, VIII and IX and a concomitant shortening of the corresponding terga. In Trichodectidae this may lead to the division of tergite VIII longitudinally by segment IX (Fig. 212). The re-positioning of the genital opening has increased its proximity to the anus, and in Trichodectidae the anus is contained within the genital chamber with the recuced segments X and XI projecting from the genital opening (Fig. 19). The curvature required of the abdomen has been further limited in some Trichodectidae by two distinct adaptations. In some species of *Felicola* segment IX is developed into a long, slender posterior process and the genital opening is dorsal and apical (Fig. 187). The basal apodeme and parameres are elongate and slender (Fig. 205). Most of the curvature required is probably developed at the base of segment IX and the junction of the parameres and the basal apodeme. Constriction of the endophallus at the latter fold is prevented by the presence of a reduced, circular mesomeral arch, lacking an extension, which, being fused to the endophallus, prevents the structure from being pinched shut. In some *Lorisicola* species segment IX projects dorsally from segment VIII, the genital opening being dorsal (Fig. 114). This positioning limits the degree of curvature required of the abdomen by increasing the proximity of the genital opening to the vulva on minimum curvature.

Male terminalia

In Trichodectidae the subgenital plate is fundamentally uniform in construction, although great superficial differences may exist between species. The plate is here considered to comprise eight discrete elements: sternites VII, VIII, IX (and, occastionally, VI); a pair of rods (referred to as 'subgenital plate rods' or 's.g.p.r.' in this study) which lie laterally to the sternites and sometimes fuse them together (Figs 19, 165, 212); the two pleurites of segment IX, and the post-genital sclerite, which is of uncertain homology (Fig. 19). Any of these elements may be present, reduced or absent, or fused to adjacent sclerites. The sternites and the post-genital sclerite may be whole or medially divided. In cases of extreme reduction only the lateral rods may be left (Fig. 163) or all the sclerites absent (Fig. 187). In the most complete form (Fig. 68), all the sclerites are fused, forming a squared plate; usually there are membranous areas surrounding the sternal setae ('perisetal gaps'), but these may be absent (Fig. 115).

The subgenital plate rods on sternum VIII are always connected to the ventral wall of the genital chamber in Trichodectidae, a feature also observed in some Anoplura. The function of this attachment is not known, although in species with ventrally-positioned parameres and a median posterior extension to the mesomeral arch, the difference in lengths between the dorsal wall of the genital chamber and the membrane between the basal apodeme and the subgenital plate might cause divergence of the apices of the parameres and mesomeral arch extension during extrusion of the genitalia to allow evertion of the endophallus.

In some Trichodectidae the posterolateral angles of the subgenital plate are greatly extended into setose lobes termed 'styli' by Eichler (1963) (Figs 46, 68). Abdominal sternal sclerites are probably derived from a fusion of the sternal plate and the coxal elements of the paired abdominal appendages (coxopodites) (Matsuda, 1976; Richards & Davies, 1977). In the subgenital plate of the Acercaria the paired nature of the gonocoxopodite component may be expressed as a concavity of the posterior margin of the plate and concomitant projection of the posterolateral angles (Matsuda, 1976). True abdominal styli are derived from the paired abdominal appendages and are serially homologous with either the shaft of the thoracic legs or the coxal styli (spurs of Matsuda, 1976) of the thoracic legs as present in the Machilidae (Thysanura) (Matsuda, 1976; Richards & Davies, 1977). Styli are not, therefore, homologous with the coxopodites, but arise from them, being separated by a clear sulcus. Although true styli are present in some Psocoptera (Matsuda, 1976), the posterior extensions of the subgenital plate of Trichodectidae are not demarcated by a sulcus and thus are not homologous with true styli. The so-called styli of the Trichodectidae are an indication of the gonocoxopodite component of the subgenital plate, and are here termed 'pseudostyli'. Taxonomic use may be made of the form of the pseudostyli, which is very variable in the Trichodectidae, but the difficulty of assigning polarity to transformation series limits the applicability of this character within phylogenetic studies. The distribution of the pseudostyli through the Trichodectidae, however, is utilised in the construction of the phylogeny of the family (see below).

Male genitalia

The structure of the male genitalia of lice and the homologies of the major parts are discussed by Lyal (1983 and in prep., *b*). The genitalia consist of a more or less sclerotised basal apodeme supporting caudally a pair of parameres which may be fused ventrally and a pair of mesomeres which may be fused dorsally; fused to the interior faces of the parameres and mesomeres is the permanently-everted portion of the eversible endophallus (Lyal, 1983 and in prep., *b*). In most Trichodectidae both parameres and mesomeres are present, the latter usually being fused apically (Figs 170, 198), the fused portion generally being extended posteriorly (Fig. 224). The parameres may also be fused, forming a median ventral plate (Fig. 250). The parameres and mesomeres may meet the basal apodeme together (Fig. 170) or separately (Fig. 250). The full range of variation of the male genitalia is discussed in the character analysis and taxonomy sections below.

During copulation the endophallus everts into the female genital chamber. As described above, the interior of the femlae genital chamber is roughened and lined with scales. The endophallus is likewise roughened, being covered with small chitinous spicules or larger sclerites. The probable function of this adaptation is to maintain a firm connection between the male and female genitalia during copulation. The form of the endophallus and the distribution of the spicules and sclerites are species-specific and very variable, possibly functioning as pre-zygotic isolating barriers.

Character survey

As noted above, the characters and character states listed below were selected from a much larger set of characters and states. In some cases reasons for rejection are discussed below. The full list of characters and the complete data matrix are presented in Lyal (1983) and are deposited in the library of the British Museum (Natural History).

1	Posterior of basal apodeme lateral struts ('b.a.l.s.')	symmetric in vertical plane	0	
		asymmetric in vertical plane (Figs 193, 195)	1	g
2	Anterior end of basal apodeme	flat, convex, concave (Figs 91, 200, 250)	0	
		deeply concave (Fig. 52)	1	g
		acuminate (Fig. 173)	1′	g
3	Posterior bifurcation of b.a.l.s.	absent	0	
		present (Fig. 173)	1	g
4	Posterior of b.a.l.s.	lacking lateral extension	0	
		with lateral extension to mesomeres (Fig. 239)	1	g
5	Anteposterior spur of b.a.l.s.	absent	0	
		present (Fig. 83)	1	g

6	Shape of basal apodeme	not long and 'waisted'	0	
		very long, with median 'waist' (Fig. 119)	1	g
7	Posterior of b.a.l.s.	not modified as below	0	
		broad and obtuse in meeting parameres (Fig. 198)	1	g
8	Posterior of b.a.l.s.	not modified as below	0	
		sharply inturned and convex (Fig. 200)	1	g
9	Posterior of b.a.l.s.	not modified as below	0	
		incurved to parameres (Figs 144, 145)	1	g
10	Basiparameral sclerites	absent	0	
		present, fused to parameres	1	g
		present, free	2	g
11	Paramere fusion	not fused to mesomeral arch	0	
		fused to mesomeral arch in part (Figs 60, 75)	1	g
		completely fused to mesomeres (Fig. 74)	2	g
12	Paramere fusion	not fused to basal apodeme	0	
		fused exteriorly to basal apodeme (Fig. 75)	1	g
		fused medially or completely to basal apodeme (Figs 145, 172, 174)	1′	g
13	Paramere fusion	not fused together or closely associated	0	
		fused together	1	g
		not fused but closely associated, with line of division apparent (Figs 223, 224)	1′	g
14	Parameral apices	unfused	0	
		fused	1	g
15	Paramere shape	not as described below	0	
		fused to shield-shaped plate (Figs 239, 242)	1	g
16	Paramere shape	not as described below	0	
		fused as described in character 15, with antero-median projection (Fig. 238)	1	g
17	Parameral plate shape	not as described below	0	
		produced apically into incurving points (Fig. 171)	1	g
18	Parameral orientation	similar	0	
		at right-angles to each other (Fig. 170)	1	g
19	Paramere shape	more or less broad, thick	0	
		very thin, deflected asymmetrically (Fig. 174)	1	g
20	Paramere shape	more or less broad	0	
		narrow rods (Figs 196, 197)	1	g
21	Paramere shape	not as described below	0	

		very broad, lanceolate, scoop-shaped (Fig. 172)	1	g
22	Median internal projection of parameres	absent	0	
		present	1	g
23	Paramere size	large or moderate	0	
		small discs (Fig. 84)	1	l
24	Paramere shape	not as described below	0	
		cylindrical (Figs 169, 205)	1	g
25	Paramere shape	not as described below	0	
		basally very narrow, medially broad (Fig. 198)	1	g
26	Paramere shape	not as described below	0	
		with characterically-differentiated base and blade (Fig. 51)	1	g
27	Base of parameres	not as described below	0	
		broad, club-like (Fig. 192)	1	g
		block-like (Fig. 201)	1′	g
		cuboid (Fig. 52)	1″	g
28	Base of parameres	lacking flange	0	
		with flange (Fig. 118)	1	g
29	Paramere and mesomere shape	not as described below	0	
		of characteristic asymmetric form (Fig. 249)	1	g
30	Reduction of parameres and mesomeres	not reduced as below	0	
		characteristically reduced (Fig. 52)	1	l
		characteristically greatly reduced (Fig. 53)	2	l
31	Mesomeres	present	0	
		absent	1	l
32	Mesomeral position	reach or fail to reach b.a.l.s.	0	
		extend mesad of b.a.l.s.	1	g
33	Mesomere fusion	apically fused to form arch	0	
		not apically fused	1	l
34	Lateral desclerotisations of mesomeral arch	absent	0	
		present (Fig. 118)	1	g
35	Lateral flexions of mesomeral arch	absent	0	
		present (Figs 107, 225)	1	g
36	Mesomeral arch	not as described below	0	
		modified into tripartite arch (Fig. 93)	1	g
37	Mesomeres basally, between b.a.l.s.	not modified as below	0	
		sharply directed posteriad (Fig. 224)	1	g
38	Mesomeral arch mesally	smooth or with projection	0	
		with two nipples (Fig. 221)	1	g
39	Diameter of mesomeral arch	less than half the length of the permanently-everted endophallus	0	
		more than half the length of the permanently-everted endophallus	1	g

		as great as the length of the permanently-everted endophallus	2	g
40	Shape of mesomeral arch	not as described below	0	
		with median anterior deflection (Figs 191, 192)	1	g
41	Shape of mesomeral arch	circular or elliptical	0	
		rectangular (Fig. 198)	1	g
42	Shape of mesomeral arch	not as described below	0	
		extension lost, arch 'looped' (Fig. 247)	1	g
43	Shape of mesomeral arch	not as described below	0	
		widely circular (Fig. 55)	1	g
44	Shape of mesomeral arch	not as described below	0	
		pentagonal, convex distally (Fig. 62)	1	g
45	Shape of mesomeral arch	smoothly curved	0	
		sharply inturned to parameres (Fig. 81)	1	g
		extending anteriad to posterior end of basal apodeme and sharply recurved (Figs 82, 219)	2	g
46	Shape of mesomeres	not as described below	0	
		very slender, string-like (Fig. 52)	1	g
47	Median extension of mesomeral arch	present	0	
		absent	1	l
48	Apex of mesomeral arch extension	not bifurcate	0	
		bifurcate	1	g
49	Shape of mesomeral arch extension	not as described below	0	
		broadly expanded, lanceolate	1	g
50	Tongue-like sclerite between parameres	absent	0	
		present	1	g
51	Everted part of endophallus	not sclerotised	0	
		sclerotised	1	g
52	Endophallus spiculation	not as described below	0	
		numerous 'V'-shaped rods	1	g
53	Endophallus spiculation	not as described below	0	
		comprising large hook-like spines (Fig. 107)	1	g
54	Endophallus spiculation	not concentrated about gonopore	0	
		concentrated about gonopore	1	g
		with dense 'V'-shaped patch about gonopore	2	g
55	Endophallus spiculation	not as described below	0	
		including median row of hook-like scales	1	g
56	Endophallus spiculation	not as described below	0	
		dense and refrigent in part	1	g
57	Gonapophysis setae	present	0	
		absent	1	l
58	Gonapophysis setae	lacking sclerotised tubercles	0	

		some having sclerotised basal tubercles (Fig. 150)	1	g
59	Gonapophysis setal tubercles	absent, or present and not characteristically fused	0	
		present and characteristically fused (Fig. 111)	1	g
60	Gonapophysis setal tubercles	absent, or present and in characteristic pattern (Fig. 153)	0	
		present and modified from characteristic pattern by loss of apical non-tuberculate seta (Fig. 146)	1	l
61	Gonapophysis shape	not as described below	0	
		spoon-shaped (Fig. 156)	1	g
62	Gonapophysis shape	not as described below	0	
		hook-shaped (Fig. 66)	1	g
		hook-shaped with spur (Fig. 67)	1′	g
63	Gonapophysis shape	not explanate ventrally (other than as discrete lobe)	0	
		thinly explanate ventrally (other than as discrete lobe)	1	g
64	Gonapophysis lobe	absent	0	
		present	1	g
65	Apex of gonapophysis	acute or obtuse	0	
		not projecting beyond lobe (if present); apparently absent	1	l
66	Gonapophysis lobe	not very thick	0	
		very thick	1	g
67	Gonapophysis lobe	absent, or not as described below	0	
		broad, formed of fused tubercles (Fig. 233)	1	g
68	Gonapophysis lobe	absent, or not as described below	0	
		narrow, rectangular, formed from 2 or 3 fused tubercles (Fig. 177)	1	g
69	Gonapophysis lobe	negative for character 67 or, if positive, flattened	0	
		positive for 67 and folded anteriorly	1	g
		positive for 67 and greatly folded	2	g
70	Gonapophysis lobe	absent, or not as described below	0	
		produced into spines posteriorly (Fig. 211)	1	g
71	Gonapophysis junction with ventral vulval margin	acute	0	
		smoothly continuous	1	g
72	Ventral vulval margin	unsclerotised	0	
		sclerotised	1	g
73	Ventral vulval margin	no shorter than length of gonapophyses	0	

		shorter than length of gonapophyses (Fig. 102)	1	g
74	Ventral vulval margin	lacking setal tubercles	0	
		with setal tubercles (Fig. 156)	1	g
75	Ventral vulval margin	not expanded	0	
		expanded (Figs 94, 126)	1	g
76	Ventral vulval margin	not as described below	0	
		greatly produced and rounded (Fig. 113)	1	g
77	Ventral vulval margin	not as described below	0	
		with median narrow projection	1	g
78	Subgenital lobe	absent	0	
		present	1	g
79	Subgenital lobe margin	not serrate	0	
		serrate	1	g
		very serrate	2	g
80	Subgenital lobe surface	smooth dorsally and ventrally	0	
		with overlapping pointed scales (Fig. 210)	1	g
		with small spines (Fig. 208)	2	g
		with many overlapping spines (Fig. 207)	3	g
81	Subgenital lobe, basally	lacking lateral processes	0	
		with lateral processes	1	g
82	Subgenital lobe processes (ch. 81)	not as described below	0	
		thinly sclerotised and directed posteriad	1	g
83	Subgenital lobe processes (ch. 81)	not as described below	0	
		membranous and serrate (Figs 155, 157)	1	g
84	Subgenital lobe	not bifurcate (Fig. 210)	0	
		bifurcate (Fig. 208)	1	g
85	Subgenital lobe bifurcations (ch. 84)	not as described below	0	
		rectangular, widely separate (Fig. 176)	1	g
86	Subgenital lobe	lacking submarginal setal patch	0	
		with submarginal setal patch	1	g
87	Sub-vulval area	lacking pointed scales	0	
		with pointed scales	1	g
88	Dorsal vulval face	not spinous	0	
		spinous	1	g
89	Post-vulval sclerites	present	0	
		absent	1	l
90	Post-vulval sclerites	broad, triangular	0	
		long, narrow, oriented parallel to longitudinal axis	1	g
91	Common oviduct	not as described below	0	
		with folded ‘collar’ at branching-point	1	g
92	Female genital chamber	lined with overlapping scales	0	

		lined with sclerotised nodules, some fused	1	g
93	Female genital chamber	not as described below	0	
		with median dorsal longitudinal fold	1	g
94	Female genital chamber	not as described below	0	
		with median dorsal area clear of scales	1	g
95	Female genital chamber	not as described below	0	
		with median anterior dorsal area clear, thinly sclerotised	1	g
96	Female genital chamber	not as described below	0	
		with spines on dorsal face	1	g
97	Female sternum VII	lacking processes	0	
		with two long spikes on posterior margin (Fig. 73)	1	g
98	Reproduction	sexual	0	
		parthenogenetic	1	g
99	Male tergite VIII (if present)	with posterior element absent or, if present, not fused to tergite IX	0	
		with posterior element fused to tergite IX	1	g
100	Posterior margins of male tergum IX	not as described below	0	
		greatly expanded (Fig. 79)	1	g
101	Male segment IX	without two longitudinal strengthening sclerites	0	
		with two longitudinal sclerites	1	g
102	Pseudostyli	absent	0	
		present	1	g
103	Pseudostyli (if present)	not as described below	0	
		broad, rounded, long (Fig. 68)	1	g
104	Pseudostyli (if present)	rounded apically	0	
		angular, pointed apically (Fig. 78)	1	g
105	Male segment IX	lacking single apical projection	0	
		with single apical projection (?fused pseudostyli)	1	g
106	Male sternite VIII	not as described below	0	
		characteristically enlarged (Fig. 159)	1	g
107	Male sternite VIII (if present)	not convex posteriorly	0	
		characteristically convex posteriorly (Fig. 218)	1	g
108	Male perisetal gap	present	0	
		absent	1	l
109	Male sternum VI	not as described below	0	
		with anterior and posterior sclerites	1	g

110	Female flagellomeres	unfused (three flagellomeres)	0	
		fused to form two flagellomeres	1	g
		fused to form one flagellomere	2	g
111	Male flagellomeres	unfused	0	
		fused	1	g
112	Male scape	greatly or slightly expanded	0	
		not expanded	1	l
113	Male scape setae	randomly scattered on posterior face	0	
		in longitudinal row on posterior face	1	g
114	Male scape setal row (if present)	numbering at least three setae on posterior face	0	
		reduced to two setae on posterior face	1	l
115	Male flagellum	lacking apical 'teeth'	1′	l
		with single apical 'tooth'	1	l
		with two apical 'teeth'	0	
		with three apical 'teeth'	1″	g
		with four apical 'teeth'	1⁗	g
		with eight apical 'teeth'	1‴	g
116	Male flagellar 'teeth'	not on protuberance	0	
		on protuberance	1	g
117	Male flagellar 'teeth'	articulated basally	0	
		fused to flagellum	1	g
118	Male flagellum	lacking basal projection	0	
		with simple basal projection	1	g
		with basal projection of linked 'teeth'	1′	g
		with broad, rough, basal projection	2′	g
119	Male flagellum	not as described below	0	
		with simple median and basal projections only	1	g
120	Inner face of male flagellum	not serrate	0	
		serrate	1	g
121	Male scape	lacking apical projection	0	
		with apical projection	1	g
122	Female pedicel	lacking projections	0	
		with membranous projection	1	g
123	Male flagellum	not very long	0	
		very long	1	g
124	Flagellar sensilla placodea and coeloconica	not in pit	0	
		in pit with marginal tongue-like processes	1	g
125	Sitophore sclerite	not as described below	0	
		with posterior arms extended (Fig. 12)	1	g
126	Posterior temple angles	lacking projections	0	
		with projections (Fig. 129)	1	g
		with very long projections (Fig. 138)	2	g
127	Posterior temple margins	not as described below	0	
		produced and convex	1	g

128	Osculum	not deep	0	
		deep and with characteristic anterior marginal convexity (Fig. 69)	1	g
129	Pretarsus	bearing two claws	0	
		bearing one claw	1	l
130	Pretarsal claws	lacking ventral spines	0	
		with blunt ventral spines	1	g
		with sharp ventral spines	1′	g
131	Post-coxale of leg III	not fused to abdominal pleurum II	0	
		fused to abdominal pleurum II, at least in female	1	g
132	Sternum II	not as described below	0	
		with sclerotised apophysis articulated to pleurum II	1	g
133	Atrium of thoracic spiracle	spherical	0	
		tubular	1	g
134	Abdominal spiracles	all of similar size	0	
		spiracle VIII of male very small	1	l
		spiracles VII and VIII very small in both sexes	1′	l
135	Abdominal spiracle VIII	present	0	
		absent	1	l
136	Abdominal spiracle VII	present	0	
		absent	1	l
137	Abdominal spiracle VI	present	0	
		absent	1	l
138	Abdominal spiracle III	present	0	
		absent	1	l
139	Setae of posterior setal row of pleurum III	not stout	0	
		stout	1	g
140	Pleurum VII	lacking tuft of very long setae	0	
		with tuft of very long setae (Figs 88, 90)	1	g
141	Abdominal tergal setae	short or of medium length (Figs 105, 188)	0	
		generally very long, obscuring p.l.s. (if present) (Fig. 158)	1	g
142	Male tergum II	lacking specialised setae as described below	0	
		with long stout setae not found on other terga (Figs 180, 188)	1	g
143	Male tergum III	lacking specialised setae as described below	0	
		with isolated pair of long median setae, longer than those of tergum IV (Fig. 187)	1	g
144	Male terga II–IV	without specialised setae as described below	0	
		each with single pair of long median setae (Fig. 182)	1	g

145	Female terga I–VIII	without specialised setae as described below	0	
		each with single pair of long stout median setae	1	g
146	Female terga I–IV	with median setae	0	
		lacking median setae	1	l
147	Male terga II and III	without specialised setae as described below	0	
		with group of characteristically specialised long setae (Fig. 178)	1	g
148	Female terga I–VIII	without specialised setae as described below	0	
		each with single pair of median setae	1	g
149	Male terga II–III	without specialised setae as described below	0	
		with long setae arranged in straight rows of four or more (Figs 161, 244)	1	g
150	Male tergum II	without specialised setae as described below	0	
		with long setae arranged in curved rows (Fig. 41)	1	g
151	Postero-lateral setae	absent or possibly present but not clearly distinguished from lateral setal group	0	
		clearly present on terga II–VI	1	g
152	Male terga II–VI	with two median setae the same size as other setae of median group	0	
		with two median setae appreciably smaller than other setae of median group	1	g
153	Setae of abdominal sterna II–IV	not as described below	0	
		short, stout (Fig. 136)	1	g
154	Female abdominal setae	not as described below	0	
		very long, fine	1	g
155	Setae of male tergum II	not arising from modified sclerite	0	
		arising from very long, medially-divided sclerite	1	g
156	Abdominal setal bases	not enlarged	0	
		enlarged	1	g
157	Abdominal pleurum II	not as described below	0	
		extending narrowly onto sternum II	1	g
		extending broadly onto sternum II	1′	g
158	Dorsal projection of pleurum II	absent	0	
		present, unsclerotised	1	g
		present, sclerotised	2	g
159	Dorsal projection of pleurum IV	absent	0	
		present	1	g
160	Ventral projection of	absent	0	

	pleurum IV	present	1	g
161	Projections of pleurum IV (if present)	not as described below	0	
		very long (Fig. 136)	1	g
162	Male terga VI–VIII (or VI, if VII–VIII without sclerites)	not as described below	0	
		with anterior sclerite longitudinally divided medially	1	g
163	Male terga VI–VII	not as described below	0	
		with posterior sclerite longitudinally divided medially	1	g
164	Abdominal lateral flecks	absent	0	
		present	1	g

Character analysis

The character analysis is performed in two interconnected parts, the determination of character polarity and the construction of the cladogram. These are linked through the process of 'reciprocal illumination' (Hennig, 1966), and thus, although they are considered individually in the two sections below, there is some interaction between the two processes which will be manifested in discussion. The following two sections are intended to explain the reasons for the polarity assigned to the characters listed above, and for those groups developed in the cladogram where characters are apparently arranged non-parsimoniously.

To increase clarity and conciseness the distributions of characters and character states discussed below are related to taxa and clades developed in the analysis. Clades are referred to by the names of the taxa (species or genera) on the extreme left (top) and right (bottom) of the clade as depicted on the cladogram (Figs 23 to 34), reading from left (top) to right (bottom).

Identification of apomorphic states

In many cases an apomorphic character state is identified as such by its distinct complexity and very limited distribution and, to avoid pointless repetition in the following discussion, such instances are not examined individually.

The characters are examined under the following headings:
Male genitalia (characters 1–56); Female genitalia (characters 57–97); Reproduction (character 98); Male terminal abdominal segments (characters 99–109); Antennae (characters 110–124); Head (characters 125–128); Legs (characters 129–130); Postcoxale (character 131); Spiracles (characters 133–138); Abdominal setae (characters 139–156); Abdominal pleural projections and modifications (characters 157–161); Abdominal sclerae (characters 132, 162–164).

Male genitalia (characters 1–56)
Most species of Psocodea have symmetric male genitalia and this state is consequently assumed to be plesiomorphic for the superorder. In a few species of Trichodectidae the genitalia are asymmetric, but differences in the form of the asymmetry in different species (Figs 170, 174, 249) suggest that several independent autapomorphies have been developed. In some cases a characteristic asymmetry is limited to a single species and is therefore of no relevance to phyletic analysis, but the asymmetries described in characters 1, 18, 19 and 29 are more widely distributed and are all employed. The distribution of other apomorphies indicates that character 1, the vertical asymmetric deflection of the lateral struts of the basal apodeme ('b.a.l.s.'), has been developed twice, once in *Felicola (S.) bedfordi* (Fig. 195), and once in the common ancestor of *F. (F.) cynictis* and *F. (F.) setosus* (Fig. 193).

In most Psocodea the basal apodeme is not fused to the parameres, but in a few Trichodectidae this fusion, considered to be apomorphic, has taken place (character 12). In the *Damalinia (D.) theileri–harrisoni* clade the posterior ends of the b.a.l.s. are broad and fused exteriorly to the parameres (Fig. 75); this fusion (character 12:1) is unlike that found elsewhere in the family and is believed on that account to be autapomorphic. In the *Trichodectes (S.) retusus–mustelae* clade, the *T. (S.) fallax–potus* clade, *Neolutridia lutrae* and *Lutridia exilis* the parameres are also fused to the b.a.l.s. (character 12:1′), but there are no features in the fusion pattern to indicate whether the apomorphy is homologous or convergent in the four clades. There are a number of possible sequences of gains and reversals. The fusion may have taken place three or four times with no reversals; once, to be lost at least four times; or twice, to be lost at least twice. The genitalia of *Lutridia* spp. differ from those found in the sister-group (the *Trichodectes–Neolutridia* clade), being more similar to those of *Protelicola*. Comparison of *L. exilis* and *L. matschiei* (Figs 144, 145) indicates fusion of the parameres and b.a.l.s. in the former species to be associated with the virtual detachment of the basal fused portion of the parameres, a unique feature. For this reason the fusion in *L. exilis* is deemed to be autapomorphic. The *Trichodectes (S.) retusus–mustelae* clade and the *T. (S.) fallax–potus* clade are placed by character 144 in a trichotomy with *T. (S.) emeryi*, a species in which the parameres are not fused to the b.a.l.s. If the fusion is homologous in *Trichodectes (Stachiella)* and *Neolutridia*, then it must have been lost in *Werneckodectes, Trichodectes (Trichodectes)* and *T. (Paratrichodectes)*, and *T. (S.) emeryi*. Parsimony suggests that fusion was developed independently in *Neolutridia* and the common ancestor of the two clades in *Trichodectes (Stachiella)* that possess the character, these latter being united as sister-groups. Fusion of the parameres to the b.a.l.s. is thus postulated to have taken place four times in the Trichodectidae, three of those times in the *Trichodectes–Lutridia* clade.

In most Psocodea the parameres are not fused together, but such fusion is present, probably apomorphically, in a number of species of Trichodectidae (character 13:1). In some species parameral fusion is difficult to observe, as the portion of the permanently-everted endophallus lying between the parameres is faintly sclerotised, giving the impression that the parameres are fused together; fusion has probably developed in some cases through sclerotisation of the endophallus. The distribution of other apomorphies suggests that parameral fusion exhibits more homoplasy than any other apomorphy in the analysis, being derived 24 times and lost once. In the *Lorisicola (P.) bengalensis–juccii* clade the parameres are closely associated with each other but are not fused (Figs 223, 224), although fusion has sometimes been assumed (e.g. Werneck, 1948). This proximity is believed to be autapomorphic for the clade (character 13:1′). The form of the fused parameres (parameral plate) may be apomorphic for groups of species (characters 15, 17).

In a few Trichodectidae the parameres and mesomeres are fused, a probable apomorphy (character 11). The distribution of other apomorphies and slight differences in the fusion pattern (Figs 60, 74, 75, 81, 225) indicate some homoplasy in the character.

As described above, the mesomeres are frequently fused apically in the Psocodea, and consequently this fusion, when found in the Trichodectidae, is deemed to be plesiomorphic. Loss of fusion (i.e. reduction to two unfused mesomeres) is therefore believed to be apomorphic within the Trichodectidae (character 33), and distribution relative to other apomorphies indicates that it has occurred several times in the family (see cladogram). In most species of the *Procaviphilus–Eurytrichodectes* clade there is a lateral desclerotisation on each side of the mesomeral arch (Figs 118, 122, 135). This character state is not found elsewhere and this, its structure, and the distribution of other apomorphies, all indicate its apomorphic status (character 34). The mesomeral arch may also have lateral flexions (Figs 107, 108, 225), which can give the arch the appearance of being broken (see Werneck, 1948). This modification is found in species of the *Lorisicola (P.) lenicornis–neoafricanus* clade and of *Procavicola (Condylocephalus)*, which on the basis of other apomorphies are widely separated on the cladogram; the lateral flexion of the mesomeral arch (character 35) is consequently believed to be a convergent apomorphy in the two clades named. In most species of the genus *Eutrichophilus* the mesomeral arch is divided into three parts by total desclerotisations laterally (Figs 91, 93). This feature is unique within the Phthiraptera and therefore considered apomorphic (character 36).

In many Trichodectidae a rod-like sclerite terminating posteriorly in a Y-shape or a broad plate is present longitudinally between the b.a.l.s. (Figs 55, 82, 148). Although this sclerite (the 'central sclerotisation') is very clear in some species, it is poorly sclerotised in others, and may be either absent or obscured by the sclerotisations of the endophallus in mounted specimens. The uncertainty attached to the observation of this structure has precluded its use in analysis, although it may be of value taxonomically. The central sclerotisation is probably a derivative of the basal apodeme, developed for muscle attachment.

A sclerite or pair of sclerites is present anteriorly to the parameres in some Trichodectidae, and are referred to here as the 'basiparameral sclerites' (Figs 107, 225) (character 10: 1+2). They may be fused to the parameres (Fig. 225) or to each other (Fig. 93). Their presence is believed to be apomorphic and their derivation is probably from the basal ventral flanges of the parameres found apomorphically (character 28) in a number of Trichodectidae (Figs 118, 122). If they are formed (as suggested here) by detachment of the flange from the main body of the paramere (Fig. 21), fusion of the sclerites and the parameres is a stage in the transformation series to the development of free sclerites, but fusion of the basiparameral sclerites to each other is a 'terminal' apomorphic state (although it is not used in the cladistic analysis because of its extremely limited distribution).

The anterior end of the basal apodeme may be heavily or lightly sclerotised, or apparently not sclerotised at all. This degree of sclerotisation is very susceptible to modification during preparation of the specimen, and thus is difficult to assess accurately. The character is not used in analysis. The most prominent features of the basal apodeme are the lateral struts (b.a.l.s.), which are generally fairly heavily sclerotised. These struts may approach the anterior of the basal apodeme in parallel, convergently or divergently; this character is not used in cladistic analysis because of the difficulty in assigning polarity to the different forms, but is useful taxonomically, and can help in the determination of the form of the anterior margin of the basal apodeme. This anterior margin may be straight or broadly convex, shallowly concave, very deeply concave (Fig. 52) or acuminate (Fig. 173) (character 2). Of these forms the last two are almost certainly apomorphic within the Trichodectidae; the elongation of the apodeme and the concomitant parallel-sided concavity is found only in the *Bovicola alpinus–tibialis* clade (character 2:1), and the acuminate form is found only in three species of *Trichodectes*, although in fact the latter apomorphy imparts little useful information for the construction of the cladogram. The polarity of the character for the other three states is difficult to assess, and they are therefore not used in phyletic analysis.

In some species of *Damalinia (Tricholipeurus)* the b.a.l.s. develop a lateral spur before the junction with the parameres, probably at the point at which the dorsal and ventral layers of the basal apodeme separate; this feature (the 'anteposterior spur', Fig. 83) is not found elsewhere in the Trichodectidae and is considered apomorphic (character 5). The posterior ends of the b.a.l.s. are most frequently not, or only slightly, expanded laterally, but in some Trichodectidae they are greatly broadened and scoop-shaped. This very broad form, whilst believed to be apomorphic, is not used as an apomorphy in phyletic analysis because of difficulties in delimiting the state. The posterior forking of the b.a.l.s. (Fig. 173) is also considered apomorphic (character 3), but was probably developed twice in *Trichodectes* (see cladogram). The basal apodeme probably extends anteriorly as far as segment VI in the plesiomorphic state, but in a few Trichodectidae it extends up to segment II; in some cases this lengthening has been accompanied by a width restriction or 'waisting' medially, and this is believed to be apomorphic (character 6). Other features of the basal apodeme are, by virtue of their restricted distribution and concordance with the distributions of other apomorphies, believed to be apomorphic (characters 4, 7, 8, 9).

Whilst it is not possible to be certain of the plesiomorphic form of the parameres in the Trichodectidae, it is assumed that this is fairly unspecialised, and that the forms of the parameres found in groups of species that are also linked by other apomorphies are apomorphic (characters 20–27).

As noted above, apical fusion of the mesomeres is plesiomorphic for the Trichodectidae, so loss of apical fusion, reduction in size and complete loss of the mesomeres are all considered to be apomorphic within the family (characters 30, 31, 33). The presence of a median longitudinal extension to the mesomeral arch is also considered plesiomorphic, as it is present in a number of taxa outside the Trichodectidae. Loss of this extension, or modification of its form from 'simple lanceolate' (Fig. 118), are considered apomorphic within the family (characters 47–49). In the plesiomorphic state the mesomeres articulate basally with the basal apodeme; articulation of the basal apodeme with any other part of the mesomeres is considered apomorphic. Mesad extension of the mesomeres between the b.a.l.s. (character 32) has apparently arisen twice, once in the Dasyonyginae, and once in the *Lorisicola*, and in each case providing an autapomorphy for the clade named. In *Lorisicola (P.) bengalensis* and *philippinensis* the parts of the mesomeres between the b.a.l.s. are apomorphically deflected posteriad (Fig. 224) (character 37). A similar recurving of the mesomeres occurs elsewhere in the Trichodectidae (character 45), but in this case the mesomeres are exterior to the b.a.l.s., and their recurved portions lie ventrally to the b.a.l.s. This apomorphy is seen as a transformation series of states in *Damalinia (Tricholipeurus)* (character 45:1–45:2), the most apomorphic of which (45:2) is also exhibited by *Lorisicola mjoebergi*, although in this case the recurved parts of the mesomeres are very difficult to see (Fig. 219). Other modifications to the mesomeres believed to be apomorphic are present in restricted groups within the Trichodectidae (characters 38–46).

The endophallus may be sclerotised in a number of apomorphic ways within the Trichodectidae (characters 51–56).

Female genitalia (characters 57–97)

The gonapophyses of most Trichodectidae and many other Psocodea bear at least some setae, which arise directly from the structure and not from tubercles. Absence of setae (character 57) and development of sclerotised setal tubercles (character 58) are therefore both believed to be apomorphic within the Trichodectidae. Setal tubercles are found in *Protelicola, Procaviphilus* and the *Trichodectes–Neolutridia* clade (*T–N*), but as a sister-group relationship between the latter two is not supported by other apomorphies, and the form of the tubercles differs between the two clades (Figs 111, 157), the character is probably convergent. The relationship between *Protelicola* and the *T–N* clade is discussed below. The characteristic pattern taken by the tubercles in each clade is modified by loss (character 60) or fusion (character 59); in both cases these are believed to be apomorphic modifications because of their concordance with other apomorphies. Tuberculate setae are also found on the ventral vulval margin of most species in *Trichodectes* (Fig. 157); concordance with other apomorphies suggests the apomorphy of this character (character 74).

The plesiomorphic form of the gonapophyses is not certain, but some forms, because of their very restricted distribution, are believed to be apomorphic (characters 61, 62, 63); some convergence in character 62 is indicated by the distribution of other apomorphies. The development of a lobe on the ventral margin of the gonapophysis is restricted to the Trichodectidae and, for this reason, is believed to be apomorphic within the clade (character 64). Distribution of other apomorphies suggests that the lobe developed independently in several different clades, sometimes taking only one form in a clade (character 70), sometimes being apomorphically modified (characters 66–69). The reduction of the 'spur' – the portion of the gonapophysis distal to the lobe – is considered apomorphic, as it is confined to two small groups of taxa within the family (character 65). Where present, the gonapophyses in most Phthiraptera meet the ventral vulval margin at an angle (Figs 94, 175), but in some Trichodectidae they meet in a smooth curve (Fig. 154), which may be sclerotised (characters 71, 72). The ventral vulval margin may extend in a more or less smooth curve between the gonapophyses, as is most frequently the case in lice with gonapophyses, or it may be produced in some manner (characters 75–78). Each of these projections is considered apomorphic, although the distribution of other apomorphies suggests that some are homoplastically developed in different clades of the family. The distinction between the subgenital lobe (character 78) and the expansion of the ventral vulval margin (character 75, and its apomorphic derivative, character 76), may not be immediately clear, but whilst the former term is applied to structures that arise abruptly from the margin, the latter is a more extensive posterior production of the whole of the margin. Both of these apomorphies occur more than once in the Trichodectidae. The form of the subgenital lobe is variable, though frequently it is marginally serrate, sometimes with the serrations greatly developed (character 79:2). Several other apomorphies, of restricted distribution within the Trichodectidae, are found in the form of the subgenital lobe (characters 80–83, 85, 86). Two probable apomorphies, the presence of an internal sclerite in the subgenital lobe and the presence of lateral setal patch, are not used in the cladistic analysis. The internal sclerite is not readily observable, but this is probably due to the sclerite being rendered undetectable during preparation of the specimens (especially the smaller species), and this likelihood precludes its use. The distribution of the sclerite, where detected, suggests it to be plesiomorphic within the Trichodectinae, possibly linked to the development of the subgenital lobe in this clade. The lateral marginal setae appear to share part of the distribution of the lateral processes of the lobe (character 81), being absent in a few species only, and the two characters are probably closely associated; for this reason the setal character is not used.

The plesiomorphic form of the genital chamber in the Trichodectidae is not known, but observations on other Phthiraptera suggest light sclerotisation with a few internal spicules. The development, in some restricted groups of Trichodectidae, of particular patterns of spicules, scales, spines and broad sclerotised areas (characters 92–96) is considered apomorphic.

Reproduction (character 98)

Parthenogenetic reproduction (character 98) occurs in a few Trichodectidae, mostly in the Bovicolinae, but also in the species *Geomydoecus scleritus*. As all other Phthiraptera reproduce bisexually, the character is taken as apomorphic. Parthenogenesis appears to have developed at least four times in the Trichodectidae.

Male terminal abdominal segments (characters 99–109)

The sclerites of the terminal segments of the male trichodectid abdomen are very variable in presence or absence states, extent, and degree of subdivision. This variability is not, in many cases, readily associated with transformation series of other characters to which polarity has been applied, and the plesiomorphic state (and hence apomorphic states) of the characters of these sclerites is, in most cases, not known. In a few instances the sclerites are distinctly modified in a restricted group of species, and thus polarity can be assigned (characters 99, 101, 106, 107, 108, 109).

Segment IX and the genital opening are apomorphically positioned more or less dorsally in many species of Trichodectidae, as discussed above. Distortion due to preparative processes obscures the position in many of the specimens examined, however, and characters associated with this positioning cannot be used with any confidence, and are excluded from analysis.

In some species of Trichodectidae the posterior margin of tergum IX is greatly expanded to produce a double convex lobe (character 100); this development is believed to be apomorphic, although the distribution of other apomorphies indicates that it developed twice.

The presence of pseudostyli, discussed in detail above, is believed to be apomorphic for the Trichodectidae (character 102). The plesiomorphic form of the pseudostyli is not known, as the extant forms are very variable and cannot, in most cases, be resolved into transformation series. In two cases (characters 103, 104), the pseudostyli are of very distinct form and restricted to groups of species believed to be holophyletic on other grounds; these character states are believed to be apomorphic. The presence of a single projection posteriorly on segment IX in some species of Trichodectidae, believed to be formed of fused pseudostyli, is also considered apomorphic (character 105). Although found in only three species, the distribution of other apomorphies suggests two independent developments of this character state.

Antennae (characters 110–124)

In all Trichodectidae the male flagellomeres are fused together (character 111), a state found elsewhere only in the anopluran families Echinophthiriidae and Hamophthiriidae and therefore considered apomorphic for the Trichodectidae. Fusion of the flagellomeres has also occurred in some female Trichodectidae (character 110), but the distribution of other apomorphies suggests four homoplastic derivations of this apomorphy in the family. The expansion of the scape in the male to house the enlarged musculature is probably plesiomorphic for the Trichodectidae, as similar expansion is found in many Ischnocera and Anoplura. Reduction of this expansion is, however, apomorphic within the family (character 112), and is believed to have taken place three times. The flagellum of most male Trichodectidae bears a number of setae modified into broad pointed 'teeth' (Figs 13, 231), a feature not found in the same form in any other Phthiraptera, and therefore considered apomorphic for the family. The plesiomorphic number of 'teeth' is almost certainly two, as this number is the most common in all groups of Trichodectidae; any variation from this number (to zero, one, three, four or eight) is believed, therefore, to be apomorphic (character 115). The loss of the basal articulation of the 'teeth' (character 117) and the development of a supporting protuberance (character 116) are both apomorphic. In order that the male antennae should clasp the female with maximum efficiency the 'inner' (posterior) surface of some or all of the antennal segments may be roughened or bear projections; such developments are considered apomorphic in each form (characters 118–121). The presence of a membranous projection on the female antenna (character 122) is also believed to be apomorphic. In most Phthiraptera the setae of the scape are scattered over its surface in no coherent pattern, and this is true of some Trichodectidae (Fig. 70); in most Trichodectidae, however, the setae of the dorsoposterior surface of the scape are apomorphically arranged in a line along the segment (Fig. 13) (character 113). In some cases where a row of setae might be expected from the construction of the cladogram, the number of the setae involved in the putative row is only two, and this is believed to represent an apomorphic reduction in number (character 118).

The sensilla of the antennae in Trichodectidae and other Phthiraptera have been discussed above; the presence of a fringed pit surrounding the sensilla of the flagellum in two species of Trichodectidae is unique and believed to be apomorphic (character 124).

Head (characters 125–128)

Although the sitophore sclerite is variable in most Phthiraptera (Haub, 1973), it is comparatively uniform in the Trichodectidae. The form found in most Trichodectidae (Fig. 11) is believed on this account to be plesiomorphic, and is departed from in *Bovicola (Spinibovicola)*, *Dasyonyx* and *Eurytrichodectes*, where the posterior arms are extended (Fig. 12) (character 125). The distribution of other apomorphies indicates that the modification is convergent in *Bovicola (Spinibovicola)* and *Dasyonyx* plus *Eurytrichodectes*.

The posterior margins of the temple are generally broadly rounded in Trichodectidae, but in species of the genus *Eutrichophilus* the convexity is much greater than in the rest of the family (Fig. 87); this development is believed to be apomorphic (character 127). In the three species of the genus *Eurytrichodectes* (only two of which are described) and the four of *Procavicola (Condylocephalus)* the posterior temple angles are developed into pointed projections (character 126), these being very long in the former genus (character 126: 2). This modification is not found elsewhere in the Trichodectidae, although small rounded projections are found in some *Dasyonyx* spp. and some *Damalinia* spp. The presence of pointed projections is believed, on the basis of the distribution of other characters, to be homoplastic in the two genera mentioned.

The form of the osculum has been largely excluded from consideration in the cladistic analysis because of the direct influence of the hair of the host (see above). However, in the *Damalinia (D.) theileri–baxi* clade it is quite different from other species of Trichodectidae (Fig. 69), and is here suggested to be apomorphic (character 128).

Legs (characters 129, 130)

The loss of one tarsal claw on each leg (character 129) is an apomorphy associated with ectoparasitism on mammals. This character is proposed as an autapomorphy of the Trichodectidae, although it may be autapomorphic for a postulated holophyletic group comprising the Anoplura, Rhyncophthirina and Trichodectidae (Lyal, 1985).

A number of Psocodea have teeth on the 'inside' face of the tarsal claws, and many Trichodectidae have what appears to be a single basal tooth (Fig. 15). The occurrence of teeth all along the 'inside' face of the tarsal claws (Figs 14, 15) is restricted in the Trichodectidae to *Dasyonyx*, and is believed to be autapomorphic for the genus (character 130). The two subgenera of *Dasyonyx* have tarsal claw teeth of different forms: *D. (Dasyonyx)* have sharp slender teeth (Fig. 14), whilst *D. (Neodasyonyx)* have blunter, broader teeth (Fig. 15). These two forms may be co-apomorphies, indicating that the subgenera are sister-groups, or one may be the plesiomorphic state. No other characters have been found within *Dasyonyx* that indicate reliable sister-group relationships within the genus. In this study the two tooth forms are accepted as co-apomorphies and the subgenera retained, but further work on the genus may cause this hypothesis to be challenged.

Postcoxale (character 131)
In most species of Trichodectidae the metathoracic postcoxale is either not sclerotised or sclerotised and small, but the polarity of the transformation series with the extreme states 'sclerotised' and 'not sclerotised' is not known. In *Procaviphilus (Meganarionoides)* and some species of *Dasyonyx (Dasyonyx)* the postcoxale is greatly enlarged and heavily sclerotised, an apomorphic state not included in the analysis for reasons given below. A further apomorphic condition, the fusion of the postcoxales, is also found in some members of the same subgenera. The presence of the sclerotised postcoxale is difficult to determine in some of the smaller species of *Dasyonyx*, but in any case the distribution of other apomorphies indicates convergence of the postcoxale characters in the two subgenera. Neither apomorphy is used in the analysis.

In *P. (Meganarionoides)*, uniquely, the postcoxale is fused to abdominal pleurum II (character 131), and this apomorphy is used in the analysis.

It is interesting that the great development of the postcoxales, restricted to lice parasitic on hyraxes, is morphologically convergent on the development of the apophysis of abdominal sternum II (character 132), which is found in another group of hyrax lice.

Spiracles (characters 133–138)
For the Phthiraptera (and the Trichodectidae) the plesiomorphic number of spiracles is a single thoracic pair and six abdominal pairs; further reduction in the number of abdominal spiracles is apomorphic. The numbers of abdominal spiracles in the different species of Trichodectidae are summarised in Table 1. Each reduction is considered to be an apomorphy (characters 135–138), though some homoplasy has occurred. Inspection of the distribution of other apomorphies indicates that reduction to five, four and one pair of spiracles has occurred once, reduction to three and two pairs twice, and reduction to none eight times. Because of the sequential pattern of spiracle loss, apomorphy 136 is always associated on the cladogram with apomorphy 135, 137 with 136 and 135, and 138 with 137, 136 and 135.

In most species of lice all of the abdominal spiracles have atria of roughly the same size; as has been pointed out in earlier discussion, however, some Trichodectidae have posterior spiracles with atria much smaller than those more anterior on the abdomen (character 134). This difference in size is believed to be an apomorphic reduction.

In most species of lice the atrium of the thoracic spiracle is as broad or broader than long; species of the genus *Cebidicola*, however, have a tubular atrium associated with the thoracic spiracle (character 133). This modification of form is believed to be apomorphic.

Abdominal setae (characters 140–156)
Study of abdominal setal patterns throughout the Psocodea suggests that the plesiomorphic pattern is a row of setae running around the abdomen on each of segments I to VIII. On trichodectid abdominal pleura II–VII this row of setae (referred to here as the posterior setal row or 'p.s.r.') is generally clear, and is absent in only a few species. The distribution of other apomorphies indicates this absence to be apomorphic, although limited to a very few, distantly-related, species. In some Trichodectidae, the p.s.r. of pleura II, III and IV comprises setae that are much stouter than those of other pleura, and the distribution of other apomorphies suggests the apomorphic status of each of these, although each exhibits some homoplasy. Preliminary analysis indicated that specialisation of the p.s.r. on pleura II and IV conveys little phylogenetic information, and only character 139 (specialisation of the p.s.r. on pleurum III) is used in the final cladistic analysis. The setae on pleura VIII and IX are frequently longer than the setae of

the p.s.r. on anterior pleura; the extreme length of these setae in *Eutrichophilus* is, however, recognised as apomorphic (character 140).

The setal row on sterna II and III is usually similar to the row on other sterna, but in the two species of *Eurytrichodectes* the setae of these two rows are short, stout and conical (Fig. 136). This unique feature is believed to be apomorphic (character 153).

The tergal setal row of many Trichodectidae, especially males, is clearly composed of four discrete groups – two lateral and two median – each separated by a gap (Fig. 22). The positioning of the groups and the number of setae in them are useful taxonomic characters, and may be utilised as landmarks for the identification of particular setae. The groups are, however, difficult to use in phyletic analysis because of the difficulty of assigning polarity to any transformation series.

In some Trichodectidae (and in no other Phthiraptera) a seta – termed here the 'posterolateral seta' or 'p.l.s.' – is present posterolaterally on each side of terga II–VI (Fig. 22). The restriction of distribution of this seta within the Phthiraptera suggests that its presence is apomorphic (character 151). In some cases there is more than one p.l.s. on each side of the tergum (Fig. 201); this is believed to be an apomorphy but its sporadic occurrence (in terms of clades indicated by other apomorphies) has led to its omission from the cladistic analysis. The presence of the p.l.s. is difficult to assess in some species, either because the lateral group may be reduced in number or because the lateral group is composed of very long setae. In the former case, a single seta in the position of the p.l.s. may be this seta (the lateral group being absent), or it may be the sole remaining seta of the lateral group (the p.l.s. being absent) (Fig. 159). In the latter case (most *Trichodectes* species and the Neotrichodectinae), the most lateral seta of the lateral group frequently lies slightly posterior to the rest of the row (Fig. 158) and a more differentiated p.l.s. is absent. In both these cases the p.l.s. is postulated to be present, though modified. The

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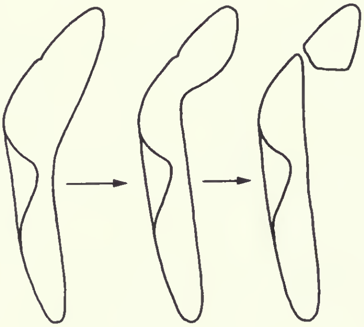

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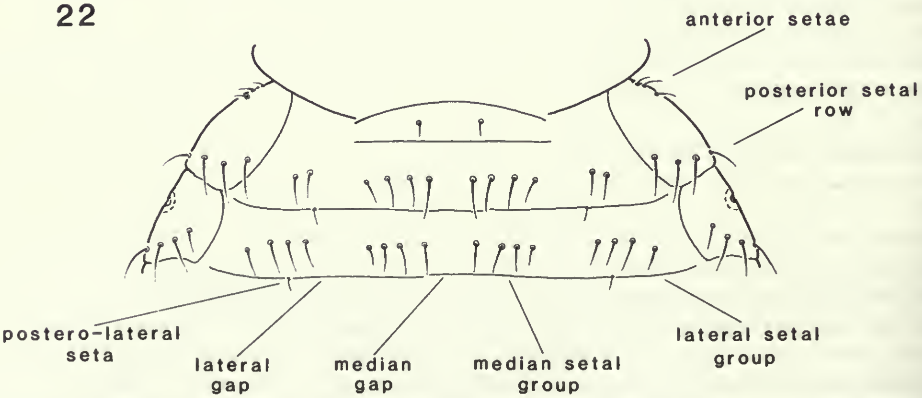


Figs 21, 22 Trichodectid morphology. 21, postulated evolution of basi-parameral sclerite by detachment of basal flange of paramere. 22, Abdominal setal arrangement, illustrated by anterior terga and pleura of male.

distribution of other characters suggests, however, that secondary loss of the p.l.s. has occurred within some taxa.

Some setae of the median tergal group, particularly in males, may be specialised. In males of *Neotrichodectes* spp. the two central setae of the united median groups, or two setae very near the centre (perhaps separated by one or two unmodified setae) are very much smaller than the other setae of the row (Fig. 229). These 'tergocentral microsetae' (character 152) are found nowhere else, and this and the concordance of their distribution with that of apomorphy 118: 1′+2′ suggests the apomorphy of the character state. In *Felicola (S.) pygidialis* and *F. (S.) macrurus* the median group of tergum III is modified in a distinctive manner in the males (Fig. 178), and this modification is assumed to be apomorphic for the two species (character 147). Some or all of the setae of the median group on terga II and III of male Trichodectidae may be enlarged relative to the other tergal setae. This enlargement occurs sporadically both within and outside the family, and each case is believed to be autapomorphic. Within the Trichodectidae, in males of *Geomydoecus (Thomomydoecus), G. (G.) copei, Trichodectes (Paratrichodectes) ovalis* and *ugandensis*, and the undescribed sister-subspecies of *Trichodectes (T.) galictidis*, the setae of the median row on both terga II and III are enlarged but remain in a straight row (Figs 161, 244); this arrangement is believed to be apomorphic, but probably convergent in each of the four groups (character 149). In *Bovicola (Spinibovicola) hemitragi* and *multispinosa* a similar enlargement is confined to some of the setae of tergum II, and the lines are curved (Fig. 41) (character 150). In males of *Felicola*, the holophyly of which is supported by several apomorphies, the median setal group is reduced to a single, greatly enlarged seta (Fig. 188). The apomorphic status of this character (character 142) is indicated by its restricted distribution and correlation with other apomorphies. It is notable that the setae are single, but of normal size (very small) in the *Felicola (F.) rahmi-viverriculae* clade (Fig. 183), and secondarily increased in number to six in *Felicola (S.) bedfordi* and *F. (F.) setosus* (Figs 180, 189). On the basis of other apomorphies, the former is believed to be a single autapomorphic reversal, whilst the latter is believed to be a convergent gain.

The sclerite from which the pair of setae arises may be long and of characteristic shape (Fig. 181); this feature is found only in conjunction with the enlarged setae (character 142) and is postulated to be apomorphic (character 155).

In many males of *Felicola* the median setal group on terga III–VII is also reduced to a single seta, although in most cases this does not approach the size of the seta of tergum II. In the *Felicola (S.) cooleyi–quadraticeps* clade this reduction has taken place on terga III–VII, but the setae are similar in length to those of tergum II, the latter being reduced relative to those of other species of *Felicola* and the former enlarged (Fig. 186) (character 143). This apomorphy is convergent on the apomorphic setal pattern of the males of *Trichodectes (Stachiella)* (character 144), although in this case the setae are all generally long and stout. The median setal group of the female tergum may also be reduced to a single seta (character 145) or lost (character 146). The distribution of these female apomorphies is as follows. The reduction of the median group to a single seta is found only in the *Trichodectes (S.) fallax–octomaculatus* clade; the sister-species, *T. (S.) potus*, and the sister-group to this clade, the *T. (S.) retusus–mustelae* clade, lack the female median group entirely. The sister-species to the whole *T. (S.) retusus–potus* clade, *T. (S.) emeryi*, has the median group unreduced, numbering three setae, on terga I and II, reduced to one seta or absent on tergum III, and absent on terga IV–VIII. It is not certain whether setal loss in the female has taken place only once, the setae being regained in the *fallax–octomaculatus* clade, or has taken place independently three times (in *emeryi*, the *retusus–mustelae* clade, and *potus*).

The length of the abdominal setae is difficult to employ in phyletic analysis because of the problem of establishing the polarity of the transformation series 'very short – medium – very long'. The restricted distributions of the two extremes of the series (concordance with other apomorphies) indicate their apomorphic status, however. The very short, sparse setae (Fig. 183) are found in no other Phthiraptera but the *Felicola–Lorisicola* clade and some *Trichodectes* spp., and are probably apomorphic but convergent in the two groups. The very long refringent setae of some Trichodectidae (Fig. 158) are considered apomorphic for a similar reason (character

141), though in this case similar setae are found in some Philopteridae. These long setae probably evolved twice in the Trichodectidae: once in *Trichodectes* and once in the Neotrichodectinae. The fine, long setae of the females of the *Felicola (S.) cooleyi–quadraticeps* clade are found in no other group and are considered apomorphic (character 154).

The setal bases – the circular 'pits' of the setal articulations – are of fairly constant size relative to the setae in most Trichodectidae. However, in the *Bovicola (B.) alpinus–tibialis* clade the bases are noticeably large in relation to the setae, and seem to have a double margin. This feature needs to be examined using the scanning electron microscope to elucidate its true structure, but examination using the light microscope is sufficient to detect its presence. This feature is here considered as apomorphic (character 156).

Abdominal pleural projections and modifications (characters 157–161)
In many Trichodectidae the dorsoposterior and/or the ventroposterior pleural angles project on pleura II, III or IV (see discussion above, and Table 2). Projections on these segments of the type found here do not occur elsewhere in the Phthiraptera, and are therefore considered as apomorphic (characters 158–160). Preliminary analysis reveals that the projections on pleurum III contribute no useful phyletic information, so the apomorphy is omitted from the final cladistic analysis. Variation in the degree of development of the dorsal and ventral lobes of the projection on pleurum IV is omitted for the same reason, except for the extreme development in *Eurytrichodectes* (character 161). Both the presence of a dorsal and a ventral projection on pleurum IV (characters 159 and 160 respectively) are included in the analysis, though the latter apomorphy is reversed in some clades. The presence of a projection on pleurum II (character 158) provides a synapomorphy for *Geomydoecus* spp.,which are also united as a holophyletic group on other grounds; the projection on this pleurum is found convergently in *Trichodectes (Paratrichodectes) zorillae*. The sclerotisation of the dorsal projection on pleurum II (character 158:2) is an autapomorphy of *Geomydoecus (Thomomydoecus)* (and some species in *Geomydoecus* s.str. – see discussion below –) and *T. zorillae*, but sclerotisation of the projections on the other pleura is very variable, and is not used in cladistic analysis.

In *Damalinia (Damalinia)* pleurum II extends on to sternum II, and the pleurite is expanded at the expense of the sternite (character 157). This extension may be broad (character 157:1′) or narrow (character 157:1), but the more plesiomorphic state of these two (should they not be co-apomorphies) is not known. The species with a broad ventral extension of pleurite II also possess a more or less extensive dorsal extension, but this is not found in species with a narrow ventral extension. In this treatment the two forms of the ventral extension are used to characterise each of two sister-groups, but this hypothesis is open to challenge, as the group indicated by character 157:1 has no other supporting apomorphy.

Abdominal sclerae (characters 132, 162–164)
As noted above, in species of the trichodectid genus *Procavicola* sternite II is greatly developed as a heavily sclerotised internal apophysis, articulated to pleurum II (character 132). The presence of this unique structure is considered apomorphic.

The presence of the lateral flecks and their associated small sclerite is considered apomorphic, as the structure occurs in no Phthiraptera other than the Trichodectidae (character 164).

The pleura, sterna and terga of the trichodectid abdomen may be sclerotised or not; although some groups (identified on the basis of other apomorphies) may, in general, be more or less sclerotised, the polarity of the transformation series 'sclerotised – not sclerotised' for each segment cannot be determined, and these characters are not used in the cladistic analysis. The male abdomen may have a characteristic sclerotisation dorsally, in that the terga may have anterior and posterior sclerites; this feature is present in some Anoplura, but is probably convergent in this suborder. The presence of doubled tergal sclerites in male Trichodectidae is believed to be apomorphic for the family, but is not used in cladistic analysis because of the large number of reversals. The tergal sclerites are not further modified in most male Trichodectidae, but in some there is longitudinal division of the anterior or posterior sclerites (characters 162 and 163 respectively), this division being accepted as apomorphic.

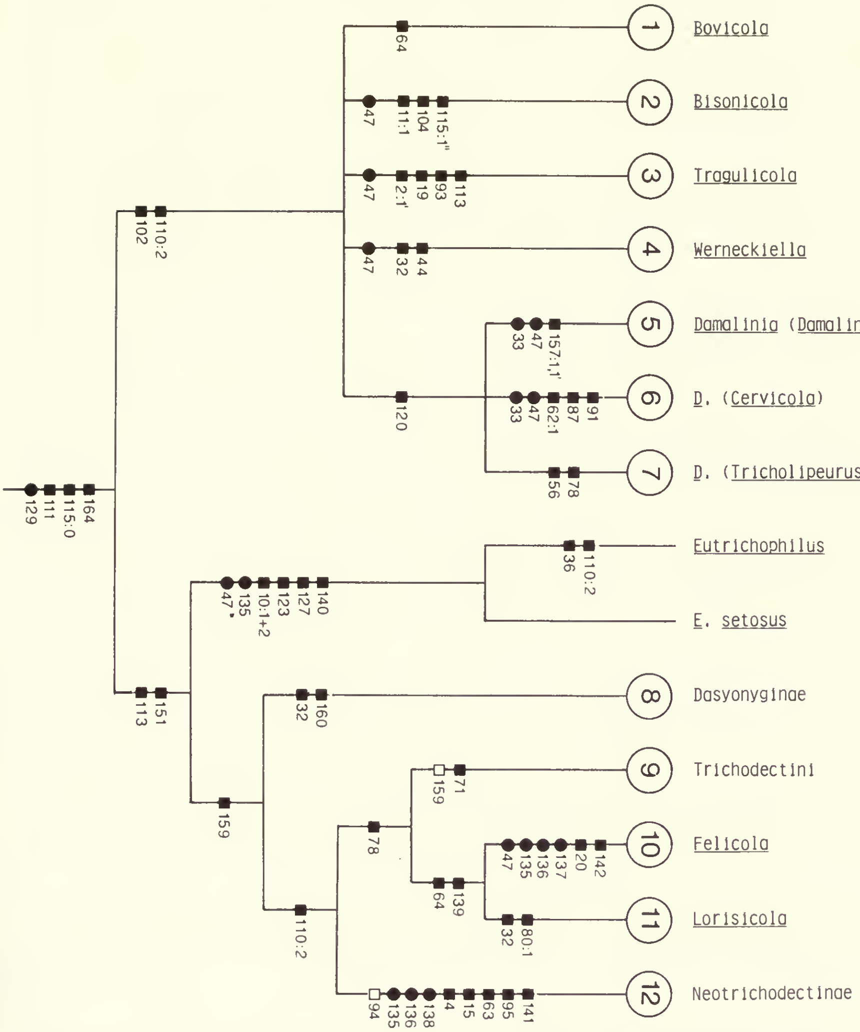


Fig. 23 Cladogram of Trichodectidae. Clades numbered 1–12 are resolved in Figs 24–34. The Eutrichophilinae (Genus *Eutrichophilus* only) is not resolved further. For explanation of numbered apomorphies see text.

Cladistic analysis

The holophyly of both monotypic and polytypic species is accepted without the need for justification, so species-level autapomorphies have not been indicated unless they are homoplastic with character states elsewhere on the cladogram. Omission of the autapomorphies of species saves both space in the data matrix and time taken for analysis, and for the same reasons many sister-species pairs are justified on the cladogram with fewer autapomorphies than are available.

Of the 187 apomorphic character states used in the analysis, 86 are postulated to have been developed more than once or to have been secondarily lost, 363 such homoplasies being proposed. When, in the analysis, a choice is available between postulating one reversal or a pair of homoplastic gains (i.e. three clades in a holophyletic group are involved and the topography of the tree is not affected whichever the choice), the latter is chosen (e.g. character 13:1 in the *Damalinia theileri–appendiculata* clade). This choice is made so that the distribution of apomorphic character states can more easily be discerned on the cladogram. The number of

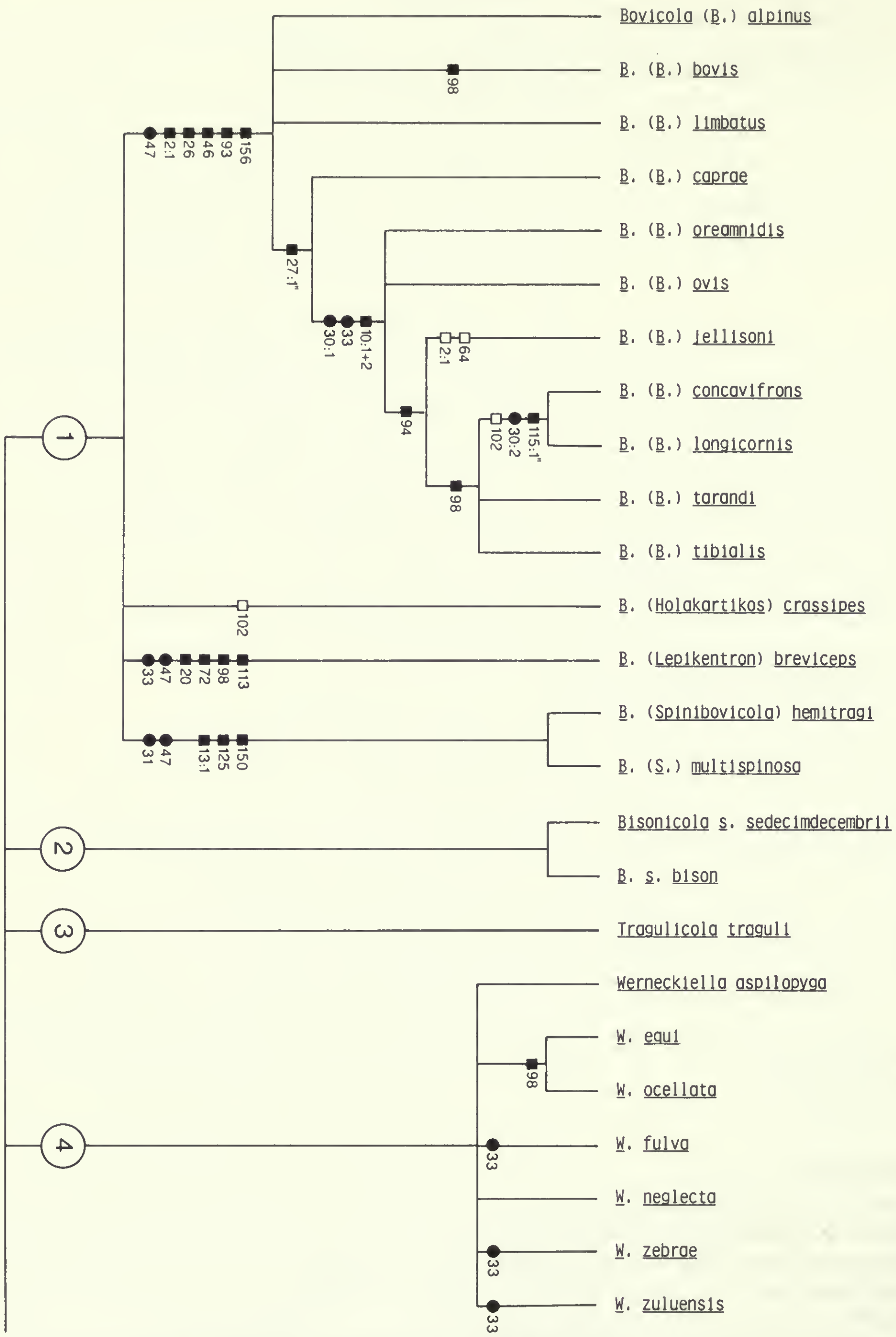


Fig. 24 Cladogram of Bovicolinae (part) (clades 1–4 of Fig. 23: genera *Bovicola, Bisonicola, Tragulicola* and *Werneckiella*). For explanation of numbered apomorphies see text.

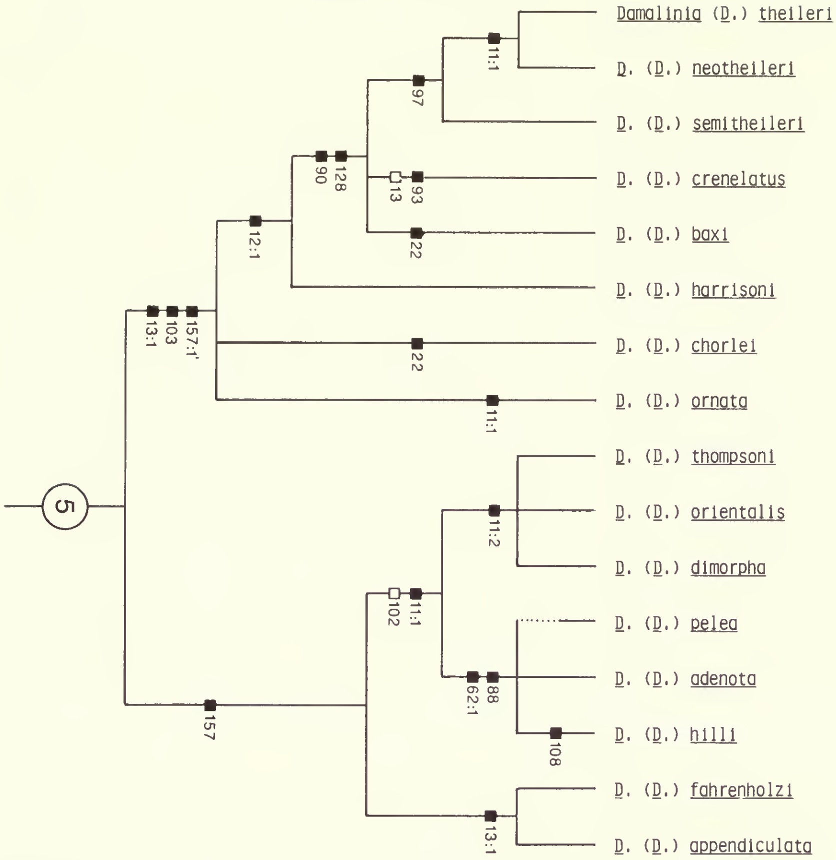


Fig. 25 Cladogram of *Damalinia (Damalinia)* (clade 5 of Fig. 23). For explanation of numbered apomorphies see text.

homoplasies could be slightly reduced without affecting the topology of the tree because, as explained below, the less parsimonious presentation is sometimes chosen to make the cladogram more informative and less potentially misleading. In a number of places in the discussion of apomorphic state identification above, reference is made to single apomorphic character states arising more than once. This is superficially contradictory, especially if the terms apomorphy and homology are equated. Such situations have been detected during one 'round' of reciprocal illumination. Should all such convergent apomorphic states be recoded as separate apomorphies (which they are believed to be, even if they cannot be differentiated morphologically) the cladogram would appear more parsimonious.

The loss of the median extension of the mesomeral arch (character 47) is placed on the cladogram 17 times, frequently in combination with the loss of apical fusion of the mesomeres (character 33). These apomorphies are not arranged in the most parsimonious manner on the cladogram, as can be seen by inspection of the Bovicolinae. As presented, the cladogram depicts the loss of the extension 11 times in this subfamily. A more parsimonious arrangement of the apomorphies is achieved by postulating characters 33 and 47 as synapomorphic for *Damalinia (Damalinia)* and *Damalinia (Cervicola)*, and character 47 as synapomorphic for two clades: *Werneckiella* plus *Tragulicola* and *Bisonicola*, and *Bovicola (Bovicola)* plus *B. (Lepikentron)* and *B. (Spinibovicola)*. This arrangement reduces the number of proposed homoplasies of character 47 to six within the Bovicolinae, and reduces the number of polychotomies on the cladogram. Alternatively, the loss of the extension might be postulated to have occurred only once, in the common ancestor of the Bovicolinae, and regained six times (*B. crassipes, D.*

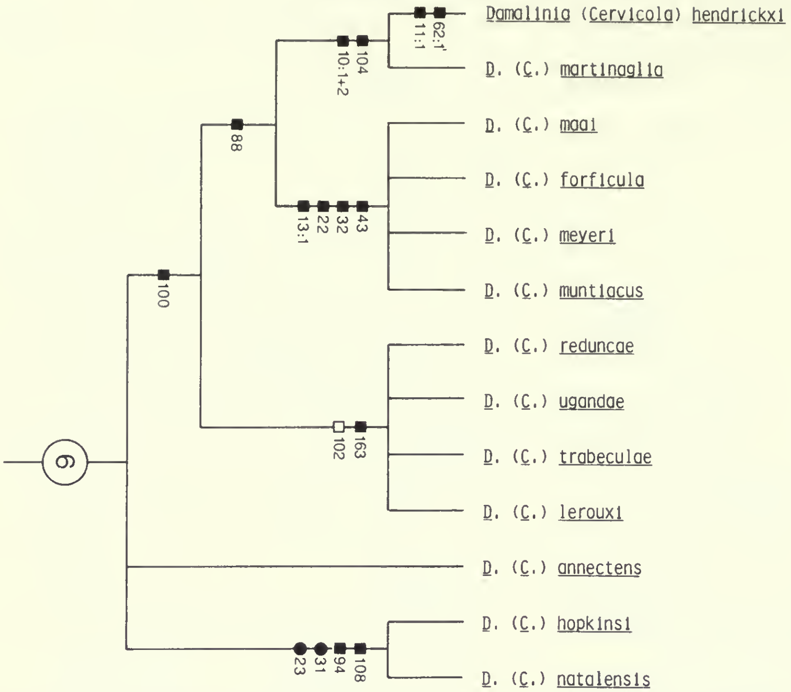


Fig. 26 Cladogram of *Damalinia (Cervicola)* (clade 6 of Fig. 23). For explanation of numbered apomorphies see text.

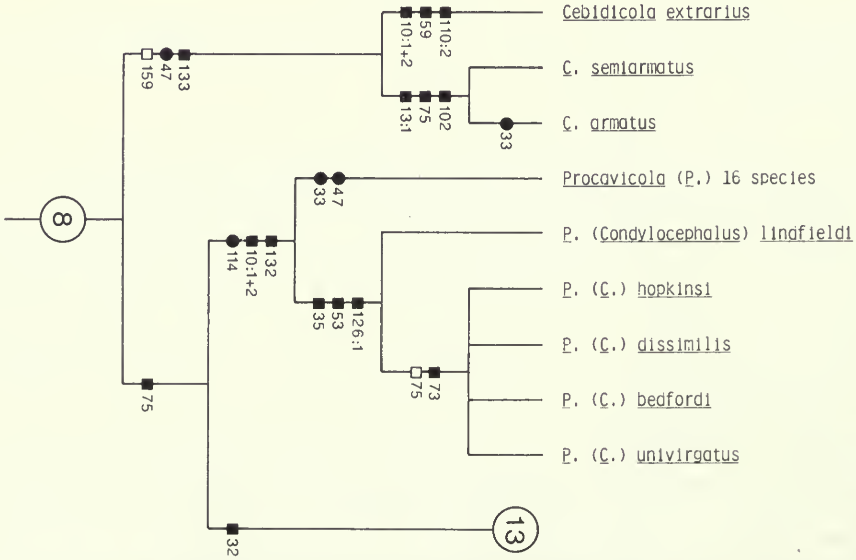


Fig. 28 Cladogram of Dasyonyginae (clade 8 of Fig. 23, part: genera *Cebidicola* and *Procavicola*). Clade 13 is resolved in Fig. 29. For explanation of numbered apomorphies see text.

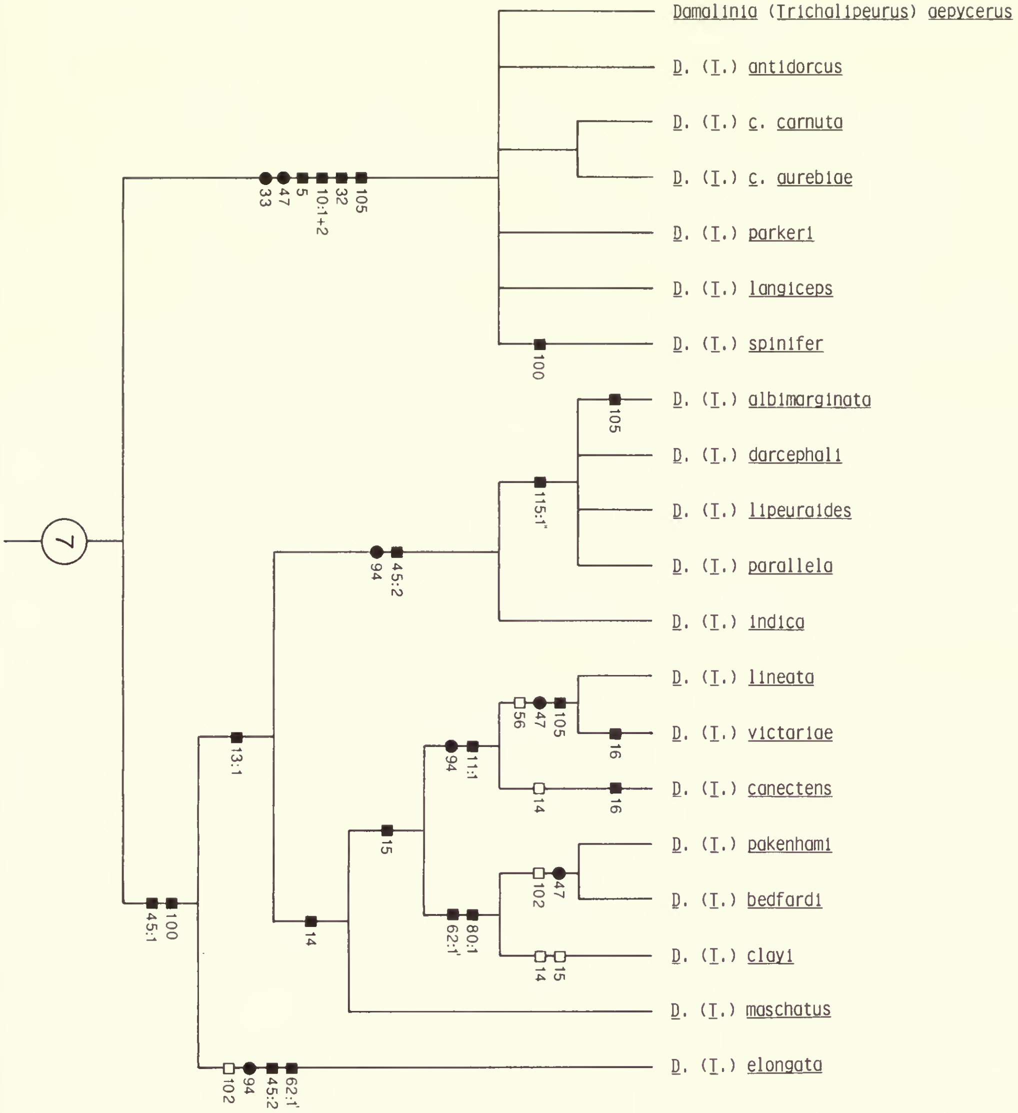


Fig. 27 Cladogram of *Damalinia (Tricholipeurus)* (clade 7 of Fig. 23). For explanation of numbered apomorphies see text.

elongata, D. moschatus, D. clayi and the *D. albimarginata–indica* clade). The most parsimonious hypothesis is that the structure was lost in the ancestor of Bovicolinae as suggested above, regained twice (*B. crassipes* and the *D. (T.) albimarginata–elongata* clade), and secondarily lost twice (*D. (T.) lineata–victoriae* and *D. (T.) pakenhami–bedfordi*). This last hypothesis, although more parsimonious than the distribution on the tree presented, does not change the topology of the tree. The distribution of character 47 is not as apparent from inspection of the tree in its most parsimonious distribution as it is in the tree presented, as the more scattered distribution of the losses and reversals obscures the alternative possible distributions and implies a spurious confidence in the tree as supported by them.

The distribution of character 33 (the loss of mesomeral fusion) in *Werneckiella* is not presented in the most parsimonious manner. There is great difficulty in the observation of this character state in *Werneckiella*, and the morphological difference between 'loss of fusion' and 'fusion' is very slight. A detailed examination of the species of this genus for other characters to

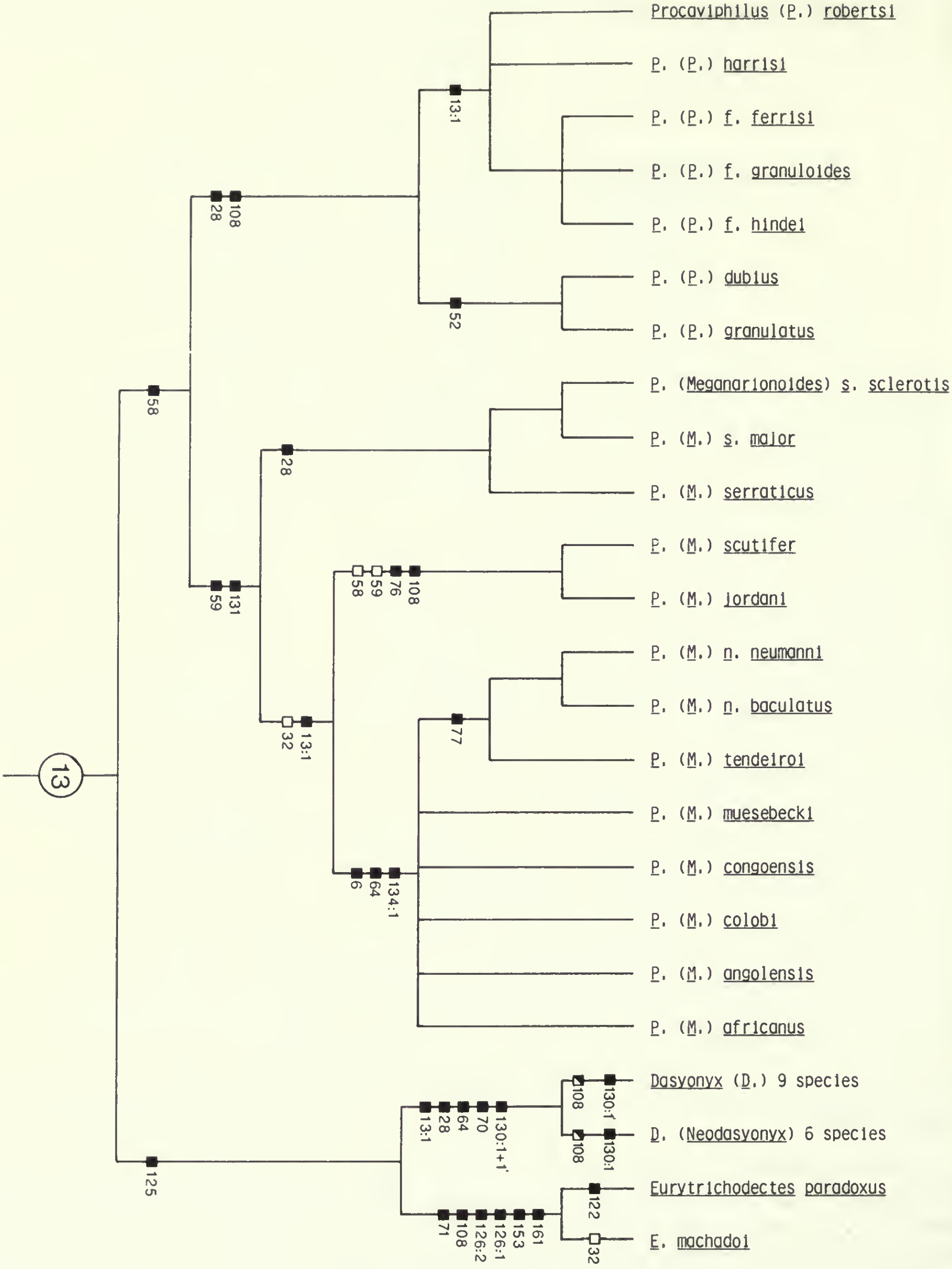


Fig. 29 Cladogram of Dasyonyginae (part; clade 13 of Fig. 28: genera *Procaviphilus*, *Dasyonyx* and *Eurytrichodectes*). For explanation of numbered apomorphies see text.

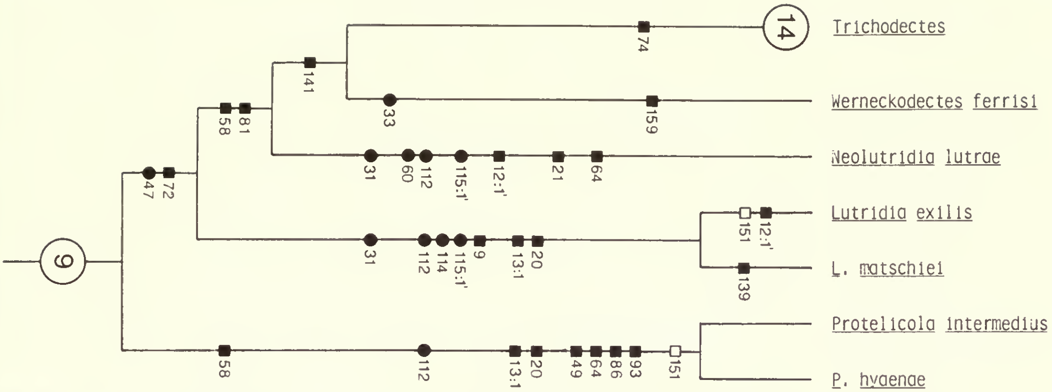


Fig. 30 Cladogram of Trichodectini (clade 9 of Fig. 23, part: genera *Protelicola, Lutridia, Neolutridia* and *Werneckodectes*). Clade 14 is resolved in Fig. 31. For explanation of numbered apomorphies see text.

complete a full analysis was not made, character 33 only being noted because it occurs elsewhere on the cladogram. It is possible but not likely that the distribution of character 33 as observed is supported by other apomorphies, but the proposal of holophyletic groups within the genus on the basis of the observations made of this single character would be unwise. It is notable that *Werneckiella fulva* and *W. neglecta*, which differ in the state of character 33, are otherwise very similar, the females apparently being indistinguishable (Emerson & Price, 1979), and it is very likely that they are sister-species.

The arrangement of *Protelicola, Lutridia* and the *Trichodectes–Neolutridia* clade (*T–N*) on the cladogram (Figs 30, 31) does not accord with the most parsimonious distribution of the apomorphies. The cladogram contains four convergences for 'gain' apomorphies: 12:1′ (fusion of parameres and b.a.l.s.) is postulated as homoplastic in *Lutridia, Neolutridia* and *Trichodectes (Stachiella)*; 13:1 (fusion of parameres to each other) is postulated as homoplastic in *Protelicola* and *Lutridia*; 20 (development of rod-shaped parameres) is postulated as homoplastic in *Protelicola* and *Lutridia*; and 58 (development of tubercles for the gonapophysis setae) is postulated as homoplastic in *Protelicola* and *T–N*. Apomorphy 12:1′ has been discussed in detail above, and the distribution suggested in the cladogram is believed consistent with the morphological evidence. Apomorphy 58 could be considered in two ways other than that presented: as an autapomorphy supporting the sister-group relationship of *Protelicola* and *T–N*, or as an autapomorphy of the Trichodectini (the *Trichodectes–Protelicola* clade), reversed in *Lutridia*. The first alternative is not supported by the distribution of any other apomorphies, whereas the two alternative arrangements are each indicated by more than one apomorphy (see below); the sister-group relationship of *Protelicola* and *T–N* is therefore rejected. The plesiomorphic arrangement of the gonapophysis tubercles in *T–N* is clearly distinct from the arrangement in *Protelicola*. If the tubercles are postulated to be homologous in the two clades two further apomorphies (the form of the tubercles in each clade) would have to be proposed, as neither form appears to be plesiomorphic with respect to the other. This manipulation does not affect the topology of the cladogram (whatever the position of *Lutridia*), and does not clarify the relationships of the clades involved, so the hypothesis of convergence of character 58 in *Protelicola* and *T–N* is retained. The other two apomorphies may now be considered together as they both suggest the sister-group relationship of *Protelicola* and *Lutridia*. The alternative hypothesis (of the cladogram as presented) is supported by apomorphies 72 (development of a sclerotisation along the ventral vulval margin) and 47 (loss of the median extension of the mesomeral arch). 'Loss' characters are given much less weight than 'gain' characters in this analysis, so character 47 should be left out of consideration. The sister-group relationship of *Protelicola* and *Lutridia* is therefore supported by two apomorphies and the relationship proposed on the cladogram supported by one. As noted in the generic descriptions below, however, an undescribed species of *Protelicola* has been seen which does not share apomorphy 20. The cladistic position of this species with respect to the other two species in the genus has not

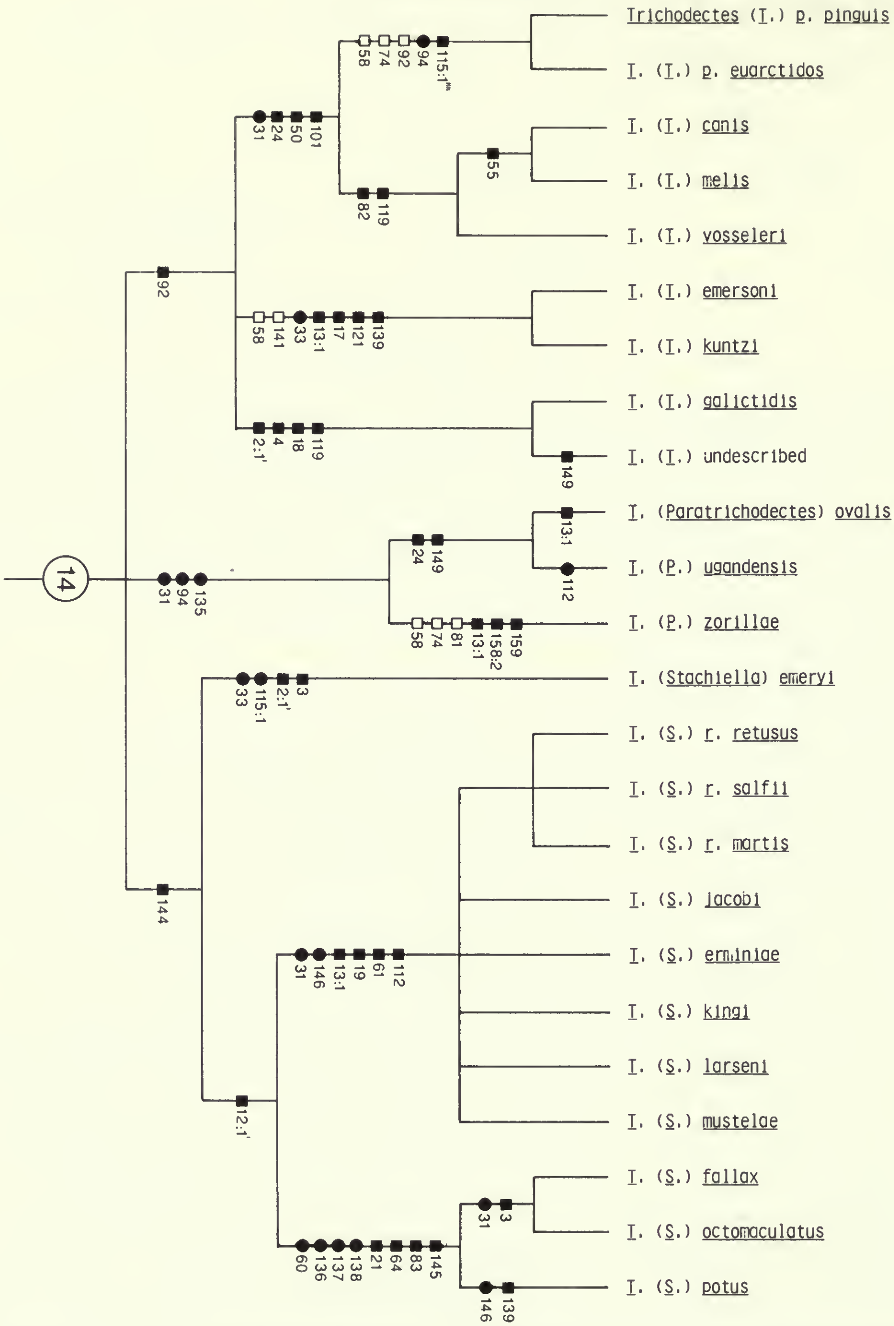


Fig. 31 Cladogram of *Trichodectes* (clade 14 of Fig. 30). For explanation of numbered apomorphies see text.

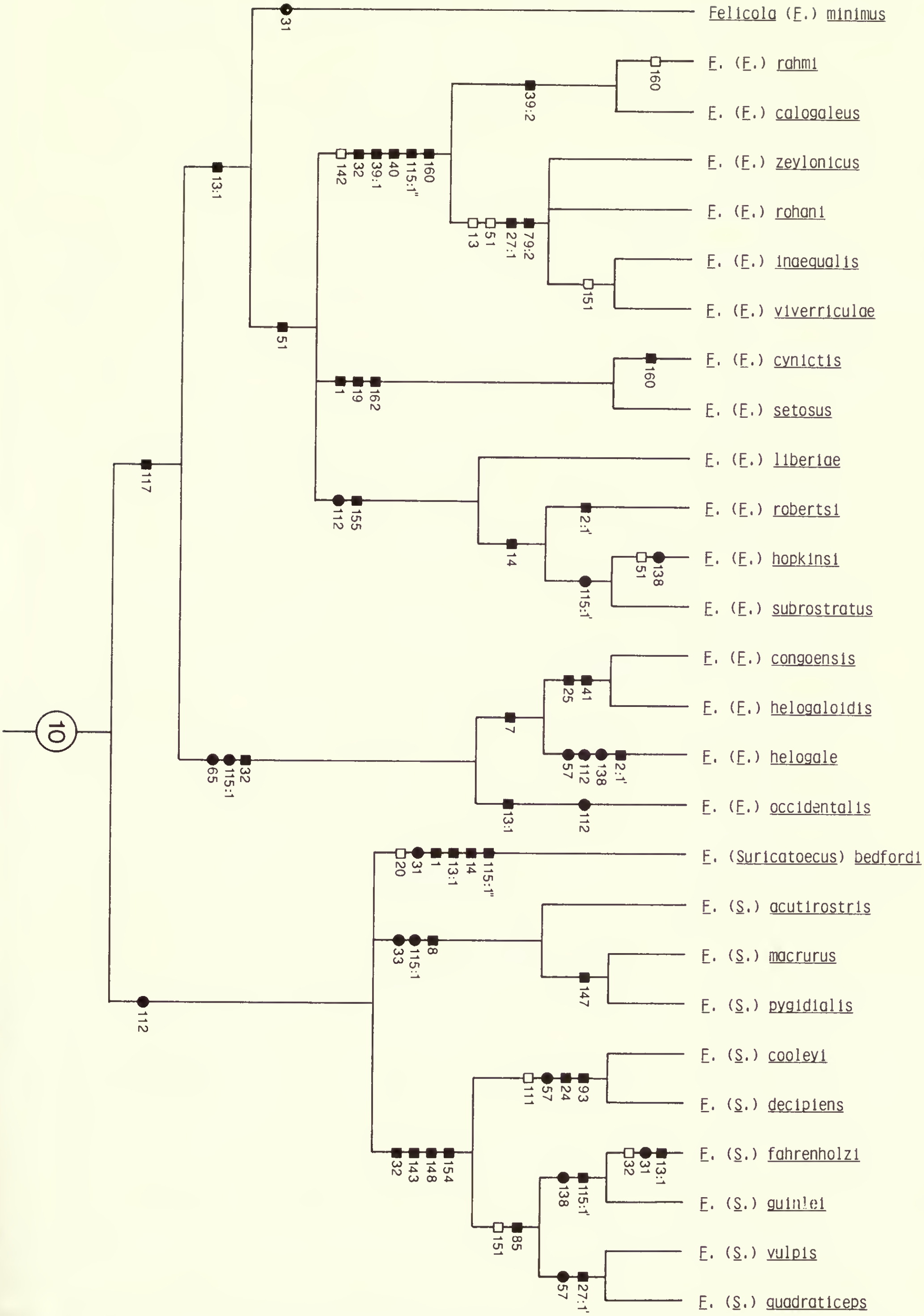


Fig. 32 Cladogram of *Felicola* (clade 10 of Fig. 23). For explanation of numbered apomorphies see text.

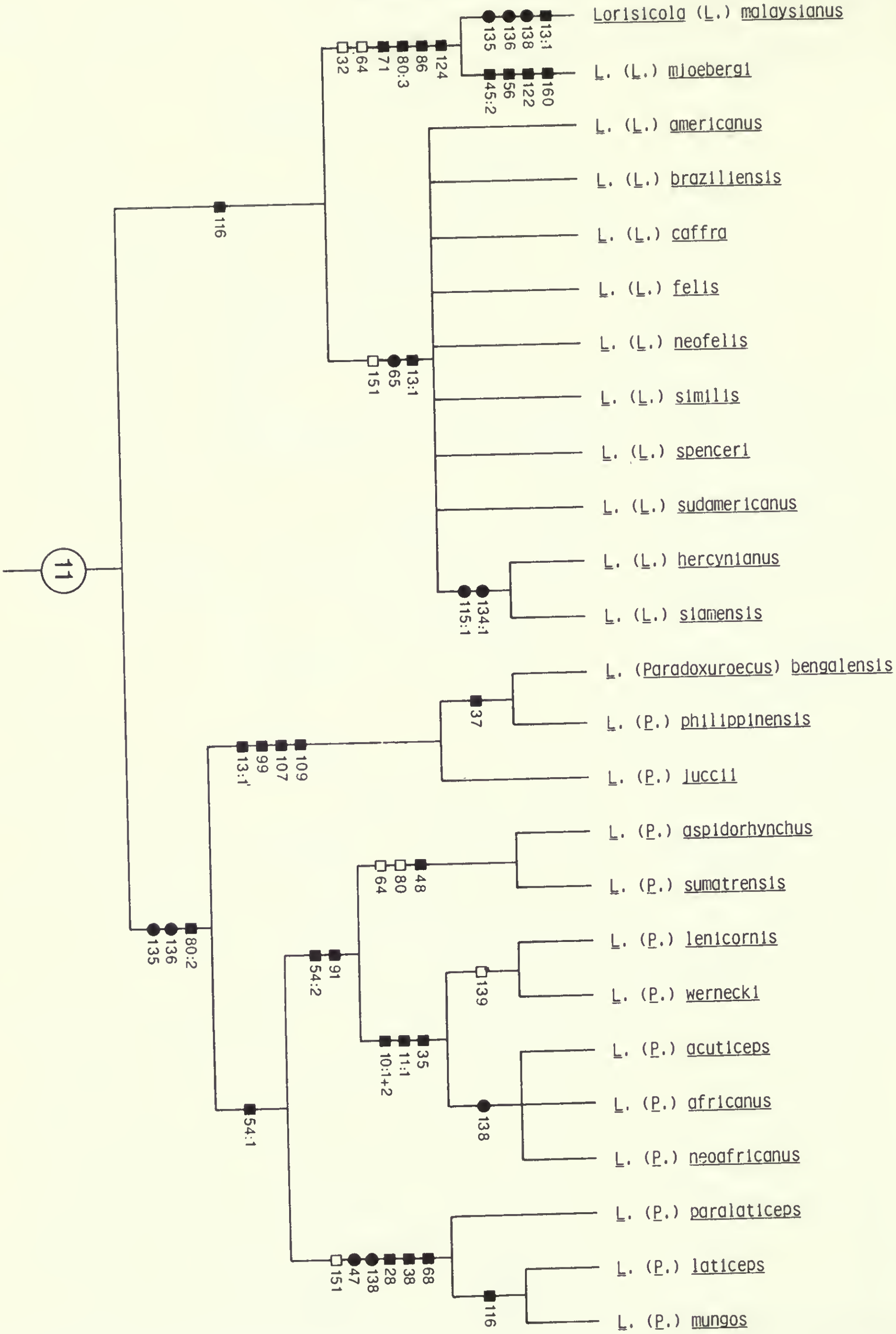


Fig. 33 Cladogram of *Lorisicola* (clade 11 of Fig. 23). For explanation of numbered apomorphies see text.

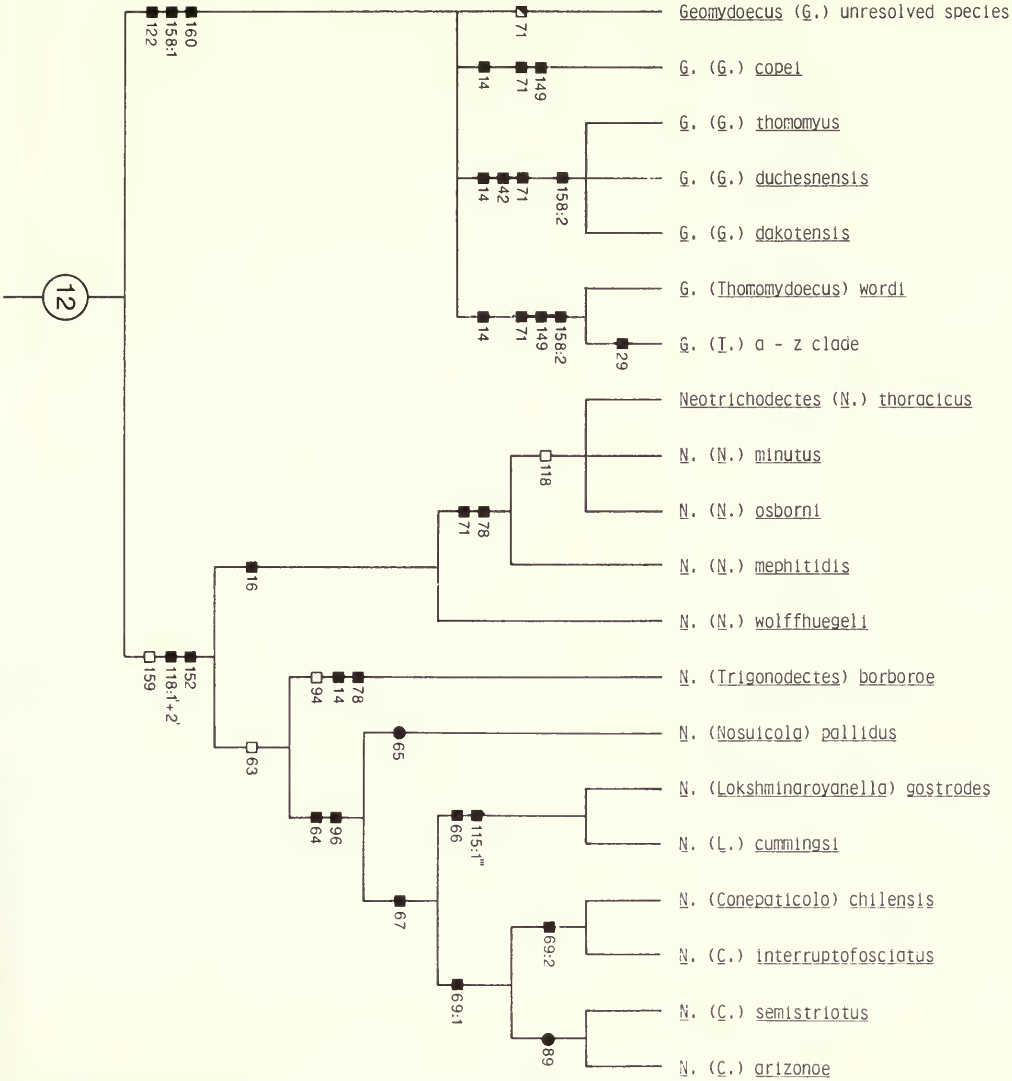


Fig. 34 Cladogram of Neotrichodectinae (clade 12 of Fig. 23: genera *Neotrichodectes* and *Geomydoecus*). For explanation of numbered apomorphies see text.

been determined because of the poor state of preservation of the specimens, but its existence raises the possibility that character 20 is an apomorphy not of *Protelicola* but of only two species within the genus (the alternative being a reversal in the undescribed species). Character 20 is also homoplastically developed in *Felicola* and *Bovicola (Lepikentron)*. If this character is disregarded, apomorphies 72 and 13:1 must be compared for their comparative likelihood of homoplasy. Apomorphy 13:1 is homoplastically developed at 22 other points on the cladogram whilst 72 is found elsewhere only in *Bovicola (Lepikentron)*. Apomorphy 72 should clearly be given much more weight than 13:1 in construction of the cladogram, and 20 is considered of uncertain value in view of the undescribed species of *Protelicola*. For these reasons the cladogram is retained as proposed, even though it is not maximally parsimonious.

The dorsal projection of pleurum IV (character 159) is lost in the Trichodectini, but postulated as secondarily regained in *Werneckodectes* and *Trichodectes (Paratrichodectes) zorillae*. The form of the projection is different in the two species, however, which indicates the independent development of the structure.

Whilst the genus *Geomydoecus* s.l. is almost certainly holophyletic, this probably does not apply to either of the two included subgenera (Fig. 34). The question of holophyly should be addressed first in the smaller subgenus *Geomydoecus (Thomomydoecus)*. All but one of the included species (*G. (T.) wardi)* have characteristically asymmetric male genitalia (character 29), and are proposed on this basis to be a holophyletic group (the *asymmetricus–zacatecae* clade or '*a–z* clade'). *G. (T.) wardi* and the *a–z* clade share the following apomorphies: posterolateral temple margin with single stout seta and associated shorter, finer setae (a character not included in the data matrix); male parameral plate apically pointed (character 14); gonapophysis smoothly continuous with ventral vulval margin (character 71); male abdominal terga II and III with median setal group comprising exceptionally long, stout setae (character 149); and pleural projections sclerotised, especially in females (character 158:2). The possession of a single stout temple seta is unique to these species, but may be a reduction from the two stout setae found in this position in some *Geomydoecus (Geomydoecus)*. Apomorphies 14, 71 and 149 are also shared by *G. (G.) copei*, and this species has the mesomeral arch and parameral plate very slender, approaching the shape of the genitalia of the *a–z* clade more closely than does *G. (T.) wardi*; the posterolateral temple margin lacks any specially-modified setae, but this may be due to secondary loss. Apomorphies 14, 71 and 158:2 are shared by the *G. (G.) thomomyus–dakotensis* clade, but the male genitalia are considerably broader than those of *G. (T.) wardi*, and the mesomeral arch lacks a median extension (an autapomorphy of the clade). This clade has a further autapomorphy in the form of the posterolateral setae of the temple margin, which comprise a single long fine seta and associated shorter fine setae. As with *G. (G.) copei*, the plesiomorphic form of the temple setae is unknown, and could have been the form found in *G. (Thomomydoecus)*. Other species of *G. (Geomydoecus)* have a single apex to the parameral plate (character 14), but do not share any of the other apomorphies mentioned. *G. (T.) wardi*, the *a–z* clade, and the *G. (G.) thomomyus–dakotensis* clade are all parasitic on *Thomomys* spp., whilst *G. (G.) copei* is a parasite of *Orthogeomys hispidus*; both host genera are parasitised by other members of *Geomydoecus (Geomydoecus)*.

The apomorphies listed above plainly do not support unequivocally any of the three possible sister-group relationships of the *a–z* clade without invoking homoplasy to an unjustifiable extent. It is apparent, however, that *G. (Geomydoecus)* is paraphyletic with respect to *G. (Thomomydoecus)* and that the latter subgenus is possibly polyphyletic. A full phylogenetic analysis of the 102 species and subspecies of *Geomydoecus*, which would have been necessary to resolve the problem, was not attempted. The hosts of the genus are all geomyid rodents, the systematic and taxonomic understanding of which is of questionable accuracy (Price, pers. comm.). For the purposes of this study the subgeneric concepts proposed by Price & Emerson (1972) are retained.

Taxonomic history of Trichodectidae

Burmeister (1838) divided the Mallophaga into two families, Liotheidae and Philopteridae, the latter comprising the two genera *Philopterus* and *Trichodectes*. Kellogg (1896) proposed the suborders Amblycera and Ischnocera for Liotheidae and Philopteridae (sensu Burmeister) respectively, and erected the family Trichodectidae for the genus *Trichodectes*.

Mjöberg (1910) described *Damalinia* and *Eutrichophilus*, the second and third genera of Trichodectidae, and Stobbe (1913*a*) described a fourth genus, *Eurytrichodectes*. Stobbe (1913*b*) revised the family for the first time. Ewing (1929) described four further genera and provided a key to all eight, although Ferris (1929) regarded Ewing's new genera as of 'most dubious value'. Bedford (1929, 1932*a*, 1932*b*, 1936) described a further 10 genera, two of which were junior synonyms of genera proposed by Ewing (1929), thus bringing the total to 16; Ewing (1936) provided a key to 14 of these. Kéler (1938*a*) recognised 24 genera, 10 of them new (although one of these had been published previously by Kéler, 1934 as a nomen nudum). The two genera omitted by Kéler (1938*a*) were the same two previously omitted by Ewing (*Cebidicola* Bedford, 1936 and *Lorisicola* Bedford, 1936); the three species included in these genera were placed by Kéler with two others, also from primates, in his new genus *Meganarion* (although with the proviso 'without, of course, intending to establish the congeneric status of these species'). Kéler

(1938*a*) provided a key to most of the genera described in his paper (with the sole exception of *Meganarion*) and to many of the species. Werneck (1941) introduced the subgenus concept to the taxonomy of Trichodectidae, describing three new subgenera in two of the four genera of the family parasitic on hyraxes. During the decade following Kéler's (1938*a*) review of the family a number of new genera were described, bringing the total number of available names in the genus-group to 43 by the end of 1948. Werneck (1948, 1950) reviewed all the Trichodectidae, and recognised 20 genera (though one of these doubtfully) and three subgenera. No genera and only one subgenus have been described since 1948. The most recent name to be added (*Lakshminarayanella* Eichler, 1982) was published as a replacement name for a junior homonym, and brings the total of available names to 45. There have been no revisionary works of the family since those of Werneck (1948, 1950), although Hopkins & Clay (1952), when cataloguing the 'Mallophaga', accepted 13 genera, some of these doubtfully, and Eichler (1963) recognised 38 genera (with no subgenera).

The problem of establishing criteria by which taxa can be distinguished at the generic level received early attention. An attempt to identify morphological characters for this purpose was initiated by Bedford (1929). Bedford (1932*a*) provided a more thorough discussion, and concluded that whilst the shape of the head, the presence or absence of abdominal sclerites and the form of the female gonapophyses were of value, the form of the male genitalia and the number of abdominal spiracles provided no useful guide. Ewing (1936) came to a quite different conclusion, regarding abdominal spiracle number as 'the most important generic character'. Bedford (1939) realised the unworkability of any system involving *a priori* assessment of morphological characters for generic discrimination, although he still felt that abdominal spiracle number was not of value at the generic level, and noted that (morphological) generic characters 'may not be very striking'. To supplement or replace morphological characters Bedford (1939) made use of host data, the possibility of which was first discussed by Kellogg (1913, 1914) and Harrison (1916*b*). Bedford (1939) wrote: 'Before placing a species in a new genus one should ask oneself: would it be possible to say from what kind of host the parasite was taken off had it not been recorded? If it is impossible to answer the question, then one should be justified in placing it in a new genus.' Hopkins (1941) used this principle to a certain extent in his discussion of *Felicola*. He also discussed the morphological characters used for the discrimination of the genus from others, and pointed out that 'the singling out of one character [on which to base genera] . . . only tends to obscure natural relationships'. Werneck (1936) perceived and treated the problem of generic discrimination in a rather different way from those described above. He noted that whilst the type-species (and sometimes a few species similar to the type) of each of the described genera were quite distinct, other species showed intermediate characters. The existence of these 'transitional forms' convinced Werneck that there was no validity in the separate genera, so he synonymised them all (with the exception of some genera not found in South America, which were outside the scope of the paper). Bedford (1939) regarded this action as 'unwarrantable' and reinstated all the genera. Hopkins (1942, 1943) reviewed the characters used to separate the genera of Trichodectidae parasitic on carnivores and antelopes respectively. In each case he found annectent species as described by Werneck (1936), and took similar action, though modified by the belief that louse genera should somehow reflect host taxa. Hopkins (1942) therefore accepted three genera of Trichodectidae parasitic on carnivores and later (1943) accepted one genus parasitic on antelopes. Werneck (1948, 1950), although less influenced by the host data, recognised more genera than had Hopkins. He accepted the morphologically 'distinct' species and species groups as genera, and placed annectent species in the genus which they most closely resembled. Hopkins (1949) 'conceded subgeneric status to many groups which seem likely to be accepted by systematists whose views . . . differ from mine' and recognised 14 genera and 20 subgenera. Hopkins & Clay (1952) synonymised some of the subgenera accepted by Hopkins (1949), but raised others to generic status. Ledger (1980) held views similar to Hopkins & Clay (1952), although in some cases followed the views of Hopkins (1949); the resultant generic arrangement still involved fewer genera than accepted by Werneck (1948, 1950), and many more subgenera. Emerson & Price (1981), however, could 'find no basis for rejecting the classification of Trichodectidae given by Werneck (1948, 1950)', and suggested that the 'question of genera vs subgenera will perhaps continue until Mallophaga have been described from all likely hosts'. A number of other workers also follow these views. A third group of taxonomists (e.g. Eichler, 1963; Zlotorzycka, 1972) have accepted not only all the genera recognised by Werneck (1948, 1950), but also a number of genera that Werneck considered as junior synonyms; the subgenus category is not used, however. The present generic placement of most of the Trichodectidae is thus a matter of some contention and a review of the variations in status of some genera and subgenera is presented in Tables 3–5.

	Ewing (1936)	Kéler (1938*a*)	Eichler (1941)	Hopkins (1943)	Hopkins (1949)	Werneck (1950)	Hopkins & Clay (1952)	Eichler (1963)	Ledger (1980)	Emerson & Price (1981)	Present study
1. *Damalinia* Mjöberg, 1910	1	1	1	1	1	1	1	1	1	1	1
2. *Bovicola* Ewing, 1929	2	2	2	= 1	1 (2)	2	1 (2)	2	1 (2)	2	2
3. *Tricholipeurus* Bedford, 1929	3	3	3	= 1	1 (3)	3	1 (3)	3	1 (3)	3	1 (3)
4. *Cervicola* Kéler, 1938*a*		4	4	-	1 (4)	= 1	=1 & =2	4	=1 s.l.	= 2	1 (4)
5. *Holakartikos* Kéler, 1938*a*		5	5	-	5	= 2	= 2	5	=1 s.l.	= 2	2 (5)
6. *Lepikentron* Kéler, 1938*a*		6	6	-	6	= 2	1 (6)	6	=1 s.l.	= 2	2 (6)
7. *Rhabdopedilon* Kéler, 1938*a*		7	7	-	1 (7)	= 2	= 6	7	=1 s.l.	= 2	= 2
8. *Werneckiella* Eichler, 1940			8	-	1 (8)	= 2	= 2	8	=1 s.l.	= 2	8
9. *B.* (*Spinibovicola*) subgen. n.											2 (9) [from 2]
10. *Bisonicola* gen. n.											10 [from 2]
11. *Tragulicola* gen. n.											11 [from 1]

Table 3 Generic concepts in the Bovicolinae. The genera included in the table are represented by numbers 1–11; '2' indicates that the genus (*Bovicola*) is given full generic status, '1(2)' indicates that the genus (*Bovicola*) is considered a subgenus (of *Damalinia*) and '=1' indicates that the genus is considered as a junior synonym (of *Damalinia*). The generic name *Bovidoecus* Bedford, 1929 is omitted, as it was synonymised with *Bovicola* by Bedford (1932*a*) and has not since been used. There is no reference in the table to Werneck (1936), who treated all genera of Trichodectidae as synonyms of *Trichodectes*.

	Kéler (1938*a*)	Eichler (1941)	Hopkins (1942)	Werneck (1948)	Hopkins (1949)	Hopkins & Clay (1952)	Eichler (1963)	Ledger (1980)	Emerson & Price (1981)	Present study
1. *Trichodectes* Nitzsch, 1818	1	1	1	1	1	1	1	1	1	1
2. *Neotrichodectes* Ewing, 1929	2	2	= 1	2	1 (2)	1 (2)	2	1 (2)	2	2 [to Neotrichodectinae]
3. *Galictobius* Kéler, 1938*b*	3	3	= 1	= 1	1 (3)	= 1	3	= 1	= 1	= 1
4. *Lutridia* Kéler, 1938*a*	4	4	= 1	4	1 (4)	4	4	1 (4)	4	4
5. *Stachiella* Kéler, 1938*a*	5	5	= 1	5	1 (5)	1 (5)	5	1 (5)	5	1 (5)
6. *Ursodectes* Kéler, 1938*a*	6	6	= 1	= 1	1 (6)	= 1	6	= 1	= 1	= 1
7. *Potusdia* Conci, 1942				= 1	1 (7)	= 1	7	= 1	= 1	= 1
8. *Trigonodectes* Kéler, 1944				= 1	1 (8)	= 1	8	= 1	= 1	2 (8) [to Neotrichodectinae]
9. *Werneckodectes* Conci, 1946				= 1	1 (9)	= 1	9	= 1	= 1	9
10. *Neolutridia* gen. n.										10 [from 4]
11. *T.* (*Paratrichodectes*) subgen. n.										1 (11) [from 5]

Table 4 Generic concepts in the Trichodectini (plus *Neotrichodectes* and *Trigonodectes*). Coding as for Table 3. *Protelicola* is included in Table 5. The generic name *Grisonia* Kéler, 1938*a* is omitted and its replacement name, *Galictobius* Kéler, 1938*b*, used throughout.

	Bedford (1936)	Kéler (1938*a*)	Eichler (1941)	Hopkins (1941)	Werneck (1948)	Hopkins (1949)	Hopkins & Clay (1952)	Eichler (1963)	Ledger (1980)	Emerson & Price (1981)	Present study
1. *Felicola* Ewing, 1929	1	1	1	1	1	1	1	1	1	1	1
2. *Protelicola* Bedford, 1932	-	2	2	2	= 1	1 (2)	= 1	2	1 (2)	= 3	2 [to Trichodectini]
3. *Suricatoecus* Bedford, 1932	= 1	3	3	= 1	3	1 (3)	1 (3)	3	1 (3)	3	1 (3)
4. *Lorisicola* Bedford, 1936		-	4	-	4	4	4	4	-	4	4
5. *Fastigatosculum* Kéler, 1939			5	= 1	= 3	-	= 3	5	= 1 s.l.	= 3	= 1
6. *Eichlerella* Conci, 1942					= 3	-	= 3	6	= 1 s.l.	= 3	= 3
7. *Paradoxuroecus* Conci, 1942					= 1	-	= 1	7	= 1 s.l.	= 1	4 (7)
8. *Neofelicola* Werneck, 1948					8	1 (8)	1 (8)	8	1 (8)	8	= 7
9. *Parafelicola* Werneck, 1948					9	1 (9)	1 (9)	9	1 (9)	9	= 7

Table 5 Generic concepts in the Felicolini (plus *Protelicola*). Coding as for Table 3. The generic names *Bedfordia* and *Felicinia* (a junior homonym and an absolute synonym respectively) have not been included as their status has not varied; they are discussed in the comments following the description of *Felicola* s. str. below.

Hopkins (1941) presented an explanation for the presence of so many annectent species in the Trichodectidae and a justification for synonymising many of the genera, writing: 'I believe the explanation to be that the Trichodectidae are in the process of dividing up into genera; in some cases the divergence has proceeded far enough for us to recognise the segregates as generically distinct, but in a much greater number of cases extreme members of a group may have become strikingly distinct whilst the others remain as connecting-links which entirely undo our attempts to find characters peculiar to the group.' Hopkins' statement implies that the species in a genus are somehow evolving as a unit, and is linked to the typological approach to taxonomy. Relationships between three or more taxa, if assessed by a simple count of character states (i.e. not distinguishing between plesiomorphies, apomorphies and homoplasies) are frequently reticulate in aspect (Simpson, 1961; Hennig, 1966; Mayr, 1969). The greater the number of homoplasies the more complex the reticulum is likely to be, and the more difficult it is to combine the taxa into groups. If genera are constructed on this principle some morphologically distinct species and species-groups will be distinguished, 'linked' by annectent species, with the concomitant absence of 'gaps' between genera – precisely the problem with traditional groupings of the Trichodectidae. The 'problem' of annectent species is therefore engendered by the typological approach; the difficulties in distinguishing supra-specific groups are also a result of this, but combined in the Trichodectidae with a high degree of homoplasy.

The difficulties discussed above have discouraged authors from attempting to produce keys to genera of the Trichodectidae. Since the key to genera published by Kéler (1938*a*), very few have been published, and none included all the genera. Kéler (1944) produced a key to some genera, slightly emended from Kéler (1938*a*), but a promised second half to the paper containing the rest of the key was never published. Werneck (1948, 1950), despite describing all of the genera, did not attempt to produce a key. A few keys have since been published in faunistic works, for example Toulechkoff (1955) produced a key (in Bulgarian) to the genera found in Bulgaria, and Zlotorzycka (1972) published a rather inaccurate key (in Polish) to the genera found in Poland.

Although most authors follow Kellogg (1896) in their conception of the Trichodectidae, and retain familial rank for the group (e.g. Hopkins & Clay, 1952; Hopkins, 1960; Ledger, 1980; Emerson & Price, 1983), the rank of the group has been raised by others. Kéler (1938*a*) raised the Trichodectidae to superfamily level and included three families: Trichodectidae, Bovicolidae and Dasyonygidae, the latter two being described as new. In the Trichodectidae he placed four subfamilies, all of which he indicated to be new: Trichodectinae, Felicolinae, Eurytrichodectinae and, dubiously placed in this family, Eutrichophilinae (Fig. 35). Eichler (1940)

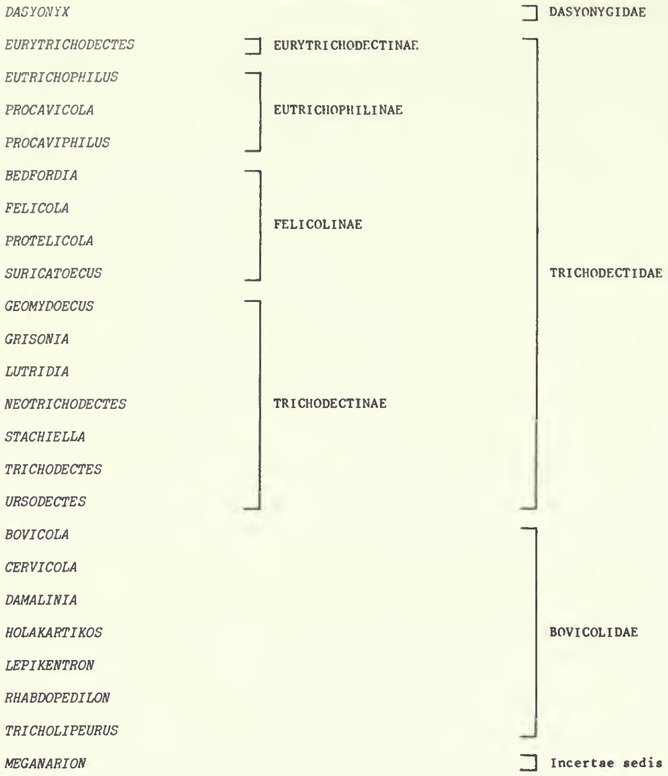


Fig. 35 Classification of 'Trichodectoidea' according to Kéler (1938*a*).

described two further subfamilies in the Trichodectidae (sensu Kéler, 1938*a*): Lymeoninae and Cebidicolinae. Eichler (1941) described the new subfamily Damaliniinae in the Bovicolidae, attributing the nominate subfamily to himself. He also transferred the Eurytrichodectinae and the Eutrichophilinae to the Dasyonygidae, again attributing the newly-defined nominate subfamily to himself. Eichler (1941) considered the rank of the whole group to be not superfamily but 'family group' and termed it the Trichodectiformia (attributed to Kéler, 1938*a*); the subfamily Trichodectinae is also attributed to Kéler (1938*a*) but the nominate family is attributed to Burmeister (1838). The classification proposed by Eichler (1941) is depicted in Fig. 36. Kéler (1944) retained the Eurytrichodectinae in Trichodectidae and moved the Eutrichophilinae to Bovicolidae; the subfamilies described by Eichler (1940, 1941) were not mentioned (Fig. 37). The Trichodectidae were attributed by Kéler (1944) to Kellogg (1896) but the nominate subfamily to Kéler (1938*a*). The superfamily rank was retained and the 'family group' not mentioned. Hopkins (1949) regarded the families proposed by Kéler (1938*a*) as subfamilies and the subfamilies as at most tribes. Hopkins also, following his synonymy of *Bovicola* with *Damalinia*, considered that 'Bovicolinae must be known as Damaliniinae'. Eichler (1963) retained the higher ranks and included 'interfamilia Trichodectiformia' within the superfamily Trichodectoidea. He moved the Lymeoninae to Dasyonygidae (wherein he retained Eurytrichodectinae), but accepted the move of Eutrichophilinae to Bovicolidae proposed by Kéler (1944). Eichler (1963) also proposed the division of the Trichodect(oidea) into tribes, indicating their existence and composition by variations in typography in the list of genera presented (Eichler, 1963: 159, lines 31–37). Eichler (1963) did not publish any of the tribal names, but Lakshminarayana (1976) listed all of them. Neither Eichler (1963) nor Lakshminarayana (1976), however, gave any statement that purported 'to give characters differentiating the tax(a); or . . . a definite bibliographic reference to such a statement' as is required by the *International Code of Zoological Nomenclature* for any name published after 1930 (Article 13).

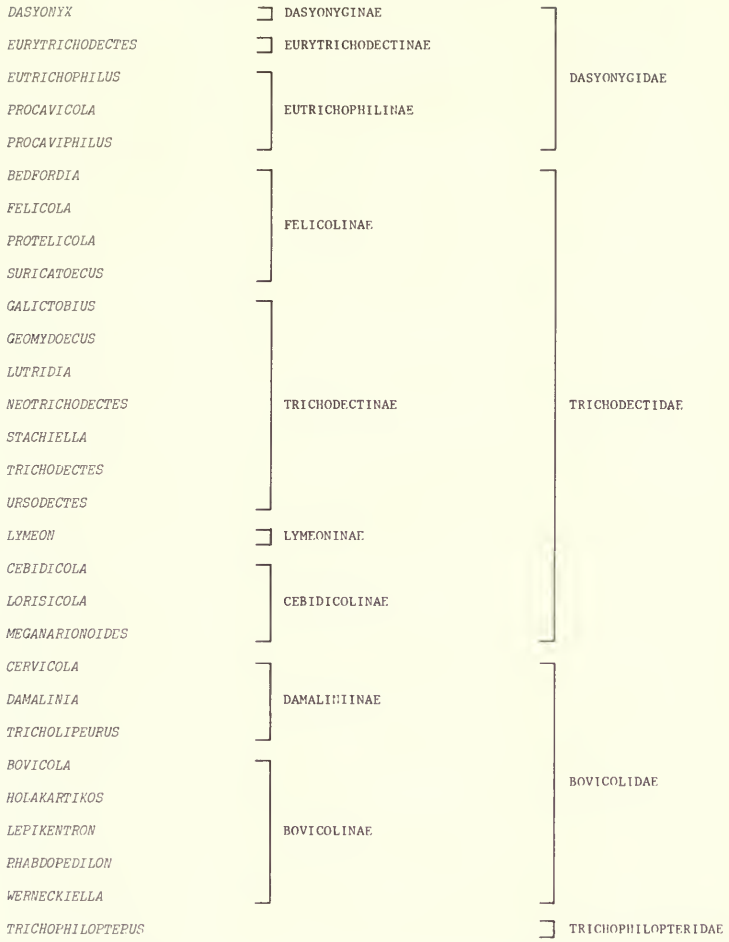


Fig. 36 Classification of 'Trichodectiformia' according to Eichler (1941).

None of the (11) names, therefore, are available for taxonomic use. Eichler (1963) attributed Trichodectoidea, Trichodectiformia, Trichodectidae and Trichodectinae to Burmeister (1838) but, whilst (correctly) attributing Bovicolidae and Dasyonygidae to Kéler (1938*a*) he attributed the nominate subfamilies of both to Eichler (1941). The classification proposed by Eichler (1963) is depicted in Fig. 38. Kéler (1969) proposed a classification similar to that proposed by Kéler (1944), but omitting a number of genera (Fig. 39).

Article 36 of the *International Code of Zoological Nomenclature* (1984) states that all categories in the family-group (tribe, subfamily, family, superfamily and any supplementary categories, according to Article 35a) are co-ordinate, and a name established for any category within the group is available with its original date and author for a taxon with the same type genus in each of the categories. The Trichodectinae, Trichodectidae, Trichodectiformia and Trichodectoidea should therefore all have the same date and author. The first use of a family-group name based on the type genus *Trichodectes* was by Kellogg (1896), who ranked 'the Nitzschian families as suborders, the Nitzschian genera as families, and the Nitzschian subgenera, the genera of present-day writers, as genera.' Kellogg (1908) attributed the Trichodectinae (the only subfamily included in the Trichodectidae, which bore no attribution) to 'Burmeister (?)'. As explained above, subsequent attribution has frequently been to Burmeister (1838) and, in the case of some co-ordinate names, to Kéler (1938*a*). Burmeister (1838) did not mention any taxon in the family-group with the type genus *Trichodectes*. All

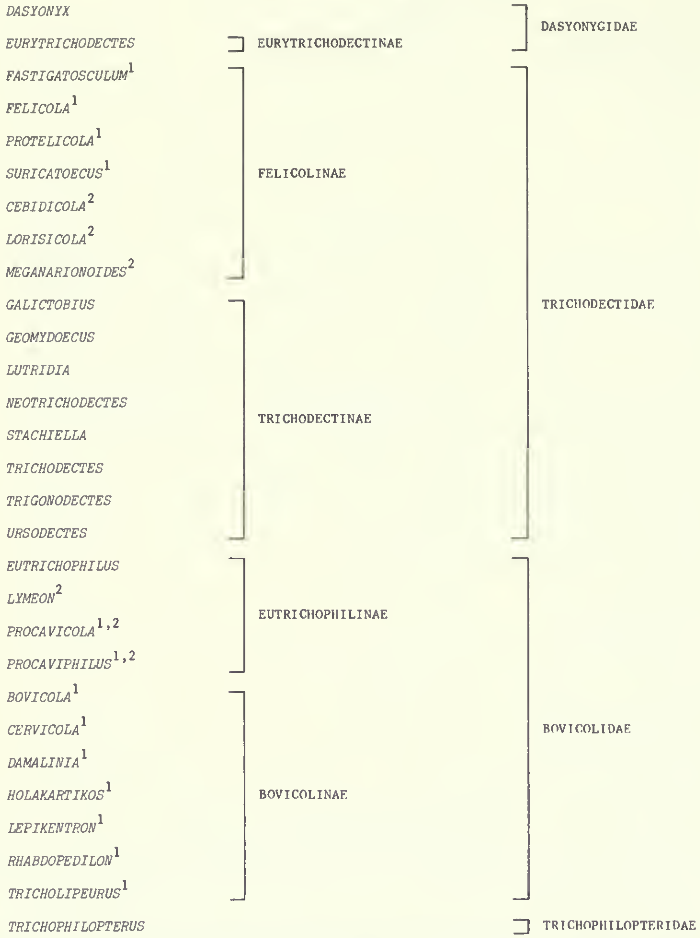


Fig. 37 Classification of 'Trichodectoidea' according to Kéler (1944). [1]Position of genus inferred from Kéler (1938*a*). [2]Position of genus inferred from key in Kéler (1944).

family-group names with the type genus *Trichodectes* should therefore be attributed to Kellogg (1896). Trichodectidae Kellogg, 1896 has been placed on the Official List of Family-group Names in Zoology (Opinion 627, *Bull. zool. Nom.* **19**: 91–96, (1962)). The names Bovicolinae, Bovicolidae, Dasyonyginae and Dasyonygidae should all be attributed to Kéler (1938*a*), not Eichler (1941). The action of Hopkins (1949) is synonymising the senior family-group (Bovicolinae) with the junior (Damaliniinae) was taken because he believed *Bovicola* and *Damalinia* (the type-genera) to be synonyms, and *Damalinia* is senior to *Bovicola*. This action is incorrect under Article 40 of the *Code*, however, which states that, at least after 1961, in the case of type-genus synonymy the senior family-group name is to be used for the family-group taxon that contains both senior and junior synonyms. This Rule can be set aside for such an action if taken before 1961, if the name has 'won general acceptance' (Article 40b). The subfamily Damaliniinae sensu Hopkins (1949) has rarely if ever been used since, whilst the name Bovicolidae (= Damaliniinae sensu Hopkins) has been employed by Eichler (1963) and Kéler (1969). The action of Hopkins (1949) is therefore rejected.

Kéler (1944) included the Trichophilopteridae – a family containing a single genus, parasitic on Lemurs – within the Trichodectoidea, although Kéler (1969) referred this family to the Philopteroidea. Eichler (1963) retained the Trichophilopteridae in the Trichodectoidea, but distinguished it as 'interfamily Trichophilopteriformia' as opposed to 'interfamily Trichodectiformia'. Stobbe (1913*a*), Ferris (1933) and Werneck (1948) all considered the affinities of

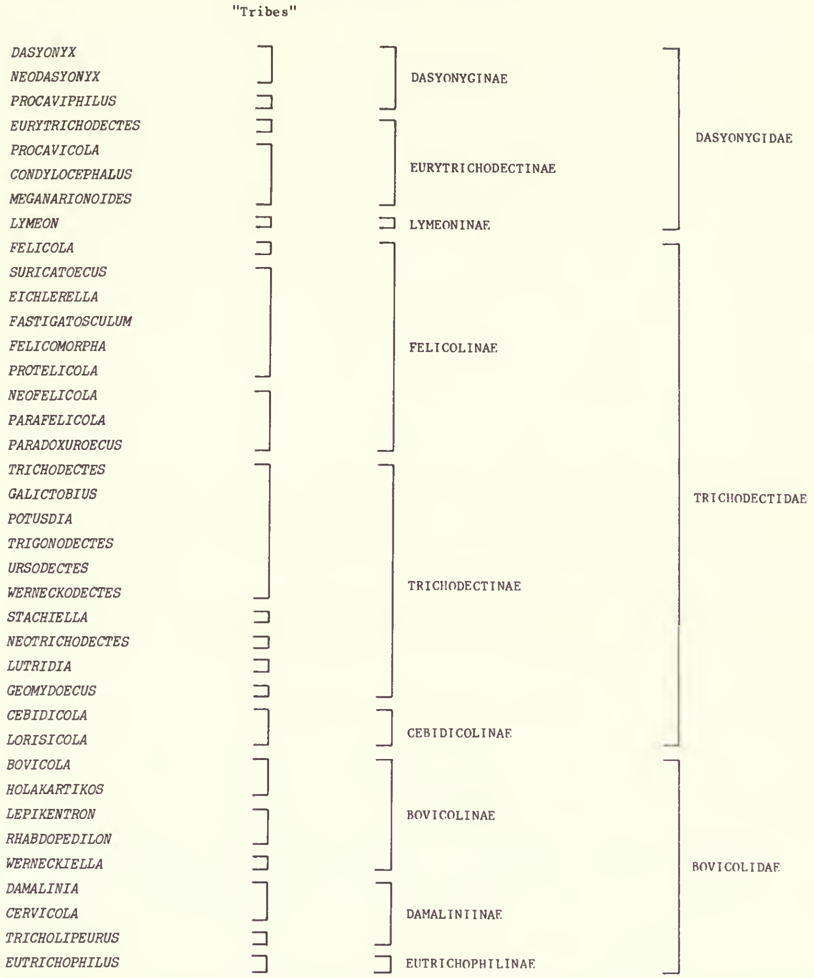


Fig. 38 Classification of 'Trichodectiformia' according to Eichler (1963). The 'tribes' are indicated by square brackets in the appropriate column, the first genus in each 'tribe' being intended by Eichler (1963) as the type-genus. See text.

Trichophilopterus to lie with the 'Philopteridae' rather than with the Trichodectidae. In this study no apomorphies were found to indicate a sister-group relationship between *Trichophilopterus* and all or part of the Trichodectidae.

Proposed classification

The proposed classification is derived from the results of a cladistic analysis of the Trichodectidae (Trichodectiformia sensu Eichler, 1963) at the species level (Figs 23–34). The species are grouped on the four criteria discussed below, and ranked according to the principles of phyletic sequencing.

Holophyly. The classification includes, as far as possible, only holophyletic groups. Some genera and subgenera, however, may be found not to follow this criterion (see discussion of *Damalinia* s. str., *Dasyonyx* and *Geomydoecus* below).

Utility. Genera are ideally of 'moderate' size and relative morphological uniformity. If a genus is large and diverse, recognition is difficult and useful discussion on many aspects of biology or distribution prohibited; if genera are too small, identification is time-consuming and discussion

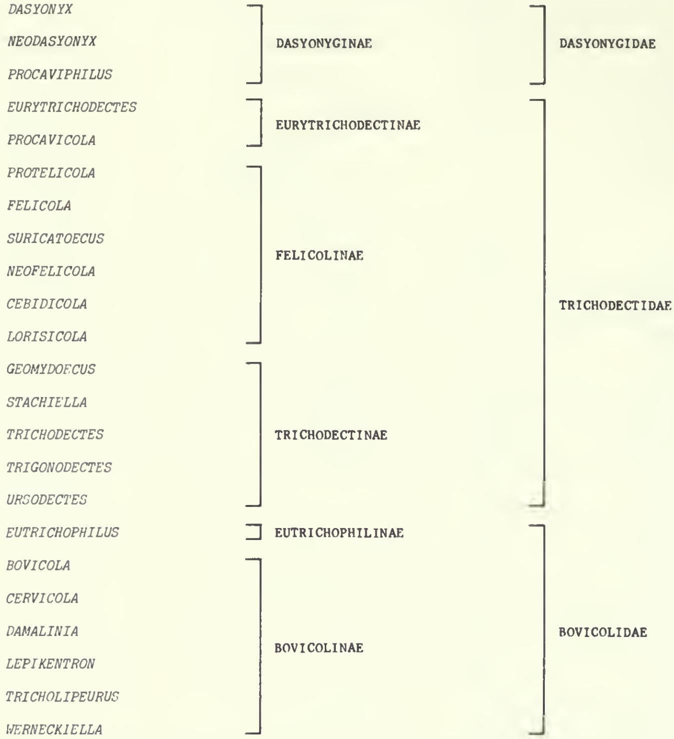


Fig. 39 Classification of 'Trichodectoidea' according to Kéler (1969).

again impeded. No 'absolute' size can be recommended, however, as the most satisfactory size will depend on a number of properties of the species, and must (in this study) conform to such limitations as are imposed by the criterion of holophyly. Subfamilies are chosen in this study to aid discussion by providing names for holophyletic groups of genera, and to fulfil the logic of the phyletic sequencing convention.

Stability. To ensure that the classification has maximal stability the generic concepts accepted in this study conflict as little as possible with established usage.

Distinctness. To facilitate identification, taxa in the genus-group should be as distinct from one another as possible. The requirements of Mayr (1969) that genera must be separated by a decided gap, and that the 'size' of the gap should be inversely proportional to the size of the taxon, are not necessarily compatible with the criterion of holophyly followed here, however, and the problem of annectent species (that 'fill' any such gap) has been discussed above. Despite the apparent drawback of adherence to holophyletic groups at the expense of inter-generic 'gaps', it has been possible in this study to produce a key to the genera of Trichodectidae (see discussion of keys to genera of Trichodectidae above).

The formation of the genera of Trichodectidae is discussed below, to give an indication of the rationale behind each decision. The genera are discussed by subfamily, and the division into subfamilies is discussed last.

Bovicolinae (Figs 24–27, 40)

This clade was not resolved fully in the analysis, and a primary pentachotomy was obtained. The clade has been treated as a single genus (see Table 4), but the diversity of morphology and of hosts indicates that this concept is too broad to be of great value. Subdivision of the clade into smaller holophyletic groups increases the value of the classification for information retrieval, and leads to the acceptance of genera that approach the concepts of Werneck (1950). To obtain a measure of conformity each of the five branches of the clade has been accorded generic status.

The monobasic genera *Bisonicola* and *Tragulicola* require no comment, and the genus *Werneckiella* was revised by Moreby (1978). Of the two remaining clades, one corresponds approximately to a restricted concept of *Bovicola*, the other to *Damalinia* plus *Tricholipeurus* (sensu Werneck, 1950). The *Bovicola* clade (genus *Bovicola*) has a primary tetrachotomy, with most of the species belonging to only one of the four resultant clades (Fig. 24). The species in this large clade are morphologically more similar to one another than they are to any of the species in the other three clades. To recognise this morphological divergence (and thus facilitate identification), and to demonstrate in the classification the extent of the phylogenetic knowledge, the four branches are each accorded subgeneric status. The *Damalinia* plus *Tricholipeurus* clade (genus *Damalinia*) has a primary trichotomy (Fig. 23), and it is clear that discussion of the genus will be facilitated by the recognition of each of these branches as a subgenus. *Damalinia* s. str. comprises two major clades, each characterised by the form of an apomorphic development of abdominal pleurum II onto the sternum. As discussed above, these two forms may be co-apomorphies, or may represent two states in a transformation series. If the latter interpretation is correct, one of the clades is probably paraphyletic with respect to the other.

Eutrichophilinae

Only the single genus *Eutrichophilus* is included, with no change in generic concept.

Dasyonyginae (Figs 28, 29)

The previously-accepted generic concepts in this subfamily remain essentially unchanged at the subgenus level. The only change is the transfer of the subgenus *Meganarionoides* from *Procavicola* to *Procaviphilus*, and the inclusion of *Procaviphilus sclerotis* and *P. serraticus* in *P. (Meganarionoides)*. Subgenera are used (as in Werneck, 1941, 1950; Ledger, 1980) as no advantage accrues from regarding each of the clades so recognised as a full genus, and application of the principles of phyletic sequencing allows retention of all the currently-used generic and subgeneric names with no higher taxa required, whereas recognition of all these as genera would require the description of a number of intercalating family-group taxa.

It is notable that one of the two subgenera of *Dasyonyx* may be paraphyletic with respect to the other, as the subgenera are characterised by apomorphic developments of the teeth of the tarsal claws. These may be co-apomorphies or two states in a transformation series (see above). If the latter interpretation is correct, one of the subgenera is probably paraphyletic with respect to the other.

Trichodectinae (Figs 23, 30–33, 40)

The first dichotomy in this clade splits it roughly into *Felicola* (sensu Ledger, 1980, but without *Protelicola* and with *Lorisicola*) on one side and *Trichodectes* (sensu Ledger, 1980, but without *Neotrichodectes* and *Trigonodectes*, and with *Protelicola*) on the other. The diversity of morphology of the lice, and the variety of hosts infested, indicates that the very broad generic concepts endorsed by Ledger (1980) are too inclusive to be of great value in data-retrieval and discussion. For this reason the genera proposed here are smaller than those of Ledger (1980) and, in some cases, approach the concepts held by Werneck (1948).

Most of the species in the *Trichodectes* side of the initial dichotomy arise from the three branches of an apical trichotomy (Figs 30, 31). The branch of this trichotomy comprising the *pinguis–galictidis* clade corresponds roughly to the concept of *Trichodectes* held by Werneck (1948), whilst the other two branches (the *ovalis–zorillae* clade and the *emeryi–potus* clade) correspond roughly to *Stachiella* sensu Werneck (1948) (though *fallax*, *octomaculatus* and *potus* were placed in *Trichodectes* by Werneck, 1948). However, placing two of the three clades of the trichotomy in a taxon *Stachiella* and excluding the third results in a group that is not holophyletic. Recognising each of the three branches of the trichotomy as a separate genus is undesirable, as the three intergrade phenetically. The course followed here is to recognise the genus *Trichodectes* comprising all three branches, each of these being considered a subgenus (Fig. 40). Using the principle of phyletic sequencing the sister-group of *Trichodectes* is also considered a genus, for which the name *Werneckodectes* is available. Likewise the next three branches of this clade are also considered genera. This process necessitates dividing Werneck's genus *Lutridia* into two genera, but retention of the genus as it stood calls for recognition of a paraphyletic group in the classification, and, although the species in the two clades comprising *Lutridia* (sensu Werneck, 1948) are superficially similar, some of these similarities may be homoplastic.

The other branch of the initial dichotomy of the Trichodectinae clade comprises, as noted above, most of the species consigned to *Felicola* by Ledger (1980) plus the single species of the genus *Lorisicola* (sensu Werneck, 1950). The two branches of this clade (Fig. 23) are each considered as genera which, taking the most senior available names, are known as *Felicola* and *Lorisicola*. For reasons of utility, each genus is divided into two holophyletic subgenera. None of the genera or subgenera coincides with any previous generic concept, as such concepts relied heavily on head shape and abdominal spiracle number, both of which characters have proved to be subject to a considerable degree of homoplasy.

In order to maintain the logic of phyletic sequencing, if the *Felicola–Lorisicola* clade is to be considered as comprising two genera, the rank of this clade and of the *Trichodectes–Protelicola* clade must be equal and formally recognised. Use of the tribal category permits this, and the family-group names Trichodectini and Felicolini are available (see full classification below). It must be stressed that these tribes are inserted to maintain the formal structure of the classification, and are not intended (or believed) to have any other significance.

Neotrichodectinae (Fig. 34)

The first dichotomy in this subfamily divides the clade into those species previously assigned to the genus *Geomydoecus* on one side, and species from *Neotrichodectes, Lakshminarayanella* and *Trichodectes* (sensu Werneck, 1948) on the other. The two branches will be discussed separately.

The genus *Geomydoecus* as previously recognised is fairly uniform in morphology, distribution and host species, and may be identified readily. To divide this genus into others would inhibit rather than encourage discussion, and the genus is retained in its present form. The two subgenera as proposed by Price & Emerson (1972) are also retained though, as indicated above, neither are holophyletic groups.

The other branch of the primary dichotomy comprises the 10 species previously assigned to the genus *Neotrichodectes* (considered a subgenus of *Trichodectes* by Hopkins, 1949 and Ledger, 1980), the two species previously assigned to the genus *Lakshminarayanella* (formerly *Lymeon*), and a single species formerly placed in *Trichodectes* by most authors (*T. barbarae*). The clade is plainly close to the established concept of *Neotrichodectes*, and it is preferable that this name is applied to as much of the group as possible. The 10 species of *Neotrichodectes* auctt. do not form a holophyletic group, however, though morphologically they are quite uniform. Inclusion of *T. barbarae* is unlikely to create problems, but *Lakshminarayanella* (as *Lymeon*) has been placed by some authors in a subfamily of its own (Eichler, 1940, 1963), and considered close to the hyrax lice (Kéler, 1944; Hopkins, 1949; Eichler, 1963). If *Lakshminarayanella* is synonymised with *Neotrichodectes* and given no formal recognition it is likely to be raised from synonomy by future workers because of its distinctive morphology, leaving *Neotrichodectes* paraphyletic. The course taken here is to recognise *Lakshminarayanella* as a subgenus of *Neotrichodectes*, which necessitates recognition of four other (holophyletic) subgenera, names already being available for two of these. Application of the principles of phyletic sequencing permits equal ranking of the subgenera within the genus.

Subfamilies (Fig. 40)

To divide the family into 'manageable' holophyletic groups for the purposes of discussion and to maintain the logic of phyletic sequencing, supra-generic groupings had to be employed. Use of

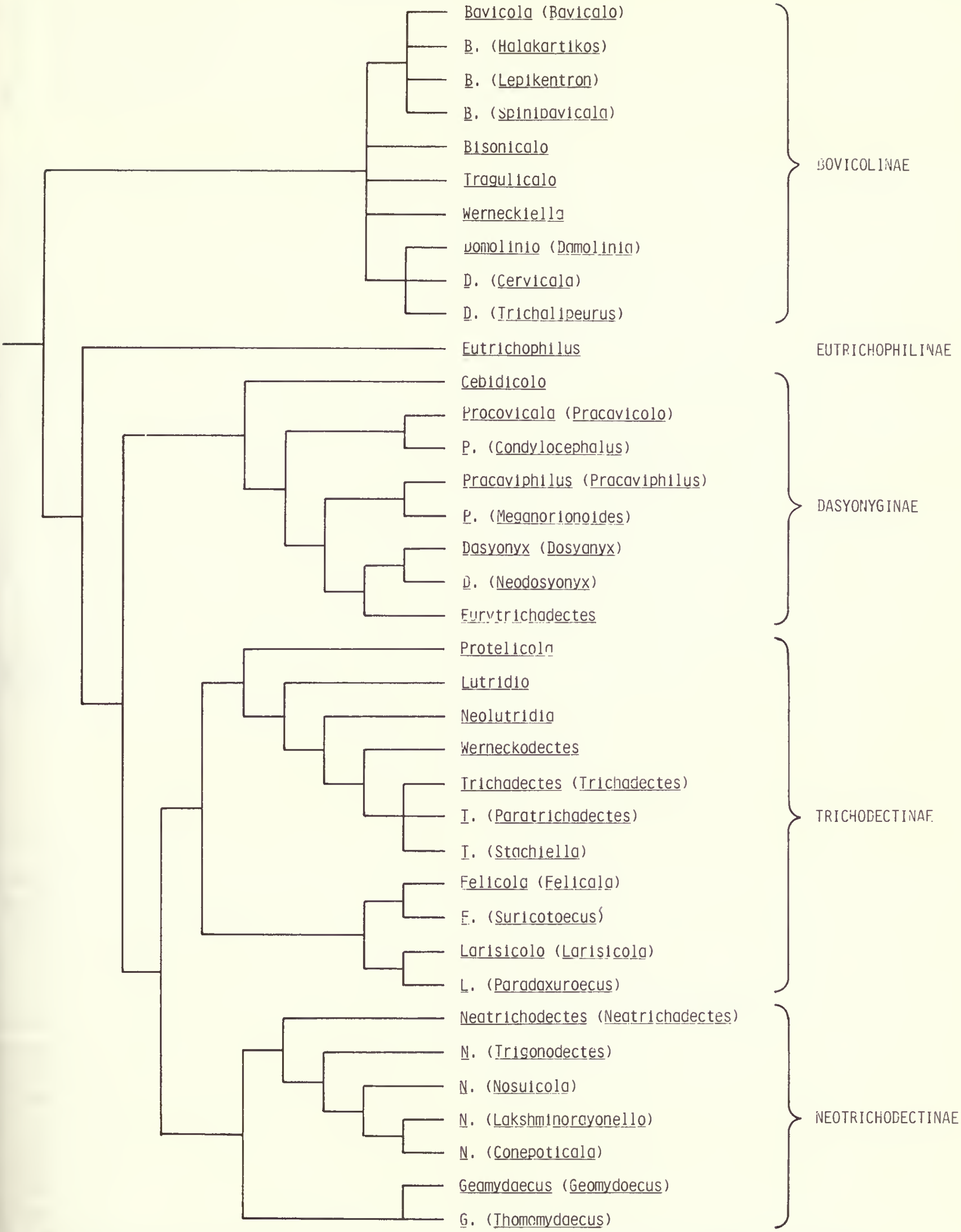


Fig. 40 Cladogram of the genera and subgenera of Trichodectidae, with subfamily assignments.

the principles of phyletic sequencing permitted the use of the subfamily category throughout (with the addition of the tribes mentioned above). The limits of the subfamilies were chosen for maximum utility, modified by the dictates of the sequencing convention. It would be surprising, given the high degree of homoplasy of structures in the Trichodectidae, if the subfamilies fulfilled the criterion 'distinctness' described above and were readily distinguishable. A key to subfamilies is provided, however, largely to satisfy the requirements of the *International Code of Zoological Nomenclature* (Article 13) for a description to accompany any new name for, although names were available for most of the subfamilies, a single new name is required.

A complete classification of the Trichodectidae to generic level is set out below in phyletic sequence (as recommended by Wiley, 1979, 1981).

Sequenced classification of the Trichodectidae

- Family **TRICHODECTIDAE** Kellogg, 1896
  - Subfamily **BOVICOLINAE** Kéler, 1938 (all genera *sedis mutabilis*)
    - Genus ***BOVICOLA*** Ewing, 1929 (all subgenera *sedis mutabilis*)
      - Subgenus ***BOVICOLA*** Ewing, 1929
      - Subgenus ***HOLAKARTIKOS*** Kéler, 1938
      - Subgenus ***LEPIKENTRON*** Kéler, 1938
      - Subgenus ***SPINIBOVICOLA*** subgen. n.
    - Genus ***BISONICOLA*** gen. n.
    - Genus ***WERNECKIELLA*** Eichler, 1940
    - Genus ***TRAGULICOLA*** gen. n.
    - Genus ***DAMALINIA*** Mjöberg, 1910 (all subgenera *sedis mutabilis*)
      - Subgenus ***DAMALINIA*** Mjöberg, 1910
      - Subgenus ***CERVICOLA*** Kéler, 1938
      - Subgenus ***TRICHOLIPEURUS*** Bedford, 1929
  - Subfamily **EUTRICHOPHILINAE** Kéler, 1938
    - Genus ***EUTRICHOPHILUS*** Mjöberg, 1910
  - Subfamily **DASYONYGINAE** Kéler, 1938
    - Genus ***CEBIDICOLA*** Bedford, 1936
    - Genus ***PROCAVICOLA*** Bedford, 1932
      - Subgenus ***PROCAVICOLA*** Bedford, 1932
      - Subgenus ***CONDYLOCEPHALUS*** Werneck, 1941
    - Genus ***PROVCAVIPHILUS*** Bedford, 1932
      - Subgenus ***PROCAVIPHILUS*** Bedford, 1932
      - Subgenus ***MEGANARIONOIDES*** Eichler, 1940
    - Genus ***DASYONYX*** Bedford, 1932
      - Subgenus ***DASYONYX*** Bedford, 1932
      - Subgenus ***NEODASYONYX*** Werneck, 1941
    - Genus ***EURYTRICHODECTES*** Stobbe, 1913
  - Subfamily **TRICHODECTINAE** Kellogg, 1896
    - Tribe **TRICHODECTINI** Kellogg, 1896
      - Genus ***PROTELICOLA*** Bedford, 1932
      - Genus ***LUTRIDIA*** Kéler, 1938
      - Genus ***NEOLUTRIDIA*** gen. n.
      - Genus ***WERNECKODECTES*** Conci, 1946
      - Genus ***TRICHODECTES*** Nitzsch, 1818 (all subgenera *sedis mutabilis*)
        - Subgenus ***TRICHODECTES*** Nitzsch, 1818
        - Subgenus ***PARATRICHODECTES*** subgen. n.
        - Subgenus ***STACHIELLA*** Kéler, 1938
    - Tribe **FELICOLINI** Kéler, 1938
      - Genus ***FELICOLA*** Ewing, 1929
        - Subgenus ***FELICOLA*** Ewing, 1929
        - Subgenus ***SURICATOECUS*** Bedford, 1932
      - Genus ***LORISICOLA*** Bedford, 1936
        - Subgenus ***LORISICOLA*** Bedford, 1936
        - Subgenus ***PARADOXUROECUS*** Conci, 1942
  - Subfamily **NEOTRICHODECTINAE** subfam. n.
    - Genus ***NEOTRICHODECTES*** Ewing, 1929
      - Subgenus ***NEOTRICHODECTES*** Ewing, 1929
      - Subgenus ***TRIGONODECTES*** Kéler, 1944
      - Subgenus ***NASUICOLA*** subgen. n.
      - Subgenus ***LAKSHMINARAYANELLA*** Eichler, 1982

Subgenus **CONEPATICOLA** subgen. n.
Genus **GEOMYDOECUS** Ewing, 1929
Subgenus **GEOMYDOECUS** Ewing, 1929 (paraphyletic)
Subgenus **THOMOMYDOECUS** Price & Emerson, 1972 (polyphyletic?)

Descriptions of genera and subgenera

The generic and subgeneric descriptions below are arranged by subfamily in the order of the sequenced classification of the Trichodectidae (see above).

Descriptions are set out in the following order: paragraph one – head, both sexes, with details of sexually-dimorphic features of antennae, if present; paragraph two – thorax, both sexes, omitting mention of the anterior setae (on the post-temporal margin) which are present in all species; paragraph three – abdomen, both sexes, with details of sexually-dimorphic features of the setae, sclerites or shape, if present; fourth paragraph – female terminalia and genitalia; fifth paragraph – male subgenital plate, terminalia and genitalia. Descriptions are given of each genus as a whole, even where subgenera are present. The descriptions of subgenera (if any are present) follow that of the genus in which they are placed, and give only subgeneric characters, so that some of the paragraphs listed above may be omitted. Characters that vary between subgenera, if mentioned in the generic description, are indicated by an asterisk (*).

Each description is followed by an indication of the host group or groups parasitised, and by any pertinent comments on the taxonomy, morphology or biology of some or all of the included species. A check-list of all species included in each genus or subgenus is also given, the names being placed in alphabetical order. Following each species name in the check-lists is an indication of the number of specimens of each sex examined in the study.

Two species have not been placed, and are considered *incertae sedis*. *Trichodectes baculus* Schömmer, 1913; type-host: *Capra hircus* Linnaeus. *Trichodectes tigris* Ponton, 1870; type-host: *Felis tigris* Linnaeus. These species are discussed by Werneck (1950).

The subfamilies, genera and subgenera are keyed (p. 335).

BOVICOLINAE Kéler

Genus *BOVICOLA* Ewing

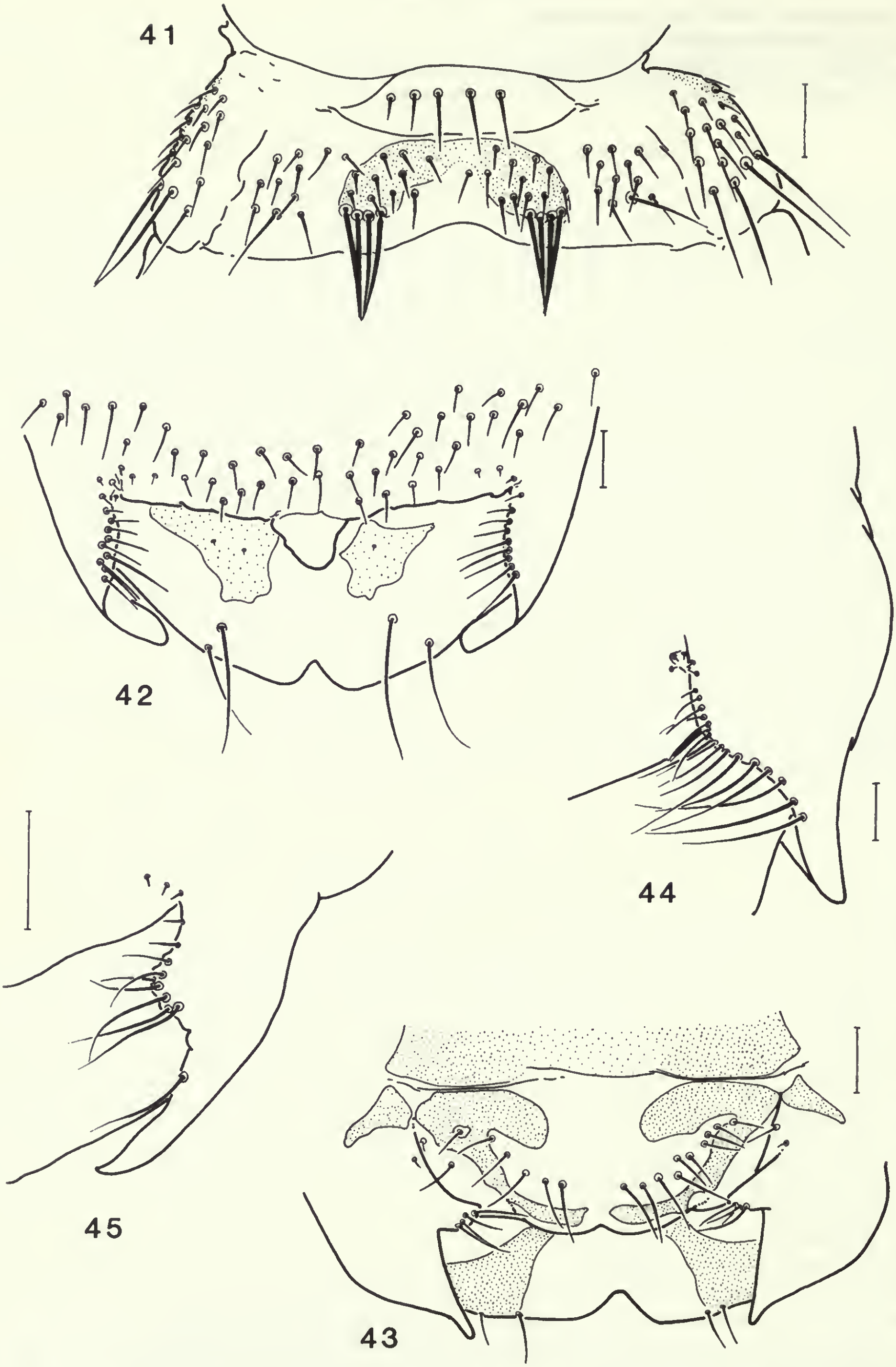
The genus *Bovicola* comprises four subgenera.

DESCRIPTION. Anterior of head with osculum absent or, if present, broad and shallow*; pulvinus of normal length or short and not attaining anterior margin of head; dorsal preantennal sulcus present or absent*; clypeal marginal carina not or only slightly broadened medially, or broadened to variable degree into bar with posterior and anterior margins roughly parallel, bar either straight and at right angles to long axis of head or curved and parallel to anterior margin of head*; anterolateral margin of head smoothly rounded; preantennal portion of head short, outline broadly rounded or trapezoid*. Temple margin smoothly convex or with posterior projection*, sometimes convexly produced posteriad*. Male scape expanded or not expanded*, with setal row apparently present or setae randomly scattered; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth' and interior face not 'roughened'. Dorsum of head with more or less abundant setae, short, long or of moderate length*. Sitophore sclerite unmodified or with posterior arms extended*.

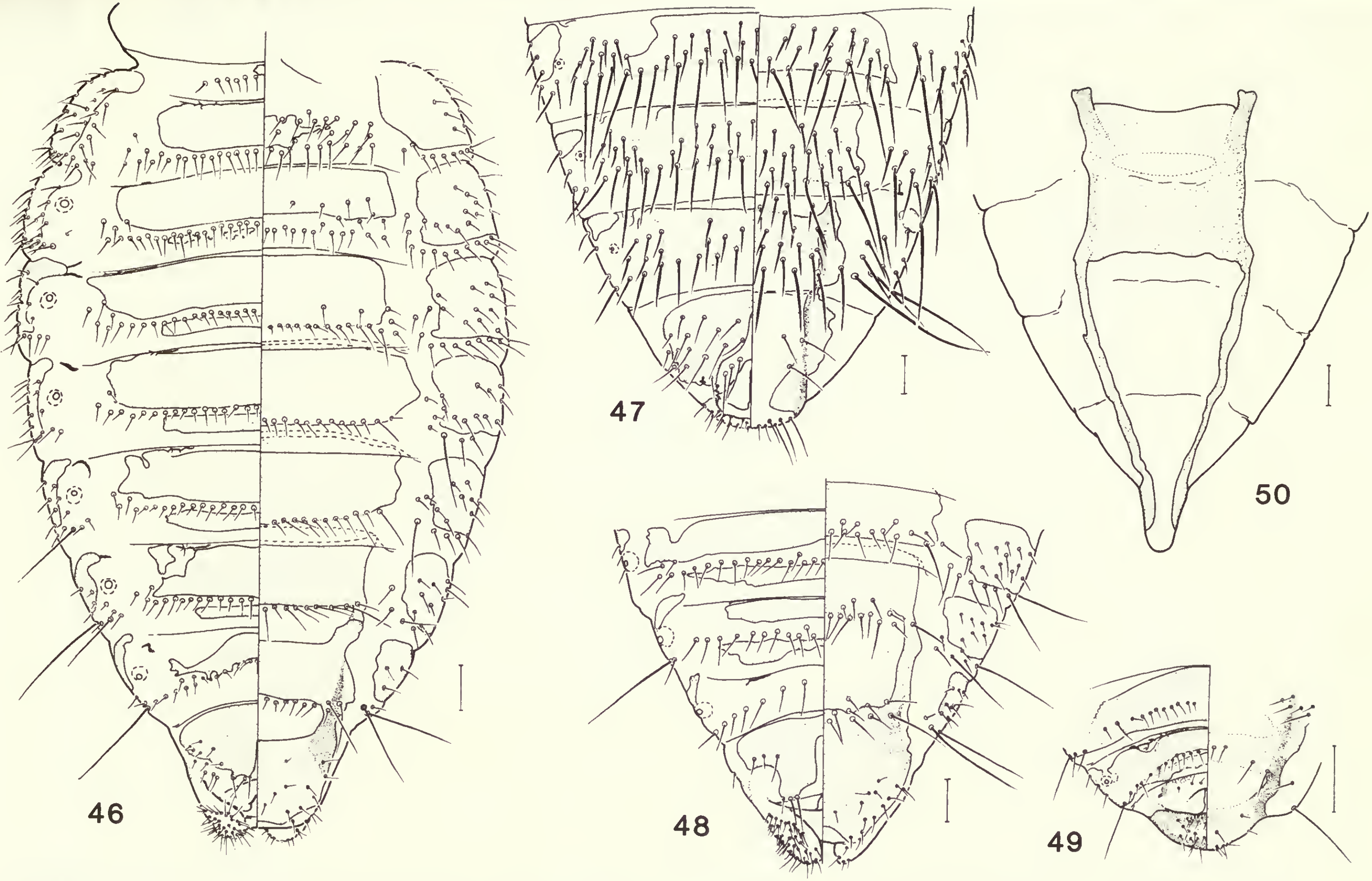
Thorax with more or less abundant setae, short, long, or of moderate length, frequently longest on postero-lateral margin of pterothorax*.

Abdomen oval or elongate, frequently tapering posteriorly more in male than in female*. Abdominal spiracles present on segments III–VIII. Abdominal setae variable*; anterior setae always present on pleura, sometimes on sterna and terga; postero-lateral setae absent. Abdominal pleural projections absent. Sclerites present at least on sterna III–VII (males) and III–VIII (females), terga II–VII (males) and III–IX (females) and pleura II–VIII; male terga with posterior sclerites present or absent*.

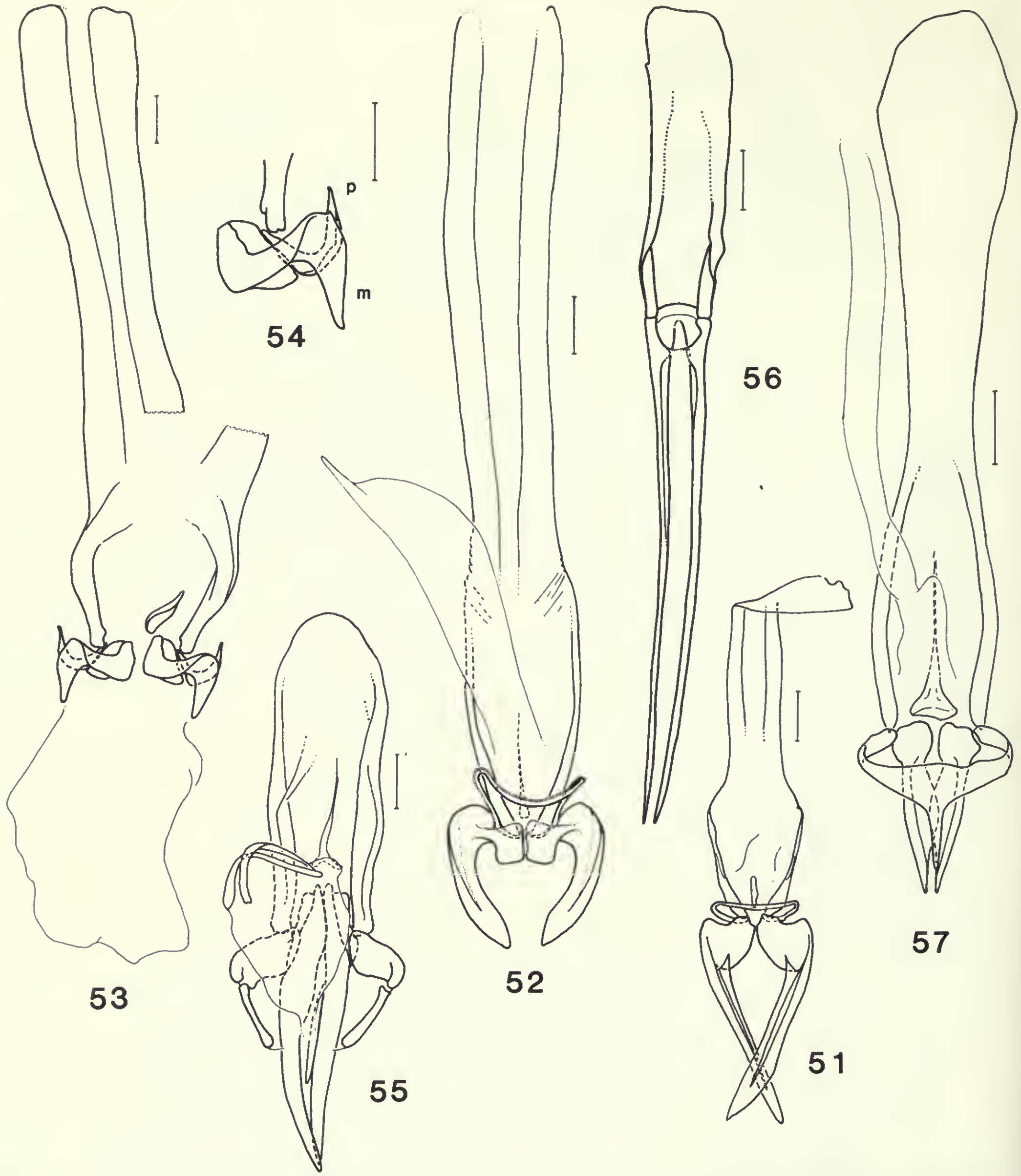
Gonapophyses with marginal setae; ventral lobe present, though sometimes not pronounced*. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised, or sclerotised only medially; subgenital lobe absent, though small median membranous projection may be present (Fig. 42)*. Genital chamber sometimes with median antero-dorsal area lacking scales or spicules*.



Figs 41–45 *Bovicola* species. 41, *B. (Spinibovicola) hemitragi*, ♂ abdominal terga I and II. 42, *B. (B.) jellisoni*, ♀ terminalia, ventral. 43, *B. (Lepikentron) breviceps*, ♀ terminalia, ventral. 44, *B. (Holakartikos) crassipes*, ♀ gonapophysis, ventral. 45, *B. (B.) caprae*, ♀ gonapophysis, ventral.



Figs 46–50 *Bovicola* species. 46, *B.* (*B.*) *caprae*, ♂ abdomen. 47–49, male terminalia of (47) *B.* (*Holakartikos*) *crassipes*; (48) *B.* (*B.*) *bovis*; (49) *B.* (*B.*) *concavifrons*. 50, *B.* (*Spinibovicola*) *hemitragi*, ♂ subgenital plate, setae omitted.



Figs 51–57 *Bovicola* species, ♂ genitalia. 51, *B. (B.) bovis*. 52, *B. (B.) caprae*. 53, *B. (B.) concavifrons*. 54, *B. (B.) concavifrons*, detail of right paramere (p) and mesomere (m). 55, *B. (Lepikentron) breviceps*. 56, *B. (Spinibovicola) hemitragi*. 57, *B. (Holakartikos) crassipes*.

Male subgenital plate variable*. Pseudostyli present or absent*. Male genital opening dorsal or postero-dorsal. Male genitalia variable*.

HOSTS. Bovidae, Cervidae and Camelidae (Artiodactyla).

COMMENTS. Some species of *Bovicola* are parthenogenetic, males being rare or unknown.

A summary of the varying taxonomic treatments of *Bovicola*, its subgenera and synonyms, is presented in Table 3.

Subgenus *BOVICOLA* Ewing

(Figs 3, 42, 45, 46, 48, 49, 51–54)

Bovicola Ewing, 1929: 193. Type-species: *Trichodectes caprae* Gurlt, by original designation.
Bovidoecus Bedford, 1929: 518. Type-species: *Pediculus bovis* Linnaeus, by original designation. [Synonymy by Bedford, 1932*a*: 356.]
Rhabdopedilon Kéler, 1938*a*: 453. Type-species: *Trichodectes longicornis* Nitzsch, by original designation. [Synonymy by Werneck, 1950: 59.]

Description. Clypeal marginal carina not broadened medially, or more or less broadened into bar with posterior margin straight or matching curvature of osculum. Temple margin smoothly convex, lacking projection on postero-lateral angle, not convexly produced posteriad to great extent. Male scape not expanded or only slightly expanded. Dorsum of head with setae short or of moderate length, of greater abundance anteriorly than posteriorly. Sitophore sclerite unmodified.

Thorax with lateral and dorsal setae long and of moderate length, sometimes abundant and numerous on disc of prothorax and pterothorax, otherwise less abundant and sparsely scattered on disc of pterothorax with only two setae present on disc of prothorax; setae present along lateral margins and posteriorly (dorsally) on prothorax and pterothorax; posterior setal row of prothorax marginal, with median gap present or absent; posterior setal row of pterothorax submarginal, with median gap absent, row incorporating two very long setae between postero-lateral and postero-median angles or, if setae generally abundant on thorax, postero-lateral setae of pterothorax longer than others.

Abdominal setae short, long or of medium length; setal bases, at least of setae of posterior setal row on sterna and terga, enlarged, clearly with doubled margins. Pregenital sclerites present on sterna and terga (where present) of all segments, except sometimes tergum I and (independently) tergum VIII of males; terga of males, at least of segments IV–VI, with both anterior and posterior sclerites.

Gonapophyses with lobe rectangular, acute, rounded or not pronounced; marginal setae confined to lobe, long. Ventral vulval margin not sclerotised; convex, biconvex with median indentation, or convex with small median membranous projection (Fig. 42); margin smooth or spinose. Postgenital area lacking spinose patch. Genital chamber with antero-median dorsal area lacking spicules, scales or other decoration, either very narrow and strongly-defined or wide and ill-defined, or with very narrow longitudinal fold.

Male subgenital plate variable; sternites VII and IX present, fused to s.g.p.r., sternite VIII absent or, if present, fused or not fused to s.g.p.r. (Figs 46, 48). Pseudostyli absent (Fig. 49) or, if present, setose and lobulate (Figs 46, 48). Basal apodeme very concave anteriorly, the sides of the concavity frequently being parallel, though sometimes obscure. Parameres with broad basal flange or block; sometimes very reduced. Basiparameral sclerites present and fused, or absent. Mesomeres, if fused apically, forming very narrow arch lacking median extension; otherwise mesomeres not fused, sometimes very reduced and obscure. Male genitalia depicted in Figs 51–54.

Hosts. Bovidae and Cervidae (Artiodactyla).

Comments. Some of the species in this subgenus are parthenogenetic.

Species included
alpinus Kéler, 1942 (5 ♂, 3 ♀)
bovis (Linnaeus, 1758) (7 ♂, 137 ♀)
caprae (Gurlt, 1843) (*c.*50 ♂, *c.*50 ♀)
concavifrons (Hopkins, 1960) [Recalled from synonymy with *longicornis* (Nitzsch).] (2 ♂, 98 ♀)
jellisoni Emerson, 1962 (10 ♂, 10 ♀)
limbatus (Gervais, 1844) (*c.*50♂, *c.*65 ♀)
longicornis (Nitzsch, 1818) (44 ♀)
oreamnidis (Hopkins, 1960) (holotype ♂)
ovis (Schrank, 1781) (59 ♂, 64 ♀)
tarandi (Mjöberg, 1910) (2 ♀, 7 nymphs)
tibialis (Piaget, 1880) (*c.*100 ♀)

Subgenus *HOLAKARTIKOS* Kéler **gen. rev., stat. n.**

(Figs 44, 47, 57)

Holakartikos Kéler, 1938*a*: 461. Type-species: *Trichodectes pilosus* Piaget (nec Giebel) [= *Trichodectes crassipes* Rudow], by original designation.

Description. Anterior of head with osculum absent; pulvinus very short, not attaining anterior margin of head; dorsal preantennal sulcus absent, though ventral preantennal sulcus sometimes present; clypeal marginal carina not always pronounced and not, or only slightly, broadened medially; preantennal portion of head very short, outline smoothly and shallowly rounded. Temple margin smoothly convex, lacking projection on postero-lateral angle, convexly produced posteriad. Male scape very slightly expanded, with setae randomly scattered. Dorsum of head with abundant setae of moderate length; temple with long postero-lateral marginal setae. Sitophore sclerite unmodified.

Thorax with abundant setae, long and of moderate length, present on margins and disc of prothorax and pterothorax; setae longest on the rounded postero-lateral angles of prothorax and pterothorax.

Abdomen with long setae of posterior setal row, and shorter anterior setae, present on sterna, terga and pleura (where present) of all segments (Fig. 47). Pre-genital sclerites sometimes very faint, present on sterna and terga (where present) of all segments except tergum I and sternum II; male terga lacking posterior sclerites.

Gonapophyses with broadly rounded lobe smoothly continuous with ventral margin; marginal setae long, present all along ventral margin, including lobe. Ventral vulval margin not sclerotised; produced into three weakly-developed lobes. Postgenital pleural area with patch of short, spine-like setae. Genital chamber lacking dorsal non-ornamented area or fold.

Male subgenital plate with s.g.p.r. not joining sternites VII and VIII, and sometimes failing to contact either or both; sternites sometimes very faintly sclerotised, obscure; s.g.p.r. with broad lateral flange on VIII and IX (Fig. 47). Pseudostyli absent. Male genital opening dorsal. Basal apodeme long, not concave anteriorly. Parameres long, slender, with basal block and flange. Basiparameral sclerites absent. Mesomeres fused apically, with median extension present (see comments below). Male genitalia depicted in Fig. 57.

HOSTS. Bovidae (Artiodactyla).

COMMENTS. The only included species is not known to be parthenogenetic.

Werneck (1950) failed to recognise the median extension of the mesomeral arch, and considered it absent.

Holakartikos was considered a synonym of *Bovicola* by Werneck (1950) and Emerson & Price (1981); a more extensive history of the variations in status of this subgenus is presented in Table 3.

SPECIES INCLUDED

crassipes (Rudow, 1866) (24 ♂, 31 ♀)

Subgenus *LEPIKENTRON* Kéler **gen. rev., stat. n.**

(Figs 43, 55)

Lepikentron Kéler, 1938*a*: 452. Type-species: *Trichodectes breviceps* Rudow, by original designation.

DESCRIPTION. Anterior of head with osculum absent; pulvinus very short, not attaining anterior of margin of head; dorsal preantennal sulcus absent; clypeal marginal carina not pronounced, not broadened medially; preantennal portion of head shorter in male than female, outline broadly and smoothly rounded. Temple margin smoothly convex, lacking projection on postero-lateral angle, not convexly produced posteriad to great extent. Male scape expanded, with setal row apparently present, though setae may be scattered randomly. Dorsum of head with setae of moderate length, slender; setae sparsely distributed, more abundant anteriorly than posteriorly. Sitophore sclerite unmodified.

Thorax with lateral and dorsal setae slender, long and of moderate length; setae present postero-laterally and posteriorly on prothorax and along lateral margins and posteriorly (dorsally) on pterothorax; posterior setal row of prothorax submarginal, sparse, with large median gap; posterior setal row of pterothorax submarginal, with small median gap, setae shorter medially than laterally, with two long setae laterally; pair of setae, widely spaced, present on disc of prothorax dorsally; setae not present on disc of pterothorax.

Abdominal setae of moderate length, slender; anterior setae never present on sterna and terga. Pre-genital sclerites present on terga II–VII (males) and terga III–IX (females) and sterna III–VII (males) and III–VIII (females); male terga III–VII with both anterior and posterior sclerites, though the posterior elements may be very faintly sclerotised and difficult to see.

Gonapophyses with small, pronounced lobe and broad tapering spur (Fig. 43); marginal setae confined to lobe. Ventral vulval margin sclerotised medially; shallowly convex or biconvex (Fig. 43). Postgenital pleural area lacking spinous patch. Genital chamber lacking median non-ornamented area or fold.

Male subgenital plate with sternite VII fused to s.g.p.r. and sternites VIII and IX absent; s.g.p.r. broad. Pseudostyli absent. Male genital opening postero-dorsal. Basal apodeme slightly longer than parameres, convex anteriorly. Parameres long, slender. Basiparameral sclerites absent. Mesomeres not apically fused; each with median desclerotisation, and appearing as two rods (Fig. 55).

HOSTS. Camelidae (Artiodactyla).

COMMENTS. Only one male of the single included species is known and the species may be parthenogenetic.

The subgenus was treated as a synonym of *Bovicola* by Werneck (1950) and Emerson & Price (1981); a more extensive history of the variations in status of this subgenus is presented in Table 3.

SPECIES INCLUDED
breviceps (Rudow, 1866) (1 ♂, 24 ♀)

Subgenus *SPINIBOVICOLA* subgen. n.

(Figs 12, 41, 50, 56)

Type-species: *Trichodectes hemitragi* Cummings.

DESCRIPTION. Anterior of head with osculum absent; pulvinus very short, but attaining anterior margin of head; dorsal preantennal sulcus absent; clypeal marginal carina broadened medially into straight bar with posterior margin slightly irregular; anterolateral margin of head smoothly rounded; preantennal portion short, with outline rounded, almost straight anteriorly. Temple margin convex laterally, straight posteriorly, with short posteriorly-directed projection on postero-lateral angle bearing two setae. Male scape slightly expanded, with setae randomly scattered. Dorsum of head with abundant setae of moderate length. Sitophore sclerite with posterior arms extended (Fig. 12).

Thorax with dorsal and lateral setae abundant, long or of moderate length, present marginally and on disc of prothorax and pterothorax; longest setae present postero-laterally on pterothorax.

Abdomen tapering more acutely in male than in female. Abdomen with posterior setal row comprising long setae on sterna, terga and pleura, anterior setae shorter; anterior setae present on sterna, terga and pleura (where present) of all abdominal segments except sometimes tergum I; male tergum II with curved row of 3–4 long stout setae on each side, modified from posterior setal row, these setae being linked by a curved sclerite (modified tergite) (Fig. 41). Pre-genital sclerites present on terga II–VII or VIII (males) and II–IX (females) and sterna II–VII (males) and II–VIII (females); male terga lacking posterior sclerites.

Gonapophyses with broadly rounded lobe smoothly continuous with ventral margin; marginal setae long, confined to lobe. Ventral vulval margin not sclerotised; convex. Postgenital pleural area lacking spinose patch. Genital chamber lacking dorsal non-ornamented area or fold.

Male segment IX produced posteriorly into narrow, sclerotised extension; subgenital plate tapering characteristically, comprising sternites VI and VII linked by s.g.p.r. (Fig. 50). Pseudostyli absent. Male genital opening dorsal. Basal apodeme not as long as parameres, not concave anteriorly. Parameres fused basally, long and tapering to pointed apices. Basiparameral sclerites absent. Mesomeres absent, or represented by very short sclerites, not apically fused. Male genitalia depicted in Fig. 56.

HOSTS. Bovidae (Artiodactyla).

COMMENTS. Neither of the two included species is known to be parthenogenetic.

SPECIES INCLUDED
hemitragi (Cummings, 1916) (20 ♂, 26 ♀)
multispinosus Emerson & Price, 1979 (8 ♂, 11 ♀)

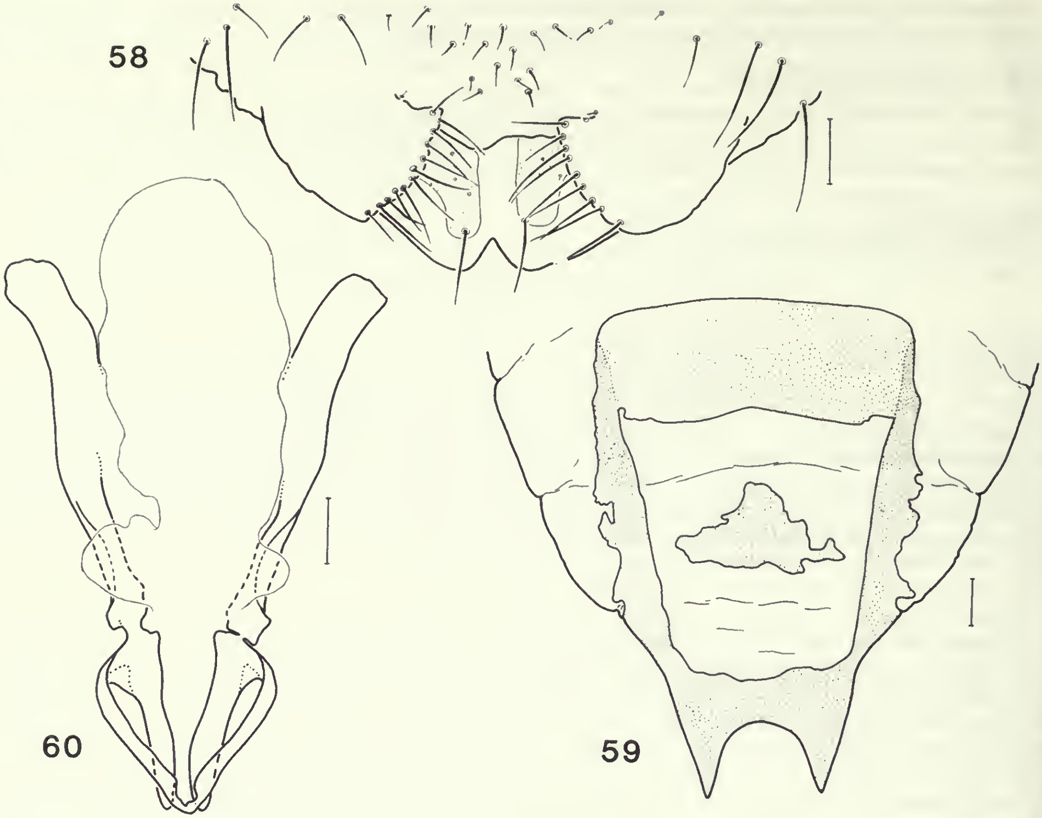
Genus *BISONICOLA* gen. n.

(Figs 58–60)

Type-species: *Bovicola sedecimdecembrii* Eichler.

DESCRIPTION. Anterior of head with osculum absent, though pulvinus attaining margin; margin anteriorly to pulvinus membranous, hyaline; dorsal preantennal sulcus present; clypeal marginal carina slightly broadened medially; anterolateral margin of head smoothly convex; preantennal portion of head short or longer, but not as long as postantennal portion, outline broadly rounded, though slightly truncate anteromedially. Temple margin broadly and smoothly convex. Male scape expanded, with setae randomly scattered; flagellomeres fused in males and females; male flagellum with two or three basally-articulated 'teeth'; male flagellum not 'roughened' on interior face. Dorsum of head with numerous setae of medium length. Sitophore sclerite unmodified.

Thorax with lateral and dorsal setae long and of moderate length; setae present along lateral margins and



Figs 58–60 *Bisonicola sedecimdecembrii*. 58, ♀ terminalia, ventral. 59, ♂ subgenital plate, setae omitted. 60, ♂ genitalia.

posteriorly (dorsally) on prothorax and pterothorax; posterior setal row on prothorax marginal, with median gap; posterior setal row of pterothorax submarginal, with median gap absent; pterothorax with posterior setal row incorporating two very long setae between postero-lateral and postero-median angles; pair of setae, widely spaced, present on disc of prothorax dorsally; scattered setae sometimes present posteriorly on disc of pterothorax dorsally. Atria of thoracic spiracles very large.

Abdomen oval. Abdominal spiracles present on segments III–VIII. Abdomen with setae short and of medium length; anterior setae present on sterna, terga and pleura; postero-lateral setae absent. Abdominal pleural projections absent. Sclerites present on sterna, terga and pleura (where present) of all pre-genital abdominal segments except tergum I; male terga V, VI and VII with anterior and posterior sclerites.

Gonapophyses broad, truncate; setae present along postero-median margin; ventral lobe absent (Fig. 58). Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; very short, more or less straight; subgenital lobe absent.

Male subgenital plate with sternites VII and IX fused to s.g.p.r., sternite VIII present but not fused to s.g.p.r.; s.g.p.r. heavily sclerotised, widest on sternum VIII (Fig. 59). Pseudostyli present, large, broadly triangular (Fig. 59). Male genital opening dorsal. Parameres separate, rod-like, fused to mesomeral arch. Basiparameral sclerites absent. Mesomeres fused apically; median extension absent. Male genitalia depicted in Fig. 60.

HOSTS. Bovidae (Artiodactyla).

SPECIES INCLUDED

sedecimdecembrii sedecimdecembrii (Eichler, 1946) **comb. n.** from *Bovicola* (5 ♂, 4 ♀)
sedecimdecembrii bison (Blagoveshtchenski, 1967) **comb. n.** from *Bovicola* (2 ♂, 1 ♀)

Genus *WERNECKIELLA* Eichler gen. rev.

(Figs 61, 62)

Werneckiella Eichler, 1940: 160. Type-species: *Trichodectes equi* Denny, by original designation.

DESCRIPTION. Anterior of head with osculum absent; pulvinus not attaining margin; dorsal preantennal sulcus present; clypeal marginal carina slightly broader medially than laterally, or not broadened; anterolateral margin of head smoothly convex; preantennal portion of head not long, outline broadly rounded, sometimes slightly flattened anteriorly. Temple margin convex or rectangular. Male scape expanded, with setae randomly scattered; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth'; male flagellum not 'roughened' on interior face. Dorsum of head with abundant short setae. Sitophore sclerite unmodified.

Thorax with lateral and dorsal setae short and of medium length; setae present along lateral margins and posteriorly (dorsally) on prothorax and pterothorax; posterior setal row on prothorax marginal, with median gap; posterior setal row on pterothorax marginal or submarginal, with no median gap; posterior setal row of pterothorax incorporating two very long setae with intervening shorter setae between postero-lateral and postero-median angles; prothorax with seta or setae on disc laterally (dorsally).

Abdomen elongate-oval. Abdominal spiracles present on segments III–VIII. Abdomen with setae short and of moderate length; anterior setae frequently present on sterna and terga, always present on pleura; postero-lateral setae absent. Abdominal pleural projections absent. Sclerites present on abdominal pleura II–VII and sterna and terga of at least abdominal segments II–VII; male terga with single sclerites only.

Gonapophyses broad, truncate, with median faces almost parallel to one another; marginal setae of moderate length; ventral lobe absent. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised, very short, straight; subgenital lobe absent.

Male subgenital plate with sternite VII present and fused to s.g.p.r., sternites VIII and IX absent; s.g.p.r. sinuate and broadest on sternum VIII (Fig. 61). Pseudostyli present, small, simple setose lobes. Male genital opening postero-dorsal. Parameres long, straight or flared and twisted medially, sometimes fused basally. Basiparameral sclerites absent. Mesomeres fused or almost fused into pentagonal mesomeral arch with median extension absent; mesomeres broadest basally (external to b.a.l.s.) and more or less broad distally; mesomeres projecting basally between b.a.l.s. to contact parameres. Male genitalia depicted in Fig. 62.

HOSTS. Equidae (Perissodactyla) and Bovidae (Artiodactyla).

COMMENTS. Some species are parthenogenetic, the males being unknown.

Werneckiella was considered a subgenus of *Damalinia* by Hopkins (1949) and a synonym of *Bovicola* by Werneck (1950); it is here raised from synonymy with *Bovicola*. A more extensive history of the variations in status of this genus is presented in Table 3. The genus was revised by Moreby (1978).

SPECIES INCLUDED

aspilopyga (Werneck, 1956) **comb. n.** from *Bovicola* (9 ♂, 11 ♀)
equi (Denny, 1842) **comb. n.** from *Bovicola* (3 ♂, *c*.100 ♀)
fulva (Emerson & Price, 1979) **comb. n.** from *Bovicola* (4 ♂, ?1 ♀)
neglecta (Kéler, 1942) **comb. n.** from *Bovicola* (5 ♂, 6 ♀)
ocellata (Piaget, 1880) **comb. n.** from *Bovicola* (17 ♀)
zebrae Moreby, 1978 **comb. rev.** from *Bovicola* (1 ♂, 2 ♀)
zuluensis (Werneck, 1950) **comb. n.** from *Bovicola* (13 ♂, 13 ♀)

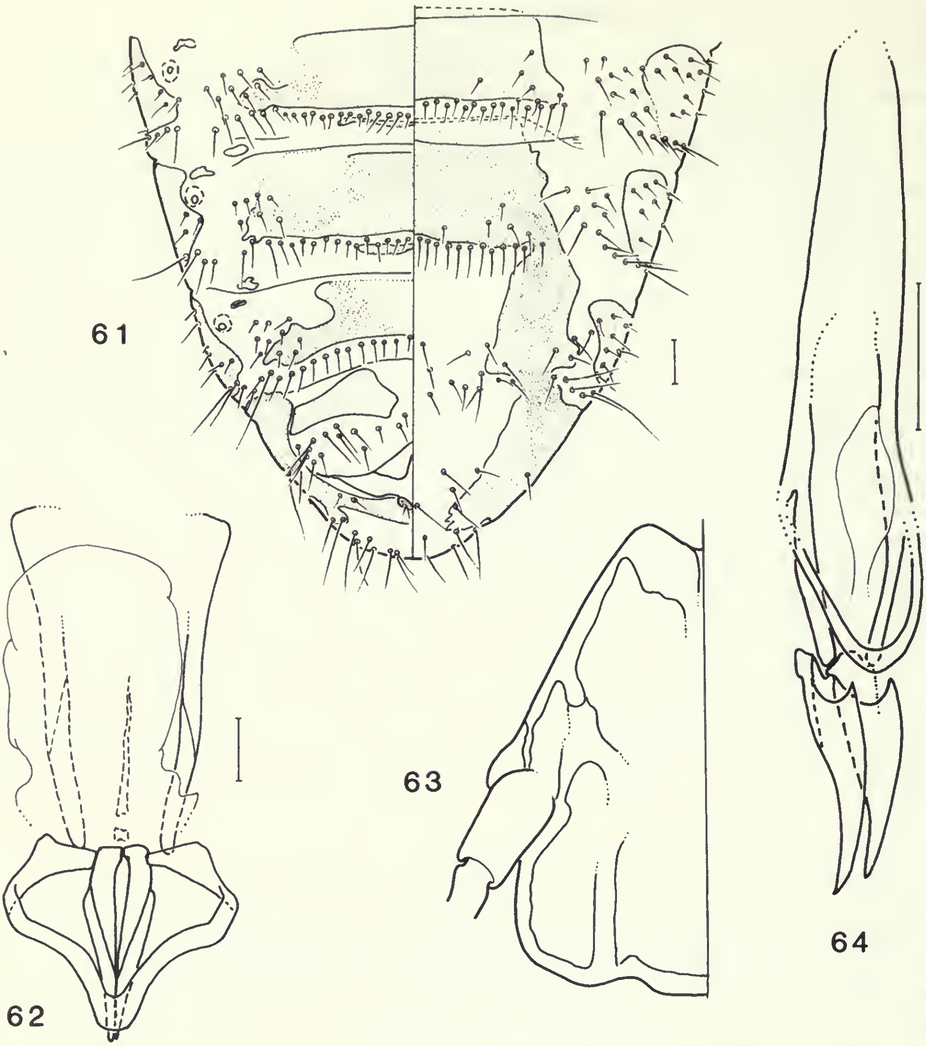
Genus *TRAGULICOLA* gen. n.

(Figs 63, 64)

Type-species: *Damalinia traguli* Werneck.

DESCRIPTION. Anterior of head with osculum present, broad; dorsal preantennal sulcus present; clypeal marginal carina broadened medially into less heavily sclerotised dorsal sclerite, which is broad, posteriorly convex and with median posterior projection (Fig. 63); anterolateral margin of head straight or slightly sinuate; preantennal portion of head as long as its maximum width, outline trapezoid. Temple margin convex or rectangular. Male scape expanded, with setal row present and comprising at least four setae; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth'. Dorsum of head with setae short posteriorly and of moderate length anteriorly. Sitophore sclerite unmodified.

Thorax with dorsal setae short or of moderate length; prothorax and pterothorax with marginal or



Figs 61–64 Bovicolinae species. 61, 62, *Werneckiella equi* ♂, (61) terminalia; (62) genitalia. 63, 64, *Tragulicola traguli*, (63) ♀ head, dorsal; (64) ♂ genitalia.

submarginal posterior setal row, the longest setae being posterolaterally except in the male, which has a pair of long setae medially on the posterior row of the pterothorax; male with setal patch centrally on disc of pronotum, but no other setae present on disc of either sex.

Abdomen elongate, with male tapering to more acute posterior angle than female. Abdominal spiracles present on segments III–VIII; atria oblate-spheroids, very large. Abdomen with setae of moderate length, the longest being those comprising the pleural posterior setal row, particularly of the posterior pleura; anterior setae present on all pleura, but not sterna or terga; postero-lateral setae absent. Abdominal pleural projections absent. Sclerites present on sterna, terga and pleura (where present) of all abdominal segments except tergum I, which is reduced and obscure; male terga III–VI with anterior and posterior sclerites.

Gonapophyses broad medially, tapering smoothly distally; ventral margin with long, abundant setae; ventral lobe absent. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; convex; subgenital lobe absent; marginal spines present, though difficult to see. Female genital chamber with dorsal wall lacking spicules over narrowly triangular area anteromedially.

Male subgenital plate with sternites IX and VIII linked by s.g.p.r., but sternite VII not attached.

Pseudostyli present, short, conical; median ventro-posterior projection also present, longer than pseudostyli. Male genital opening postero-dorsal. Basal apodeme acuminate apically. Parameres broad, triangular, poorly-sclerotised, asymmetrically deflected (may be artifact of preparation, though deflected the same way in all specimens seen). Basiparameral sclerites absent. Mesomeres fused apically, median extension absent; mesomeral arch fused to b.a.l.s. about one-third length of basal apodeme anteriad from posterior end. Male genitalia depicted in Fig. 64.

Hosts. Tragulidae (Artiodactyla).

Species included

traguli (Werneck, 1950) **comb. n.** from *Damalinia* (70 ♂, 75 ♀)

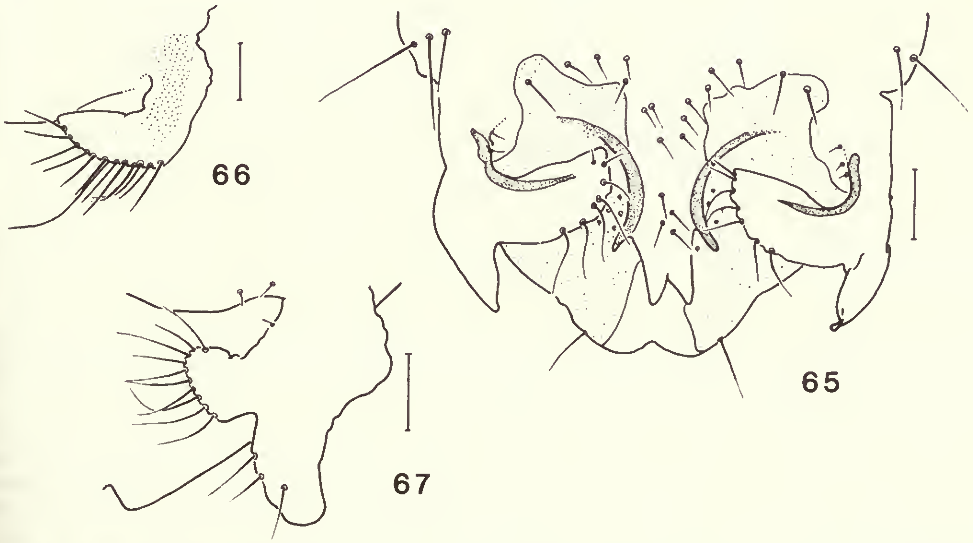
Genus *DAMALINIA* Mjöberg

The genus *Damalinia* comprises three subgenera.

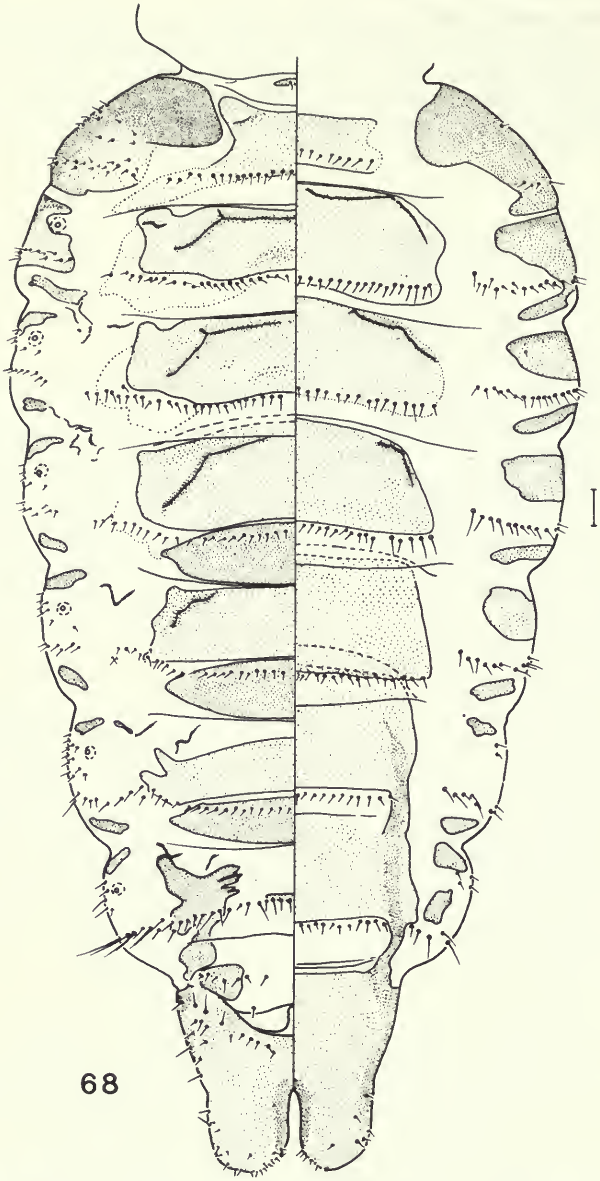
Description. Anterior of head with osculum present, narrow or broad, deep or shallow, or osculum absent, in which case head as described below for *D. (T.) conectens**; dorsal preantennal sulcus present or absent*; clypeal marginal carina more or less broadened medially and of variable form*; anterolateral margin of head straight, slightly concave, slightly sinuate or convex; preantennal portion of head of variable length, outline triangular, trapezoid, rectangular or rounded*. Temple margin smoothly convex, sometimes convexly produced posteriad*, with posterolateral angle sometimes developed laterally or with small posterior rounded projection*. Male scape expanded, with setal row present or setae randomly scattered*; flagellomeres fused in males and females; male flagellum with two or three basally-articulated 'teeth'* and interior face serrate or 'roughened'. Dorsum of head with setae sparse or more or less abundant, short or of moderate length, frequently longer along the anterolateral margins and across the clypeus than elsewhere. Sitophore sclerite unmodified.

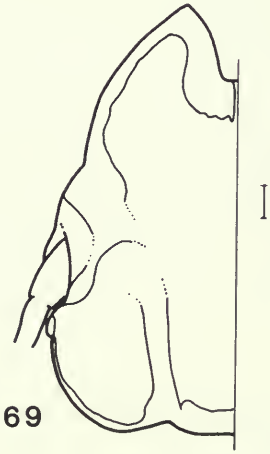
Thorax with dorsal and marginal setae short, long or of moderate length, frequently longest on posterolateral margin of pterothorax. Prothorax with setae sparse or absent on anterolateral margin; posterior setal row marginal, though directed onto disc medially and median setal pair sometimes isolated, row more or less sparse, with median gap between setae (other than isolated median pair) present, sometimes wide*; single seta frequently present on dorsal disc anterolaterally. Pterothorax with posterior setal row marginal or submarginal, sometimes irregular or 'doubled'*, median gap present or absent, posterior setal row incorporating two very long setae with intervening shorter setae between posterolateral and postero-median angles; setae absent from disc.

Abdomen oval, elongate, or very elongate and narrow*. Abdominal spiracles present on segments III–VIII. Abdominal setae short or of moderate length, frequently longer on pleura than on sterna and



Figs 65–67 *Damalinia* species. 65, *D. (Tricholipeurus) elongata*, ♀ terminalia, ventral. 66, *D. (Cervicola) meyeri*, ♀ gonapophysis, ventral. 67, *D. (C.) hendrickxi*, ♀ gonapophysis, ventral.



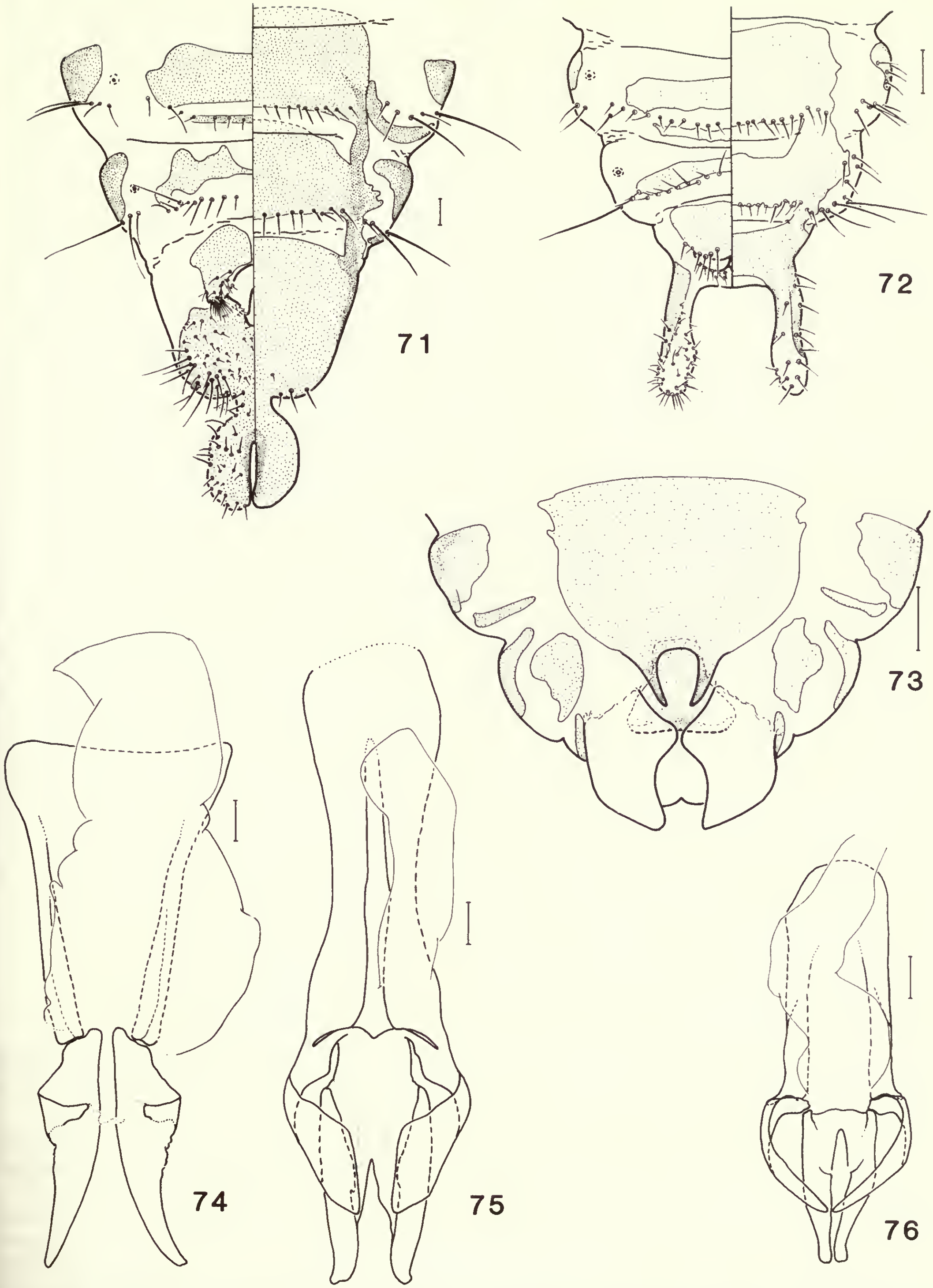


Figs 68–70 *Damalinia* species. 68, *D. (D.) crenelata*, ♂ abdomen. 69, *D. (D.) baxi*, ♀ head, dorsal. 70, *D. (Cervicola) martinaglia*, ♂ scape.

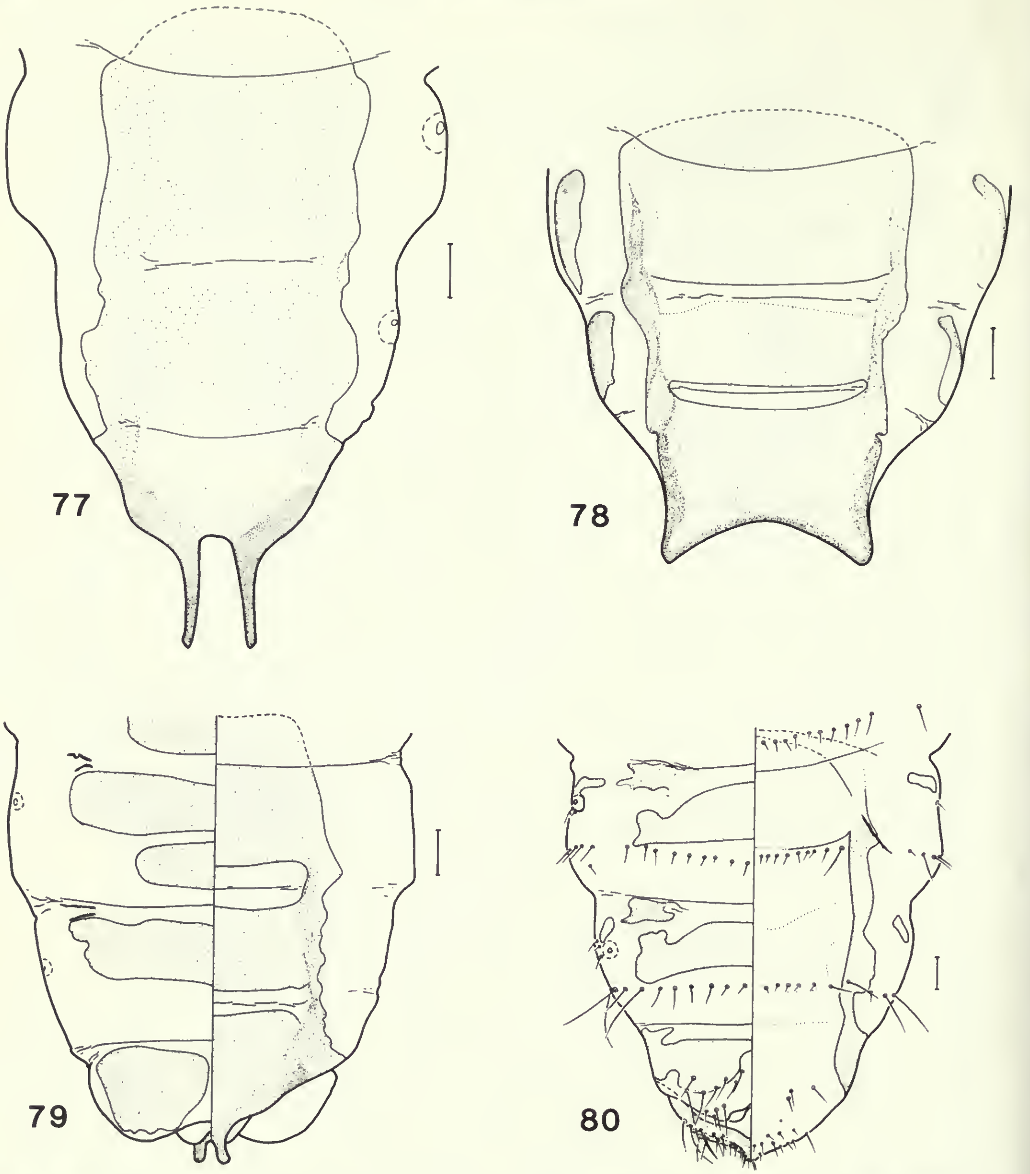
terga; anterior setae present on all pleura except, occasionally, pleurum II, rarely on sterna and terga; postero-lateral setae absent. Abdominal pleural projections absent. Pregenital sclerites present on sterna, terga and pleura (where present) of all segments except tergum I, sometimes absent or very small on pleura (Fig. 80)*; male terga with or without posterior sclerites*.

Gonapophyses variable; ventral margin without rounded lobe, but sometimes with hook-shaped projection*; marginal setae present. Gonapophyses meet ventral vulval margin acutely, not joined by sclerotised band. Ventral vulval margin sclerotised or not sclerotised; subgenital lobe present or absent*. Dorsal margin of vulva and post-vulval area with or without pointed scales*. Common oviduct, at branching point, with or without collar (see subgenus *Cervicola*)*.

Male subgenital plate variable, sternites VII and VIII always being present and fused to s.g.p.r., sternite IX sometimes modified. Pseudostyli absent or, if present, of variable form*. Posterior margins of tergum



Figs 71–76 *Damalinia (D.)* species. 71, *D. theileri*, ♂ terminalia. 72, *D. appendiculata*, ♂ terminalia. 73, *D. theileri*, ♀ terminalia. 74–76, ♂ genitalia of (74) *D. orientalis*; (75) *D. neotheileri*; (76) *D. crenelata*.



Figs 77–80 *Damalinia* species, ♂ terminalia. 77, *D. (Cervicola) natalensis*, ventral, setae omitted. 78, *D. (C.) martinaglia*, ventral, setae omitted. 79, *D. (Tricholipeurus) indica*, ventral, setae omitted. 80, *D. (T.) aepycerus*.

IX sometimes greatly expanded*. Male genital opening postero-dorsal or dorsal. Male genitalia variable*.

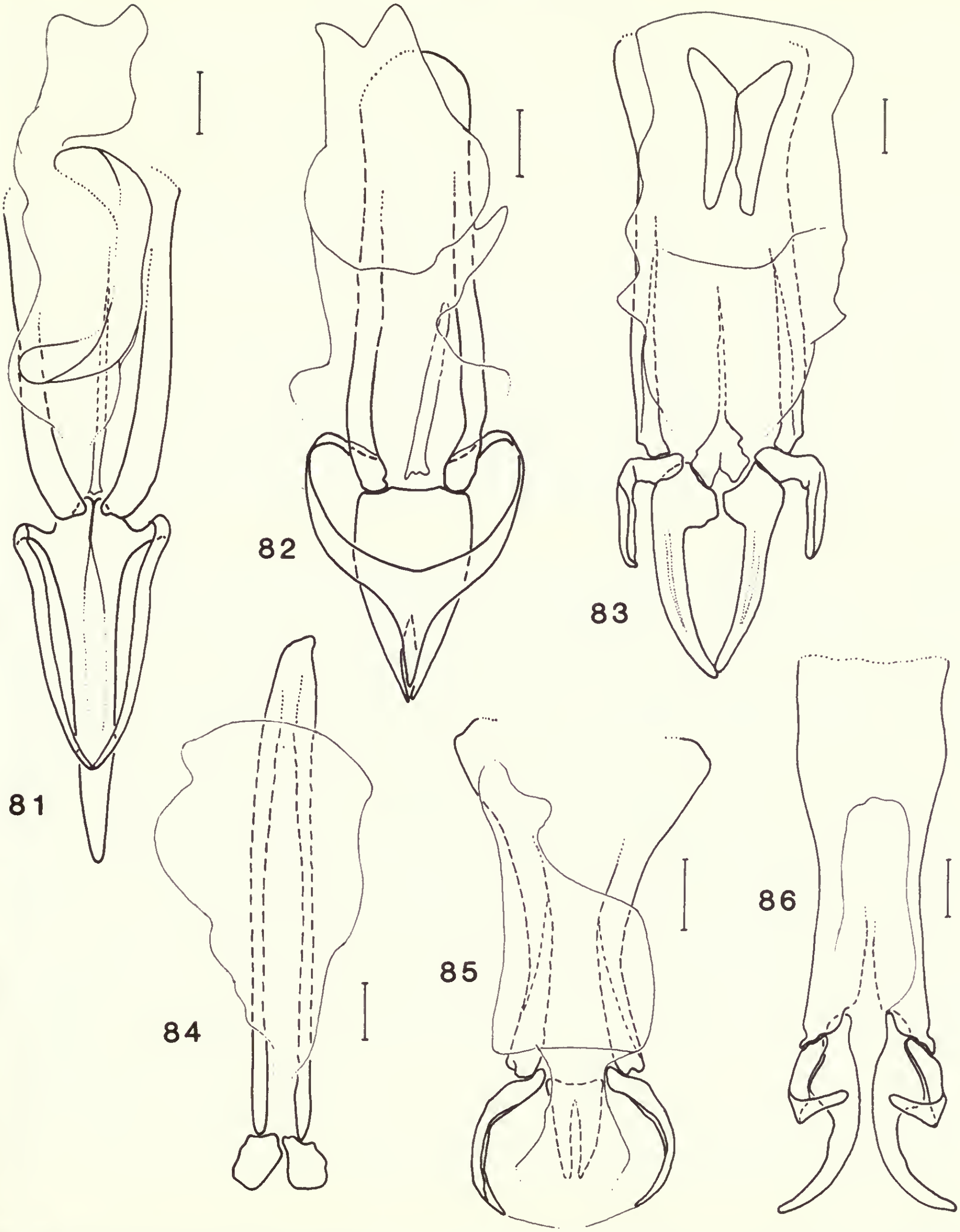
Hosts. Bovidae and Cervidae (Artiodactyla).

Subgenus *DAMALINIA* Mjöberg

(Figs 11, 68, 71–76)

Damalinia Mjöberg, 1910: 69. Type-species: *Trichodectes crenelatus* Piaget, by monotypy.

Description. Anterior of head with osculum present, narrow or broad, deep or shallow; dorsal preantennal sulcus present; clypeal marginal carina broadened medially either into more or less developed simple



Figs 81–86 *Damalinia* species, ♂ genitalia. 81, *D. (Tricholipeurus) victoriae*. 82, *D. (T.) indica*. 83, *D. (T.) aepycerus*. 84, *D. (Cervicola) hopkinsi*. 85, *D. (C.) meyeri*. 86, *D. (C.) reduncae*.

bar with posterior margin straight or concave, or into more or less broad U-shaped sclerite, or into broad, heavily-sclerotised margin of deep osculum; anterolateral margin of head convex or slightly sinuate, in the latter case slightly concave at junction of margin and clypeofrontal sulcus and convex anteriorly; preantennal portion longer or shorter than posterior portion, outline triangular, trapezoid or rounded, sometimes with slight protuberances on either side of osculum. Temple margin smoothly convex, slightly produced posteriad, sometimes with postero-lateral angle developed laterally, or with small posterior rounded projection. Male scape with setae randomly scattered; male flagellum with two basally-articulated 'teeth'. Dorsum of head with setae more or less abundant.

Pterothorax with posterior setal row sometimes irregular or 'doubled'.

Abdomen oval or elongate, sometimes very narrowly elongate. Abdominal setae present anteriorly on all pleura, occasionally on terga and sterna, but only laterally and as irregularity or 'doubling' of posterior setal row. Pleurum II with sclerite extending broadly or narrowly onto sternum II and sometimes tergum II, frequently 'crowding' sternite or tergite II (Fig. 68); pleurites not reduced in size or absent; tergum I lacking sclerite; male terga V and VI (at least) with both anterior and posterior sclerites.

Gonapophyses variable, sometimes hook-shaped, though lacking distal spur, more frequently obtuse, sometimes with ventral (median) margin concave or convex; ventral margin with setae long or of moderate length, abundant, setae sometimes also present on anterior margin. Ventral vulval margin not sclerotised, sometimes short, straight or convex; subgenital lobe absent, though posterior margin of sternum VII sometimes developed into two spikes (Fig. 73). Dorsal margin of vulva and postvulval area usually without pointed scales. Common oviduct without 'collar'.

Male subgenital plate with sternites VII, VIII and IX fused to s.g.p.r., sternite IX and postgenital sclerite sometimes fused; s.g.p.r. more heavily sclerotised than sternites (Fig. 68). Pseudostyli absent or, if present, long and broad, parallel-sided or with basal constriction (Figs 68, 71), or long and narrow (Fig. 72). Posterior margin of tergum IX not greatly expanded. Parameres more or less broad, sometimes fused together. Basiparameral sclerites absent. Mesomeres unfused apically, sometimes fused to b.a.l.s. in characteristic manner (Fig. 75) or to parameres, basally or in entirety, in the latter case apparently absent. Endophallus lacking spicular patch (cf. subgenus *Tricholipeurus*). Male genitalia depicted in Figs 74–76.

HOSTS. Bovidae (Artiodactyla).

COMMENTS. Emerson & Price (1982) distinguish their new species *orientalis* (described in *Bovicola*) from the very similar species *thompsoni* Bedford on the following grounds: 'The female of *B. orientalis* is smaller than that of *B. thompsoni* and the lateral margins of the forehead are even [sic] so slightly indented for *B. orientalis* and always even for *B. thompsoni*; the median plates on tergites II–VIII are of different shapes for the two species; the chaetotaxy of terminal abdominal segments is different, with each gonapophysis having at least 20 median and anterior setae for *B. thompsoni* [*orientalis* having, according to the preceding description, 12–17 setae]; and the posterior margin of the temple of *B. thompsoni* has small projections that are not present for *B. orientalis*. The male of *B. thompsoni* is unknown.' Five male and seven female paratypes of *B. orientalis* were examined in this study, together with a further eight males and eight females from the same host (*Capricornis crispus swinhoei*) not examined by Emerson & Price when they prepared their description of *orientalis*, and three females of *thompsoni*, including the holotype. Treating the supposed distinguishing characters in order, the three specimens of *thompsoni* are larger than any of the females from *C. c. swinhoei*; whilst none of the specimens of *thompsoni* has an indentation on the forehead (at the junction of the clypeo-frontal sulcus with the margin), not all of the specimens from *Capricornis c. swinhoei* have either; the shapes of abdominal tergites II–VIII are not significantly different in the two species; the chaetotaxy of the terminal abdominal segments is not different, and no specimen of *thompsoni* has more than 17 setae on the median and anterior margins of the gonapophyses; the small projections of the posterior temple margins are present in all specimens of *orientalis*. It seems, therefore, that the differences between the two species are twofold: host (*orientalis* being described from *Capricornis crispus swinhoei* and *thompsoni* being known only from *Capricornis sumatrensis sumartrensis*), and size. The biological significance of the latter character is not clear, and the two species may be found to differ in other characters not so far discovered. Until a larger sample can be examined, collected from more localities, no taxonomic action is taken to reduce the rank or synonymise *orientalis*, though on the basis of the information so far available the species probably should not stand.

SPECIES INCLUDED

adenota (Bedford, 1936) **comb. n.** from *Bovicola* (39 ♂, 35 ♀)
appendiculata (Piaget, 1880) (19 ♂, 25 ♀)
baxi Hopkins, 1947 (16 ♂, 24 ♀)
chorleyi (Hopkins, 1941) (21 ♂, 19 ♀)
crenelata (Piaget, 1880) (27 ♂, 20 ♀)
dimorpha (Bedford, 1939) **comb. n.** from *Bovicola* (syntype ♀)
fahrenholzi (Eichler, 1949) **comb. n.** from *Tricholipeurus*
harrisoni (Cummings, 1916) (3 ♂, 3 ♀)
hilli (Bedford, 1934) **comb. n.** from *Bovicola* (42 ♂, 27 ♀)
neotheileri Emerson & Price, 1971 (1 ♂, 6 ♀)
orientalis (Emerson & Price, 1982) **comb. n.** from *Bovicola* (108 ♂, 135 ♀)
ornata Werneck, 1957 (Holotype ♂)
pelea (Bedford, 1934) **comb. n.** from *Bovicola*

semitheileri Emerson & Price, 1971 (holotype ♂, allotype ♀)
theileri Bedford, 1928 (2 ♂. 4 ♀)
thompsoni (Bedford, 1936) **comb. n.** from *Bovicola* (3 ♀)

Subgenus *CERVICOLA* Kéler **gen. rev., stat. n.**

(Figs 66, 67, 70, 77, 78, 84–86)

Cervicola Kéler, 1934: 263. [Nomen nudum.]
Cervicola Kéler, 1938*a*: 460. Type-species: *Trichodectes tibialis* Kéler (nec Piaget) [= *Trichodectes meyeri* Taschenberg], by original designation.

DESCRIPTION. Anterior of head with osculum present, narrow or broad, deep or shallow; dorsal preantennal sulcus present; clypeal marginal carina broadened medially, either into simple bar with posterior margin straight or convex but occasionally with median posterior projection, or into longer posteriorly-developed sclerite with posterolateral angles more or less convex and more or less pronounced median posterior projection; anterolateral margin of head straight or slightly sinuate, in the latter case slightly concave at junction of margin and clypeofrontal sulcus and convex anteriorly; preantennal portion of head as long as or shorter than postantennal portion, outline triangular, trapezoid or rounded. Temple margin smoothly convex, slightly produced posteriad. Male scape with setae randomly scattered; male flagellum with two basally-articulated 'teeth'. Dorsum of head with setae more or less abundant, sometimes less so posteriorly than anteriorly.

Pterothorax with posterior setal row single.

Abdomen oval or elongate. Abdominal setae present anteriorly on all pleura except, occasionally, pleurum II, but may be very short, fine and difficult to see; anterior setae never on sterna and terga. Pleurum II never with sclerite extending onto sternum II; pleurites not reduced in size or absent; male terga V and VI (at least) with both anterior and posterior sclerites.

Gonapophyses hook-shaped, apex of curved portion acute or rounded, sometimes with distal (dorsal) spur (Figs 66, 67). Gonapophyses with setae long or of moderate length on posterior margin and sometimes on apex of 'hook', smaller setae sometimes present on anterior margin of 'hook'. Ventral vulval margin not sclerotised. Subgenital lobe absent. Dorsal margin of vulva and post-vulval area with pointed scales. Common oviduct at branching-point with folded and more or less apparent 'collar', sometimes partially sclerotised and refracting light when viewed in phase-contrast or bright field transmitted light.

Male subgenital plate with sternites VII, VIII and IX fused to s.g.p.r., though sternite IX sometimes not complete, s.g.p.r. sometimes not attaining posterior margin of segment IX, perisetal gaps sometimes absent; s.g.p.r. more heavily sclerotised than sternites. Pseudostyli absent or, if present, apically pointed and more or less broad (Fig. 78) or apically rounded and very narrow (Fig. 77). Posterior margins of male tergum IX not greatly expanded. Parameres broad or narrow, larger or smaller than mesomeres, may be reduced to small discs, in which case mesomeres absent; parameres fused or unfused; apices sometimes widely divergent. Basiparameral sclerites present or absent. Mesomeres absent or, if present, not fused apically, nor fused to parameres or b.a.l.s. Endophallus lacking spicular patch (cf. subgenus *Tricholipeurus*). Male genitalia depicted in Figs 84–86.

HOSTS. Bovidae and Cervidae (Artiodactyla).

COMMENTS. *Cervicola* was treated as a synonym of *Damalinia* by Werneck (1950), and of both *Damalinia* and *Bovicola* by Hopkins & Clay (1952, pp. 102 and 67 respectively). The history of the variations in status of *Cervicola* is presented in Table 3.

SPECIES INCLUDED

annectens Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (21 ♂, 25 ♀)
forficula (Piaget, 1880) (5 ♂, 8 ♀)
hendrickxi Hopkins, 1947 (4 ♂, 6 ♀)
hopkinsi Bedford, 1936 (15 ♂, 28 ♀)
lerouxi (Bedford, 1930) **comb. n.** from *Tricholipeurus* (9 ♀)
maai Emerson & Price, 1973 (holotype ♂, allotype ♀)
martinaglia (Bedford, 1936) (34 ♂, 27 ♀)
meyeri meyeri (Taschenberg, 1882) (5 ♂, 54 ♀)
meyeri hydropotis (Dobroruka, 1975) **comb. n.** from *Cervicola*
meyeri sika (Dobroruka, 1975) **comb. n.** from *Cervicola*
muntiacus (Séguy, 1948) (12 ♂, 12 ♀)
natalensis Emerson, 1964 (2 ♂, 2 ♀)

reduncae (Bedford, 1929) **stat. n., comb. n.** from *Tricholipeurus* [Raised from subspecies of *D. trabeculae*.] (28 ♂, 29 ♀)

trabeculae (Bedford, 1929) **comb. n.** from *Tricholipeurus* (10 ♂, 10 ♀)

ugandae (Werneck, 1950) **stat. n., comb. n.** from *Tricholipeurus* [Raised from subspecies of *D. trabeculae*.] (14 ♂, 13 ♀)

Unless otherwise stated, all species were previously considered as placed in *Damalinia* s. str.

Subgenus *TRICHOLIPEURUS* Bedford **stat. n.**

(Figs 4, 7, 8, 13, 65, 79–83)

Tricholipeurus Bedford, 1929: 514. Type-species: *Tricholipeurus aepycerus* Bedford, by original designation.

DESCRIPTION. Anterior of head variable, one of two types.

(*a*) Osculum absent; pulvinus short, not attaining anterior margin of head; dorsal preantennal sulcus absent; clypeal marginal carina insignificant, not, or only slightly, broadened medially; anterolateral margin of head straight posteriorly, convex anteriorly; preantennal portion of head as long as postantennal portion, outline rounded anteriorly (*D. (T.) conectens* only).

(*b*) Osculum present, rarely deep; dorsal preantennal sulcus present; clypeal marginal carina broadened medially either into simple bar with posterior margin straight or convex, or into longer posteriorly-developed U- or W-shaped sclerite, with posterolateral angles more or less acutely convex, and frequently with more or less pronounced median posterior projection; anterolateral margin straight, slightly sinuate, or slightly concave; preantennal portion of head longer or shorter than postantennal portion but not short, outline trapezoid or rectangular. Temple margin smoothly convex, more or less convexly produced posteriorly. Male scape with setal row frequently present, comprising four or five setae, though setae sometimes more or less randomly scattered; male flagellum with two or three basally-articulated 'teeth'. Dorsum of head with setae sometimes sparse.

Prothorax with median gap of posterior setal row sometimes almost the width of the posterior margin. Pterothorax with posterior setal row single.

Abdomen usually very elongate, narrow. Abdominal setae present anteriorly on all pleura except, occasionally, pleurum II, but may be very short, fine and difficult to see; anterior setae never on sterna and rarely on terga. Pleurum II never with sclerite extending onto sternum II; pleural sclerites frequently reduced to small anterior plate or absent; tergum I sometimes lacking sclerite; male terga lacking posterior sclerites, or with both anterior and posterior sclerites present on at least segments V and VI (though may be present on any segments up to II–VIII).

Gonapophyses variable, sometimes hook-shaped with distal spur and marginal setae on posterior (dorsal) margin of 'hook', or long with ventral margin convex, straight or sinuate (though not with lobe), apically pointed or rounded; marginal setae of moderate length. Ventral vulval margin sometimes sclerotised; subgenital lobe present, variable, not marginally serrate, ventrally smooth or scaled. Dorsal margin of vulva and post-vulval area without pointed scales. Common oviduct without 'collar'.

Male subgenital plate with sternites VII, VIII and IX fused to s.g.p.r.; perisetal gaps sometimes large, occasionally absent; s.g.p.r. heavily sclerotised and sternites sometimes very lightly scerlotised; s.g.p.r. sometimes curved or sinuate (Fig. 80). Pseudostyli absent or, if present, variable, short and rounded or apically angular, posteriorly or medially directed, narrow or broad, sometimes fused to form single caudal projection. Posterior margins of male tergum IX frequently greatly expanded (Fig. 79). Lateral struts of basal apodeme sometimes with anteposterior spur (Fig. 83). Parameres unfused or, if fused, plate apically pointed or bifurcate. Basiparameral sclerites present or absent. Mesomeres unfused apically or, if fused, symmetric or asymmetric, median extension absent or present; mesomeral arch frequently recurved abruptly at base to contact parameres, sometimes extended between b.a.l.s.; mesomeres not fused to parameres or b.a.l.s. Endophallus with patch of regularly-arranged and numerous spicules sometimes very apparent. Male genitalia depicted in Figs 81–83.

HOSTS. Bovidae and Cervidae (Artiodactyla).

COMMENTS. *Damalinia (T.) longiceps* is included following the statement of Clay & Hopkins (1955) that it resembles *D. (T.) spinifer* Hopkins 'most closely among known species'.

Tricholipeurus has been treated as a genus, synonym (Hopkins, 1943) and subgenus (Hopkins, 1949) of *Damalinia*; the history of the variations in status of *Tricholipeurus* is presented in Table 3.

SPECIES INCLUDED

aepycerus (Bedford, 1929) **comb. n.** from *Tricholipeurus* (1 ♂, 1 ♀)

albimarginata (Werneck, 1936) **comb. n.** from *Tricholipeurus* (9 ♂, 13 ♀)
antidorcus (Bedford, 1931) **comb. n.** from *Tricholipeurus* (11 ♂, 18 ♀)
bedfordi (Hill, 1922) **comb. n.** from *Tricholipeurus* (2 ♂, 2 ♀)
clayi (Werneck, 1938) **comb. n.** from *Tricholipeurus* (14 ♂, 12 ♀)
conectens Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (18 ♂, 16 ♀)
cornuta cornuta (Gervais, 1844) **comb. n.** from *Tricholipeurus* (20 ♂, 27 ♀)
cornuta ourebiae Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (18 ♂, 17 ♀)
dorcephali (Werneck, 1936) **comb. n.** from *Tricholipeurus* (2 ♂, 2 ♀)
elongata (Bedford, 1934) **comb. n.** from *Tricholipeurus* (10 ♂, 10 ♀)
indica (Werneck, 1950) **comb. n.** from *Tricholipeurus* (65 ♂, 60 ♀)
lineata (Bedford, 1920) **comb. n.** from *Tricholipeurus* (75 ♂, 83 ♀)
lipeuroides (Megnin, 1884) **comb. n.** from *Tricholipeurus* (106 ♂, 91 ♀)
longiceps (Rudow, 1866)
moschatus (Emerson & Price, 1971) **comb. n.** from *Tricholipeurus* (holotype ♂, disassociated ♂ head)
pakenhami (Werneck, 1947) **comb. n.** from *Tricholipeurus* (21 ♂, 20 ♀)
parallela (Osborn, 1896) **comb. n.** from *Tricholipeurus* (50 ♂, 106 ♀)
parkeri (Hopkins, 1941) **comb. n.** from *Tricholipeurus* (10 ♂, 10 ♀)
spinifer Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (17 ♂, 16 ♀)
victoriae Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (33 ♂, 35 ♀)

EUTRICHOPHILINAE Kéler

Genus *EUTRICHOPHILUS* Mjöberg

(Figs 87–93)

Eutrichophilus Mjöberg, 1910: 71. Type-species: *Eutrichophilus cercolabes* Mjöberg, by subsequent designation (Harrison, 1916*a*: 21).

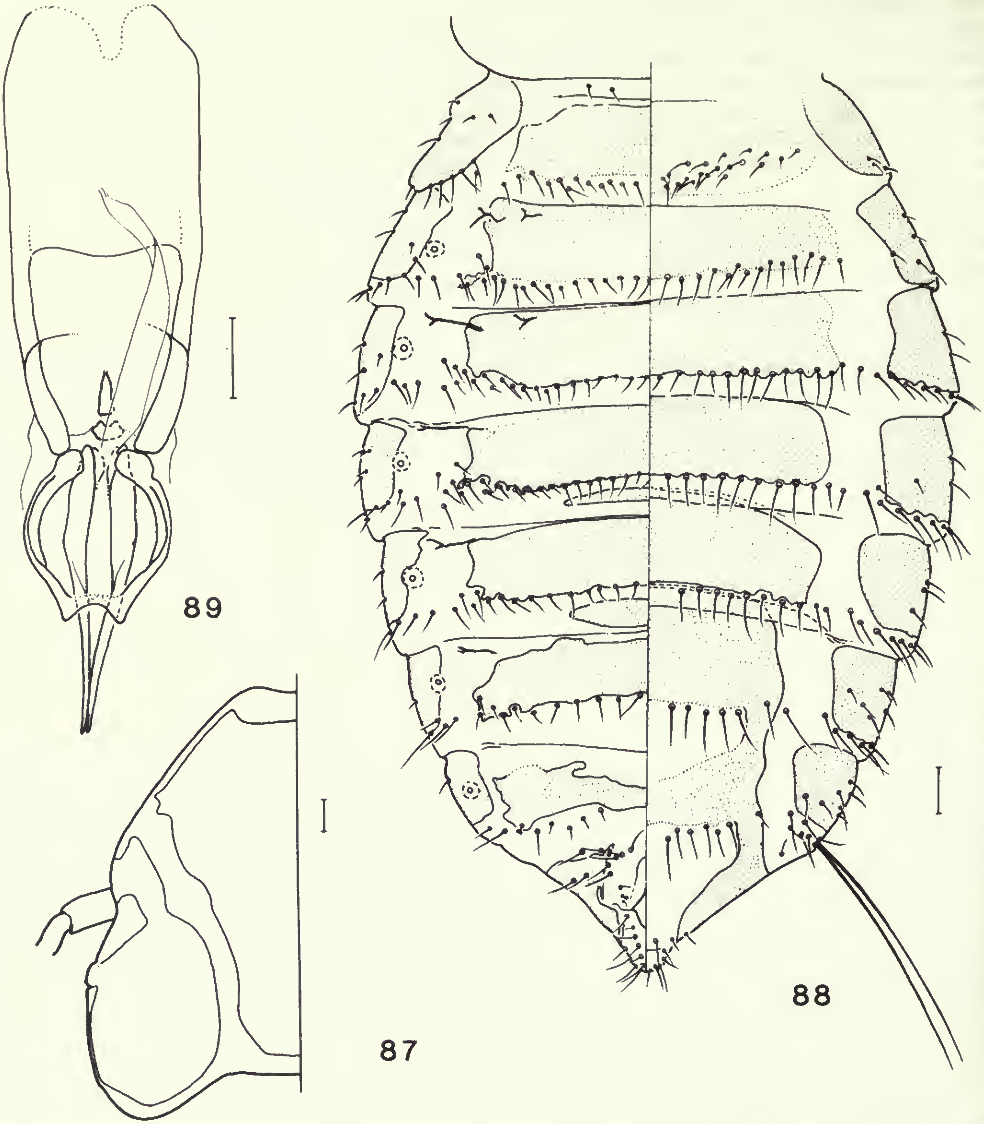
DESCRIPTION. Anterior of head with osculum present or absent, but pulvinus always attaining margin; dorsal preantennal sulcus absent; clypeal marginal carina with median expansion absent or slight, or present as broad or narrow parallel-sided bar with transverse margins convex, straight, or concave; anterolateral margin of head straight or convex; preantennal portion of head long or short; outline triangular, rounded or broadly trapezoid. Temple margin convex or with posterolateral angle apparent; temples greatly expanded posteriad (Fig. 87). Male scape expanded, with longitudinal setal row present and comprising two setae; male flagellomeres fused; female flagellomeres fused or flagellum comprising two flagellomeres; male flagellum very long, with two basally-articulated 'teeth'. Dorsum of head with setae short or long, sometimes longer anteriorly than posteriorly. Sitophore sclerite unmodified.

Thorax with dorsal setae short or of moderate length marginally or submarginally on posterior of prothorax and pterothorax, absent from disc of both; one or two long setae on posterolateral margins of pterothorax.

Abdomen oval and elongate. Abdominal spiracles present on segments III–VIII. Abdominal setae short or of moderate length, with tufts of long setae on at least pleurum VIII, sometimes also pleurum VII (males) or IX (females) (Fig. 88); anterior setae present on all pleura but absent from sterna and terga; postero-lateral setae present. Abdominal pleura lacking projections dorsally or ventrally. Sclerites present on sterna, terga and pleura (where present) of all pre-genital abdominal segments except, sometimes, tergum I, which may be very small; male terga, at least of abdominal segments V and VI, with anterior and posterior sclerites.

Gonapophyses frequently large, broadly triangular or rounded, ventral margin lacking lobe but with more or less dense marginal setae which are long or of moderate length. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; smoothly convex, with or without median indentation or setose projection; subgenital lobe absent. Female terminalia depicted in Fig. 90.

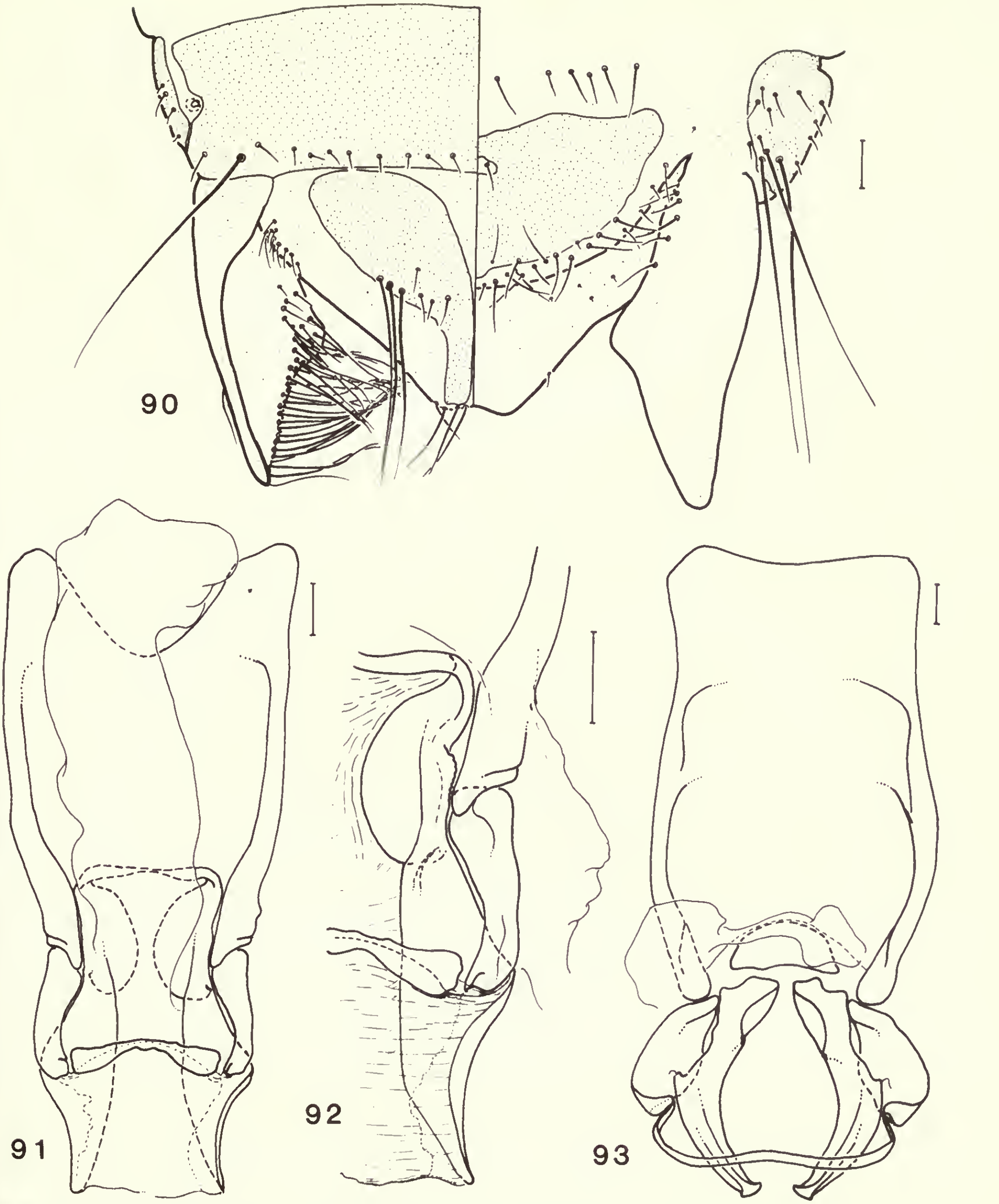
Male subgenital plate with sternites VII and VIII present and fused to s.g.p.r., IX absent or, if present, fused to s.g.p.r. (Fig. 88). Pseudostyli absent. Male genital opening dorsal, male segment IX posterior. Parameres long or short, narrow or broad; with basiparameral sclerite or flange sometimes present and fused medially, thus linking parameres, but otherwise unfused. Mesomeres present, fused apically to form arch with no median extension; arch smoothly rounded, or with lateral desclerotisations, in which case median portion is straight and at right angles to lateral portions, very poorly sclerotised and thin, or absent. Male genitalia depicted in Figs 89, 91, 92.



Figs 87–89 *Eutrichophilus* species. 87, *E. minor*, ♀ head, dorsal. 88, *E. setosus*, ♂ abdomen. 89, *E. setosus*, ♂ genitalia.

Hosts. Erethizontidae (Rodentia).

Species included
- ***cercolabes*** Mjöberg, 1910 (29 ♂, 25 ♀)
- ***comitans*** Werneck, 1950 (6 ♂, 2 ♀)
- ***cordiceps*** Mjöberg, 1910 (23 ♂, 27 ♀)
- ***exiguus*** Werneck, 1950 (holotype ♂, allotype ♀)
- ***guyanensis*** Werneck, 1950 (8 ♂, 7 ♀)
- ***lobatus*** Ewing, 1936 (5 ♂, 8 ♀)
- ***maximus*** Bedford, 1939 (11 ♂, 11 ♀)
- ***mexicanus*** (Rudow, 1866) (50 ♂, 50 ♀)
- ***minor*** Mjöberg, 1910 (34 ♂, 27 ♀)
- ***moojeni*** Werneck, 1945 (3 ♂, 3 ♀)
- ***setosus*** (Giebel, 1874) (102 ♂, 102 ♀)



Figs 90–93 *Eutrichophilus* species. 90, *E. maximus*, ♀ terminalia. 91, *E. guyanensis*, ♂ genitalia. 92, *E. guyanensis*, ♂ genitalia, detail. 93, *E. moojeni*, ♂ genitalia.

DASYONYGINAE Kéler

Genus *CEBIDICOLA* Bedford

(Figs 94–99)

Cebidicola Bedford, 1936: 52. Type-species: *Trichodectes armatus* Neumann, by original designation.

Meganarion Kéler, 1938*a*: 465. Type-species: *Trichodectes armatus* Neumann, by original designation. [Synonymy by Eichler, 1941.]

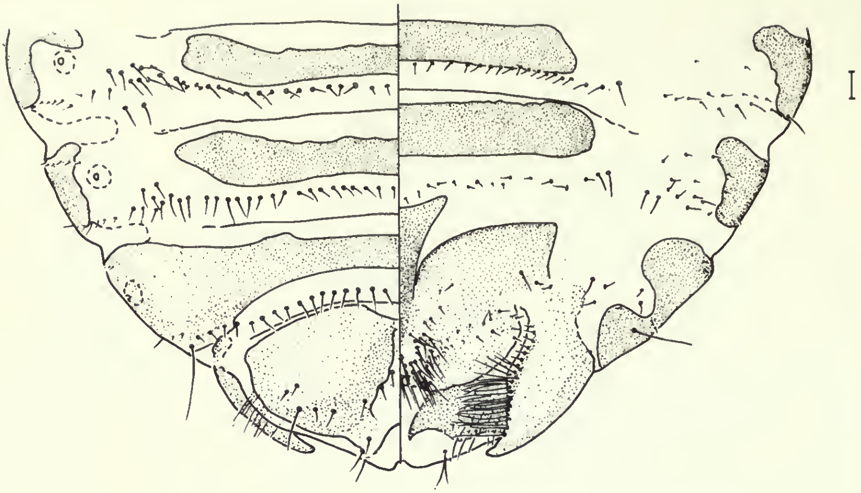
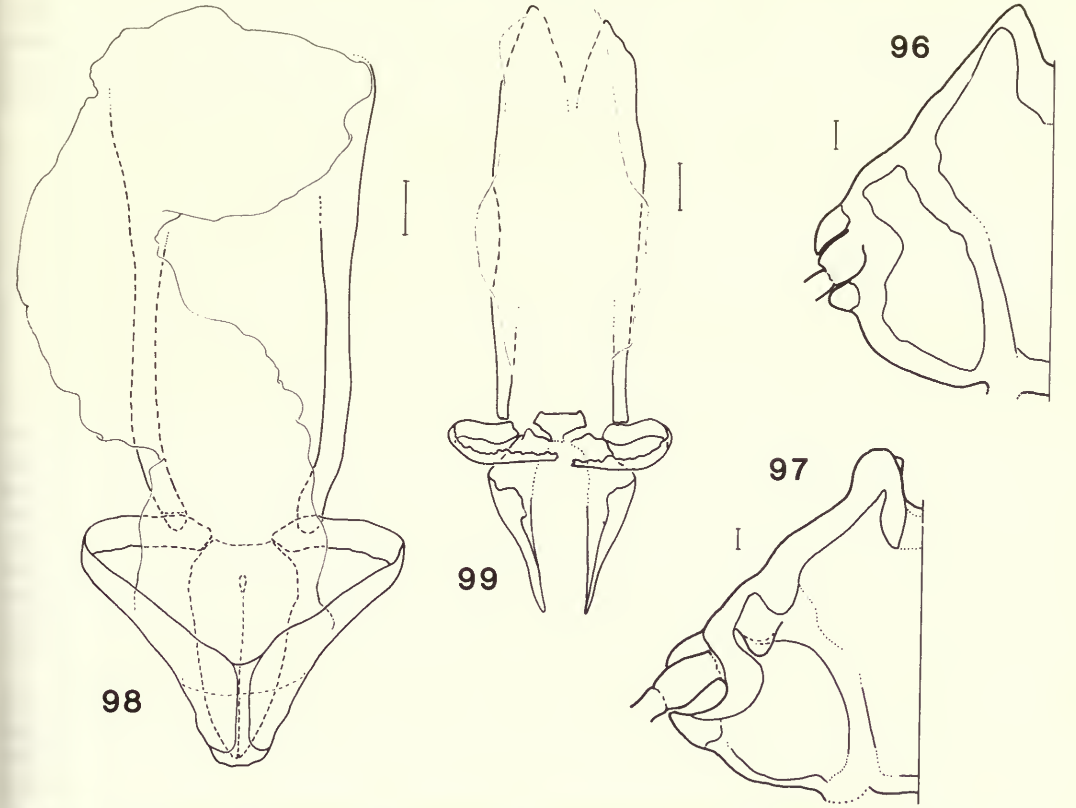


Fig. 94 *Cebidicola armatus*, ♀ terminalia.

Fig. 95 *Cebidicola armatus*, ♂ abdomen.



Figs 96–99 *Cebidicola* species. 96, *C. semistriatus*, ♀ head, dorsal. 97, *C. armatus*, ♀ head, dorsal. 98, *C. armatus*, ♂ genitalia. 99, *C. extrarius*, ♂ genitalia.

Description. Anterior of head with osculum present, deep; dorsal preantennal sulcus present or absent; clypeal marginal carina broadened medially into dorsal, posteriorly convex, sclerite; anterolateral margin straight, slightly convex, concave or sinuate anteriorly, more or less abruptly concave at junction with clypeofrontal sulcus, with or without anterior sclerotised projection on either side of osculum (Figs 96, 97); preantennal outline broadly triangular. Temple margin convex or slightly acute and angular posterolaterally, with eyes more or less prominent (Figs 96, 97). Male scape expanded, with setal row present and comprising two or more setae; male flagellomeres fused, with two basally-articulated 'teeth'; female flagellomeres fused or unfused. Dorsum of head with setae short or of moderate length, sparse. Sitophore sclerite unmodified.

Tarsal claws lacking ventral spines or teeth. Postcoxale absent or present, not greatly developed. Thoracic setae present dorsally only along posterior and posterolateral margins of pterothorax; setae short medially, longer laterally. Atrium of thoracic spiracle tubular or conical.

Abdomen oval, sometimes tapering posteriorly more in male than female. Abdominal spiracles present on segments III–VIII. Abdominal setae short or of moderate length, longest on pleura VI–VIII; anterior setae sometimes present on pleura and laterally on sterna and terga; postero-lateral setae present, sometimes numbering more than one per site. Pleural projection present ventrally on abdominal pleurum IV, large, sclerotised. Sclerites present on all abdominal pleura, on at least abdominal terga II to VIII and at least abdominal sterna V to VII; male terga, at least on segments V–VII, with anterior and posterior sclerites (Fig. 95).

Gonapophyses broad, especially medially, though lobe absent; marginal setae long, densely crowded. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; sometimes expanded, otherwise smoothly convex (Fig. 94); bilobed median spinose projection may be present, but subgenital lobe absent. Median longitudinal sclerite sometimes present on female sternum VIII (Fig. 94).

Male subgenital plate with sternite VII fused to s.g.p.r., VIII fused or not fused to s.g.p.r., and IX absent or, if present, not fused to s.g.p.r. Pseudostyli absent or, if present, small, slender, incurved (Fig. 95). Male genital opening postero-dorsal or dorsal. Parameres fused or unfused; basiparameral sclerites present, fused. Mesomeres present, fused or unfused and, if fused, median extension absent; mesomeral arch produced basally between b.a.l.s. to contact parameres, which do not meet b.a.l.s. Male genitalia depicted in Figs 98, 99.

HOSTS. Cebidae (Primates).

SPECIES INCLUDED
armatus (Neumann, 1913) (3 ♂, 4 ♀)
extrarius Werneck, 1950 (21 ♂, 13 ♀)
semiarmatus (Neumann, 1913) (12 ♂, 12 ♀)

Genus ***PROCAVICOLA*** Bedford

The genus *Procavicola* comprises two subgenera.

DESCRIPTION. Anterior of head with osculum present, semicircular; dorsal preantennal sulcus present; clypeal marginal carina broadened medially into dorsal, posteriorly convex, sclerite (Fig. 106); conus large, as long as female scape; anterolateral margin of head straight or convex anteriorly, more or less abruptly concave at junction with clypeofrontal sulcus; preantennal outline broadly triangular. Temple margin smoothly convex, sometimes produced posteriad, or with postero-lateral angle developed into posteriorly-projecting triangular or rounded process*. Male scape expanded, with setal row represented by two setae only; male flagellomeres fused, with two basally-articulated 'teeth'; female flagellomeres unfused and closely associated, fused to two closely associated annulations, or completely fused*. Dorsum of head with setae short, sparse; anterior margin of head with setae longer than on disc. Sitophore sclerite unmodified.

Tarsal claws lacking ventral spines or teeth. Postcoxale of metathoracic leg absent or present; if present, may be well developed, but not to the same degree as described for *Procaviphilus (Meganarionoides)* and not fused to abdominal pleurite II. Thoracic setae present dorsally only along posterior and latero-posterior margins of prothorax and pterothorax; setae short, except for laterally on pterothorax, where of moderate length.

Abdomen oval, more or less elongate (Figs 103, 105). Abdominal spiracles present on segments III–VIII, all approximately the same size. Abdominal setae short or of moderate length; anterior setae present on pleura only; postero-lateral setae present, sometimes numbering more than one per site*. Pleural projections present dorsally and ventrally on abdominal pleurum IV, sclerotised. Sclerites present on sterna, terga and pleura of all abdominal segments except, occasionally, tergum I*; male terga, at least of segments IV–VI, with anterior and posterior sclerites; second abdominal sternum with broad, heavily-sclerotised apophysis underlying sternite, articulating with median extensions of abdominal pleurite II (Figs 103, 105).

Gonapophyses broad, lacking lobe; marginal setae lacking tubercles, occasionally on small conical protuberances (Figs 101, 102). Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; expanded, sometimes W-shaped medially (Fig. 100), sometimes broadened posteriorly (Fig. 101), sometimes contracted, shorter than length of gonapophyses (Fig. 102)*.

Male subgenital plate with sternites VII and VIII present and fused to s.g.p.r., sternite IX absent or, if present, fused to s.g.p.r. and perisetal gaps small*; s.g.p.r. not always attaining posterior margin of segment IX*. Pseudostyli absent (Figs 103–105). Male genital opening postero-dorsal. Male genitalia very variable*; parameres not fused, basiparameral sclerites present or absent*, mesomeres fused or unfused*.

HOSTS. Procaviidae (Hyracoidea).

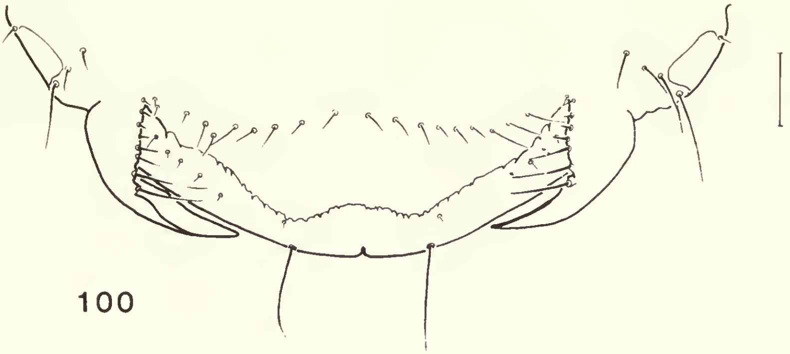
Subgenus ***PROCAVICOLA*** Bedford

(Figs 100, 104–106, 109)

Procavicola Bedford, 1932: 711. Type-species: *Trichodectes sternatus* Bedford, by original designation.

DESCRIPTION. Temple margin smoothly convex, sometimes projecting posteriorly, but never with posterior membranous or lightly-sclerotised process.

Postero-lateral setae present, single at each site. Sclerites present on sterna, terga and pleura of all abdominal segments except segment I, where tergal sclerite absent.



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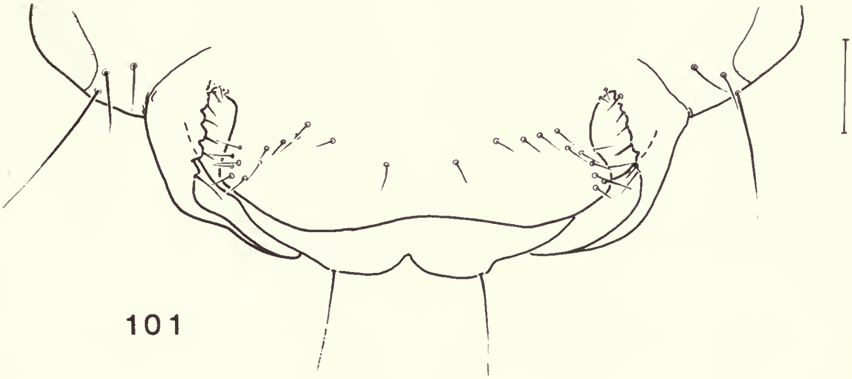

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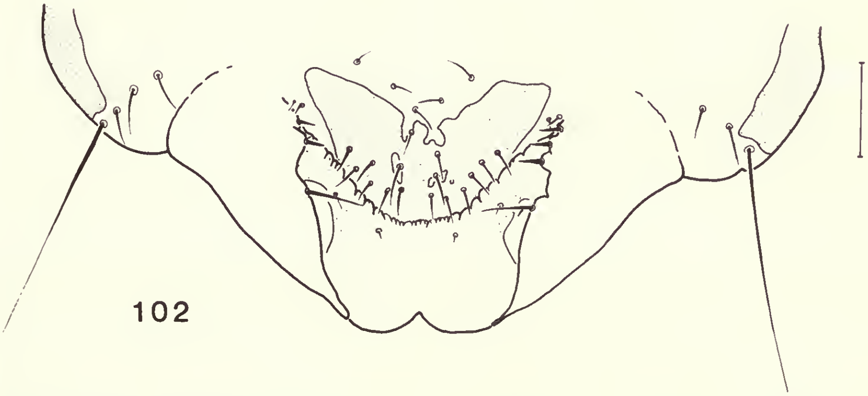

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Figs 100–102 *Procavicola* species, ♀ terminalia, ventral. 100, *P. (P.) natalensis*. 101, *P. (Condylocephalus) lindfieldi*. 102, *P. (C.) dissimilis*.

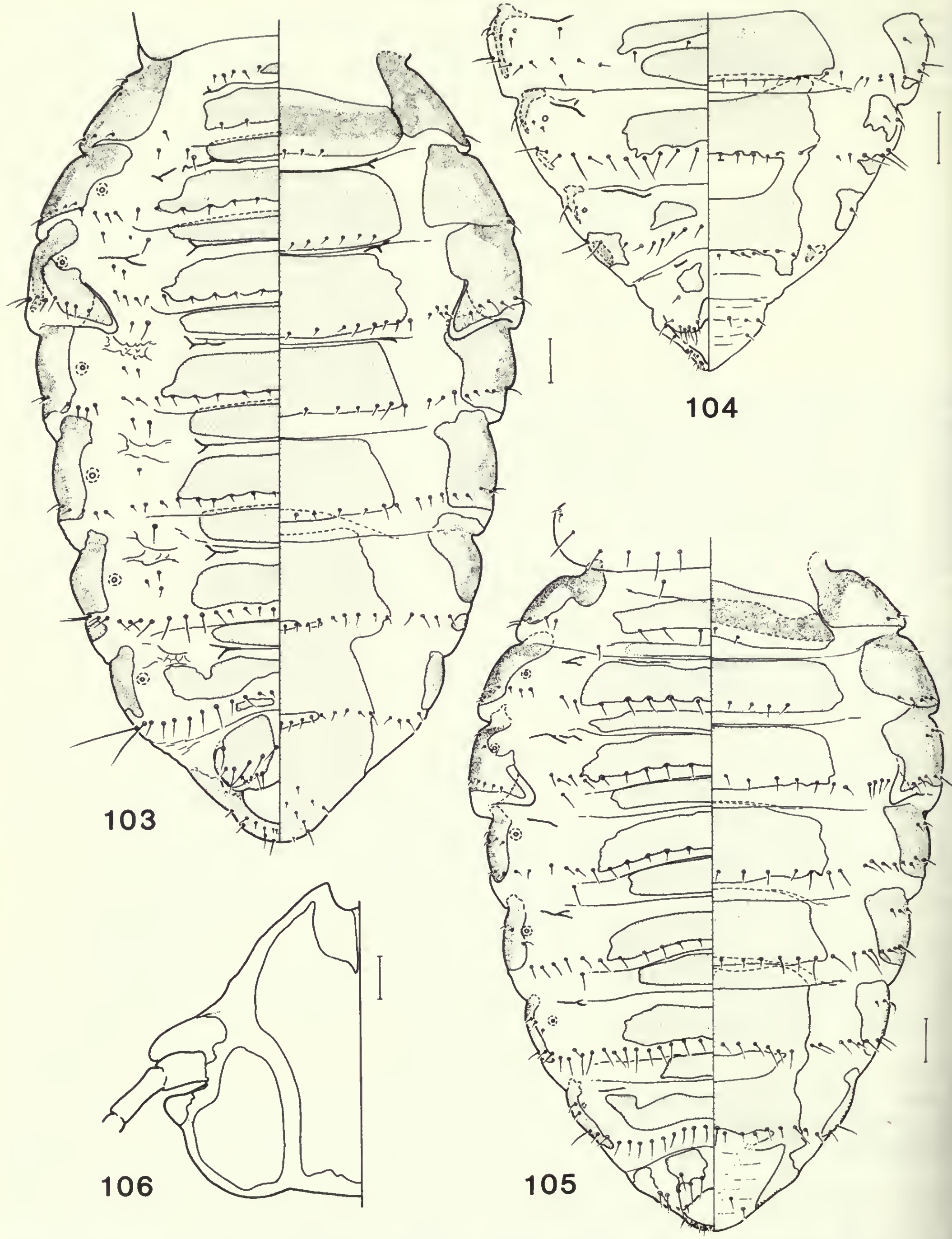
Ventral vulval margin expanded as described, much broader than length of gonapophyses (Fig. 100).

Male subgenital plate with sternites VII and VIII present and fused to s.g.p.r., sternite IX absent; s.g.p.r. may be very slender, may not attain posterior margin of segment IX (Figs 104, 105). Parameres unfused, more or less narrow, rod-like, sometimes asymmetrically curved. Basiparameral sclerites frequently present, fused or separate. Mesomeres not fused, short. Endophallus lacking large, hook-like sclerites. Male genitalia depicted in Fig. 109.

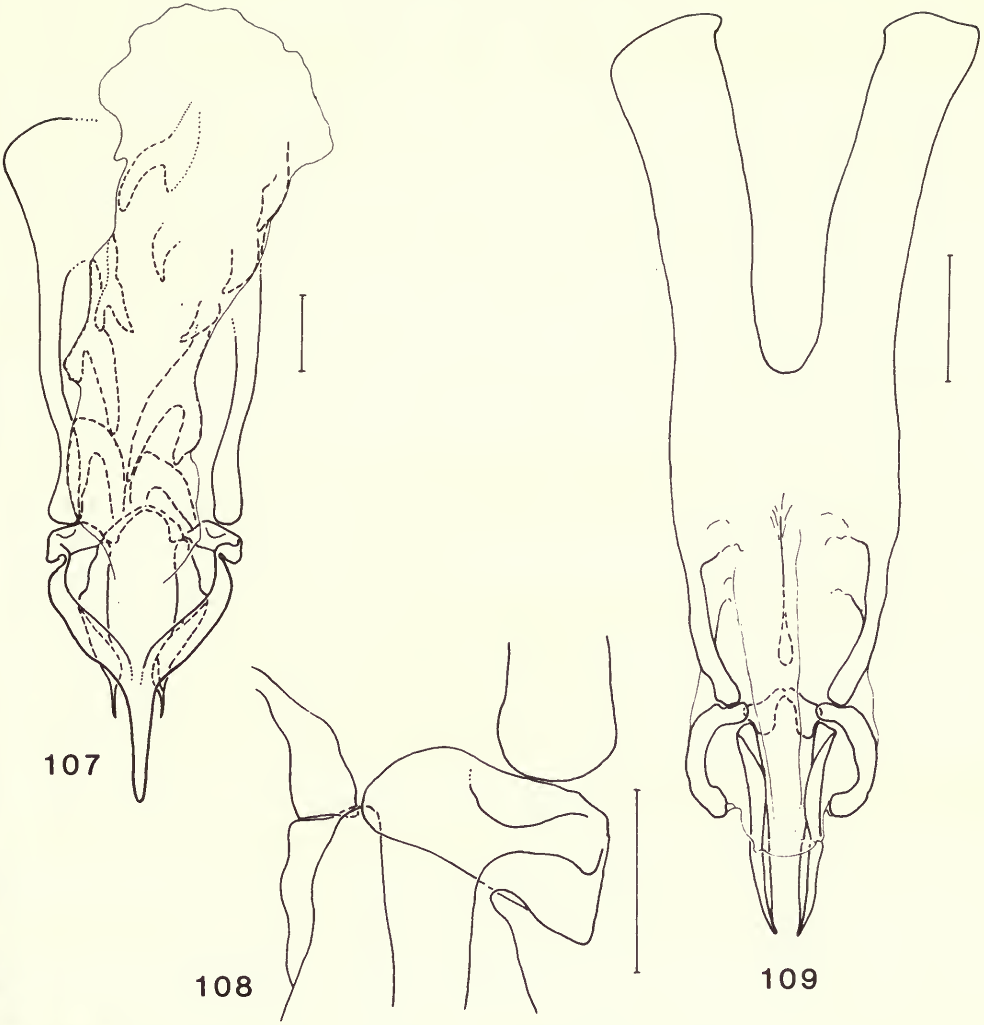
Hosts. Procaviidae (Hyracoidea).

Species included

affinis Werneck, 1941 (10 ♂, 13 ♀)



Figs 103–106 *Procavicola* species. 103, *P. (Condylocephalus) dissimilis*, ♂ abdomen. 104, *P. (P.) vicinus*, ♂ terminalia. 105, *P. (P.) eichleri*, ♂ abdomen. 106, *P. (P.) natalensis*, ♀ head, dorsal.



Figs 107–109 *Procavicola* species, ♂ genitalia. 107, *P. (Condylocephalus) dissimilis*. 108, *P. (C.) dissimilis*, detail of right paramere and mesomere at junction with basal apodeme. 109, *P. (P.) pretoriensis*.

brucei Werneck, 1941 (43 ♂, 48 ♀)
eichleri Werneck, 1941 (45 ♂, 56 ♀)
emarginatus (Bedford, 1928) (16 ♂, 19 ♀)
furca Bedford, 1939 (1 ♂)
heterohyracis Bedford, 1932 (3 ♂, 1 ♀)
lopesi lopesi Bedford, 1939 (32 ♂, 40 ♀)
lopesi vicinus Werneck, 1941 (8 ♂, 10 ♀)
mokeetsi Bedford, 1939 (20 ♂, 15 ♀)
natalensis Bedford, 1932 (23 ♂, 12 ♀)
parvus Bedford, 1932 (8 ♂, 6 ♀)
pretoriensis Bedford, 1932 (23 ♂, 21 ♀)
shoanus Maltbaek, 1937
sternatus (Bedford, 1928) (9 ♂, 8 ♀)
subparvus Bedford, 1932 (6 ♂, 9 ♀)
thorntoni Hopkins, 1942 (18 ♂, 22 ♀)
ugandensis Werneck, 1941 (17 ♂, 18 ♀)

Subgenus *CONDYLOCEPHALUS* Werneck

(Figs 101–103, 107, 108)

Condylocephalus Werneck, 1941: 497 [as subgenus of *Procavicola* Bedford]. Type-species: *Procavicola (Condylocephalus) bedfordi* Werneck, by original designation.

DESCRIPTION. Temple margin convex, with posteriorly-projecting membranous or lightly-sclerotised process, more apparent in male than female, triangular or as small rounded bump (*linfieldi* females). Female flagellomeres unfused, but closely associated.

Abdomen with postero-lateral setae present, frequently doubled, trebled or numerous at each site. Sclerites present on sterna, terga and pleura of all abdominal segments.

Ventral vulval margin expanded, sometimes broadened posteriorly and broader than length of gonapophyses (Fig; 101), otherwise narrower, width less than length of gonapophyses (Fig. 102).

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., with perisetal gaps small (Fig. 103). Parameres unfused, curved, with anterolateral projections, not asymmetric. Basiparameral sclerites present, fused or unfused. Mesomeres fused apically; mesomeral arch with median extension and lateral double flexion (Figs 107, 108). Endophallus ornamented with large, hook-like sclerites (Fig. 107).

HOSTS. Procaviidae (Hyracoidea).

COMMENTS. Though *Condylocephalus* has been treated by most authors as a subgenus of *Procavicola*, Eichler (1963) considered it to have full generic status.

SPECIES INCLUDED

bedfordi Werneck, 1941 (2 ♂, 1 ♀)
dissimilis Werneck, 1941 (64 ♂, 58 ♀)
hopkinsi Werneck, 1941 (24 ♂, 29 ♀)
lindfieldi (Hill, 1922) (77 ♂, 65 ♀)
univirgatus (Neumann, 1913) (33 ♂, 32 ♀)

Genus *PROCAVIPHILUS* Bedford

The genus *Procaviphilus* comprises two subgenera.

DESCRIPTION. Surface of head, thorax and abdomen frequently covered with clearly-visible scales or sclerotised nodules.

Anterior of head variable, one of two types: 'procaviphilus' or 'procavicola'*.

(*a*) 'procaviphilus' type. Osculum absent or, if present, slightly concave only; dorsal preantennal sulcus absent; clypeal marginal carina broadened medially into straight or slightly curved bar (Fig. 112); conus small, not as long as female scape; anterolateral margin of head straight or convex anteriorly, no abrupt concavity at junction with clypeofrontal sulcus; preantennal outline trapezoid (Fig. 112).

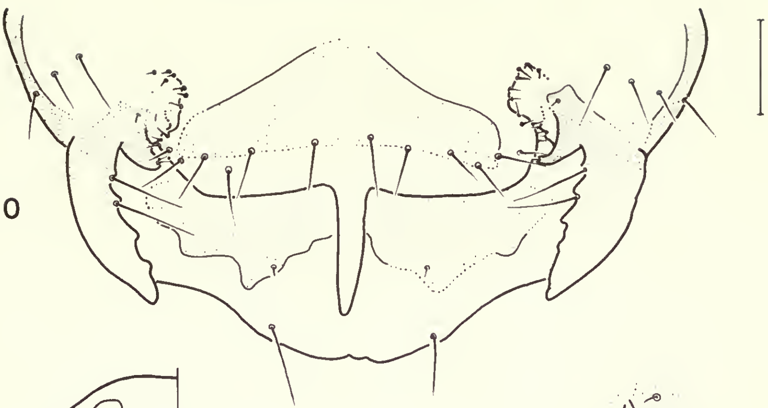
(*b*) 'procavicola' type. Osculum present, semicircular; dorsal preantennal sulcus present or absent; clypeal marginal carina broadened medially into dorsal, posteriorly convex, sclerite (Fig. 106); conus large, as long as female scape; anterolateral margin of head convex anteriorly, more or less abruptly concave at junction with clypeofrontal sulcus; preantennal outline broadly triangular.

Temple margin smoothly convex, more or less projecting posteriorly. Male scape expanded, with setal row represented by two setae only; male flagellomeres fused, with two basally-articulated 'teeth'; female flagellomeres unfused, though sometimes very closely associated. Dorsum of head with setae short, sparse. Sitophore sclerite unmodified.

Tarsal claws lacking ventral spines or teeth. Postcoxale of leg III absent or, if present, frequently enlarged, heavily sclerotised, displaced posteriad to occupy abdominal sternum II, and fused to sclerite of abdominal pleurum II, in which case gap between postcoxales sometimes obscured by sternite II*. Thoracic setae present dorsally only along posterior and lateroposterior margins of prothorax and pterothorax; setae short, except for laterally on pterothorax, where of moderate length.

Abdomen oval-elongate. Abdominal spiracles present on segments III to VIII, though sometimes very small and possibly non-functional on VIII*. Abdominal setae short or of moderate length; anterior setae present on pleura only, sparse; postero-lateral seta present. Pleural projections present ventrally and dorsally on abdominal pleurum IV, sclerotised. Sclerites, frequently faint, present on sterna, terga and pleura of all abdominal segments except I; male terga, especially tergum VI, frequently with anterior and posterior sclerites.

Gonapophyses with setae non-tuberculate and, frequently, tuberculate; setal tubercles, if present,



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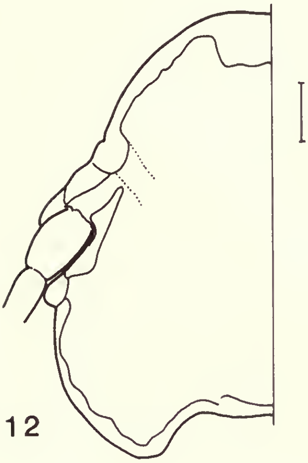

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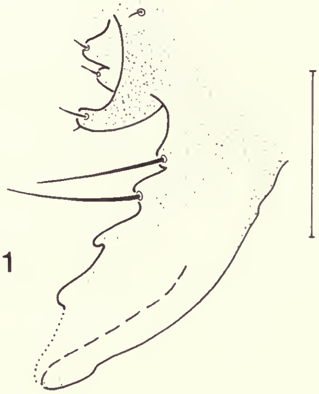

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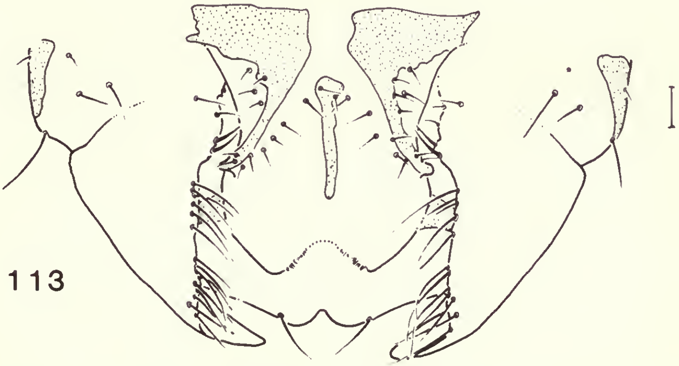

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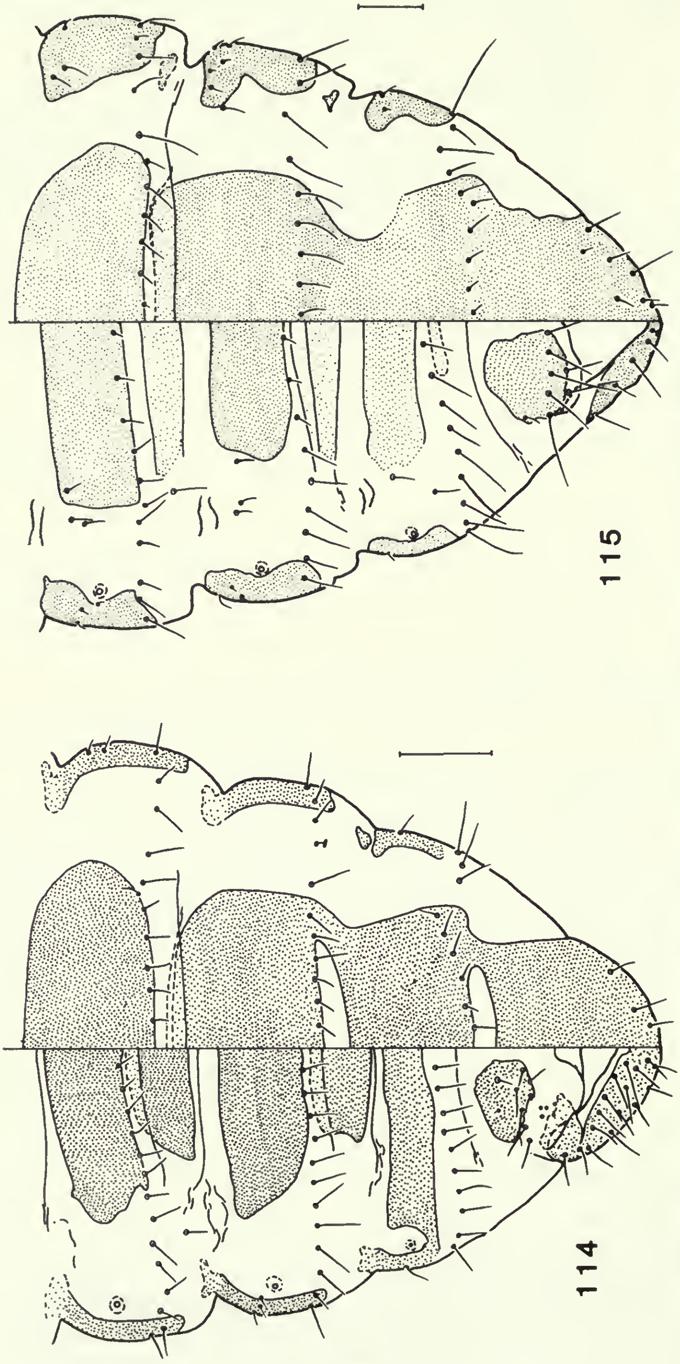
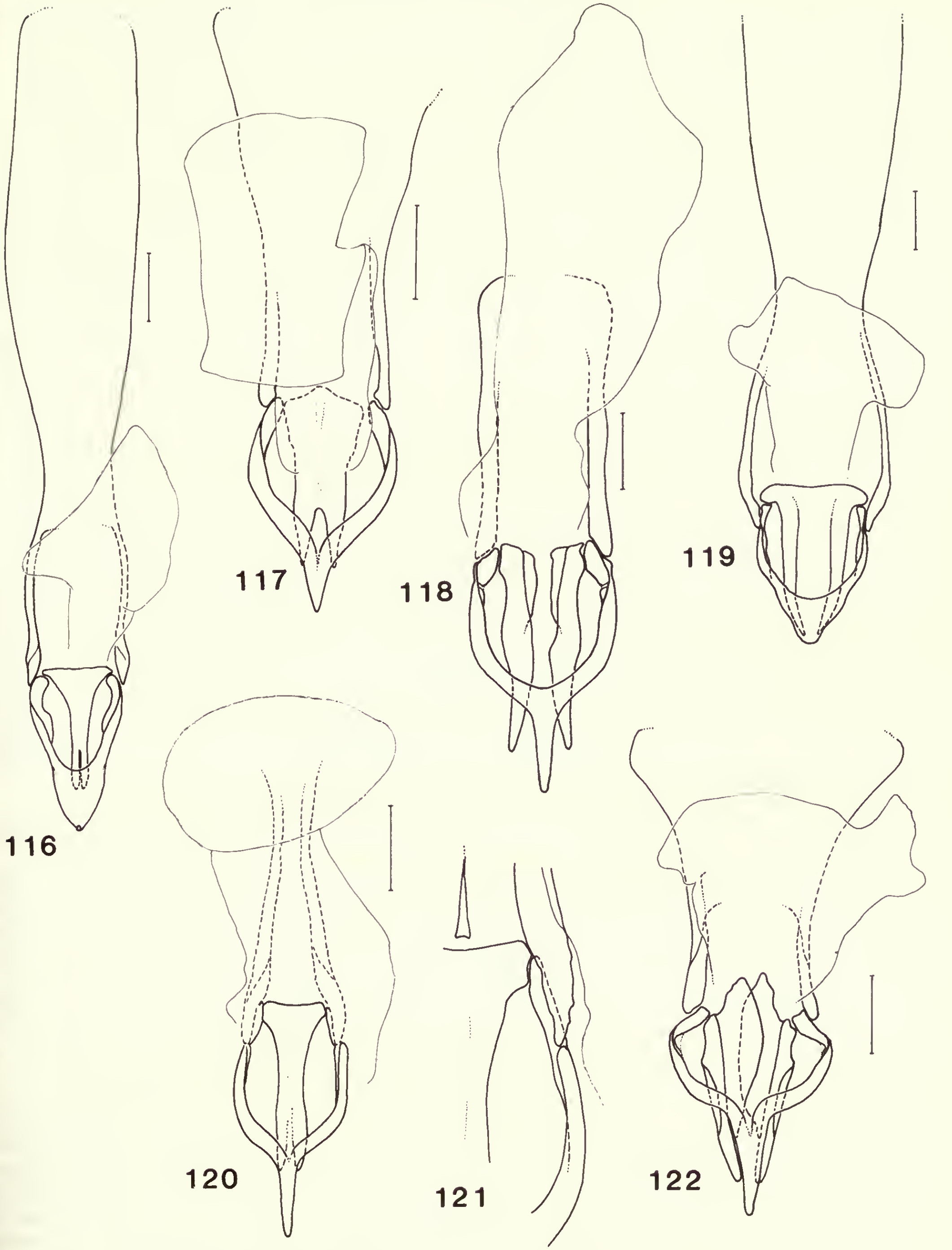
Figs 110–113 *Procaviphilus* species. 110, *P. (Meganarionoides) n. baculatus*, ♀ terminalia, ventral. 111, *P. (M.) n. baculatus*, ♀ gonapophysis, ventral. 112, *P. (P.) f. granuloides*, ♀ head, dorsal. 113, *P. (M.) scutifer*, ♀ terminalia, ventral.

sometimes fused characteristically*; lobe absent or, if apparently present, formed of fused tubercles and thick, with submarginal setae (Fig. 111). Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; expanded, frequently with posterior broadening (Fig. 110), sometimes lengthened (Fig. 113) or with median lobulate process (Fig. 110)*.

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., perisetal gaps very small or absent, rarely large (Figs 114, 115). Pseudostyli absent. Male genital opening posterodorsal. Male genitalia very variable: basal apodeme short or long with median constriction*; parameres unfused, frequently with basal flange, or fused, faintly or clearly, and parameral plate apically bifurcate. Basiparameral sclerites absent. Mesomeres fused, basally extending between b.a.l.s. to contact parameres, which



Figs 114, 115 *Procaviphilus (Meganarionoides)* species, ♂ terminalia. 114, *P. (M.) angolensis*. 115, *P. (M.) scutifer*.



Figs 116–122 *Procaviphilus* species, ♂ genitalia. 116, *P. (Meganarionoides) angolensis*. 117, *P. (P.) f. granuloides*. 118, *P. (P.) dubius*. 119, *P. (M.) n. neumanni*. 120, *P. (M.) jordani*. 121, *P. (M.) jordani*, detail of junction of mesomere, paramere and basal apodeme. 122, *P. (M.) serraticus*.

may also contact b.a.l.s. (Figs 116, 117, 119–121); mesomeral arch with median extension more or less broad, lateral desclerotisations sometimes apparent (Figs 118, 122)*.

HOSTS. Procaviidae (Hyracoidea) and Cercopithecidae (Primates).

Subgenus *PROCAVIPHILUS* Bedford

(Figs 112, 117, 118)

Procaviphilus Bedford, 1932: 725. Type-species: *Procaviphilus ferrisi* Bedford, by original designation.

DESCRIPTION. Anterior of head of 'procaviphilus' type.

Postcoxale absent or, if present, not greatly developed and not fused to abdominal pleurite II.

Abdominal spiracles all the same size.

Gonapophyses with setal tubercles present but not fused; gonapophyses not apically truncate. Ventral vulval margin expanded, sometimes W-shaped medially, not broadened posteriorly.

Male genitalia with basal apodeme short, attaining abdominal segment VII or VI, lacking median constriction; mesomeral arch with lateral desclerotisations.

HOSTS. Procaviidae (Hyracoidea).

SPECIES INCLUDED

dubius Werneck, 1941 (10 ♂, 10 ♀)
ferrisi ferrisi Bedford, 1932 (12 ♂, 5 ♀)
ferrisi granuloides Bedford, 1939 (26 ♂, 19 ♀)
ferrisi hindei Werneck, 1946 (3 ♂, 4 ♀)
granulatus (Ferris, 1930) (13 ♂, 17 ♀)
harrisi Werneck, 1946 (15 ♂, 19 ♀)
robertsi (Bedford, 1928) (16 ♂, 18 ♀)

Subgenus *MEGANARIONOIDES* Eichler

(Figs 110, 111, 113–116, 119–122)

Meganarionoides Eichler, 1940: 159. Type-species: *Trichodectes colobi* Kellogg, by original designation.
Acondylocephalus Werneck, 1941: 478 [as subgenus of *Procavicola* Bedford]. Type-species: *Trichodectes congoensis* Ferris, by original designation. [Synonymy by Werneck, 1946: 85.]

DESCRIPTION. Anterior of head of 'procaviphilus' type or, more frequently, of 'procavicola' type.

Postcoxale of leg III enlarged as described in description of *Procaviphilus* s.l., and fused to abdominal pleurite II, at least in female.

Gonapophyses with setal tubercles absent (in which case gonapophyses characteristically broad and vulval margin produced posteriad as in Fig. 113), or present basally, marginally and submarginally, and fused characteristically to form basal process (Fig. 111); gonapophyses more or less truncate. Ventral vulval margin expanded, as described for *Procaviphilus* s. str. or, more frequently, broadened posteriorly, sometimes produced posteriad (Fig. 113) or with median lobulate process (Fig. 110).

Male genitalia with basal apodeme attaining abdominal segment VII or VI or, more frequently, long, attaining segment III or II, with median constriction (Figs 116, 119); mesomeral arch with or without lateral desclerotisation.

HOSTS. Procaviidae (Hyracoidea) and Cercopithecidae (Primates).

COMMENTS. There has been some disagreement in the literature over the correct host of one species in this subgenus. Most species included in *P. (Meganarionoides)* are parasites of Procaviidae, as are all other species in the subfamily Dasyonyginae (other than the three species of *Cebidicola*, which are included in the subfamily for the first time in this study). One species, however, *P. (M.) colobi* (Kellogg, 1910), was described from the monkey *Colobus guereza caudatus* Thomas. Kéler (1938*a*) included this species with the others described from Primates in his genus *Meganarion* (an objective synonym of *Cebidicola*), although realising that the species were not truly congeneric. Eichler (1940) described the new genus *Meganarionoides* for *colobi*, and placed it with *Cebidicola* and *Lorisicola* in the new subfamily Cebidicolinae. Werneck (1946) recognised the identity of *colobi* with the hyrax lice, and synonymised *Meganarionoides* with *Procavicola (Acondylocephalus)* Werneck, 1941, the subgenus thus taking the name *Procavicola (Meganarionoides)*. Werneck (1946) also suggested that *Colobus* was not the true host of *P. colobi*, but that the louse was probably a parasite of *Dendrohydrax validus* subsp. He suggested that the host record of the type-specimens was erroneous and due to mislabelling (the collection having included both *Colobus* and *Dendrohyrax*), and that a second record was due to contamination (other hyrax-lice having been associated with the specimens of *colobi*). Hopkins (1949) reported having examined 25 skins of *Colobus polykomos*, which he identified as the 'supposed host', without having found any Trichodectidae, and agreed with Werneck (1946) that *Dendrohyrax validus* subsp. was the correct host. Hopkins & Clay (1952) also identified *D. validus* subsp. as the host, the record from '*Colobus caudatus*' being termed an 'error'. Eichler (1963) agreed, and removed *Meganarionoides* from the Cebidicolinae and placed it in the Dasyonygidae with *Procavicola* (Fig. 38). Emerson & Price (1981) include *P. colobi*, without comment, as a parasite of *Dendrohyrax validus validus*, although the association with the nominate subspecies of this animal has not appeared elsewhere in the literature. Kuhn & Ludwig (1964), however, reported a specimen of *Colobus guereza* with 'hundreds of eggs and adult and larval *Procavicola* on it, all clasping the hairs tightly; most of them on the back and on the throat', and were able to state that the monkey had not been in contact with a *Dendrohyrax* or any other Procaviidae after its death. They concluded 'There is no doubt . . . that *Colobus guereza* is a natural host of *Procavicola (Meganarionoides) colobi*.' In view of the fact that there are now three records of the species from *Colobus guereza* and none from any member of the Procaviidae, this conclusion seems fully justified.

Meganarionoides was, as described above, treated as a subgenus of *Procavicola* by Werneck (1946). In this he has been followed by most authors, although Eichler (1963) considered it to be a full genus. Before the present study *Meganarionoides* had not been placed as a subgenus of *Procaviphilus*.

SPECIES INCLUDED

africanus (Werneck, 1941) **comb. n.** from *Procavicola* (5 ♂, 5 ♀)
angolensis (Bedford, 1936) **comb. n.** from *Procavicola* (8 ♂, 11 ♀)
colobi (Kellogg, 1910) **comb. n.** from *Procavicola* (1 ♂, 1 ♀)
congoensis (Ferris, 1930) **comb. n.** from *Procavicola* (22 ♂, 25 ♀)
jordani (Bedford, 1936) **comb. n.** from *Procavicola* (2 ♂, 2 ♀)
muesebecki (Emerson & Price, 1969) **comb. n.** from *Procavicola* (10 ♂, 10 ♀)
neumanni neumanni (Stobbe, 1913) **comb. n.** from *Procavicola* (2 ♂, 1 ♀)
neumanni baculatus (Ferris, 1930) **comb. n.** from *Procavicola* (13 ♂, 14 ♀)
sclerotis sclerotis Bedford, 1932 [treated as *Procaviphilus* s. str. by previous authors] (10 ♂, 17 ♀)
sclerotis major Maltbaek, 1937 [treated as *Procaviphilus* s. str. by previous authors]
scutifer (Werneck, 1941) **comb. n.** from *Procavicola* (14 ♂, 19 ♀)
serraticus (Hill, 1922) [treated as *Procaviphilus* s. str. by previous authors] (50 ♂, 70 ♀)
tendeiroi (Emerson, 1965) **comb. n.** from *Procavicola* (3 ♂, 2 ♀)

Genus ***DASYONYX*** Bedford

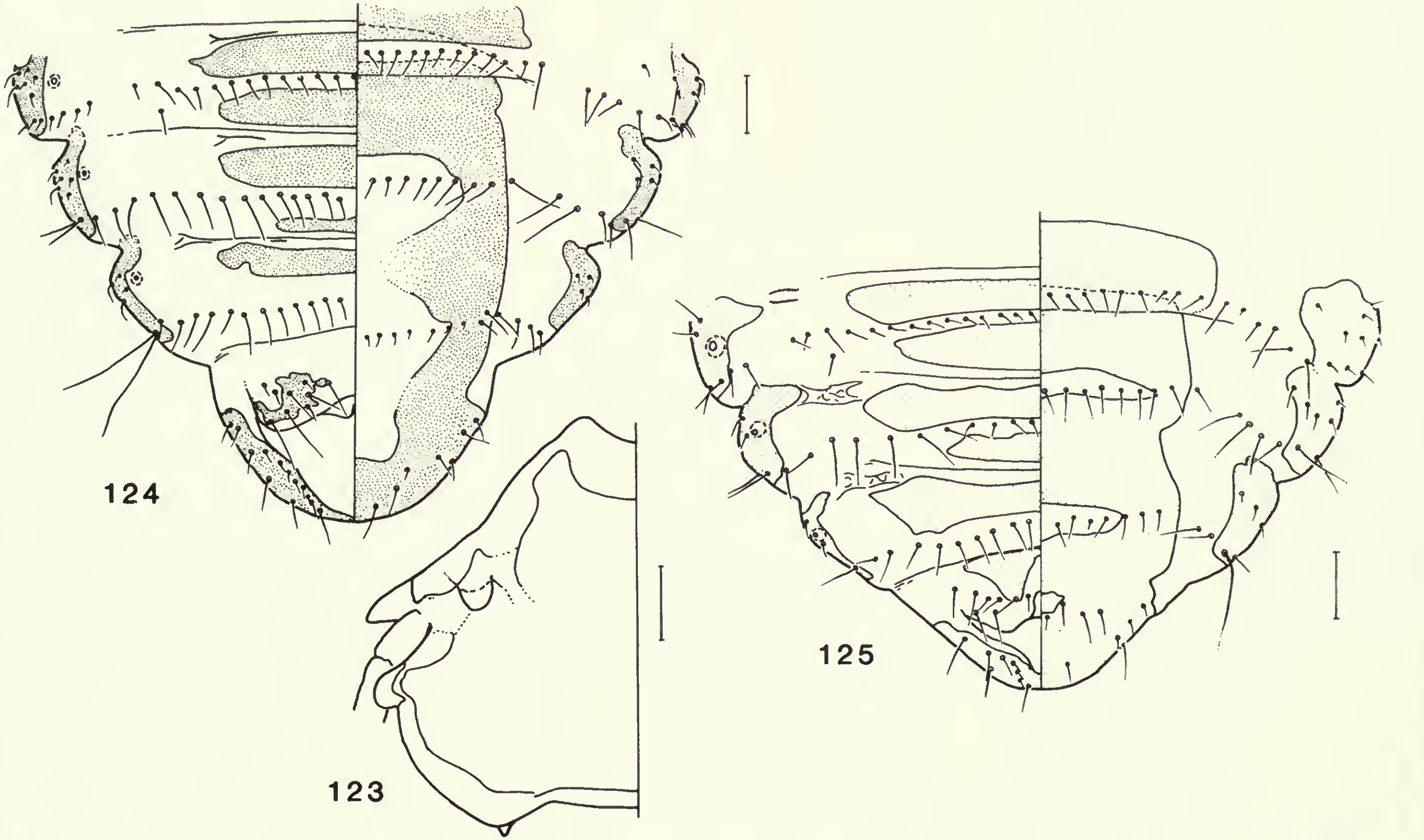
The genus *Dasyonyx* comprises two subgenera.

DESCRIPTION. Anterior of head with osculum present, variable in degree of excavation*; dorsal preantennal sulcus absent; clypeal marginal carina broadened medially, with posterior curvature of broadened portion similar to curvature of osculum* (Fig. 123); conus not large; anterolateral margin of head straight, convex or concave, though not very concave at junction with clypeofrontal suture; preantennal portion of head short or long, outline broadly triangular, trapezoidal or rounded*. Temple margin shallowly convex, sometimes with small rounded projection postero-laterally*. Male scape expanded, with setal row present; male flagellomeres fused, with two basally-articulated 'teeth'; female flagellomeres unfused. Dorsum of head with setae of moderate length. Sitophore sclerite with posterior arms extended (cf. Fig. 12), though sclerite difficult to see.

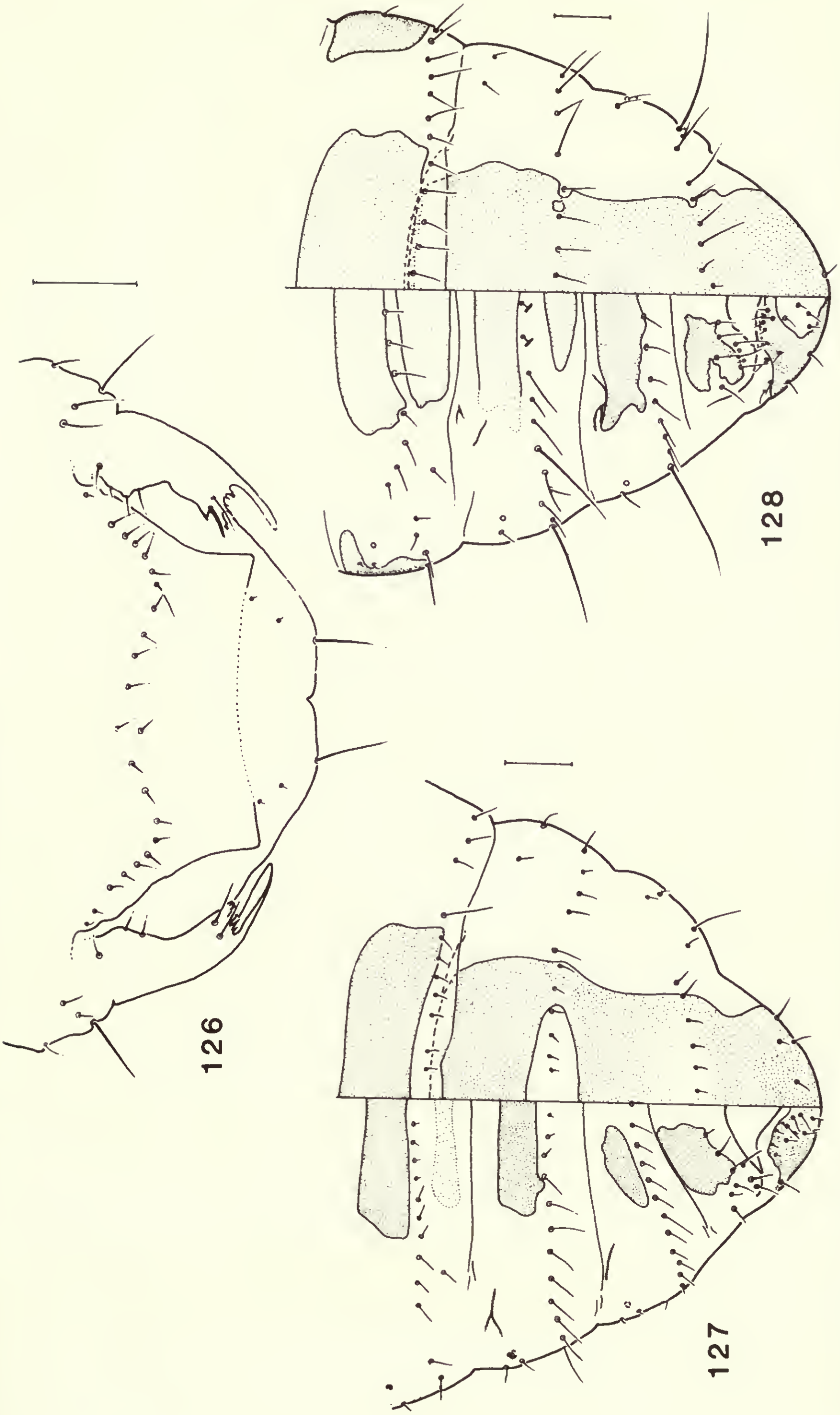
Tarsal claws with ventral spines or teeth (Figs 14, 15)*. Post-coxale of metathoracic leg absent or, if present* enlarged, though not as described for *Procaviphilus (Meganarionoides)* and not fused to abdominal pleurite II. Thorax with dorsal setae present only posteriorly on prothoracic margin and posteriorly and posterolaterally on pterothoracic margin; setae short anteriorly, longer posteriorly with the longest setae on the posterolateral margins of the pterothorax; setae generally sparse.

Abdomen broadly oval, with male segment IX not projecting greatly (Fig. 129). Abdominal spiracles present on segments III to VIII, all approximately the same size, frequently inconspicuous. Abdominal setae of moderate length; anterior setae present on pleura only; postero-lateral setae present. Pleural projections present dorsally and ventrally on abdominal pleurum IV, sclerotised. Sclerites present on sterna, terga and pleura (where present) of all abdominal segments except I; male terga, at least of abdominal segment VI, with anterior and posterior sclerites.

Gonapophyses with sparse marginal setae and variably-developed lobe ventrally, the lobe bearing two apical or subapical setae and frequently being serrate along dorsal (posterior) margin (Fig. 126).



Figs 123–125 *Dasyonyx (D.)* species. 123, *D. (D.) dendrohyracis*, ♀ head, dorsal. 124, *D. (D.) guineensis*, ♂ terminalia. 125, *D. (D.) hopkinsi*, ♂ terminalia.



Figs 126–128 *Dasyonyx* species. 126, *D.* (*D.*) *validus ugandensis*, ♀ terminalia, ventral. 127, *D.* (*D.*) *ovalis*, ♂ terminalia. 128, *D.* (*Neodasyonyx*) *nairobiensis*, ♂ terminalia.

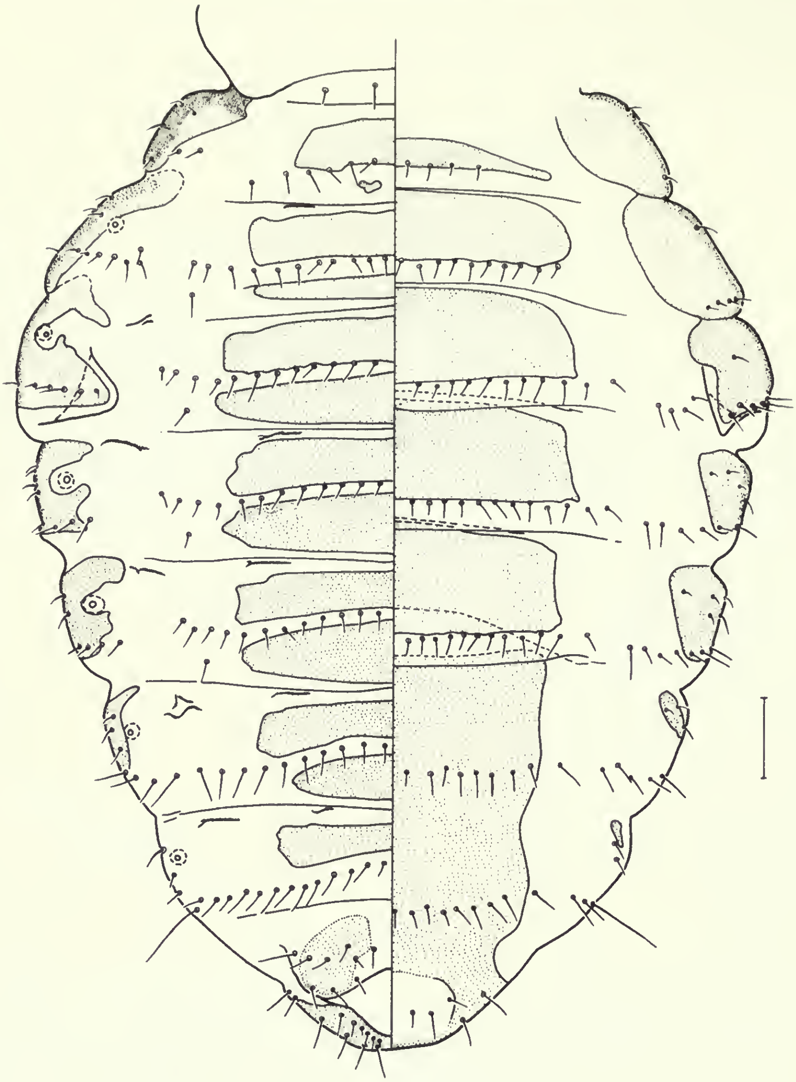


Fig. 129 *Dasyonyx (D.) validus*, ♂ abdomen.

Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; greatly expanded, sometimes with postero-lateral angular projections (Fig. 126); subgenital lobe absent.

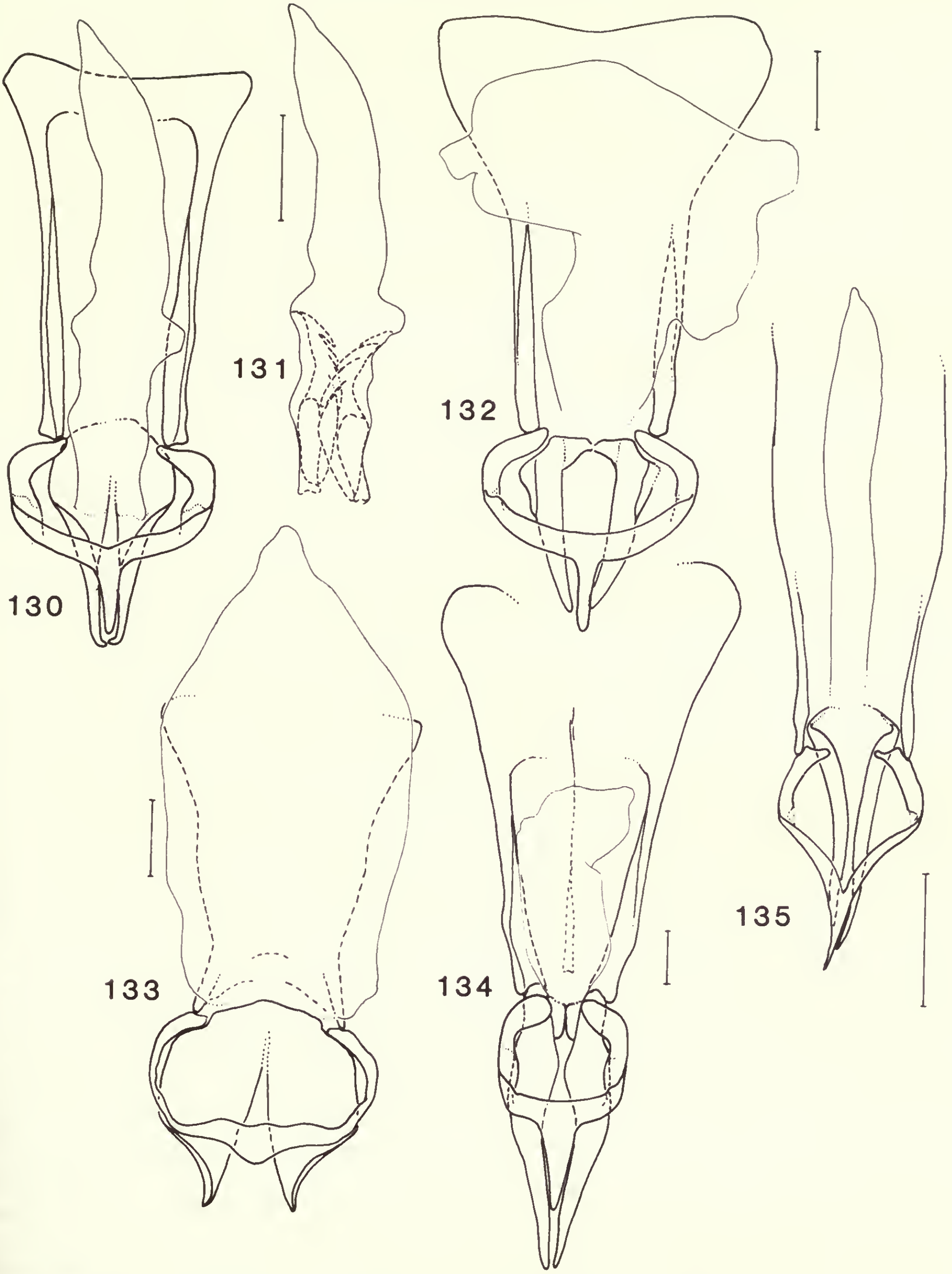
Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., but variably modified (Figs 124, 125, 127–129), frequently lacking perisetal gap. Pseudostyli absent. Male genital opening postero-dorsal or dorsal. Parameres fused or, if unfused, then with basal flanges (Figs 130, 132, 134, 135). Basiparameral sclerites absent. Mesomeres fused; mesomeral arch with median extension and lateral desclerotisations; mesomeres more or less produced basally between b.a.l.s. to meet parameres, which sometimes do not contact b.a.l.s. (Figs 130, 132–135).

Hosts. Procaviidae (Hyracoidea).

Subgenus ***DASYONYX*** Bedford

(Figs 14, 123–127, 129–132, 134, 135)

Dasyonyx Bedford, 1932*b*: 720. Type-species: *Dasyonyx validus* Bedford, by original designation.



Figs 130–135 *Dasyonyx* species, ♂ genitalia. 130, *D. (D.) validus*. 131, *D. (D.) validus*, endophallus, sclerites shown by dashed outlines. 132, *D. (D.) ovalis*, 133, *D. (Neodasyonyx) ruficeps*. 134, *D. (D.) guineensis*. 135, *D. (D.) minor*.

Description. Osculum deeply concave; preantennal outline of male head subtriangular or subtrapezoidal. Temple margin frequently with small rounded projection postero-laterally (Fig. 123).

Tarsal claws with ventral spines slender and sharp (Fig. 14). Postcoxale of metathoracic leg generally present and enlarged, though not as described for *Procaviphilus (Meganarionoides)*.

Hosts. Procaviidae (Hyracoidea).

SPECIES INCLUDED

bedfordi Werneck, 1945 (11 ♂, 16 ♀)
dendrohyracis (Ferris, 1930) (12 ♂, 15 ♀)
guineensis Werneck, 1941 (5 ♂, 3 ♀)
hopkinsi Werneck, 1941 (33 ♂, 32 ♀)
minor Bedford, 1939 (3 ♂, 1 ♀)
oculatus Bedford, 1928
ovalis Bedford, 1932 (36 ♂, 35 ♀)
smallwoodae Emerson & Price, 1969 (7 ♂, 3 ♀)
validus validus Bedford, 1932 (22 ♂, 22 ♀)
validus ugandensis Werneck, 1941 (29 ♂, 26 ♀)

Subgenus *NEODASYONYX* Werneck

(Figs 15, 128, 133)

Neodasyonyx Werneck, 1941: 543 [as subgenus of *Dasyonyx* Bedford]. Type-species: *Dasyonyx transvaalensis* Bedford, by original designation.

DESCRIPTION. Osculum shallowly concave; preantennal region of male head short, outline rounded. Temple margin lacking postero-lateral projection.

Tarsal claws with broad ventral teeth (Fig. 15). Postcoxale of metathoracic leg absent.

HOSTS. Procaviidae (Hyracoidea).

SPECIES INCLUDED

capensis Emerson, 1965 (holotype ♂, allotype ♀)
diacanthus (Ehrenberg, 1828) (9 ♂, 8 ♀)
nairobiensis Bedford, 1936 (89 ♂, 92 ♀)
ruficeps Emerson, 1964 (15 ♂, 13 ♀)
transvaalensis Bedford, 1932 (24 ♂, 31 ♀)
waterburgensis Bedford, 1932 (5 ♂, 6 ♀)

Genus *EURYTRICHODECTES* Stobbe

(Figs 9, 16, 136–138)

Eurytrichodectes Stobbe, 1913*a*: 111. Type-species: *Eurytrichodectes paradoxus* Stobbe, by monotypy.

DESCRIPTION. Anterior of head with osculum absent or, if present, very shallowly concave; dorsal preantennal sulcus absent; clypeal marginal carina slender, not greatly developed medially or, if developed, in the form of a median posteriorly-directed narrow-based triangle; anterolateral margin of head slightly sinuate; preantennal portion of head very short, outline broadly triangular or trapezoid. Temple margin produced posteriorly into broad triangular spike, almost as long as prothorax or, if shorter, attaining front of pronotum (Fig. 138). Male scape expanded, with longitudinal setal row comprising only two setae; male flagellomeres fused, though semicircular sclerite at apex may be vestige of terminal flagellomere; two basally-fused 'teeth' present on male flagellum; female flagellomeres unfused; membranous projection present on female pedicel (Fig. 138). Dorsum of head with setae short, sparse. Sitophore sclerite with posterior arms extended (cf. Fig. 12), though sclerite difficult to see.

Tarsal claws ridged ventrally, lacking teeth or spines (Fig. 16). Postcoxale of metathoracic leg absent. Thorax with dorsal setae present on posterior margin of prothorax and on posterior margin of pterothorax; setae short, sparse.

Abdomen broad and oval, sometimes with male terminal segments tapering and projecting slightly. Abdominal spiracles present on segments III to VIII, all approximately of the same size. Abdominal setae short on sterna IV to IX, terga and pleura, some tergal setae very short; sterna II and III with stout, conical setae (Fig. 136); anterior setae present, sparse on pleura; setal row on terga and sterna may be irregular; postero-lateral setae present. Pleural projections present dorsally and ventrally on abdominal pleurum IV, sclerotised, very long, reaching or almost reaching posterior margin of pleurum V. Sclerites present on sterna, terga and pleura (where present) of all abdominal segments except, sometimes, tergum I; male terga, at least of abdominal segments II to VI, with anterior and posterior sclerites.

Gonapophyses with ventral marginal setae present, each with a small, conical tubercle; ventral lobe absent. Gonapophyses meet ventral vulval margin smoothly, not linked by sclerotised band. Ventral vulval margin not sclerotised; medially expanded and trapezoid; subgenital lobe absent.

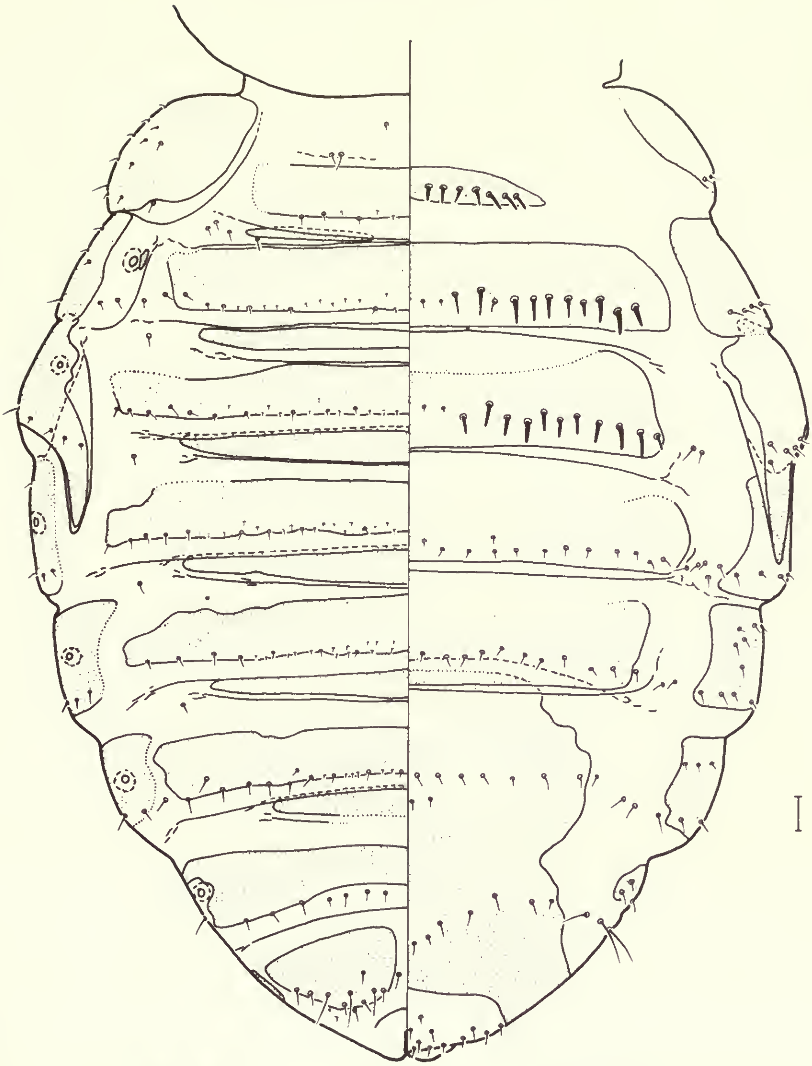


Fig. 136 *Eurytrichodectes paradoxus*, ♂ abdomen.

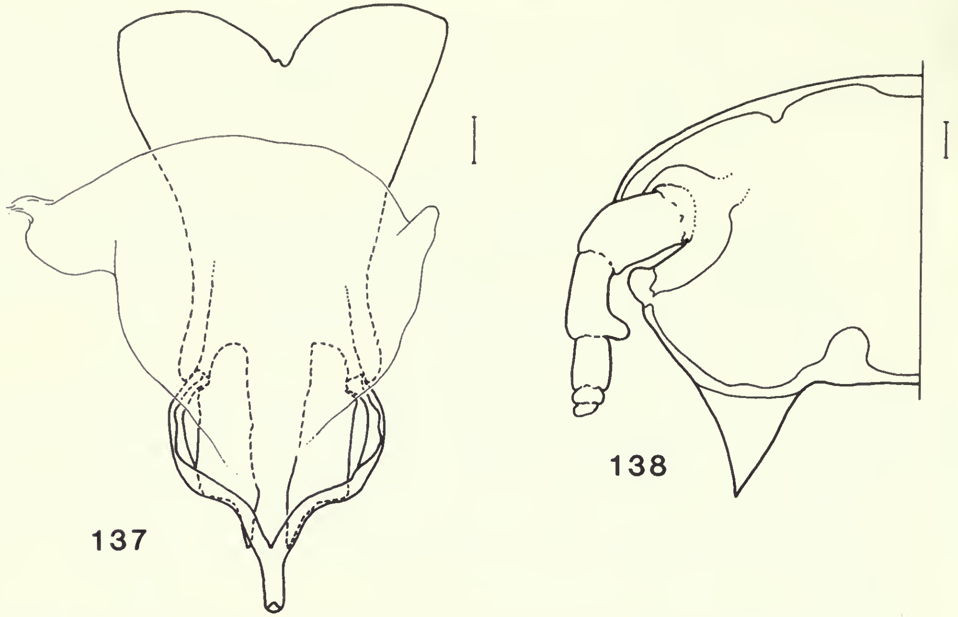
Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., with setal gaps very small or absent (Fig. 136). Pseudostyli absent. Male genital opening dorsal. Parameres not fused, sometimes apically bifurcate. Basiparameral sclerites absent. Mesomeres fused; mesomeral arch with median extension (see comments below); mesomeral arch lacking lateral desclerotisations; mesomeres sometimes produced basally between b.a.l.s. to contact parameres. Male genitalia depicted in Fig. 137.

HOSTS. Procaviidae (Hyracoidea).

COMMENTS. The illustration of the the mesomeral arch of *E. paradoxus* is reproduced upside-down in Werneck (1941: 452).

SPECIES INCLUDED

machadoi Werneck, 1958 (holotype ♂, allotype ♀)
paradoxus Stobbe, 1913 (29 ♂, 28 ♀)



Figs 137, 138 *Eurytrichodectes paradoxus*. 137, ♂ genitalia. 138, ♀ head, dorsal.

TRICHODECTINAE Kellogg

Genus *PROTELICOLA* Bedford **gen. rev.**

(Figs 139, 140)

Protelicola Bedford, 1932*a*: 355. Type-species: *Protelicola intermedius* Bedford, by monotypy.

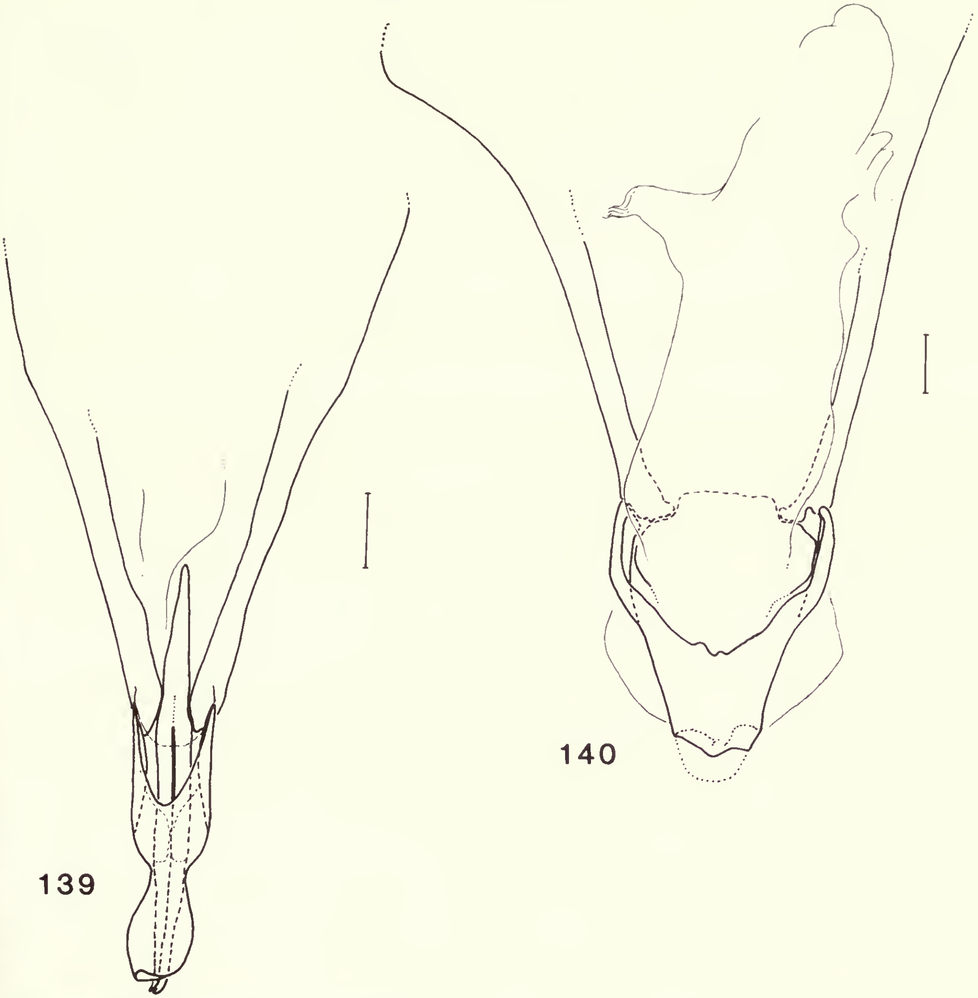
Description. Anterior of head with osculum present; clypeal marginal carina broadened just laterally to osculum, tapering medially and interrupted by dorsal preantennal sulcus; anterolateral margin of head straight or convex; preantennal outline of head triangular or rounded. Temple margin convex. Male scape slightly expanded, with longitudinal setal row present and comprising three or four setae; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth'. Dorsal setae of head short or of moderate length, longest and most abundant anteriorly. Sitophore sclerite unmodified.

Thorax with setae long or of moderate length laterally and dorsally, with setae on postero-lateral angles of pterothorax shorter, more spine-like. Prothorax with setae present sparsely on lateral and posterior margins; median gap present, wide; single seta present antero-laterally on disc. Pterothorax with setae present postero-laterally and submarginally posteriorly; median gap present, wide; no setae present on disc.

Abdomen rounded, similar in shape in males and females. Abdominal spiracles present on segments III–VIII. Abdominal setae of moderate length; anterior setae present on pleura only; postero-lateral setae absent. Abdominal pleura lacking projections. Abdominal segments with tergal sclerites absent except tergite IX in female; pleural sclerites present on pleura II and III; sternites IV–VII present in male and V–VII present in female, very slender and difficult to see in both sexes.

Gonapophyses with basal setae and rectangular lobe on ventral margin, lobe formed from more or less fused setal tubercles. Gonapophyses meet ventral vulval margin smoothly, not linked by sclerotised band. Ventral vulval margin not sclerotised. Subgenital lobe present, not marginally serrate, but sometimes with apical papillae. Female genital chamber with small lapped scales on walls, dorsal wall with median longitudinal anterior 'slit' where scales are absent.

Male subgenital plate comprising very slender sternite VII and s.g.p.r. only, s.g.p.r. not reaching posterior of sternum IX. Male genital opening dorsal or postero-dorsal. Pseudostyli absent. Basal apodeme with b.a.l.s. widely divergent anteriorly. Parameres long, slender, fused basally, projecting anteriorly between b.a.l.s. (but see second paragraph of 'comments' below). Basiparameral sclerites



Figs 139, 140 *Protelicola* species, ♂ genitalia. 139, *P. hyaenae*. 140, undescribed species.

absent. Mesomeres fused apically to form arch, with median projection present, broad (see second and third paragraphs of 'comments' below). Male genitalia depicted in Fig. 139.

Alimentary canal with numerous small spines in crop.

HOSTS. Hyaenidae and Protelidae (Carnivora).

COMMENTS. *Protelicola* was treated as a subgenus and a junior synonym of *Felicola* by Hopkins (1949) and Werneck (1948) respectively; its most recent placement (Emerson & Price, 1981) was as a synonym of *Felicola*. A more detailed history of the variations in status of *Protelicola* is presented in Table 5.

In the British Museum (Natural History) collection there is a slide bearing 1 nymphal, 3 female and 2 male (one of which is teneral) lice from *Proteles cristatus termes*. Hopkins has identified the lice as *Protelicola intermedius*. The females are indistinguishable from females of *P. intermedius* s. str., but the male genitalia are very distinct, with the parameres completely fused to form a broad plate, the mesomeral arch wide, and the b.a.l.s. with a small postero-lateral projection contacting the mesomeres (Fig. 140). In all other respects the males resemble *P. intermedius* s. str. It seems that the males represent a new species, differing from *Protelicola intermedius* by the structure of the genitalia, but the identity of the females is doubtful. In view of the limited number of specimens available, the species is not formally described.

Bedford (1932*a*) described *P. intermedius* from *Proteles cristatus*, the first louse known from a hyaena. Hopkins (1960) described *P. intermedius hyaenae* (in *Felicola*) from *Hyaena brunnea*, distinguishing it from the nominate subspecies by the size, the outline of the preantennal portion of the head, and the male genitalia. Ledger (1980) raised *P. i. hyaenae* to specific rank although Emerson & Price (1981) retained its subspecific status. Hopkins (1960) indicated three features of the male genitalia in which the two taxa differ: the greater anterior divergence of the b.a.l.s. in *P. i. intermedius*, the shape of the parameres (which he presumed to be completely fused in *P. i. intermedius*, and are only basally fused in *P. i. hyaenae*), and the absence of the mesomeral arch extension in *P. i. intermedius*. The type-series of *P. i. intermedius* has not been seen in the present study, but a series of specimens from *Proteles cristatus* has been examined; these specimens agree with Bedford's and Hopkins' descriptions of *P. i. intermedius* in all but details of the male genitalia. The male genitalia of this series were found to be very similar to those of *P. hyaenae*, with the b.a.l.s. variably divergent anteriorly, the parameres fused only basally and the mesomeral arch with a median broad extension (although this is very thinly sclerotised and difficult to see in both taxa). The male genitalia of *P. hyaenae* are depicted in Fig. 139. The two species may be distinguished by the smaller size and shorter preantennal region of *P. hyaenae* (see photographs in Hopkins, 1960).

Species included

hyaenae (Hopkins, 1960) **stat. rev., comb. n.** from *Felicola* (holotype ♂, allotype ♀)
intermedius Bedford, 1932 **comb. rev.** from *Felicola* (19 ♂, 48 ♀)

Genus ***LUTRIDIA*** Kéler

(Figs 141–145)

Lutridia Kéler, 1938*a*: 433. Type-species: *Trichodectes exilis* Giebel, by original designation.

Description. Anterior of head with osculum absent; dorsal preantennal sulcus absent; clypeal marginal carina broadened medially to form dorsal sclerite with three posteriorly-directed projections (Fig. 142); preantennal portion of head short, outline smoothly rounded. Temple margin convex or rectangular. Male scape not expanded, longitudinal setal row comprising two setae positioned distally on segment; flagellomeres fused in males and females; male flagellum lacking 'teeth'. Dorsum of head with setae short or of moderate length, sparse. Sitophore sclerite unmodified.

Thorax with dorsal setae long or of moderate length, limited to posterior and postero-lateral margins of prothorax and pterothorax.

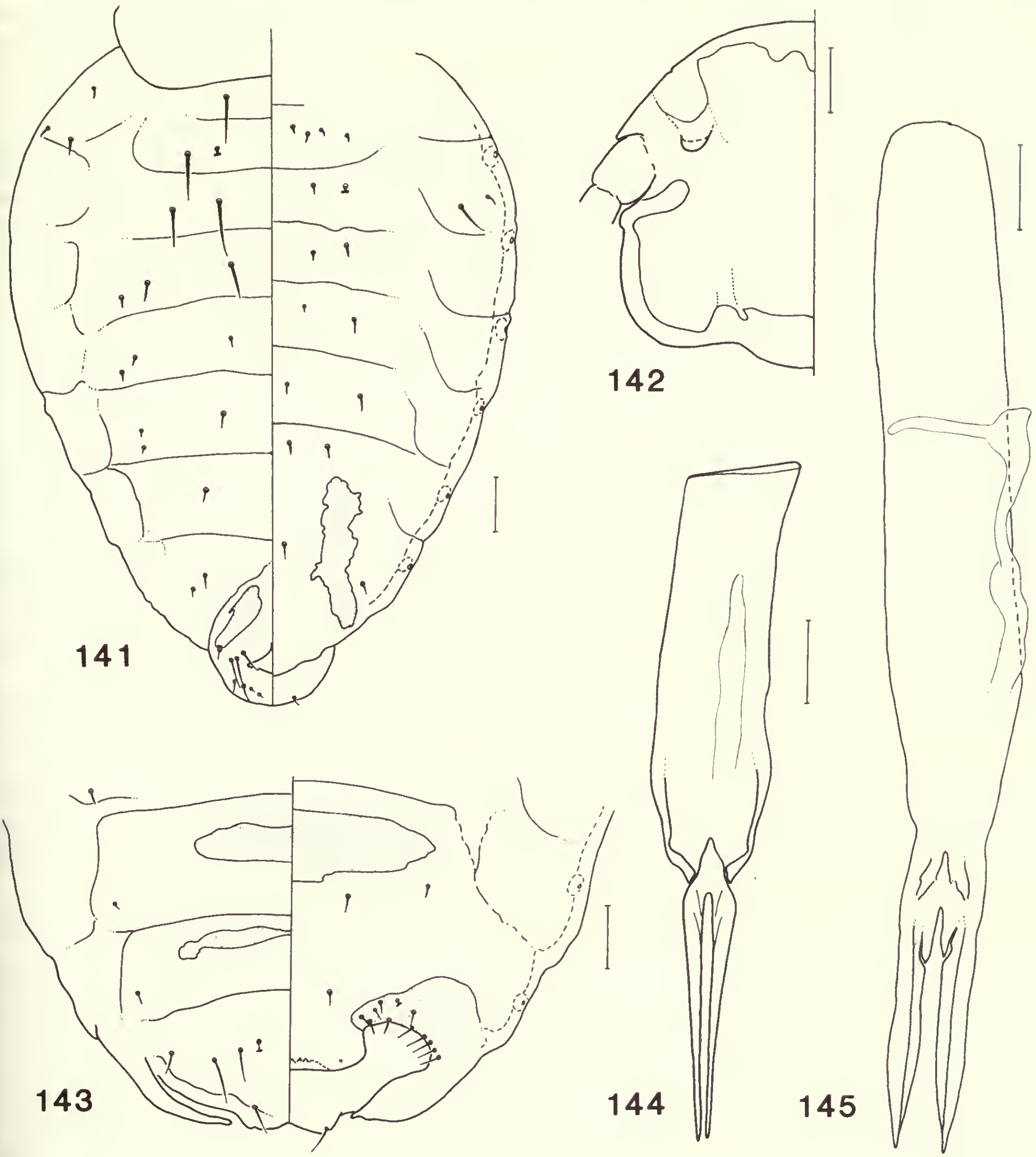
Abdomen oval or slightly elongate-oval, with male segment IX projecting slightly posteriorly (Fig. 141). Abdominal spiracles present on segments III–VIII. Abdominal setae as follows: pleurum II with setae sparse, stout and short, anterior setae and p.s.r. present; pleurum III with setae short and of moderate length, stout, very sparse (*exilis*) or with p.s.r. present (*matschiei*); pleura IV–VII or VIII lacking setae, those on VIII, if present, very small and posteriorly positioned; sternal setae short and stout or longer (about two-thirds length of segment); sternum II with median gap of posterior setal row small or absent; sterna III–IV and VII– VIII (*matschiei*) or III–VIII (*exilis*) with setae very sparse, setae absent from sterna V–VI of *L. matschiei*; terga I–IV (males) or I–III (females) with median setal group including one or two setae as long as segment, other terga with median group absent or comprising shorter setae; terga with lateral seta or setae generally present, of moderate length on terga II–III, shorter on more posterior segments (these setae may represent either lateral setal group or postero-lateral seta); anterior setae present only on pleurum II. Abdominal pleura lacking projections. Sclerites absent from abdominal pleura, present on terga IV–VIII (males) or terga IV–IX (females) and sterna III–VIII (males) or sterna IV–VIII (females); sclerites frequently very faint, may not be seen; male terga lacking posterior sclerites.

Gonapophyses with non-tuberculate setae on ventral margin; ventral lobe not present. Gonapophyses meet ventral vulval margin smoothly, linked by sclerotised band. Ventral vulval margin sclerotised, with chord at 90 degrees to long axis of abdomen, submarginal non-tuberculate setae present. Subgenital lobe present, small, rectangular, sometimes serrate along posterior margin (Fig. 143).

Male subgenital plate comprising s.g.p.r. only or with s.g.p.r. linked by broad sternite VIII (and possibly VII); in either case s.g.p.r. not attaining segment IX. Pseudostyli absent. Male genital opening dorsal. Basal apodeme slender, long, attaining at least abdominal segment III. Parameres long, slender, basally fused; basal fused portion may be partially detached from rest of parameres; parameres sometimes fused to b.a.l.s. Mesomeres absent. Male genitalia depicted in Figs 144, 145.

Hosts. Lutrinae (Carnivora: Mustelidae).

Comments. *Lutridia* has been treated as a synonym and a subgenus of *Trichodectes* (Hopkins, 1942 and Hopkins, 1949 respectively), though the most recent treatment (Emerson & Price, 1981) considered *Lutridia* as a full genus. The history of the variations in status of *Lutridia* is presented in Table 4.



Figs 141–145 *Lutridia* species. 141, *L. exilis*, ♂ abdomen. 142, *L. matschiei*, ♀ head, dorsal. 143, *L. matschiei*, ♀ terminalia. 144, *L. matschiei*, ♂ genitalia. 145, *L. exilis*, ♂ genitalia.

SPECIES INCLUDED

exilis (Nitzsch, 1861) (3 ♂, 10 ♀)
matschiei (Stobbe, 1913) (36 ♂, 38 ♀)

Genus *NEOLUTRIDIA* gen. n.

(Figs 146, 147)

Type-species: *Trichodectes lutrae* Werneck.

DESCRIPTION. Anterior of head with osculum absent, though pulvinus attaining margin; dorsal preantennal sulcus absent; clypeal marginal carina slightly broadened medially at junction with pulvinus; preantennal outline broadly and smoothly rounded. Temple margin rectangular. Male scape not expanded; longitudinal setal row present, comprising four setae; flagellomeres fused in males and females; male flagellum lacking 'teeth'. Dorsum of head with setae short or of moderate length, sparse; temple margin with two or three longer setae. Sitophore sclerite unmodified.

Prothorax with two setae of medium length on posterior margin; pterothorax with one or two short, spine-like setae anterolaterally and six to ten long setae dorsally on posterior margin.

Abdomen oval, with male segment IX projecting posteriorly. Abdominal spiracles present on segments III–VIII. Abdominal setae as follows: pleurum III with short, stout setae anteriorly and posteriorly; pleura III–VIII lacking setae; terga I–VI (males) or I–IV (females) with central seta of median groups as long as segment, setae otherwise short; terga VII–VIII (males) or V–IX (females) with short setae, sparse; sterna with stout, short setae, sparse; anterior setae present only on pleurum II; postero-lateral setae absent. Abdominal pleura lacking projections. Sclerites absent from abdominal pleura and sterna, but present, slender, on at least terga III–VII (males) or V–IX (females), though may be very faint and not seen; male terga lacking posterior sclerites.

Gonapophyses with small ventral lobes formed from fused setal tubercles. Gonapophyses meet ventral vulval margin smoothly, linked by sclerotised band. Ventral vulval margin sclerotised, with chord at 90 degrees to long axis of abdomen; submarginal non-tuberculate setae present. Subgenital lobe present, large, with lateral spine-like projections and associated setae present basally (Fig. 146).

Male subgenital plate represented by sternite VIII with lateral arms extending anteriad. Pseudostyli absent. Male genital opening dorsal. Basal apodeme attaining abdominal segment III, not slender. Parameres broad, scoop-shaped, not fused together, but fused to b.a.l.s. Mesomeres absent. Male genitalia depicted in Fig. 147.

Hosts. Lutrinae (Carnivora: Mustelidae).

Species included

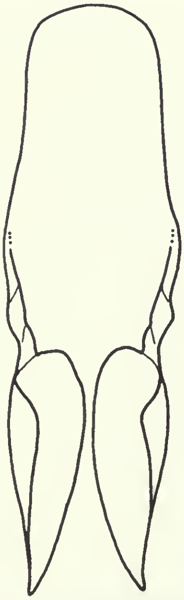
lutrae (Werneck, 1937) **comb. n.** from *Lutridia* (1 ♂, 1 ♀)

Genus ***WERNECKODECTES*** Conci **gen. rev.**

(Fig. 148)

Werneckodectes Conci, 1946: 59. Type-species: *Trichodectes ferrisi* Werneck, by original designation.

Description. Osculum absent, though pulvinus attains anterior margin of head; dorsal preantennal sulcus present; clypeal marginal carina broadened slightly medially; preantennal portion of head short, outline



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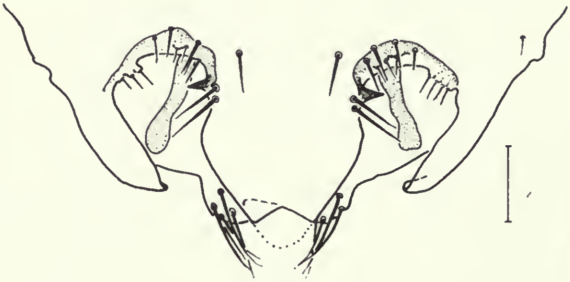

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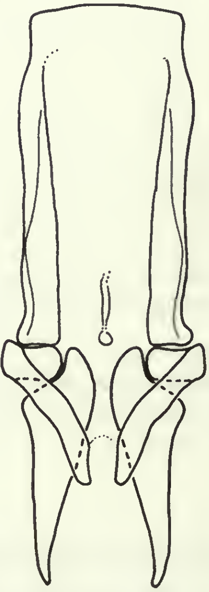

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Figs 146–148 Trichodectini species. 146, *Neolutridia lutrae*, ♀ terminalia, ventral. 147, *N. lutrae*, ♂ genitalia (after Werneck). 148, *Werneckodectes ferrisi*, ♂ genitalia (after Werneck).

smoothly and broadly rounded. Temple margin convex. Male scape expanded; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth' and basal projection. Dorsum of head with setae of moderate length.

Thorax with dorsal setae longest postero-laterally on pterothorax and along posterior margin on pterothorax; shorter setae present submarginally along posterior of pterothorax and on postero-lateral angles of prothorax, where there is a small setal patch; disc and posterior margin of pronotum each with pair of small setae.

Abdomen oval, tapering posteriorly rather more in male than female. Abdominal spiracles present on segments III–VIII. Abdominal setae numerous, anterior setae being present on sterna, terga and possibly pleura of all segments; anterior setae smaller than setae of posterior setal rows on each segment; postero-lateral setae, if present, obscured by large number of other setae. Abdominal pleurum IV with ventral projection in male, possibly with dorsal projection in female; pleurum III possibly with dorsal projection in female. Sclerites present on all abdominal pleura, on terga V–IX (males) or terga VII–IX (females) and on sterna III–VI (males only – sclerites absent on female sterna); male terga without posterior tergites, but anterior tergites, where present, with median longitudinal division.

Gonapophyses with non-tuberculate setae on ventral margin; ventral lobe present, small; setae on lobe stout, short, whilst setae distal to lobe longer, more slender. Gonapophyses meet ventral vulval margin smoothly, linked by broad sclerotised band. Ventral vulval margin sclerotised, with chord at 90 degrees to long axis of abdomen; marginal non-tuberculate setae present, stout, short. Subgenital lobe present, broad, with lateral rounded projections and associated setae present basally.

Male subgenital plate with sternite VII fused to s.g.p.r., sternites VIII and IX absent; s.g.p.r. with sinuate margins. Pseudostyli absent. Male genital opening dorsal. Parameres not as long as basal apodeme, not fused together. Basiparameral sclerites absent. Mesomeres not apically fused, abutting parameres and b.a.l.s. basally. Male genitalia depicted in Fig. 148.

HOSTS. Ursidae (Carnivora).

COMMENTS. *Werneckodectes* has been treated as a synonym and a subgenus of *Trichodectes* (by Hopkins, 1942 and Hopkins, 1949 respectively); its most recent placement was as a synonym of *Trichodectes*. A more comprehensive history of the variations in status of *Werneckodectes* is given in Table 4.

SPECIES INCLUDED

ferrisi (Werneck, 1944) **comb. rev.** from *Trichodectes*.

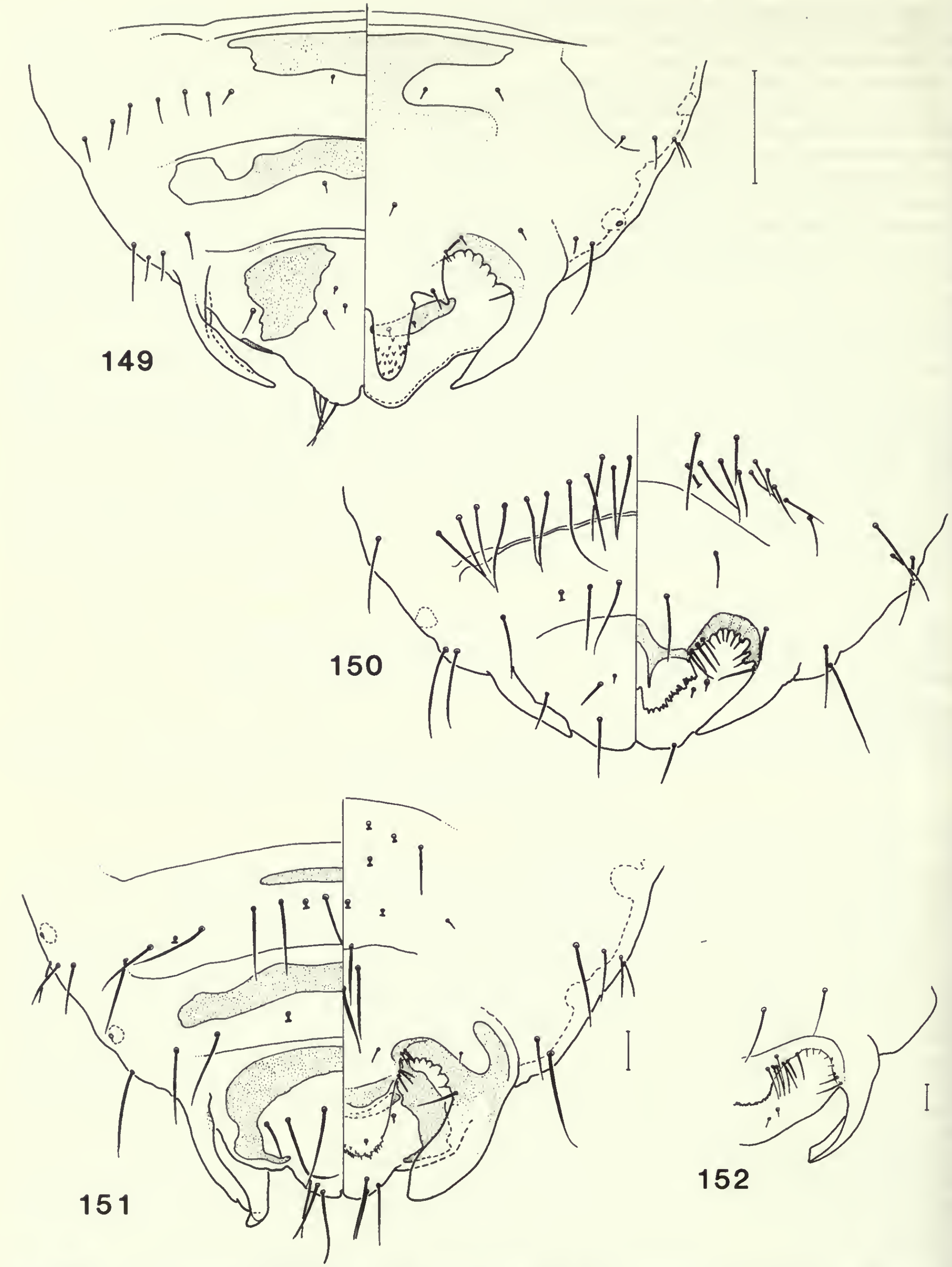
Genus *TRICHODECTES* Nitzsch

The genus *Trichodectes* comprises three subgenera.

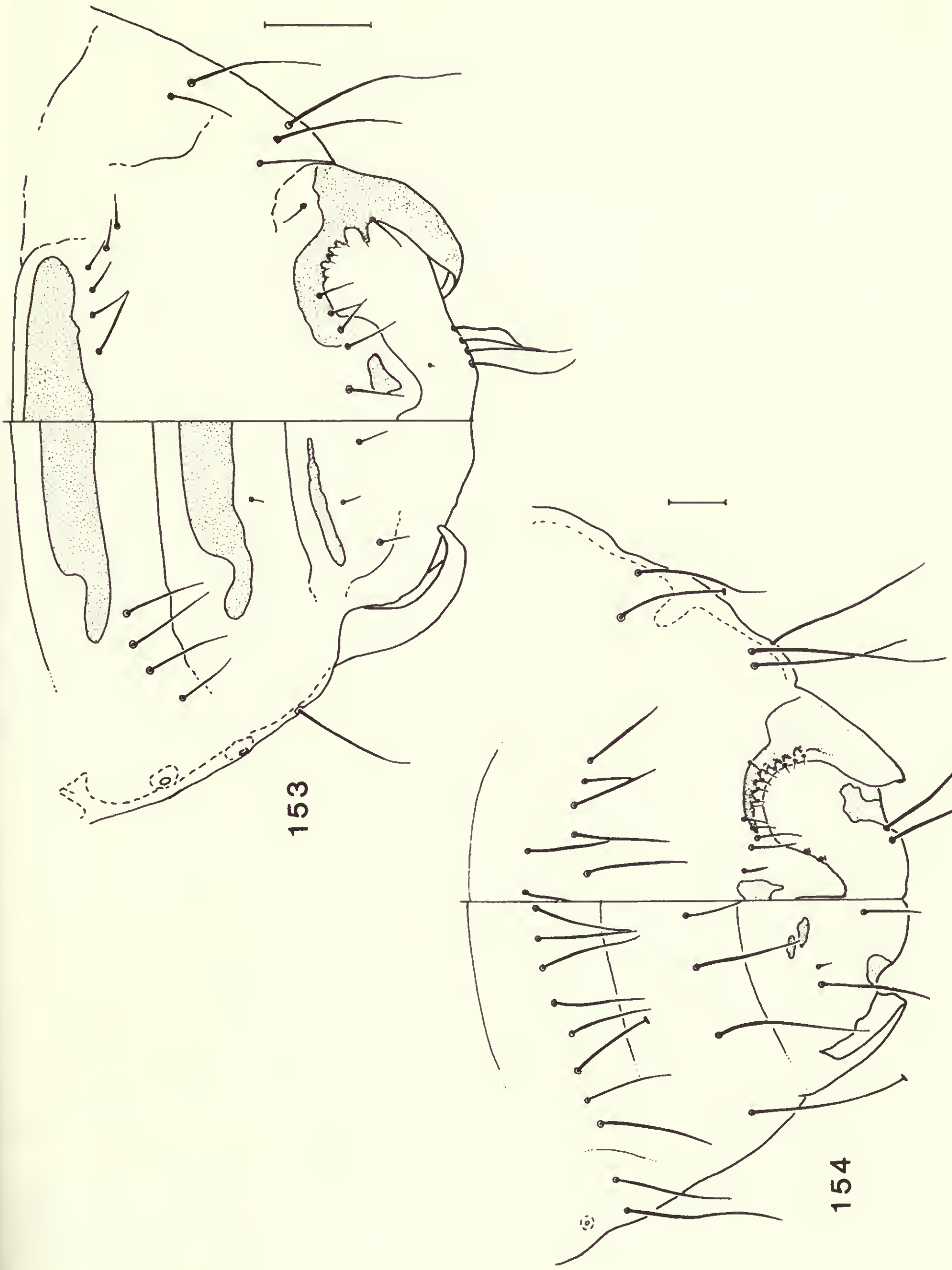
DESCRIPTION. Anterior of head with osculum present or absent*, but always with pulvinus attaining margin; dorsal preantennal sulcus present or absent; clypeal marginal carina broadened to variable extent medially to form simple bar with posterior margin straight or concave, or carina broadened into dorsal sclerite which is heavily-sclerotised laterally (dorsal to margin of clypeus and pulvinus) and lightly or very lightly-sclerotised medially (posterior to the osculum), more or less convex posteriorly or U-shaped with median posterior process*; antero-lateral margin of head straight, convex or sinuate*; preantennal portion of head long or short*, outline broadly rounded, broadly triangular, trapezoid or only slightly produced anteriad between coni*. Temple margin convex, rectangular or produced laterally*. Male scape expanded or not expanded*; longitudinal setal row present, comprising at least four setae; flagellomeres fused in males and females; male flagellum with one, two or four basally-articulated 'teeth' or 'teeth' absent*. Dorsum of head with setae short, of moderate length or long, longest setae generally present along posterior temple margin; setae sometimes sparse. Sitophore sclerite unmodified.

Thorax with prothoracic dorsal setae sparse, short or of moderate length* posteriorly and postero-laterally, absent from disc; pterothorax with setae on postero-lateral angles short and spine-like or of moderate length, dorsal setae otherwise present on posterior margin only, long or short, numerous, sparse or absent*.

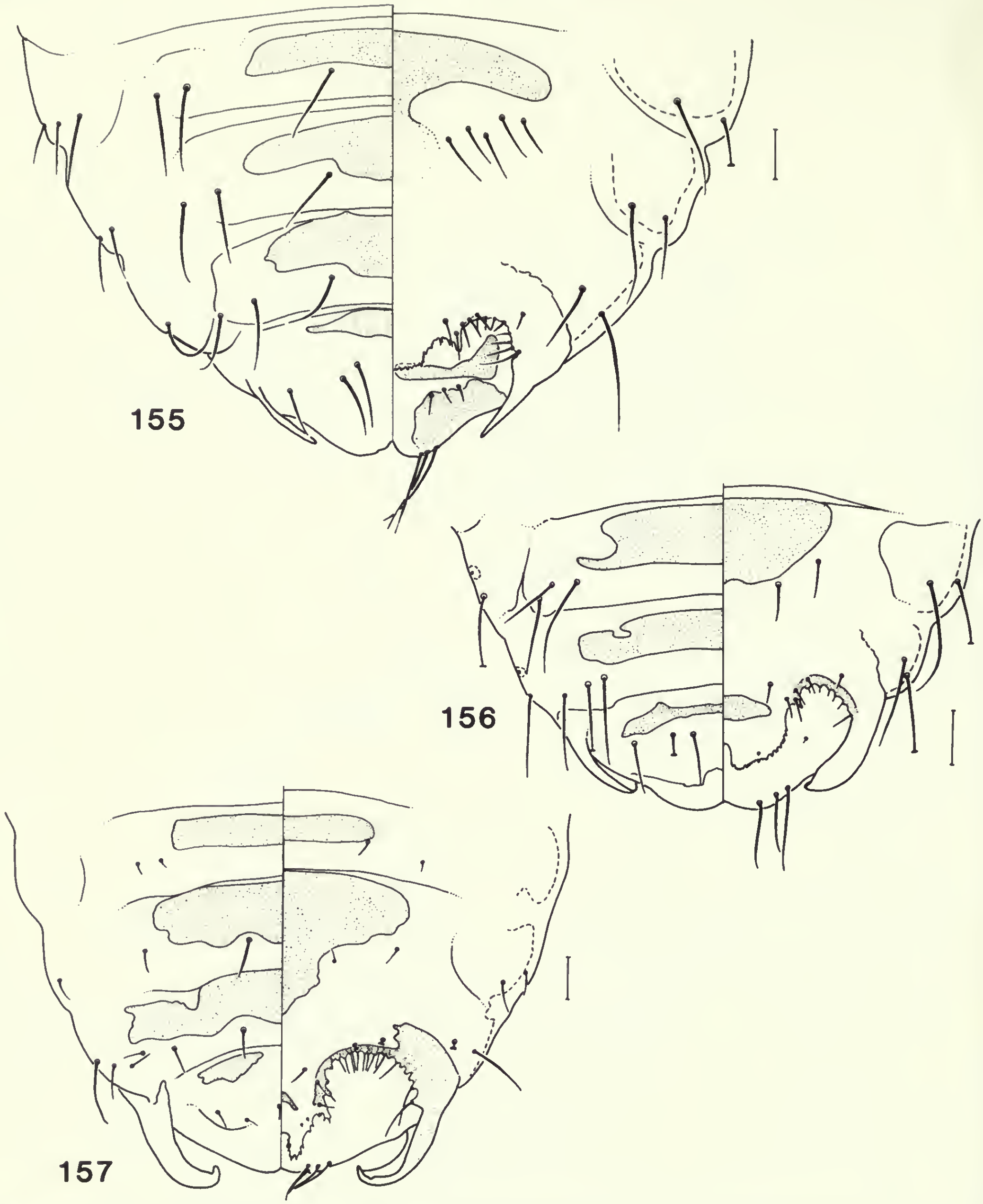
Abdomen oval, male segment IX sometimes slightly projecting posteriad, but usually positioned dorsally on the abdomen (Figs 156, 158, 160, 164, 165). Abdominal spiracles present on segments III–IV, III–V, III–VII or III–VIII*; spiracle on segment VIII, if present, sometimes much smaller than those on segments III–VII*. Abdomen with at least some tergal and sternal setae as long as segment, or setae very short, sparse and absent from pleura V and VI*; terga with lateral and median groups of setae frequently distinct; tergal setae numerous, or median group reduced to a single seta or absent*; male terga II and III sometimes with median group comprising exceptionally long, stout setae (Fig. 161)*; anterior setae



Figs 149–152 *Trichodectes (T.)* species, ♀ terminalia. 149, *T. (T.) emersoni*. 150, *T. (T.) canis*. 151, *T. (T.) galictidis*. 152, *T. (T.) p. pinguis*, ventral.



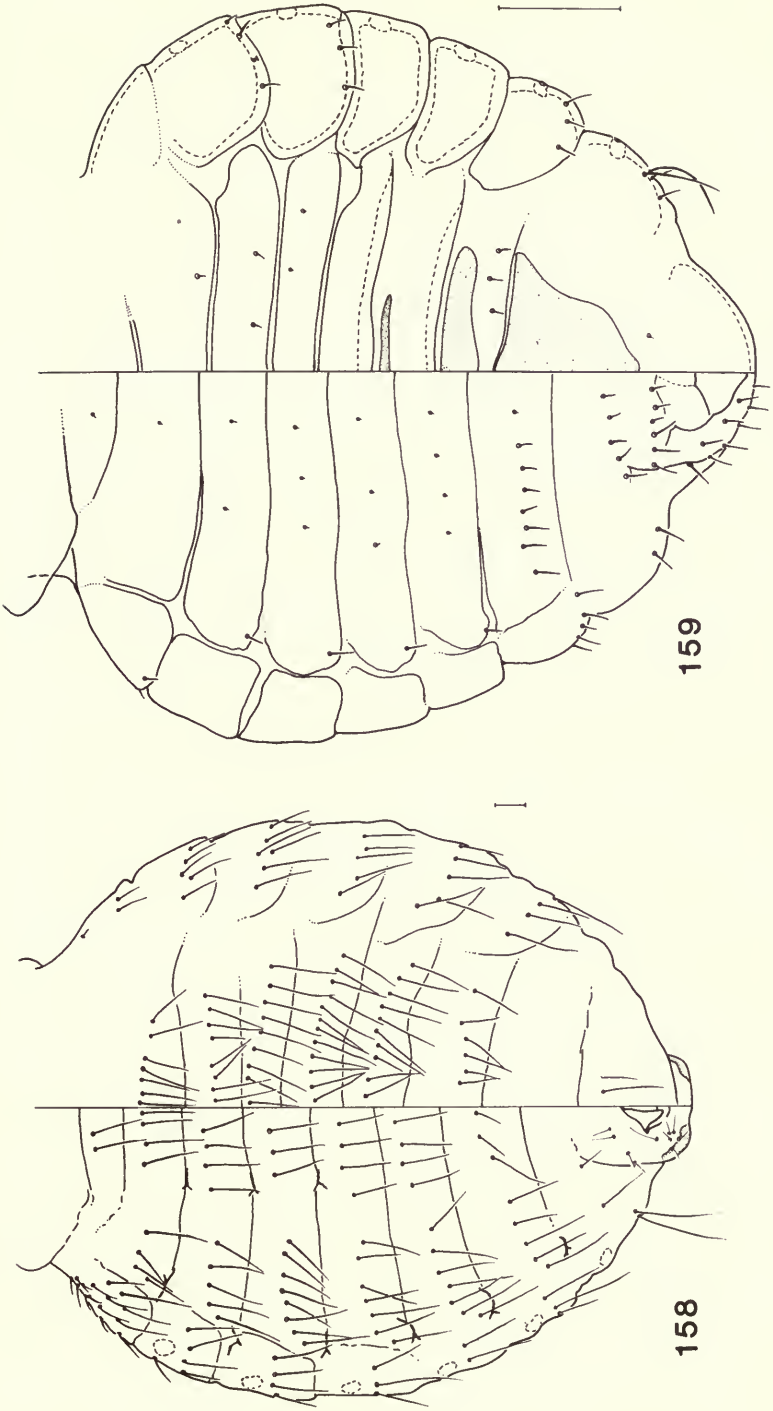
Figs 153, 154 *Trichodectes* species, ♀ terminalia. 153, *T.* (*Stachiella*) *emeryi*. 154, *T.* (*Paratrichodectes*) *zorillae*.



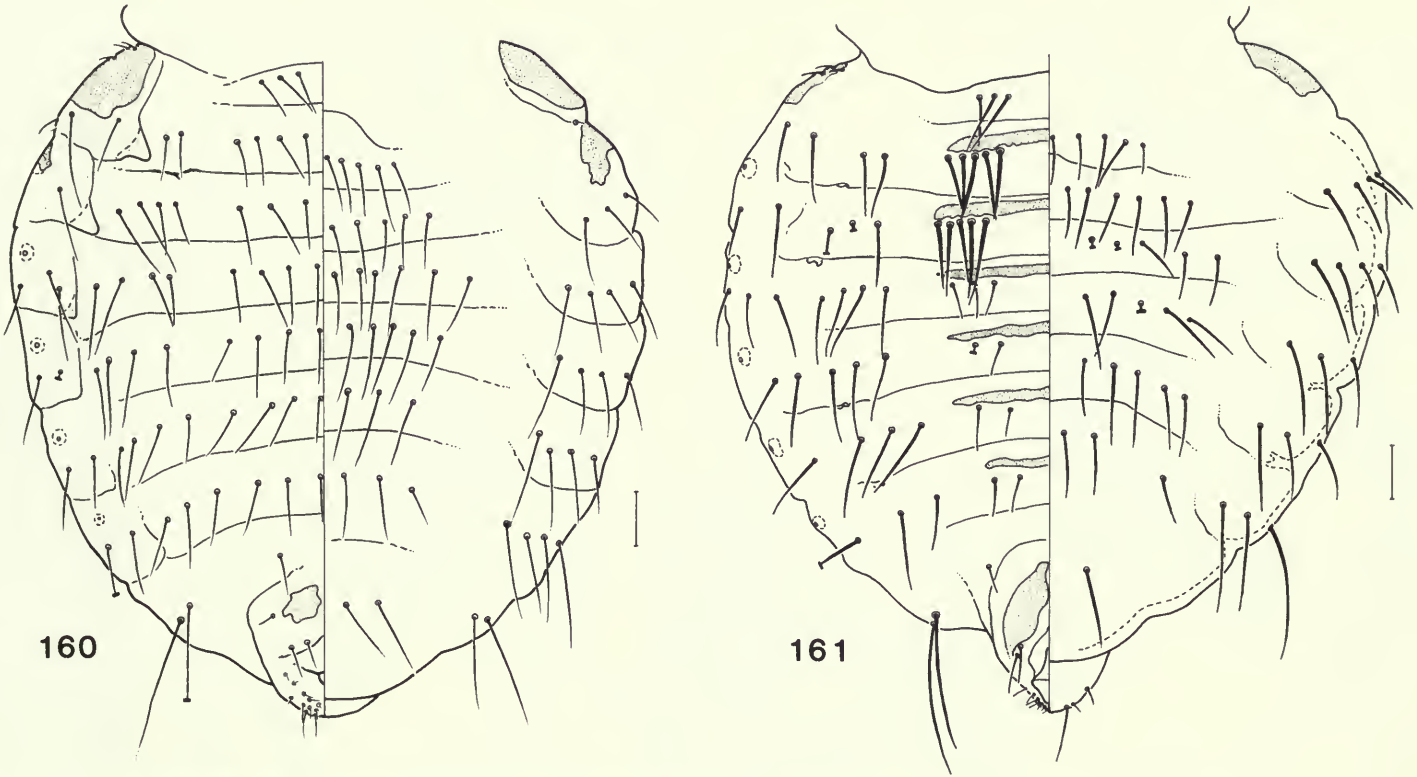
Figs 155–157 *Trichodectes (Stachiella)* species, ♀ terminalia. 155, *T. (S.) octomaculatus*. 156, *T. (S.) erminiae*. 157, *T. (S.) potus*.

present only on pleurum II; postero-lateral setae presumed absent, or presence obscured by numerous long setae or reduction (or absence) of lateral setal group. Abdominal pleura lacking projections, or projections present dorsally on pleura II, III and IV* (Fig. 160). Abdominal sclerites variable, present or absent*; male terga with or without anterior and posterior sclerites*.

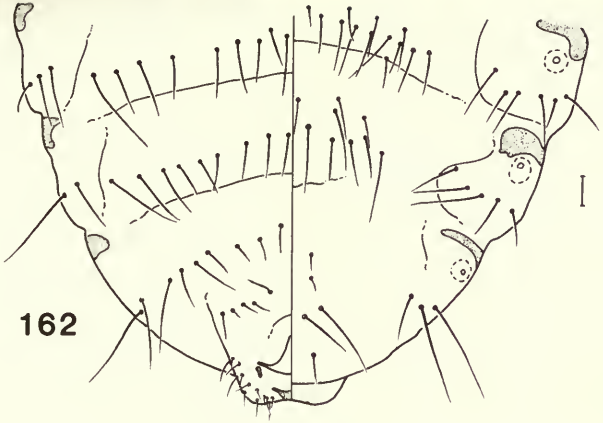
Gonapophyses with separate tuberculate setae and single apical non-tuberculate seta on ventral margin (Figs 149, 151, 153, 156, 159), or tubercles more closely associated (Fig. 155) or all setae non-tuberculate (Figs 152, 154)*; ventral lobe absent. Gonapophyses meet ventral vulval margin smoothly, linked by sclerotised band, or band absent. Ventral vulval margin sclerotised or, rarely, not sclerotised; with chord at



Figs 158, 159 *Trichodectes (T.)* species, ♂ abdomens. 158, *T. (T.) canis*. 159, *T. (T.) emersoni*.



Figs 160, 161 *Trichodectes (Paratrichodectes)* species, ♂ abdomens. 160, *T. (P.) zorillae*. 161, *T. (P.) ovalis*.



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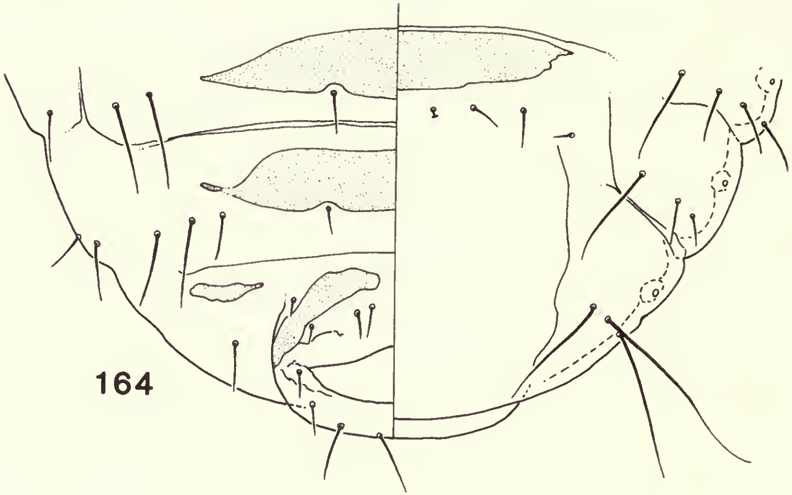

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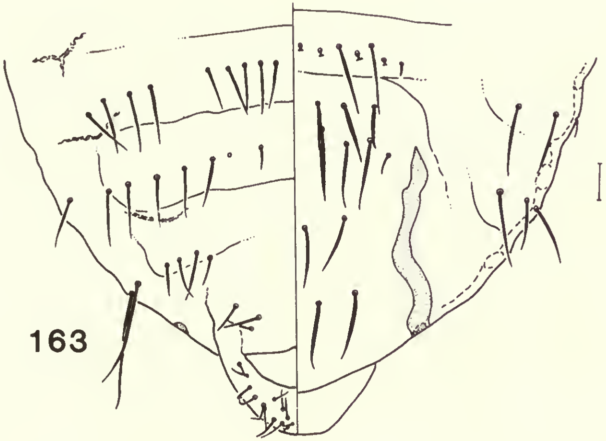

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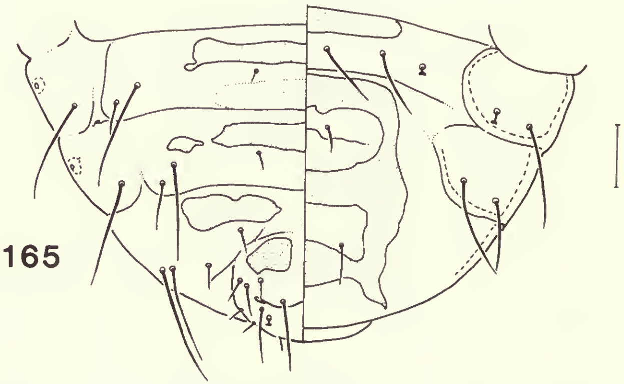

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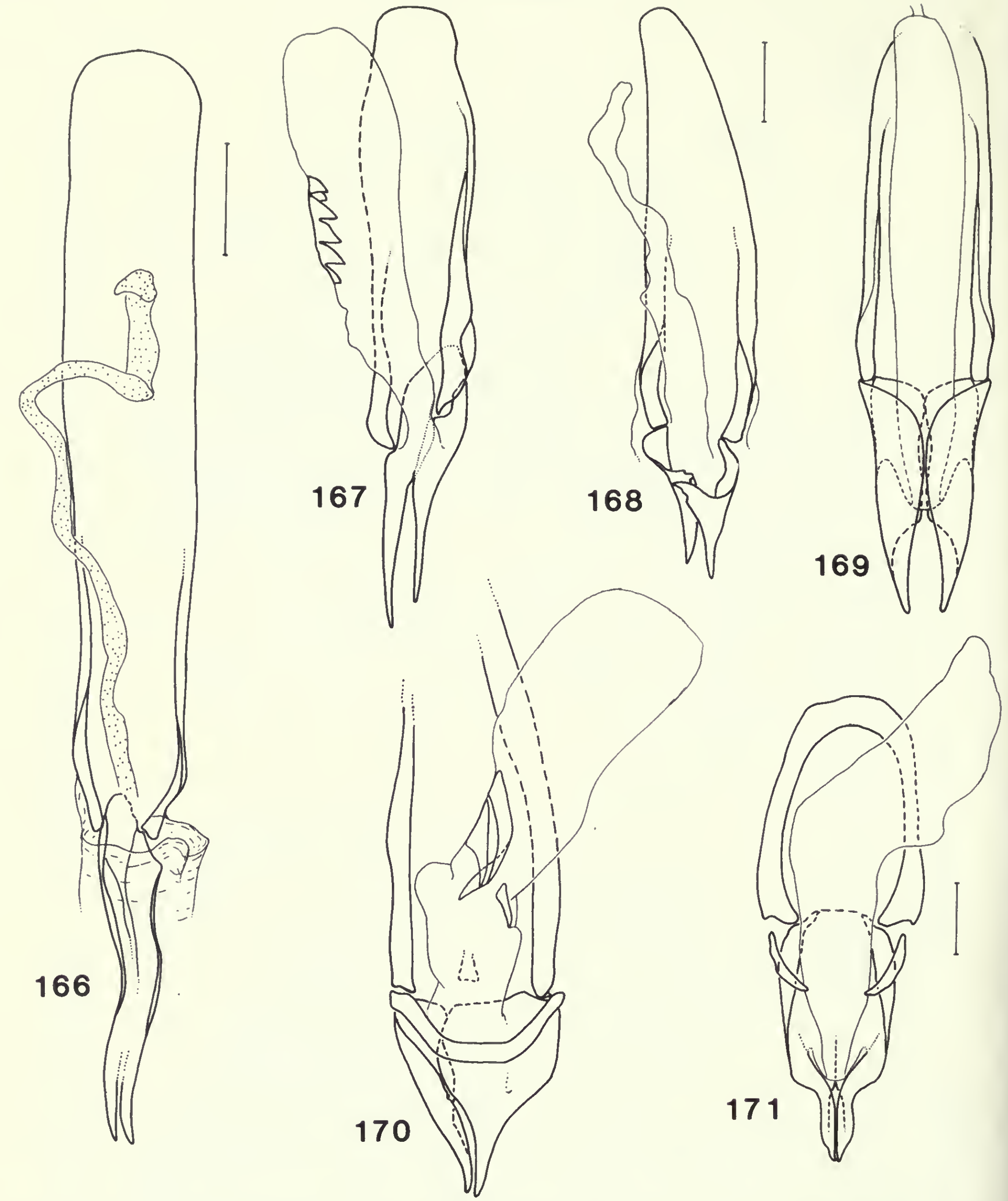
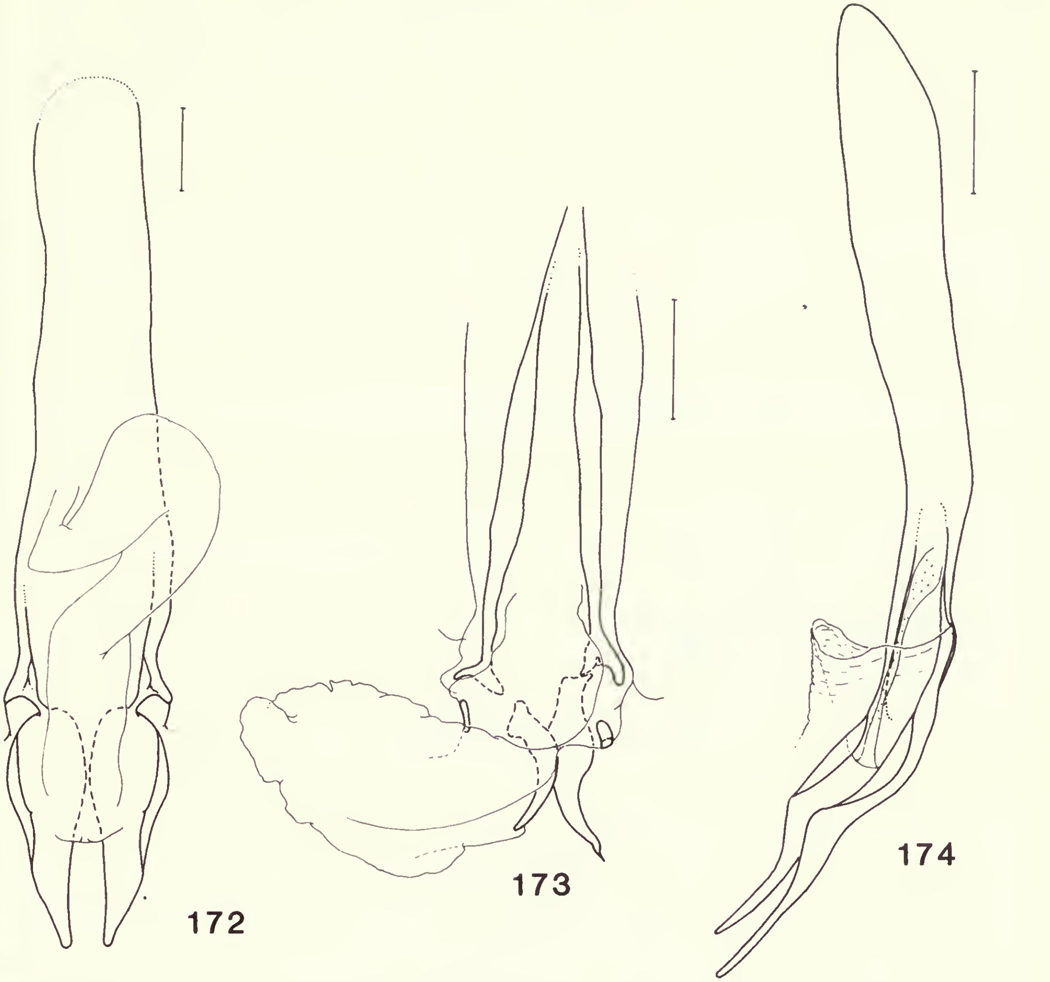
Figs 162–165 *Trichodectes* species, ♂ terminalia. 162, *T. (T.) pinguis euarctidos*. 163, *T. (T.) galictidis*. 164, *T. (Stachiella) emeryi*. 165, *T. (S.) erminiae*.



Figs 166–171 *Trichodectes* species, ♂ genitalia. 166, *T. (Paratrichodectes) ovalis*. 167, *T. (P.) zorillae*. 168, *T. (P.) ugandensis*. 169, *T. (T.) canis*. 170, *T. (T.) galictidis*. 171, *T. (T.) emersoni*.

90 degrees to long axis of abdomen; marginal setae present, tuberculate or non-tuberculate. Subgenital lobe present, usually with marginal serrations and lateral basal projections, the latter sometimes with associated setae.

Male subgenital plate absent (Figs 158, 160–162, 164), represented only by s.g.p.r. (Fig. 163) or enlarged sternite VIII (Fig. 159), with sternites VII, VIII and IX present and fused to s.g.p.r. (Fig. 165), or of the latter form but with sternite VIII divided medially. Pseudostyli absent. Male genital opening dorsal or postero-dorsal. Parameres fused or separate, fused to b.a.l.s. or free*. Basiparameral sclerites absent. Mesomeres absent or present, fused or unfused; if mesomeres fused apically, median extension absent.



Figs 172–174 *Trichodectes (Stachiella)* species, ♂ genitalia. 172, *T. (S.) octomaculatus*. 173, *T. (S.) emeryi*. 174, *T. (S.) erminiae*.

Hosts. Canidae, Mustelidae, Procyonidae, Ursidae and Viverridae (Carnivora).

Comments. The different concepts of the extent of the genus *Trichodectes* held by various workers are summarised in Table 4.

Subgenus *TRICHODECTES* Nitzsch

(Figs 10, 149–152, 158, 159, 162, 163, 169–171)

Trichodectes Nitzsch, 1818: 294. Type-species: '*Trichodectes canis* DeGeer (syn. *T. latus* N.)', by subsequent designation [Johnston & Harrison, 1911: 326].

Ursodectes Kéler, 1938*a*: 435. Type-species: *Trichodectes pinguis* Burmeister, by original designation. [Synonymy by Hopkins, 1942: 444.]

Grisonia Kéler, 1938*a*: 464. [No type-species designated] [Homonym of *Grisonia* Gray, 1843: 68].

Galictobius Kéler, 1938*b*: 228. [Replacement name for *Grisonia* Kéler.] Type-species: *Trichodectes galictidis* Werneck, by original designation. [Synonymy by Hopkins, 1942: 444.]

Description. Male scape expanded; male flagellum with two or four basally-articulated 'teeth'.

Abdominal spiracles present on segments III–VIII, spiracle on segment VIII not smaller than those on anterior segments. Abdomen with at least some tergal and sternal setae as long as segment, or setae very short, sparse and absent from pleura V and VI (*kuntzi* and *emersoni*); male terga II and III sometimes with median group comprising exceptionally long, stout setae (undescribed sister-species to *T. galictidis*), tergal setae never with median group reduced to single seta or absent (except sometimes on tergum I). Abdominal pleura lacking projections. Abdominal sternal sclerites absent, or present on sterna V–VIII only; abdominal tergal sclerites present or, more usually, absent; if tergites present on male, then not with anterior and posterior sclerites on each segment.

Female genital chamber with ventral wall frequently obscure, dorsal wall bearing sclerotised nodules, sometimes fused together.

Male subgenital plate absent, represented by s.g.p.r. only, or by enlarged sternite VIII only. Parameres fused to form plate or unfused; symmetric or asymmetric; not fused to b.a.l.s. Faintly-sclerotised tongue-like sclerite of uncertain homology sometimes present dorsally between parameres if mesomeres absent (Fig. 169). Mesomeres absent or, if present, fused or unfused. Male genitalia depicted in Figs 169–171.

Hosts. Canidae, Mustelidae, Ursidae and Viverridae (Carnivora).

Comments. *Trichodectes* Nitzsch, 1818 was placed on the Official List of Generic Names in Zoology, with the type-species *Trichodectes canis* DeGeer, by Opinion 627 of the International Commission of Zoological Nomenclature (1962, *Bulletin of Zoological Nomenclature* **19**: 91).

Species included
canis (DeGeer, 1778) (*c.*100 ♂, *c.*100 ♀)
emersoni Hopkins, 1960 (15 ♂, 12 ♀)
galictidis Werneck, 1934 (15 ♂, 16 ♀; also 2 ♂, 1 ♀ of an undescribed sister-species)
kuntzi Emerson, 1964 (15 ♂, 14 ♀)
melis (Fabricius, 1805) (*c.*60 ♂, *c.*60 ♀)
pinguis pinguis Burmeister, 1838 (1 ♂, 5 ♀)
pinguis euarctidos Hopkins, 1954 (20 ♂, 20 ♀)
vosseleri Stobbe, 1913 (2 ♂, 7 ♀)

Subgenus *PARATRICHODECTES* subgen. n.

(Figs 6, 154, 160, 161, 166–168)

Type-species: *Trichodectes ovalis* Bedford.

Description. Anterior of head with osculum present; clypeal marginal carina broadened medially into dorsal sclerite which is heavily-sclerotised laterally and lightly-sclerotised medially, more or less convex posteriorly or U-shaped with median posterior process; antero-lateral margin of head convex or sinuate; preantennal portion of head not long, outline rounded or subtriangular. Temple margin convex or rectangular. Male scape not greatly expanded; male flagellum with two basally-articulated 'teeth'.

Thorax with prothoracic dorsal setae sparse, of moderate length posteriorly and postero-laterally, absent from disc; pterothorax with setae on postero-lateral angle long dorsally, short and spine-like ventrally; dorsal posterior pterothoracic setae submarginal, long, comprising two pairs with wide median gap.

Abdominal spiracles present on segments III–VII. Abdomen with at least some tergal and sternal setae as long as segment; setae present on all pleura; tergal setae numerous, median group not reduced to a single seta or absent except sometimes on tergum I or on posterior terga of males only, if male terga II and III with median setal group comprising exceptionally long, stout setae; postero-lateral setae presumed absent, though may be present as the most lateral seta of lateral group, which is frequently situated more posteriorly than other setae. Abdominal sterna and terga with or without sclerites; male terga, if sclerites present, with anterior sclerites only.

Female genital chamber with dorsal wall not bearing sclerotised nodules.

Male subgenital plate unsclerotised. Parameres separate or thinly fused to each other; symmetric or asymmetric; not fused to b.a.l.s. Tongue-like sclerite not present. Mesomeres absent. Male genitalia depicted in Figs 166–168.

Hosts. Mustelinae (Carnivora: Mustelidae).

Species included
ovalis Bedford, 1928 **comb. rev.** from *Stachiella* (15 ♂, 12 ♀)
ugandensis Bedford, 1936 **comb. rev.** from *Stachiella* (44 ♂, 47 ♀)
zorillae Stobbe, 1913, **comb. rev.** from *Stachiella* (17 ♂, 26 ♀)

Subgenus *STACHIELLA* Kéler **stat. n.**

(Figs 153, 155–157, 164, 165, 172–174)

Stachiella Kéler, 1938*a*: 428. Type-species: *Trichodectes pusillus* Nitzsch [= *Pediculus mustelae* Schrank], by original designation.
Potusdia Conci, 1942: 141. Type-species: *Trichodectes potus* Werneck, by original designation. [Synonymised with *Trichodectes* by Werneck, 1948: 110; **syn. n.** of *Stachiella*.]

DESCRIPTION. Clypeal marginal carina broadened medially into dorsal sclerite which is heavily-sclerotised laterally and lightly or very lightly-sclerotised medially, more or less convex posteriorly or U-shaped with median posterior process; antero-lateral margin of head smoothly convex; preantennal portion of head long or short, outline broadly rounded, sometimes only slightly produced anteriad between coni. Male scape not, or only slightly, expanded; male flagellum with one or two basally-articulated 'teeth' or 'teeth' absent.

Thorax with prothoracic dorsal setae sparse, of moderate length posteriorly and postero-laterally, absent from disc; pterothorax with setae on postero-lateral angles short and spine-like or of moderate length, dorsal posterior setae submarginal, long, comprising one or more pairs with wide median gap, or absent.

Abdominal spiracles present on segments III–IV, III–V, or III–VIII; spiracle on segment VIII, if present, sometimes much smaller than those on segments III–VII. Abdomen with at least some tergal and sternal setae as long as segment; setae present on all pleura; terga with median setal group of male reduced to a single seta on most segments, lateral group small; female tergal setae of similar arrangement or with median group absent (see discussion on p. 221 above); male terga II and III never with median group comprising exceptionally long, stout setae; postero-lateral setae presumed absent, though perhaps present as the most lateral seta of lateral setal group, which is frequently situated more posteriorly than other setae of the group. Abdominal pleura lacking projections. Abdominal sterna variably sclerotised, with sternites, if present, most commonly on posterior segments; abdominal terga with sclerites present on segments III–VIII or III–IX, sometimes on I and II; male terga frequently with both anterior and posterior sclerites, though posterior sclerites may be faintly-sclerotised or absent; abdominal pleurum II frequently sclerotised, otherwise pleura unsclerotised.

Gonapophyses with separate or closely-associated tuberculate setae and single apical non-tuberculate seta on ventral margin. Gonapophyses meet ventral vulval margin smoothly, linked by sclerotised band. Ventral vulval margin sclerotised. Female genital chamber with dorsal wall not bearing sclerotised nodules.

Male subgenital plate absent, or with sternites VII, VIII and IX present and fused to s.g.p.r., or of this form but with sternite VIII divided medially. Parameres separate or thinly fused to one another; symmetric, asymmetric or asymmetrically deflected; fused or not fused to b.a.l.s. Tongue-like sclerite not present. Mesomeres absent, present, small and unfused, or present and fused. Male genitalia depicted in Figs 172–174.

HOSTS. Mustelidae: Mustelinae and Procyonidae (Carnivora).

COMMENTS. *Stachiella* has been considered a synonym and a subgenus of *Trichodectes* (Hopkins, 1942 and Hopkins, 1949 respectively), although its most recent treatment (Emerson & Price, 1981) was as a valid genus. *Potusdia* has also been considered as a valid genus, subgenus of *Trichodectes* and synonym of *Trichodectes* but has not, before this study, been considered a synonym of *Stachiella*. A more comprehensive history of the variations in status of *Stachiella* and *Potusdia* is given in Table 4.

SPECIES INCLUDED

divaricatus Harrison, 1915 **comb. rev.** from *Stachiella*
emeryi Emerson & Price, 1974 [treated by Emerson & Price (1974, 1981) as *Trichodectes* s. str.] (4 ♂, 17 ♀)
erminiae (Hopkins, 1941) **comb. n.** from *Stachiella* (92 ♂, 100 ♀)
fallax Werneck, 1948 [treated by Werneck (1948) and all subsequent authors as *Trichodectes* s. str.] (2 ♂, 2 ♀)
jacobi (Eichler, 1941) **comb. n.** from *Stachiella*
kingi McGregor, 1917 **comb. rev.** from *Stachiella* (14 ♂, 25 ♀)
larseni (Emerson, 1962) **comb. n.** from *Stachiella* (58 ♂, 57 ♀)
mustelae (Schrank, 1903) **comb. n.** from *Stachiella* (18 ♂, 23 ♀)
octomaculatus Paine, 1912 [treated by all authors as *Trichodectes* s. str.] (48 ♂, 58 ♀)

potus Werneck, 1934 [treated by Werneck (1948) and Emerson & Price (1981) as *Trichodectes* s. str.] (19 ♂, 25 ♀)

retusus retusus Burmeister, 1838 **comb. rev.** from *Stachiella* (1 ♂, 1 ♀)

retusus martis (Werneck, 1948) **comb. n.** from *Stachiella* (1 ♂)

retusus salfii (Conci, 1940) **comb. n.** from *Stachiella*

Genus *FELICOLA* Ewing

The genus *Felicola* comprises two subgenera.

Description. Anterior of head with osculum present or absent; dorsal preantennal sulcus present or absent; clypeal marginal carina, if osculum absent, with very slight median broadening, or, if osculum present, carina broadened medially into dorsal sclerite which is heavily-sclerotised laterally (dorsal to margin of clypeus and pulvinus) and very lightly-sclerotised medially (posterior to osculum); anterolateral margin of head straight, slightly sinuate or convex; preantennal portion of head long or short, outline triangular or broadly rounded*. Temple margin rectangular or convex. Male scape variably expanded or not expanded*, with longitudinal setal row present and comprising at least three setae; flagellomeres fused in males and females; male flagellum with one or three basally-articulated 'teeth', or variable number of 'teeth' fused to flagellum, or 'teeth' absent*. Dorsum of head with setae short, of moderate length or long, but in any case frequently longer than abdominal tergal setae; setae sparse, though most numerous anteriorly and along lateral margins. Sitophore sclerite unmodified.

Thorax with dorsal setae long or of moderate length though frequently short and spine-like on postero-lateral angles of pterothorax, not present on disc of prothorax or pterothorax.

Abdomen oval or elongate, frequently terminating in more or less acute projection of segment IX in the male (Figs 179, 181, 183–189). Abdominal spiracles absent, or present on segment III, segments III–IV, or segments III–V*. Abdominal setae short, of moderate length, or occasionally long and fine* (Figs 182, 186, 188); male tergum II frequently with 2–6 very long setae medially (Figs 179, 180, 187, 189); abdominal pleurum III frequently with posterior setal row comprising stout, conical setae (Figs 181, 182, 188); anterior setae, if present, only on pleurum II; postero-lateral setae present or absent. Abdominal pleurum III with projections absent, or, if present, dorsal or ventral, sclerotised or unsclerotised; abdominal pleurum IV with projections absent or, if present, dorsal and occasionally ventral, sclerotised or unsclerotised. Abdominal sclerotisation variable; sternal, tergal and pleural sclerites, if present, generally on anterior segments, becoming less clear on posterior segments; male terga sometimes with anterior and posterior sclerites, at least on tergum VI*.

Gonapophyses with non-tuberculate setae and rounded or rectangular lobe present on ventral margin; apical spur present or absent*. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; straight or concave, with chord less than 90 degrees to long axis of abdomen; subgenital lobe present, apically single or bifurcate, with margins serrate, at least posteriorly (Fig. 175) (see comment below).

Male subgenital plate not present, though sternite VIII sometimes with postero-lateral projections probably homologous with lateral rods of subgenital plate (Fig. 181). Pseudostyli absent. Male genital opening postero-dorsal or dorsal; segment IX frequently produced posteriad. Parameres generally long and slender (Figs 191, 192, 197, 201), occasionally broader (Fig. 198); frequently fused completely or, more usually, basally only. Basiparameral sclerites absent. Mesomeres present or absent; if present, unfused (Fig. 200) or, if fused, median extension absent*. Male genitalia depicted in Figs 190–206.

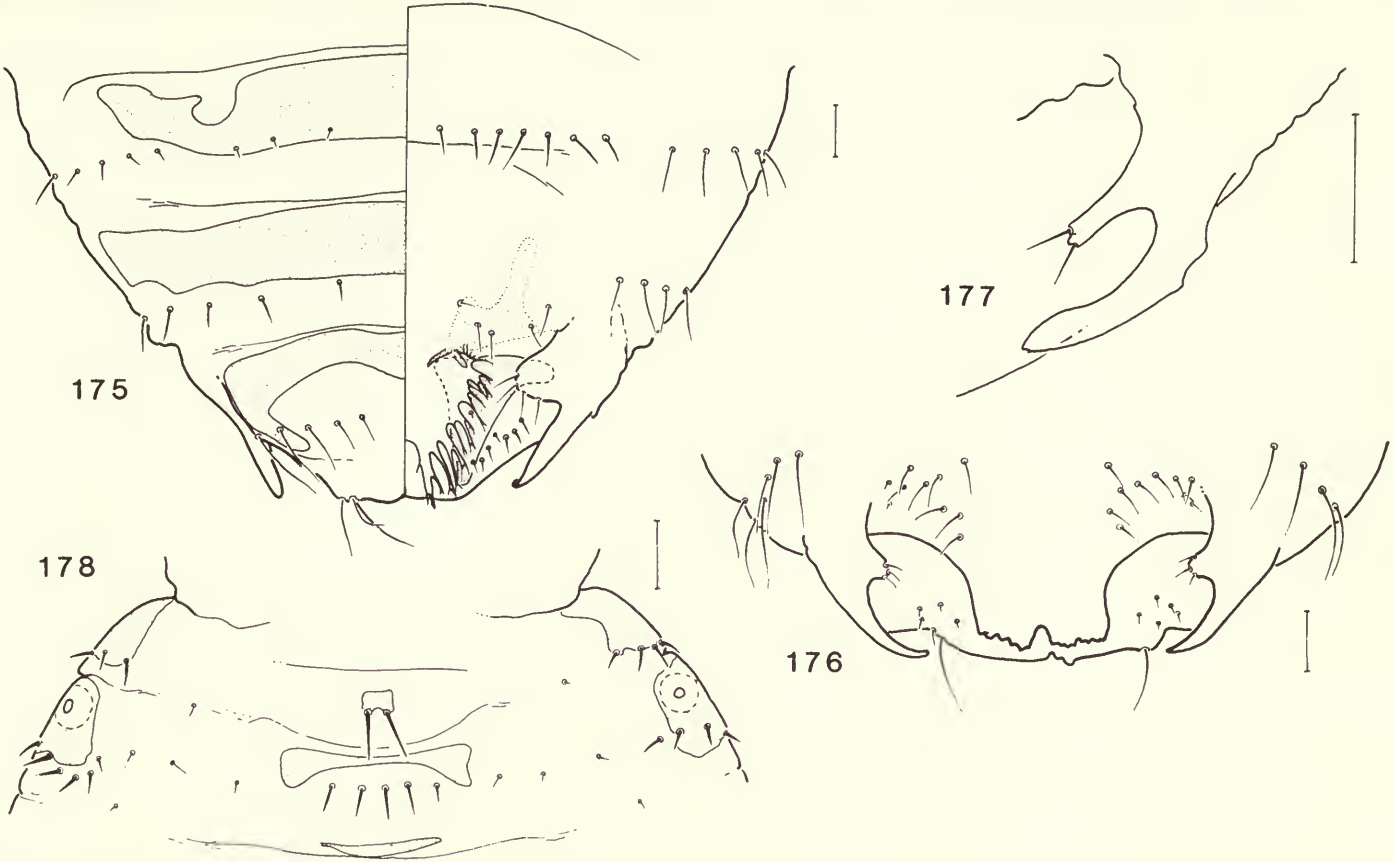
Hosts. Herpestidae, Viverridae, Felidae and Canidae (Carnivora).

Comments. Emerson & Price (1980) distinguish the females of their new species *Suricatoecus occidentalis* (transferred to *Felicola* in this study) from other species in the '*helogale* Group' (equivalent to the *congoensis–occidentalis* clade) by the presumed absence of the subgenital lobe in *occidentalis*. Examination of the type-series of this species, however, reveals that the subgenital lobe, although very fine, is present in all the females. A second species of this clade, close to *F. helogaloidis*, has been taken from skins of *Crossarchus obscurus* (the host of *F. occidentalis*) and specimens are in the collection of the British Museum (Natural History).

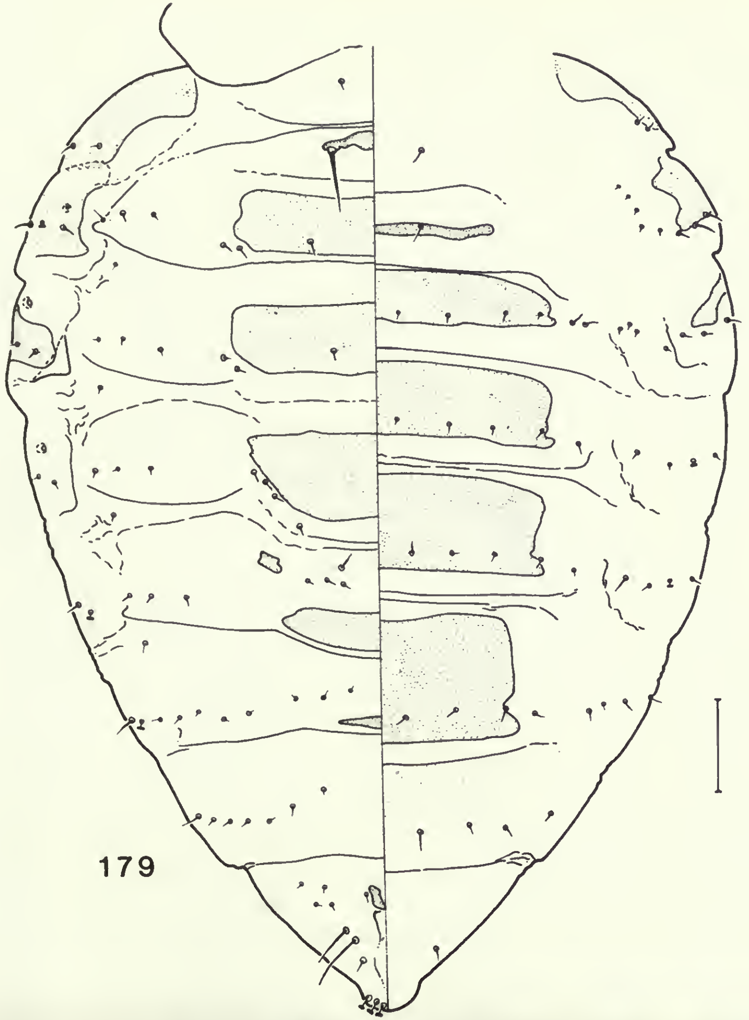
Subgenus *FELICOLA* Ewing

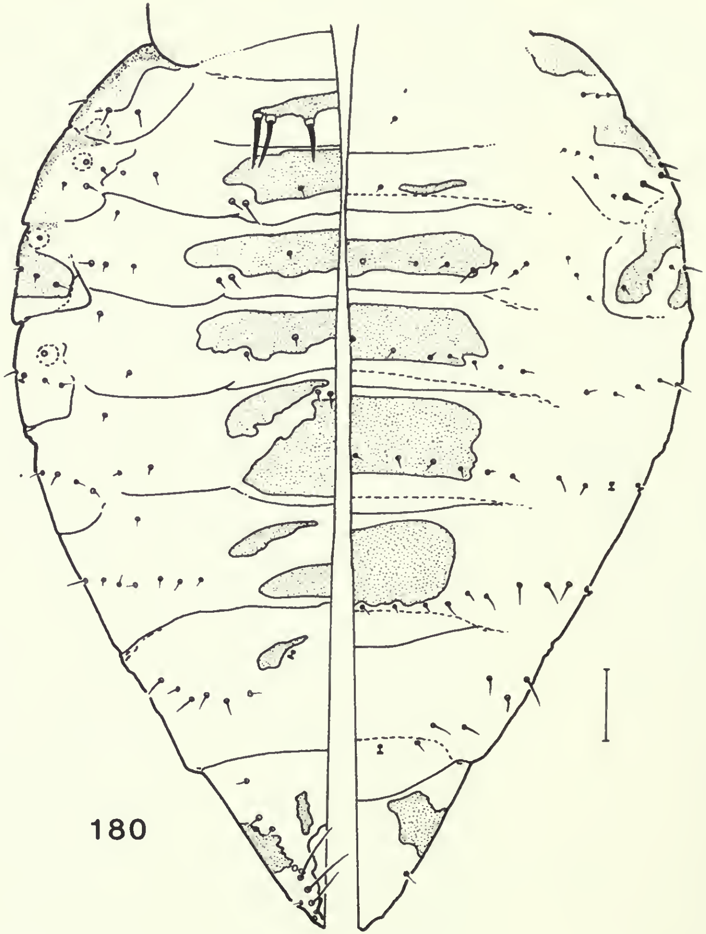
(Figs 5, 175, 179–185, 190–193, 196–198, 202–204)

Felicola Ewing, 1.vi.1929: 121, 122, 192. Type-species: *Trichodectes subrostratus* Burmeister [attributed to Nitzsch], by original designation.

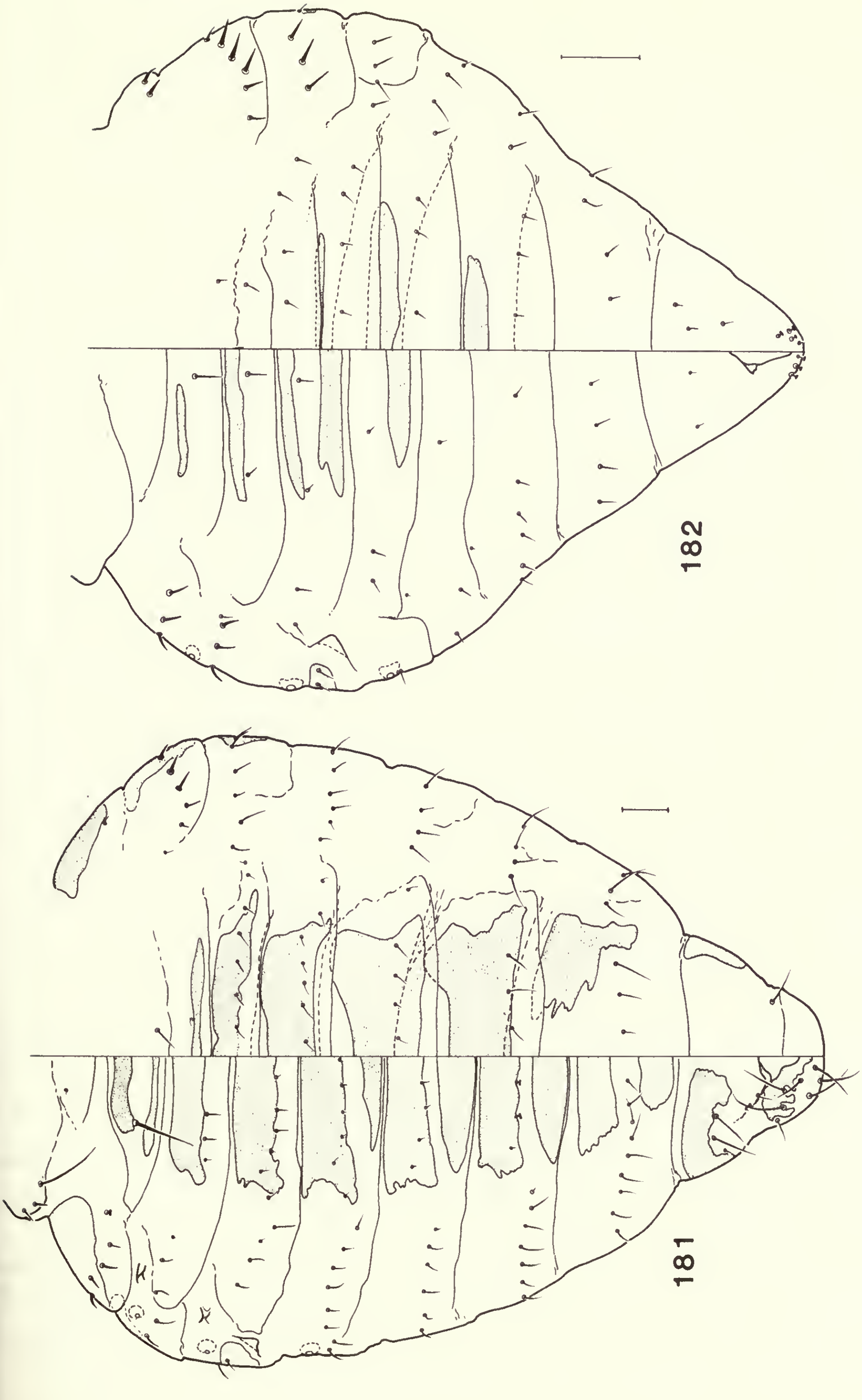


Figs 175–178 *Felicola* species. 175, *F. (F.) zeylonicus*, ♀ terminalia. 176, *F. (Suricatoecus) vulpis*, ♀ terminalia, ventral. 177, *F. (S.) decipiens*, ♀ gonapophysis, ventral. 178, *F. (S.) pygidialis*, ♂ abdominal terga I–III.

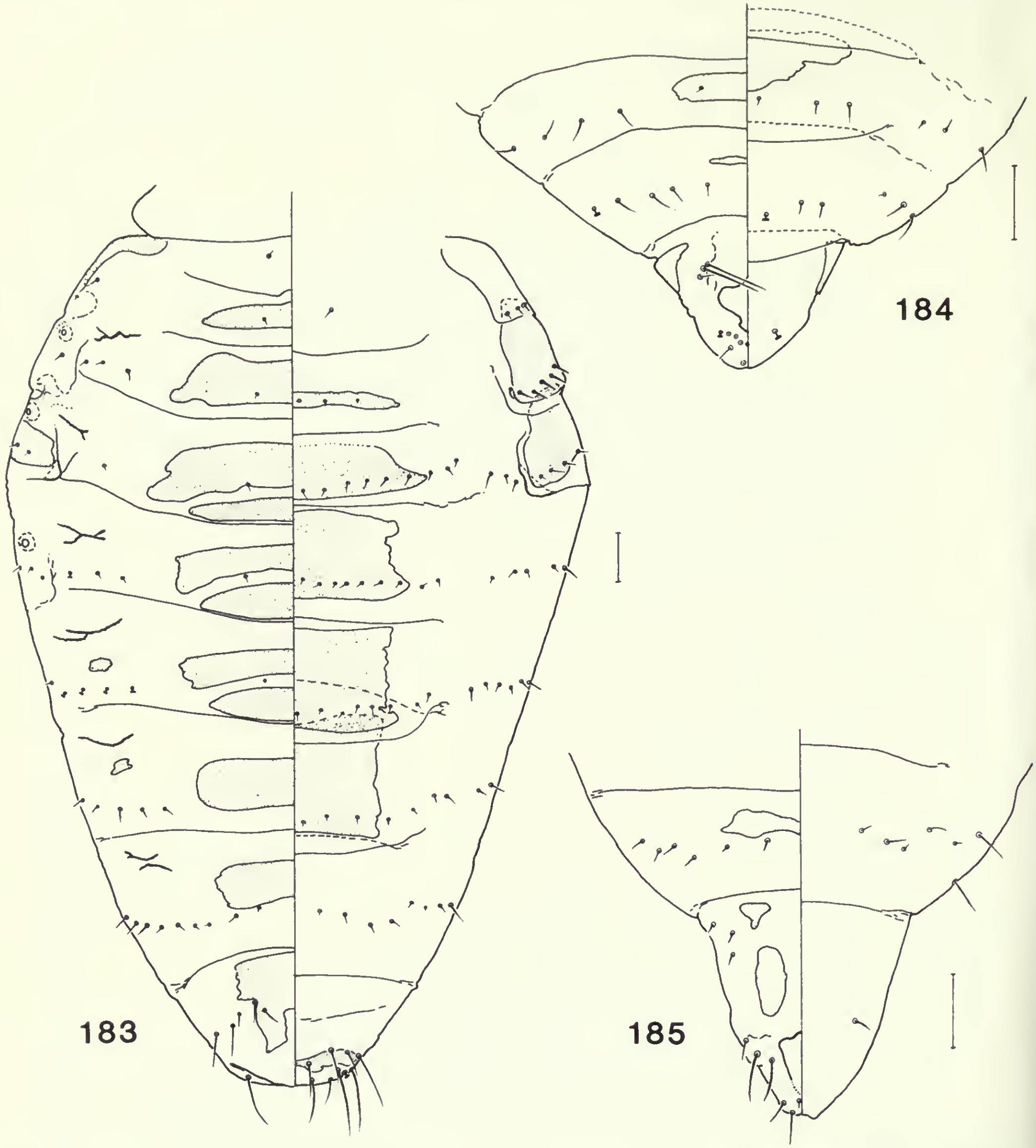




Figs 179, 180 *Felicola (F.)* species, ♂ abdomens. 179, *F. (F.) cynicitis*. 180, *F. (F.) setosus*.



Figs 181, 182 *Felicola (F.)* species, ♂ abdomens. 181, *F. (F.) congoensis*. 182, *F. (F.) minimus*.



Figs 183–185 *Felicola (F.)* species. 183, *F. (F.) calogaleus*, ♂ abdomen. 184, *F. (F.) helogale*, ♂ terminalia. 185, *F. (F.) hopkinsi*, ♂ terminalia.

Felicinia Bedford, –.x.1929: 519. Type-species: *Trichodectes subrostratus* Burmeister [attributed to Nitzsch], by original designation. [Synonymised by Bedford, 1932*a*: 536.]

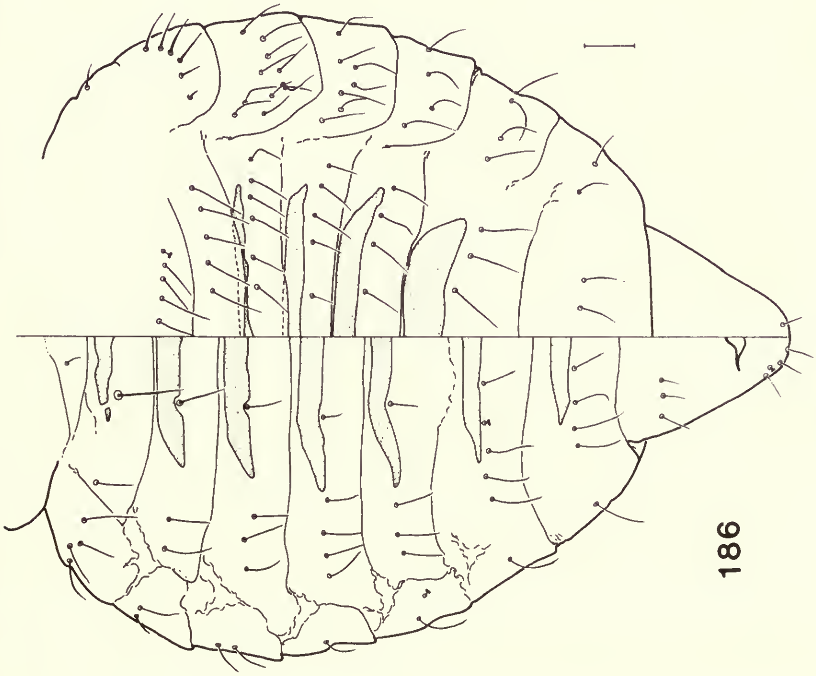
Bedfordia Kéler, 1938*a*: 463. Type-species: *Felicola helogale* Bedford, by original designation. [Homonym of *Bedfordia* Fahrenholz, 1936: 55.] [Synonymised with *Felicola* by Hopkins, 1941: 36.]

Fastigatosculum Kéler, 1939: 11. [Replacement name for *Bedfordia* Kéler.] [Synonymised with *Suricatoecus* by Werneck, 1948.]

DESCRIPTION. Preantennal portion of head with outline narrowly or broadly triangular or rounded. Male flagellum with 'teeth' absent or, if present, numbering one, two, three or four and fused to flagellum, not basally articulated.

Abdominal spiracles absent, or present on segments III–IV or III–V. Abdominal setae very short or of moderate length.

Gonapophyses with rounded lobe on ventral margin; spur present or absent.



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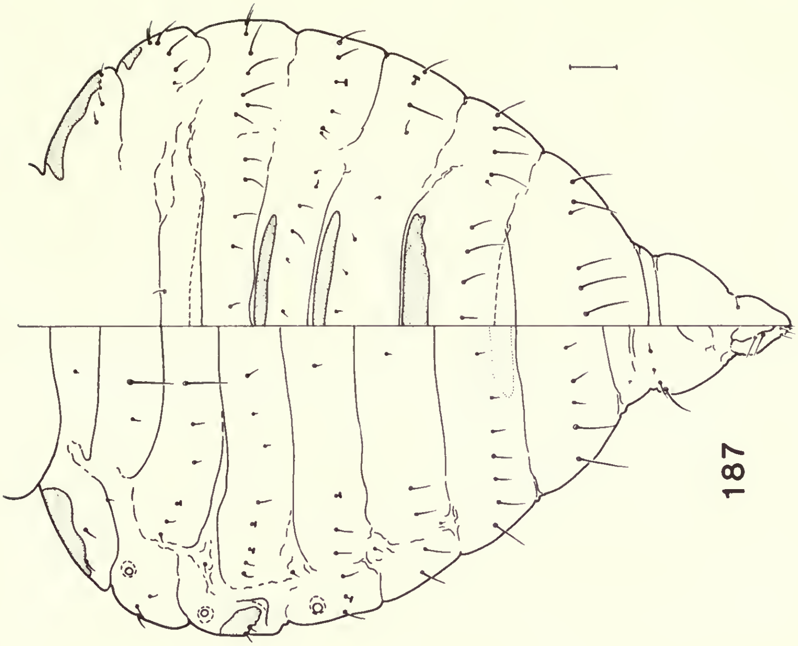

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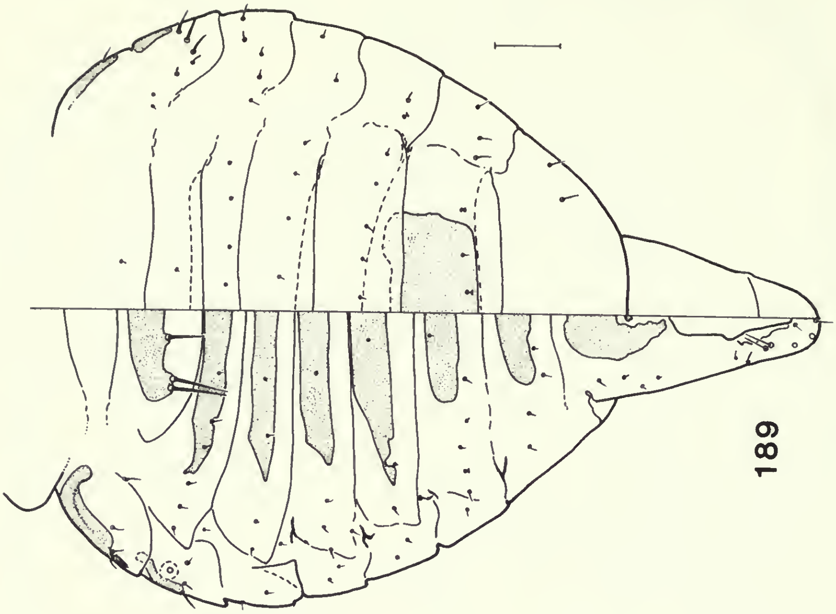
Figs 186, 187 *Felicola (Suricatoecus)*, ♂ abdomens. 186, *F. (S.) fahrenholzi*. 187, *F. (S.) decipiens*.



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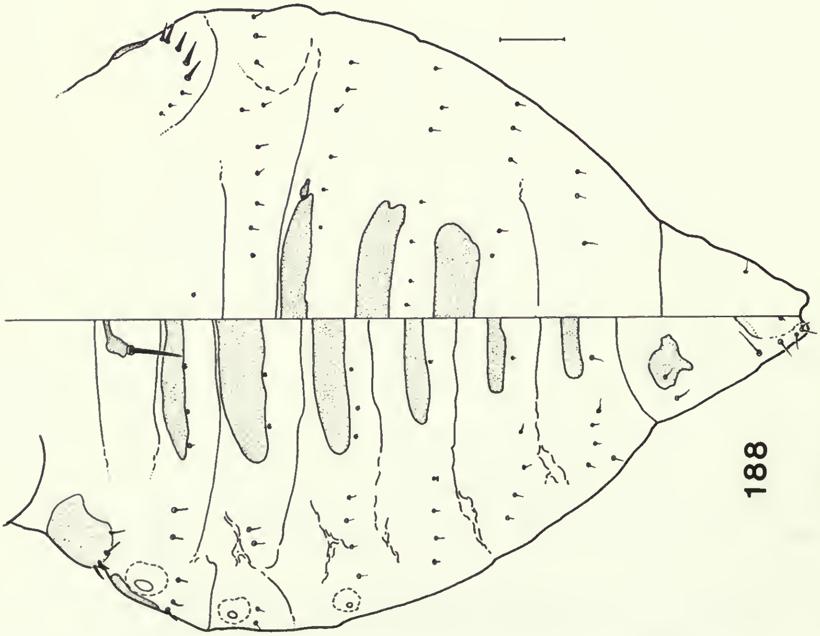

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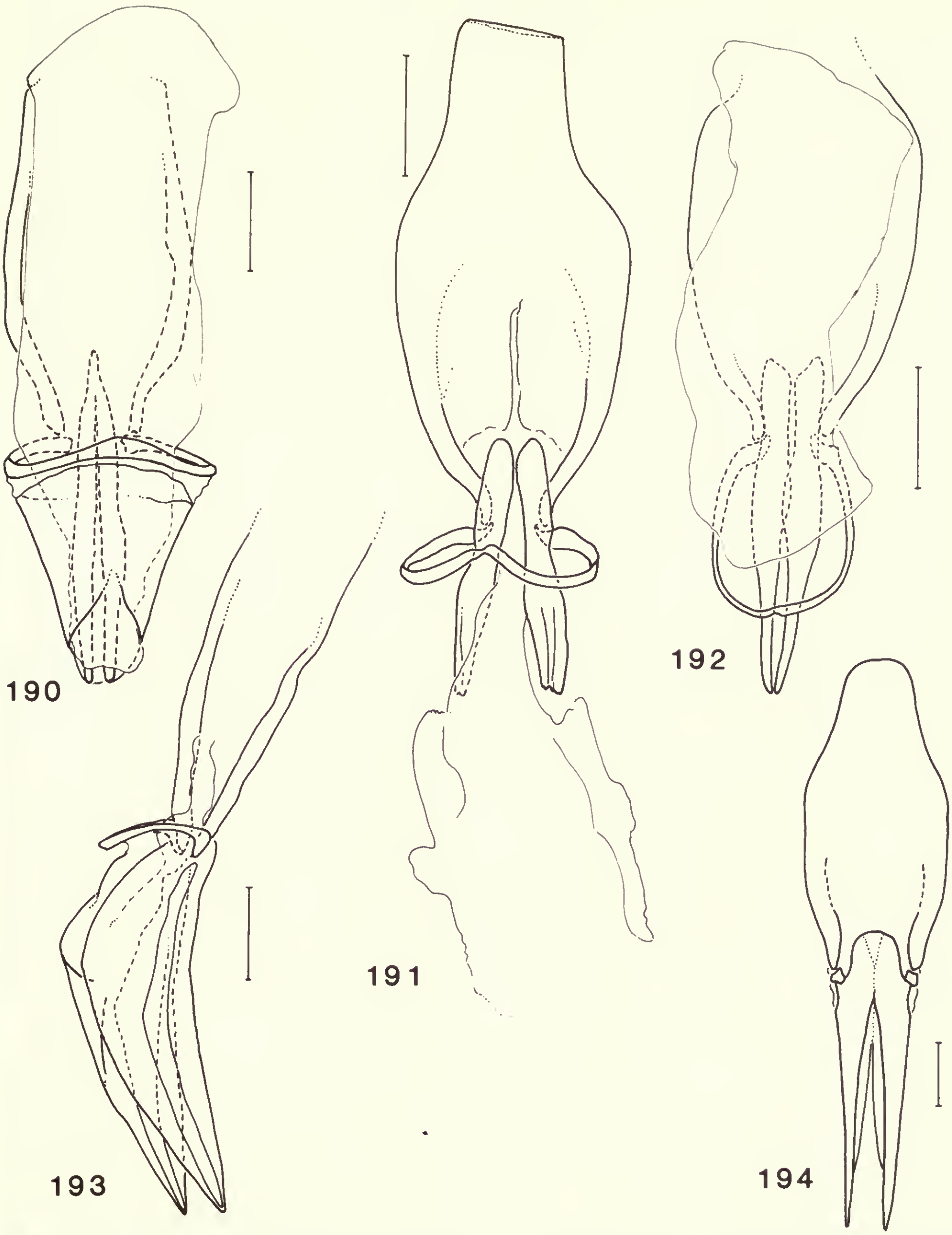
Figs 188, 189 *Felicola (Suricatoecus)*, ♂ abdomens. 188, *F. (S.) acutirostris*. 189, *F. (S.) bedfordi*.

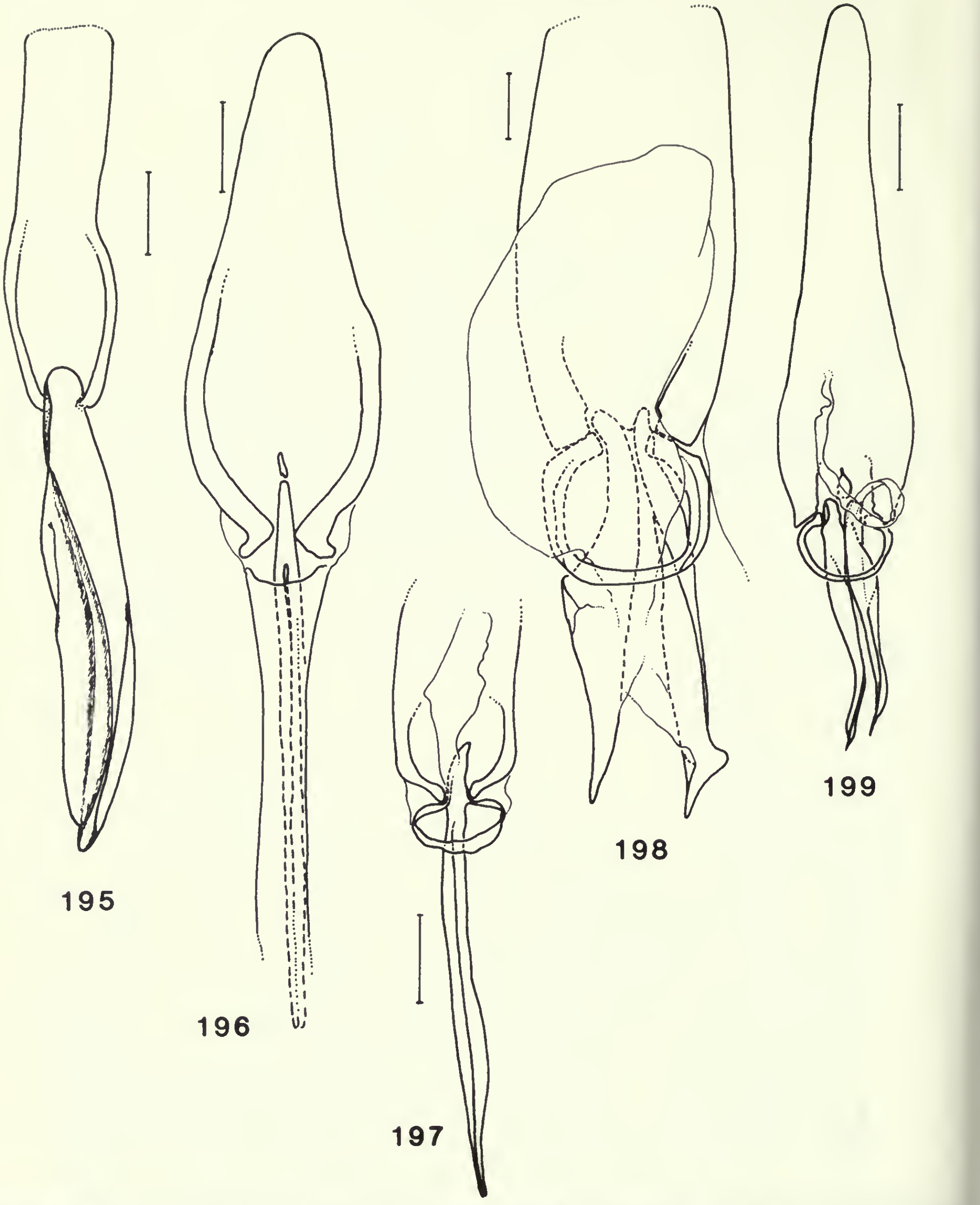


Figs 190–194 *Felicola* species, ♂ genitalia. 190, *F. (F.) calogaleus*. 191, *F. (F.) inaequalis*, endophallus partially everted. 192, *F. (F.) inaequalis*, endophallus not everted. 193, *F. (F.) setosus*; 194, *F. (Suricatoecus) fahrenholzi*.

Everted portion of endophallus frequently thinly sclerotised (Figs 190, 196, 204). Mesomeres present and fused or absent.

Hosts. Felidae, Herpestidae and Viverridae (Carnivora).

Comments. *F. genettae* (Fresca) is included on the basis of the figures and description of Fresca (1924) which, although poor, suggest an affinity with the *calogaleus–viverriculae* clade. If this is a correct placement, the host record of *Genetta genetta rhodanica* is anomalous. The various treatments of the junior

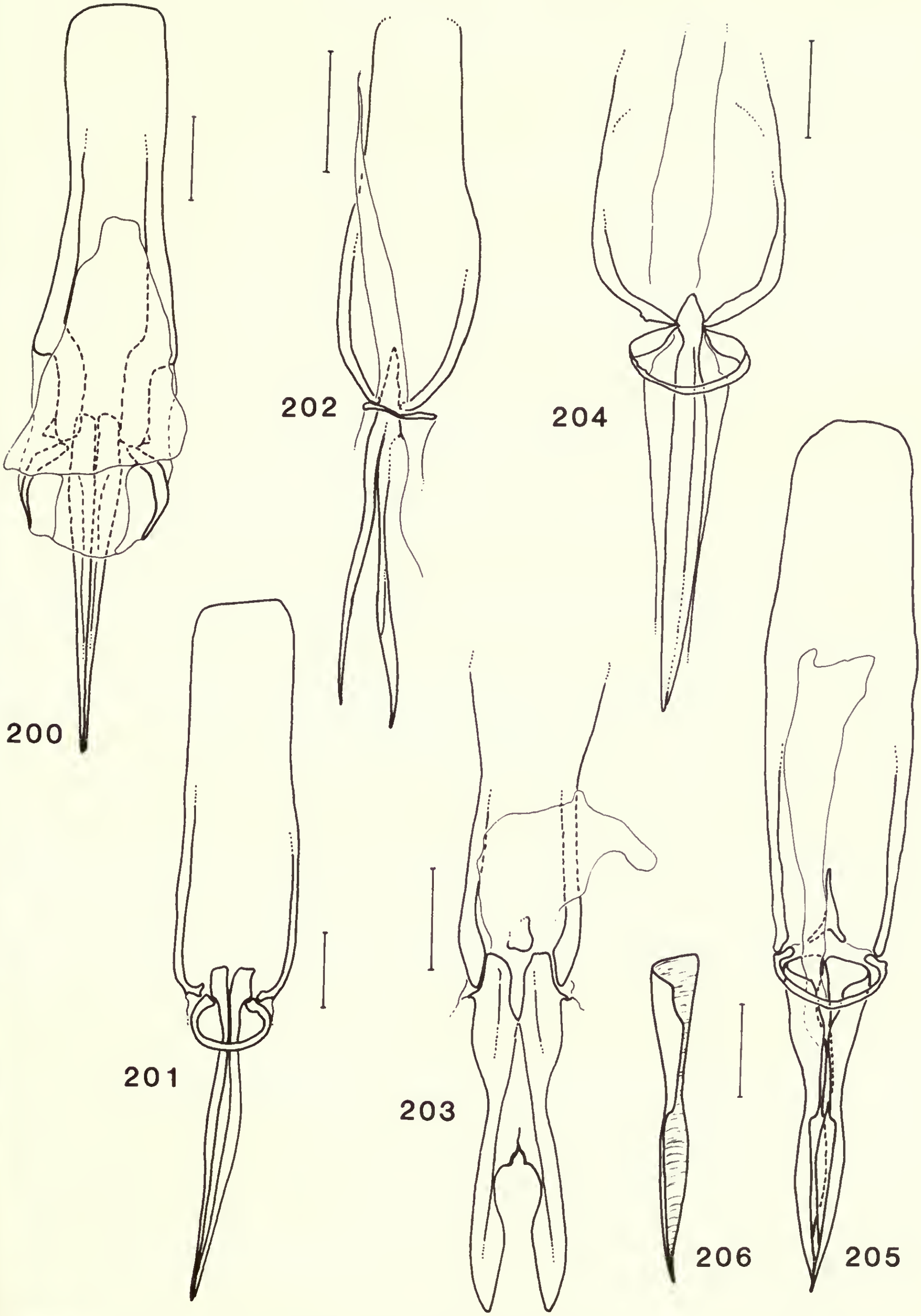


Figs 195–199 *Felicola* species, ♂ genitalia. 195, *F. (Suricatoecus) bedfordi*. 196, *F. (F.) robertsi*. 197, *F. (F.) hopkinsi*. 198, *F. (F.) congoensis*. 199, *F. (F.) helogale*.

synonyms of *Felicola* are summarised in Table 5; omitted from the table is Conci (1946) who, like Eichler (1941, 1963) regarded *Fastigatosculum* as a valid genus.

Species included

calogaleus (Bedford, 1928) (14 ♂, 24 ♀)
congoensis (Emerson & Price, 1967) **comb. n.** from *Suricatoecus* (23 ♂, 31 ♀)
cynictis (Bedford, 1938) (13 ♂, 19 ♀)
genettae (Fresca, 1924)



Figs 200–206 *Felicola* species, ♂ genitalia. 200, *F. (Suricatoecus) acutirostris*. 201, *F. (S.) vulpis*. 202, *F. (F.) liberiae*. 203, *F. (F.) minimus*, parameres displaced slightly apart. 204, *F. (F.) subrostratus*. 205, *F. (S.) decipiens*. 206, *F. (S.) decipiens*, detail of paramere.

- ***helogale*** Bedford, 1932, **comb. rev.** from *Suricatoecus* (3 ♂, 7 ♀)
- ***helogaloidis*** (Werneck, 1948) **comb. n.** from *Suricatoecus*
- ***hopkinsi*** Bedford, 1936 **comb. rev.** from *Suricatoecus* (2 ♂, 1 ♀)
- ***inaequalis*** (Piaget, 1880) (10 ♂, 19 ♀)
- ***liberiae*** Emerson & Price, 1972 (7 ♂, 3 ♀)
- ***minimus*** Werneck, 1948 (15 ♂, 28 ♀)
- ***occidentalis*** (Emerson & Price, 1981) **comb. n.** from *Suricatoecus* (4 ♂, 5 ♀)
- ***rahmi*** Emerson & Stojanovitch, 1966 (9 ♂, 16 ♀)
- ***robertsi*** Hopkins, 1944 (8 ♂, 15 ♀)
- ***rohani*** Werneck, 1956 (68 ♂, 62 ♀)
- ***setosus*** Bedford, 1932 (14 ♂, 18 ♀)
- ***subrostratus*** (Burmeister, 1838) (103 ♂, 120 ♀)
- ***viverriculae*** (Stobbe, 1913) **comb. n.** from *Parafelicola* (21 ♂, 26 ♀; 6 ♂, 6 ♀ of undescribed sister-species)
- ***zeylonicus*** Bedford, 1936 (6 ♂, 7 ♀)

Subgenus ***SURICATOECUS*** Bedford **stat. n.**

(Figs 176–178, 186–189, 194, 195, 200, 201, 205, 206)

Suricatoecus Bedford, 1932*a*: 354. Type-species: *Trichodectes cooleyi* Bedford, by monotypy.
Eichlerella Conci, 1942: 140. Type-species: *Trichodectes vulpis* Denny, by original designation. [Synonymy by Werneck, 1948: 172.]

Description. Preantennal portion of head with outline narrowly triangular or broadly rounded. Male scape not, or very slightly, expanded; male flagellum with 'teeth' absent or, if present, numbering one or three and basally articulated.

Abdominal spiracles absent, or present on segment III or segments III–V. Abdominal setae very short, of moderate length, or long and fine. Tergal and sternal sclerites generally present on abdomen, though less clear on posterior segments; male terga never with posterior sclerites.

Gonapophyses with rounded or rectangular lobe on ventral margin; spur present.

Everted portion of endophallus never sclerotised.

Hosts. Canidae and Herpestidae (Carnivora).

Comments. *Suricatoecus* has been treated not only as a genus, but also as a synonym and a subgenus of *Felicola* (Bedford, 1936 and Hopkins, 1949 respectively); a more complete history of the variations in status of *Suricatoecus* and of *Eichlerella* is provided in Table 5. Eichler (1963) included the manuscript name *Felicomorpha* in his catalogue, without providing any further details, the name therefore being a nomen nudum. In an earlier, unpublished work, Eichler had attributed this name to Kéler m.s., and noted the type-species, which is a junior synonym of *T. vulpis* Denny. *Felicomorpha* is, however, not an available name.

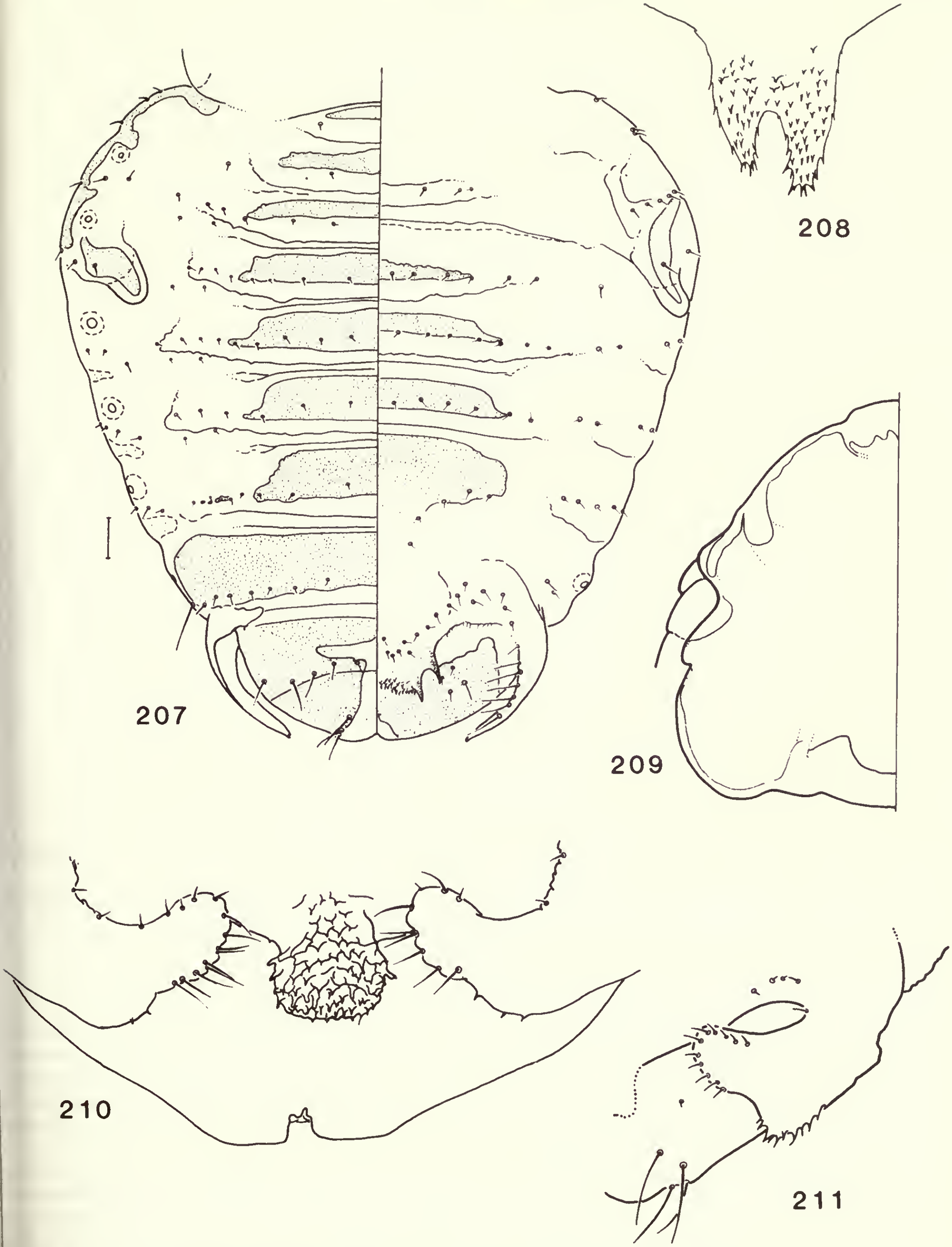
Species included

- ***acutirostris*** (Stobbe, 1913) [treated as *Felicola* s. str. by previous authors] (2 ♂, 2 ♀)
- ***bedfordi*** Hopkins, 1942 [treated as *Felicola* s. str. by previous authors] (4 ♂, 11 ♀)
- ***cooleyi*** (Bedford, 1929) **comb. n.** from *Suricatoecus* (30 ♂, 28 ♀)
- ***decipiens*** Hopkins, 1941 **comb. rev.** from *Suricatoecus* (9 ♂, 9 ♀)
- ***fahrenholzi*** (Werneck, 1948) **comb. n.** from *Suricatoecus* (16 ♂, 16 ♀)
- ***fennecus*** (Emerson & Price, 1981) **comb. n.** from *Suricatoecus*
- ***guinlei*** (Werneck, 1948) **comb. n.** from *Suricatoecus* (4 ♂, 10 ♀)
- ***macrurus*** Werneck, 1948 [treated as *Felicola* s. str. by previous authors] (23 ♂, 19 ♀)
- ***pygidialis*** Werneck, 1948 [treated as *Felicola* s. str. by previous authors] (36 ♂, 41 ♀)
- ***quadraticeps*** (Chapman, 1897) **comb. n.** from *Suricatoecus* (5 ♂, 9 ♀)
- ***vulpis*** (Denny, 1842) **comb. n.** from *Suricatoecus* (18 ♂, 25 ♀)

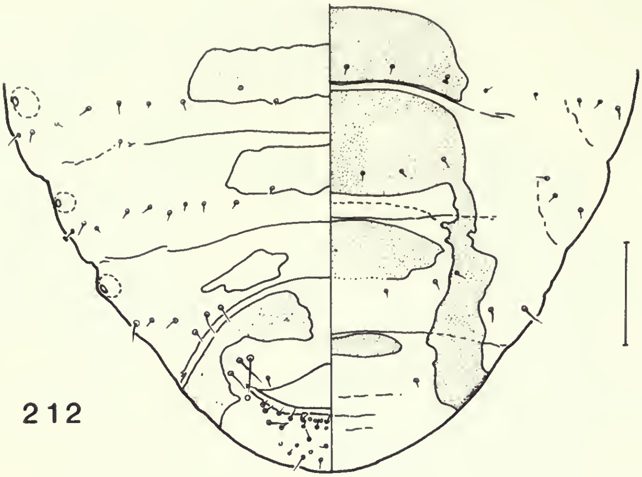
Genus ***LORISICOLA*** Bedford

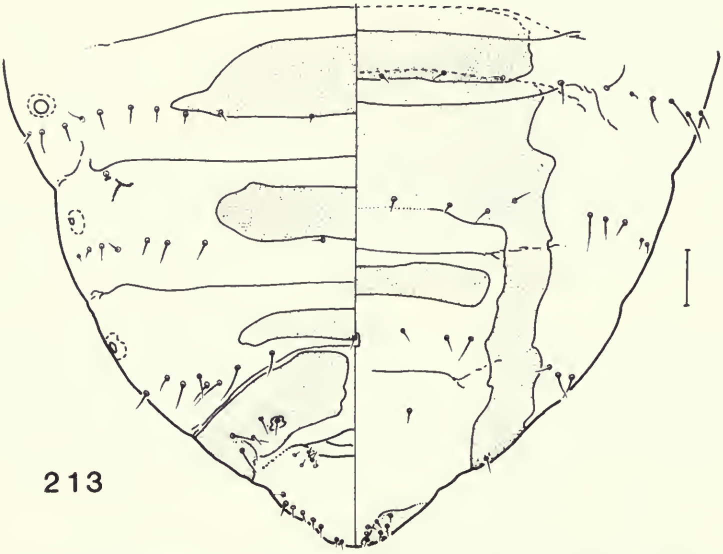
The genus *Lorisicola* comprises two subgenera.

Description. Anterior of head with osculum present or absent*; dorsal preantennal sulcus present or absent; clypeal marginal carina broadened medially, median sclerite variable*; anterolateral margin of



Figs 207–211 *Lorisicola* species. 207, *L. (L.) mjoebergi,* ♀ *abdomen. 208, L. (Paradoxuroecus) bengalensis*, ♀ subgenital lobe, ventral. 209, *L. (P.) africanus*, ♀ head, dorsal. 210, *L. (L.) spenceri*, ♀ terminalia, ventral, setae omitted apart from on gonapophyses. 211, *L. (L.) felis*, ♀ gonapophysis, ventral.



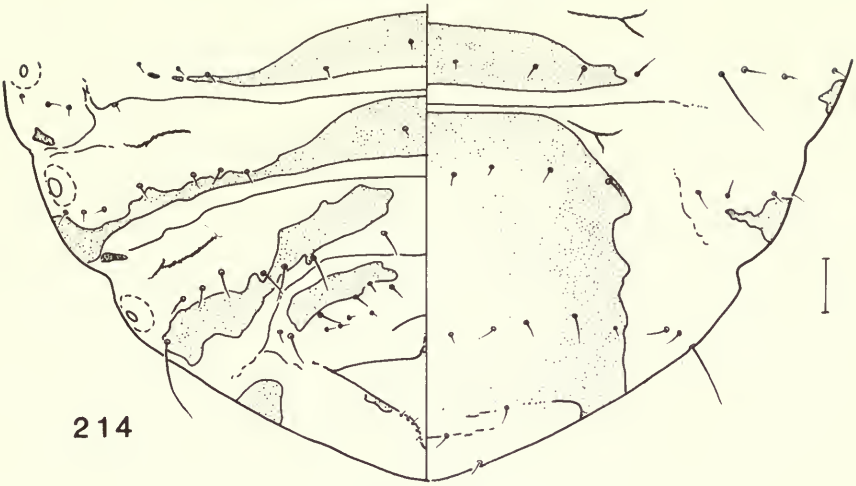


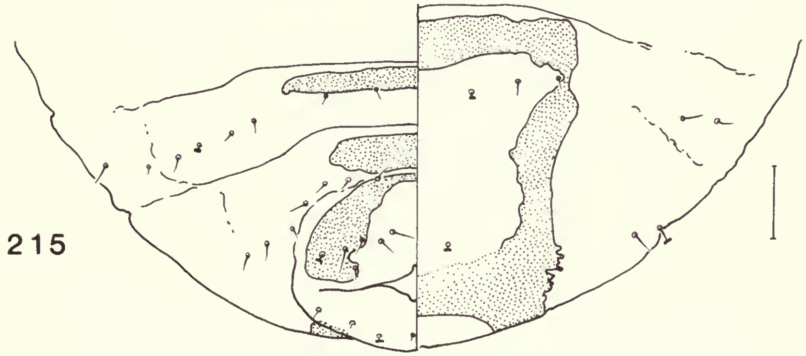
Figs 212, 213 *Lorisicola (L.)* species, ♂ terminalia. 212, *L. (L.) similis*. 213, *L. (L.) spenceri*.

head sinuate or convex; preantennal portion of head of variable length, outline more or less broadly triangular or rounded, sometimes, if osculum absent, convexly produced anteriorly*. Temple margin convex, rectangular, or slightly produced laterally*. Male scape expanded or only slightly expanded, with longitudinal setal row present and comprising at least two setae*; male and female flagellomeres fused; male flagellum with one or two basally-articulated teeth*. Dorsum of head with setae short or of moderate length, sparse. Sitophore sclerite unmodified.

Thorax with dorsal setae short or of moderate length* though frequently short and stout on postero-lateral angles of pterothorax, not present on disc or medially posteriorly on prothorax or pterothorax.

Abdomen oval or elongate, male segment IX not produced greatly. Abdominal spiracles absent, or present on segments III–VI or III–VIII; posterior two pairs of spiracles, if six pairs present, sometimes very small and possibly non-functional*. Abdominal setae short or very short, frequently sparse dorsally; abdominal pleurum III frequently with posterior setal row comprising stout, conical setae (Fig. 218); anterior setae absent except on pleurum II; postero-lateral setae present or absent, sometimes numbering more than one per site* (Fig. 207). Pleural projections present dorsally and sometimes ventrally on pleurum IV, sclerotised or unsclerotised. Abdominal sclerotisation variable; sterna with sclerites absent





Figs 214, 215 *Lorisicola* species, ♂ terminalia. 214, *L. (L.) mjoebergi*. 215, *L. (Paradoxuroecus) laticeps*.

except for subgenital plate (in male), or present on more posterior segments (VII, VI+VII, V–VII, IV–VII or III–VII); terga with sclerites on I–VIII, II–VIII, III–VIII or IV–VIII; pleura with sclerites on at least II, sometimes also on III and IV; male terga with anterior and posterior sclerites present on at least terga IV–VII, or posterior sclerites not present*.

Gonapophyses with ventral marginal non-tuberculate setae; rounded or rectangular lobe present or absent on ventral margin*; apical spur present or absent*. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; straight or concave, with chord less than 90 degrees to long axis of abdomen; subgenital lobe present, ventral surface more or less covered in overlapping scales*.

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., VII and VIII fused to s.g.p.r. and IX absent, or VII fused to s.g.p.r. and VIII and IX absent or present but not fused to s.g.p.r.*. Pseudostyli absent. Male genital opening postero-dorsal or dorsal; male segment IX lying dorsally on abdomen. Parameres short, broad, sometimes fused. Basiparameral sclerites present or absent*. Mesomeres present, fused; median extension present or absent*; mesomeres extending basally between b.a.l.s. to contact parameres, or terminating exteriorly to b.a.l.s.*. Male genitalia depicted in Figs 219–226.

HOSTS. Felidae, Herpestidae and Viverridae (Carnivora) and Lorisidae (Primates).

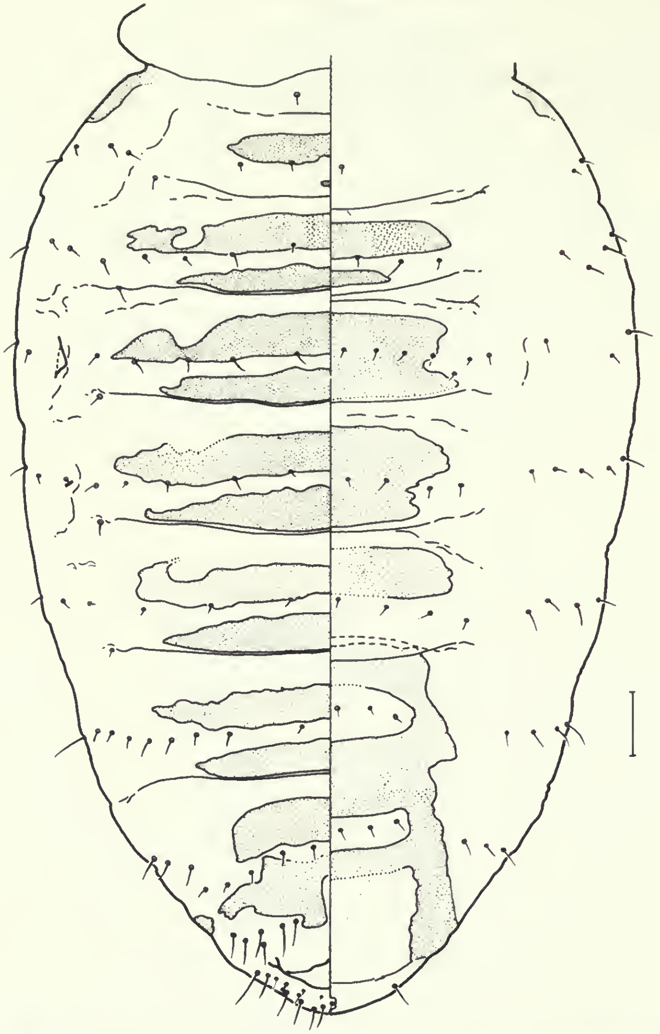


Fig. 216 *Lorisicola (Paradoxuroecus) acuticeps*, ♂ abdomen.

Subgenus ***LORISICOLA*** Bedford

(Figs 207, 210–214, 219, 220)

Lorisicola Bedford, 1936: 51. Type-species: *Trichodectes mjoebergi* Stobbe, by original designation.

DESCRIPTION. Anterior of head with osculum present; clypeal marginal carina broadened medially to form rectangular or W-shaped sclerite, or broadened slightly to either side of osculum, very lightly sclerotised posterior to osculum. Temple margin rectangular or slightly produced laterally. Male scape expanded or only slightly expanded, with setal row comprising two setae; male flagellum with basally-articulated 'teeth' on projection.

Abdominal spiracles absent, or present on segments III–VIII; posterior two pairs of spiracles, if six pairs present, sometimes very small and possibly non-functional. Males with posterior tergal sclerites absent.

Gonapophyses with rounded lobe, or lobe absent (Fig. 207); apical spur present or absent (Fig. 211). Subgenital lobe covered in overlapping pointed scales (Fig. 210) or spines (Fig. 207).

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r. (Fig. 214), or with sternite VII fused to s.g.p.r. and VIII and IX present but not fused to s.g.p.r. (Fig. 212), or of the latter form but lacking sternite IX (Fig. 213), or lacking VIII and IX but VII very broad. Basiparameral sclerites absent. Mesomeres fused, with median extension. Mesomeres extending basally between b.a.l.s. to

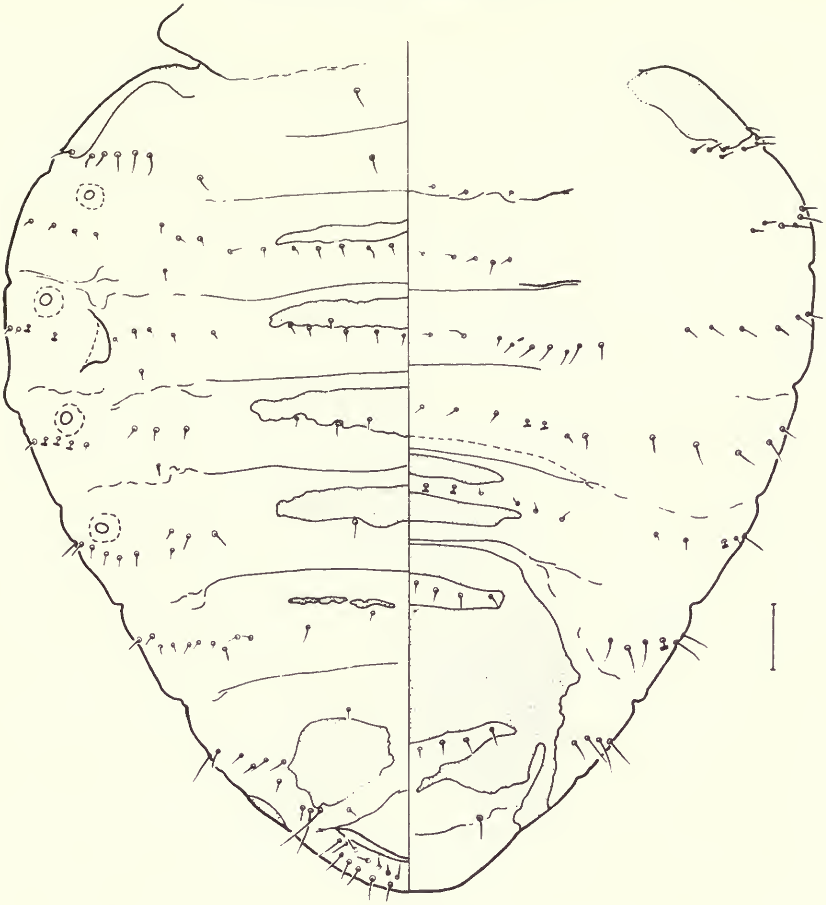


Fig. 217 *Lorisicola (Paradoxuroecus) bengalensis*, ♂ abdomen.

contact parameres (Fig. 222), terminating exteriorly to b.a.l.s. (Fig. 220), or extending anteriad to posterior end of b.a.l.s. and abruptly reversing, lying ventrally to b.a.l.s., though reversed portion is difficult to see (Fig. 219).

HOSTS. Felidae and Viverridae (Carnivora) and Lorisidae (Primates).

COMMENTS. The original spelling *mjöbergi* is emended here to *mjoebergi* in accordance with Article 32(d)(i) of the *International Code of Zoological Nomenclature* (1984).

SPECIES INCLUDED

americanus (Emerson & Price, 1983) **comb. n.** from *Felicola*
braziliensis (Emerson & Price, 1983) **comb. n.** from *Felicola*
caffra (Bedford, 1919) **comb. n.** from *Felicola* (1 ♂, 1 ♀)
felis (Werneck, 1934) **comb. n.** from *Felicola* (1 ♂, 1 ♀)
hercynianus (Kéler, 1957) **comb. n.** from *Felicola* (6 ♂, 6 ♀)
malaysianus (Werneck, 1948) **comb. n.** from *Trichodectes* (4 ♂, 5 ♀)
mjoebergi (Stobbe, 1913) (*c.*100 ♂, *c.*100 ♀)
neofelis (Emerson & Price, 1983) **comb. n.** from *Felicola*
siamensis (Emerson, 1964) **comb. n.** from *Felicola* (5 ♂, 2 ♀)
similis (Emerson & Price, 1983) **comb. n.** from *Felicola* (1 ♂, 1 ♀)
spenceri (Hopkins, 1960) **comb. n.** from *Felicola* (8 ♂, 5 ♀)
sudamericanus (Emerson & Price, 1983) **comb. n.** from *Felicola*

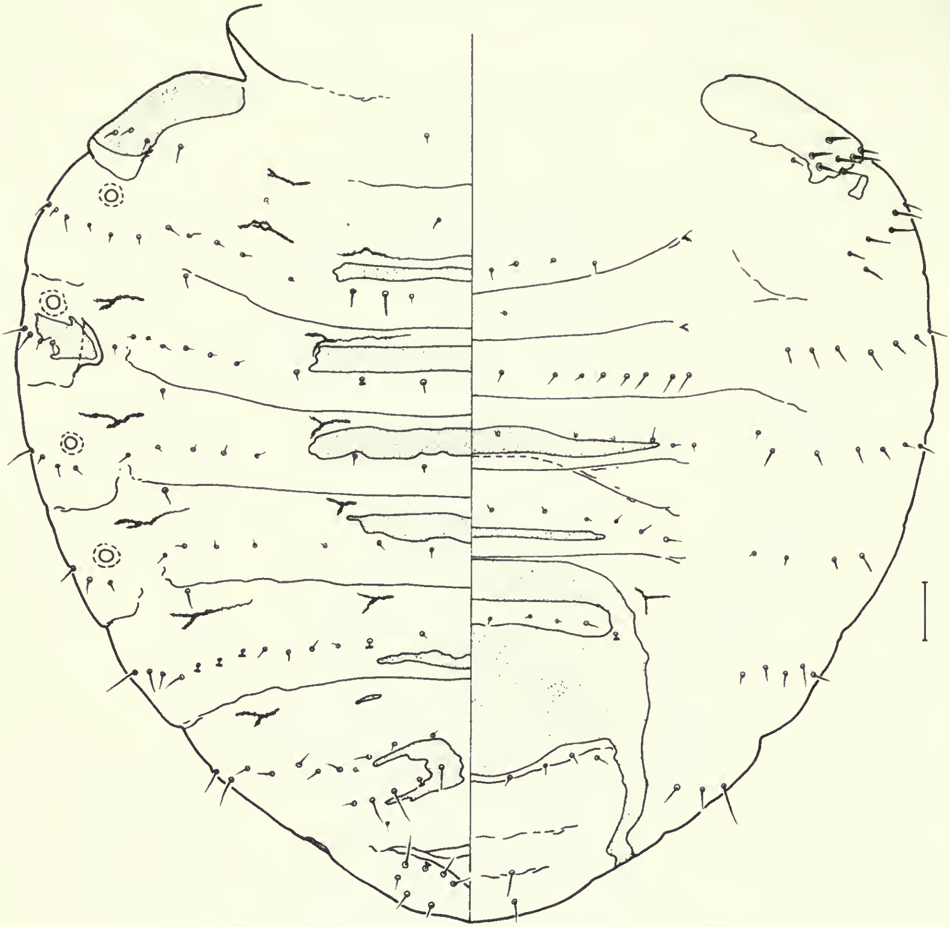


Fig. 218 *Lorisicola (Paradoxuroecus) juccii*, ♂ abdomen.

Subgenus *PARADOXUROECUS* Conci **gen. rev., stat. n.**

(Figs 208, 209, 215–218, 221–226)

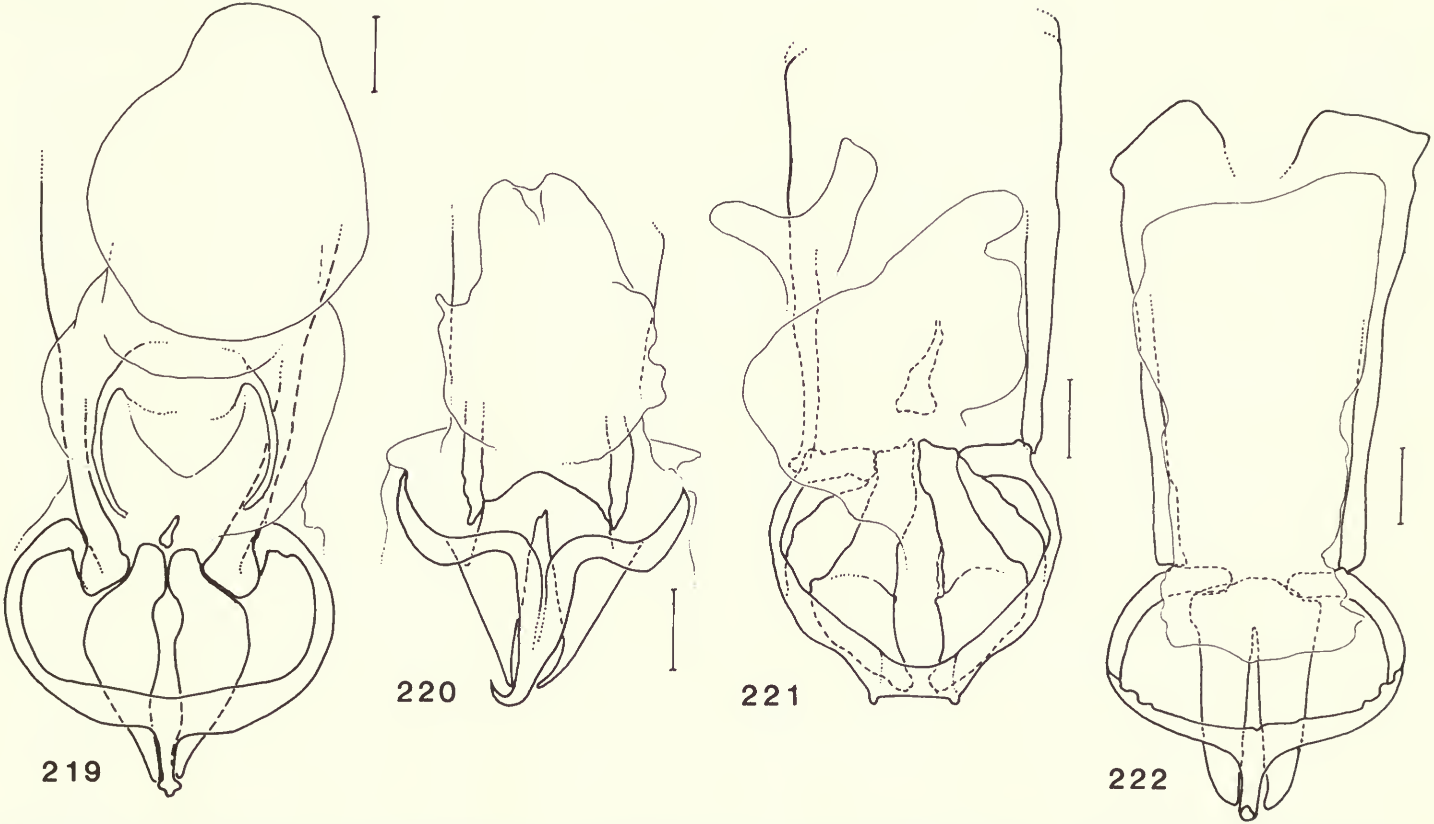
Paradoxuroecus Conci, 1942: 141. Type-species: *Paradoxuroecus juccii* Conci, by original designation.
Parafelicola Werneck, 1948: 226. Type-species: *Trichodectes acuticeps* Neumann, by original designation. **Syn. n.**
Neofelicola Werneck, 1948: 235. Type-species: *Neofelicola aspidorhynchus* Werneck, by original designation. **Syn. n.**

Description. Anterior of head with osculum present, in which case clypeal marginal carina broadened slightly to either side of osculum and very lightly sclerotised posterior to osculum, or osculum absent, in which case clypeal marginal carina broadened medially to form posteriorly-convex or straight heavily sclerotised bar (Fig. 209); outline of preantennal portion of head more or less broadly rounded or triangular, sometimes, if osculum absent, convexly produced anteriorly (Fig. 209). Temple margin convex or rectangular. Male scape expanded or only slightly expanded, with longitudinal setal row comprising at least three setae; male flagellum with two basally-articulated 'teeth', only rarely on projection.

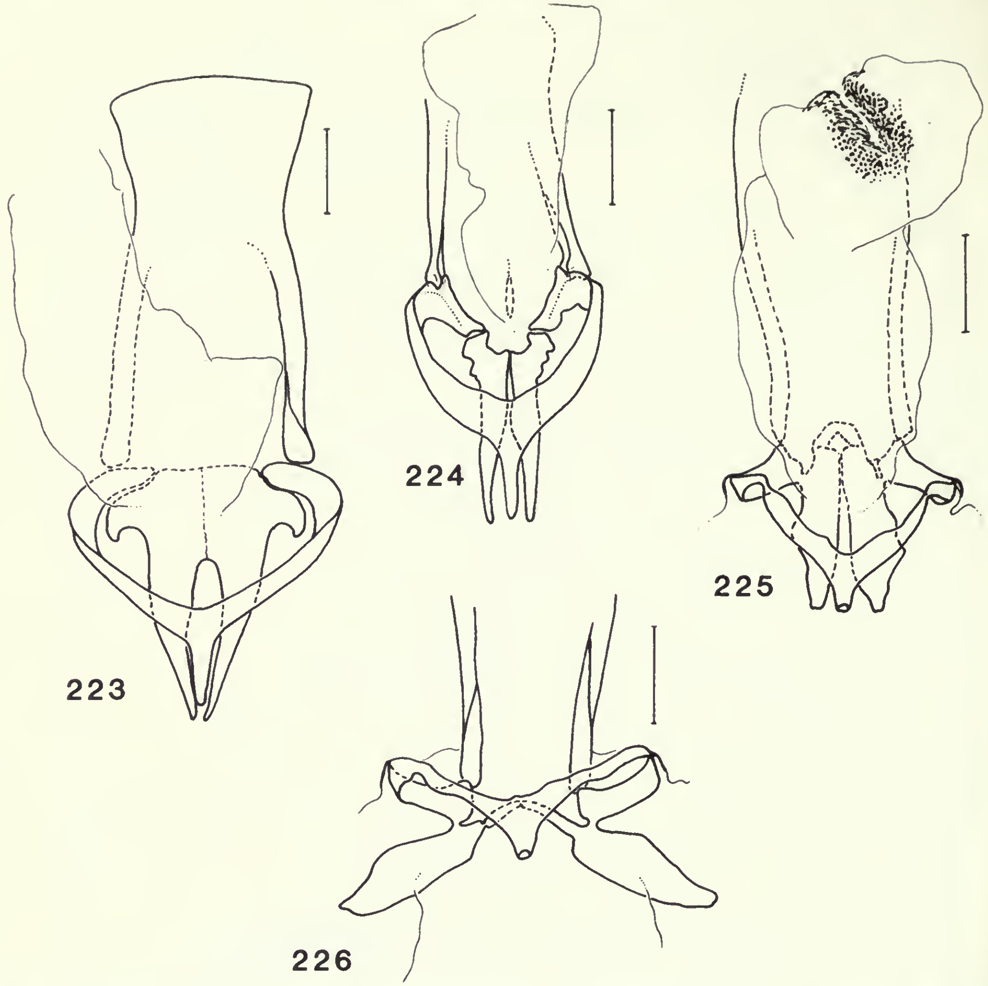
Thorax with dorsal setae short.

Abdominal spiracles absent, or present on segments III–VI. Postero-lateral setae present or absent, but never numbering more than one per site if present. Males with posterior tergal sclerites absent, or anterior and posterior sclerites present on at least terga IV–VII.

Gonapophyses with lobe present, rounded or rectangular; apical spur present. Subgenital lobe bilobate, with scales modified into short spines in some cases, though spines may be sparse (Fig. 208).



Figs 219–222 *Lorisicola* species, ♂ genitalia. 219, *L. (L.) mjoebergi*. 220, *L. (L.) malaysianus*. 221, *L. (Paradoxuroecus) laticeps*. 222, *L. (P.) spenceri*.



Figs 223–226 *Lorisicola (Paradoxuroecus)* species, ♂ genitalia. 223, *L. (P.) juccii*. 224, *L. (P.) bengalensis*. 225, *L. (P.) acuticeps*. 226, *L. (P.) acuticeps*, endophallus everted.

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r. (Fig. 216), VII and IX present and fused to s.g.p.r. but VIII absent (Fig. 215), or VII and VIII present and fused to s.g.p.r. but IX absent (Figs 217, 218). Parameres short, broad, not fused together (see second paragraph under 'comments' below), but may be very closely associated (Figs 223, 224). Basiparameral sclerites present (Fig. 225) or absent. Mesomeres fused apically with median extension present or, if absent, arch with two apical nipples (Fig. 221); mesomeral arch sometimes with lateral double flexion (Fig. 225); mesomeres extending basally between b.a.l.s. to contact parameres, sometimes sharply recurved posteriorly between b.a.l.s. (Fig. 224). Endophallus frequently with spicular collar, sometimes V-shaped, around gonopore (Fig. 225).

Hosts. Herpestidae and Viverridae (Carnivora).

Comments. *Paradoxuroecus* has been considered by most authors, following Werneck (1948), to be a synonym of *Felicola*; it is here recalled from synonymy and placed as a subgenus of *Lorisicola*. *Neofelicola* and *Parafelicola* were both considered by Hopkins (1949) to be subgenera of *Felicola*. A more complete history of the variations in the status of *Paradoxuroecus, Neofelicola* and *Parafelicola* is presented in Table 5.

Werneck (1948) figured the parameres of *aspidorhynchus, sumatrensis* and *juccii* as fused together; examination of the type-material of the first two species and of numerous specimens of the last has revealed that this is not the case, although in *L. juccii* the parameres are very closely associated with each other.

Lorisicola (Paradoxuroecus) bengalensis (Werneck, 1948) was described in *Neofelicola* from three females, the male being unknown. These females were taken from a museum skin of *Paradoxurus hermaphrodytus canus* Miller, which was itself collected in Thailand. Female lice subsequently collected from *P. hermaphrodytus* subspp. in Thailand agree with Werneck's (1948) description of *N. bengalensis*. Emerson (1965) describes the male of *bengalensis*, collected from the type host in Thailand, and distinguishes a new species, *N. philippinensis*, collected from *Paradoxurus philippinensis*.

Numerous specimens of lice from a number of subspecies of *Paradoxurus hermaphrodytus* have been examined during the course of this study, and it has become apparent that lice of two clades are present: the *Felicola (F.) zeylonicus–viverriculae* clade and the *Lorisicola (P.) philippinensis–juccii* clade.

These clades may be distinguished by the following characters.

F. (F.) zeylonicus–viverriculae clade – Three pairs of abdominal spiracles; male flagellum with 'teeth' not basally articulated; parameres long, slender, extending anteriorly between b.a.l.s.; mesomeres not basally extending between b.a.l.s.; mesomeral arch lacking median extension; female subgenital lobe broad, smooth ventrally, with long, flattened marginal spines.

L. (P.) philippinensis–juccii clade – Four pairs of abdominal spiracles; male flagellum with 'teeth' basally articulated; parameres short, broad, closely-associated with one another but not fused, not extending between b.a.l.s., if reaching them; mesomeres basally extending between b.a.l.s. to contact parameres; mesomeral arch with median extension; female subgenital lobe narrow, apically bilobate, covered ventrally with small pointed scales, lacking marginal spines.

The female described as *N. bengalensis* by Werneck (1948) is, by the structure of the subgenital lobe and the number of abdominal spiracles, a member of the *L. (P.) philippinensis–juccii* clade, as are both male and female of *N. philippinensis* as described by Emerson (1965). The male described by Emerson (1965) as *N. bengalensis* is, however, a member of the *F. (F.) zeylonicus–viverriculae* clade and therefore not the true male of *N. bengalensis*. Female lice of the latter clade are now known from *Paradoxurus hermaphrodytus* subspp., as are males of the former.

The male of *L. bengalensis* has genitalia indistinguishable from those of *L. philippinensis*. Emerson (1965) distinguishes *L. philippinensis* from *L. bengalensis* by the male genitalia, the greater number of sternal and tergal setae in both sexes of the former, and the greater number of vulval setae in the former. The characteristics of the male genitalia, as stated above, are the same in the two species. Study of the large sample of specimens now available indicates that the vulval setal number of *L. philippinensis* is not outside the range of *L. bengalensis*. The tergal and sternal setae in the males are the same, as are the sternal setae in the females. The tergal setae of the female paratype of *L. philippinensis* in the British Museum (Natural History) collection are the same as those of *L. bengalensis*, but do not agree with the figure in Emerson (1965), where far more setae are depicted. The host species *Paradoxurus philippinensis* is at best a subspecies of *P. hermaphrodytus*, and all other subspecies appear to harbour *L. bengalensis*. *L. philippinensis* (Emerson) is consequently provisionally synonymised with *L. bengalensis* (Werneck), subject to examination of the female allotype of *philippinensis*.

SPECIES INCLUDED

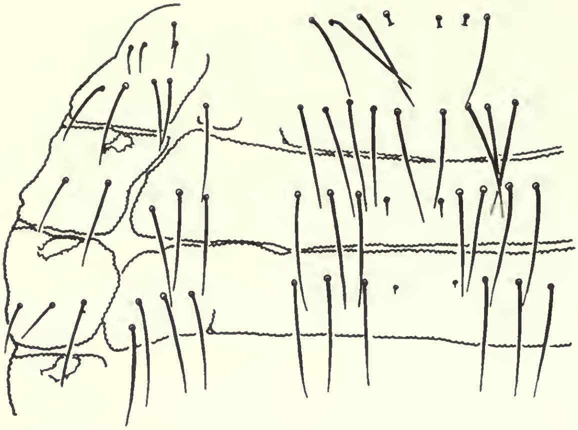
acuticeps (Neumann, 1902) **comb. n.** from *Parafelicola* (28 ♂, 34 ♀)
africanus (Emerson & Price, 1966) **comb. n.** from *Parafelicola* (15 ♂, 7 ♀)
aspidorhynchus (Werneck, 1948) **comb. n.** from *Neofelicola* (6 ♂, 7 ♀)
bengalensis (Werneck, 1948) **comb. n.** from *Neofelicola* (26 ♂, 59 ♀)
juccii Conci, 1942 **comb. n.** from *Felicola* (82 ♂, 81 ♀)
laticeps (Werneck, 1942) **comb. n.** from *Suricatoecus* (10 ♂, 13 ♀)
lenicornis (Werneck, 1948) **comb. n.** from *Parafelicola* (9 ♂, 22 ♀)
mungos (Stobbe, 1913) **comb. n.** from *Suricatoecus* (1 ♂, 3 ♀)
neoafricanus (Emerson & Price, 1968) **comb. n.** from *Parafelicola* (holotype ♂, 4 ♀)
paralaticeps (Werneck, 1948) **comb. n.** from *Suricatoecus* (1 ♂, 4 ♀)
philippinensis (Emerson, 1965) **comb. n.** from *Neofelicola* (5 ♂, 5 ♀)
sumatrensis (Werneck, 1948) **comb. n.** from *Neofelicola* (4 ♂, 4 ♀)
wernecki (Hopkins, 1941) **comb. n.** from *Parafelicola* (7 ♂, 11 ♀)

NEOTRICHODECTINAE subfam. n.

Type-genus: *Neotrichodectes* Ewing

Genus *NEOTRICHODECTES* Ewing

The genus *Neotrichodectes* comprises five subgenera.



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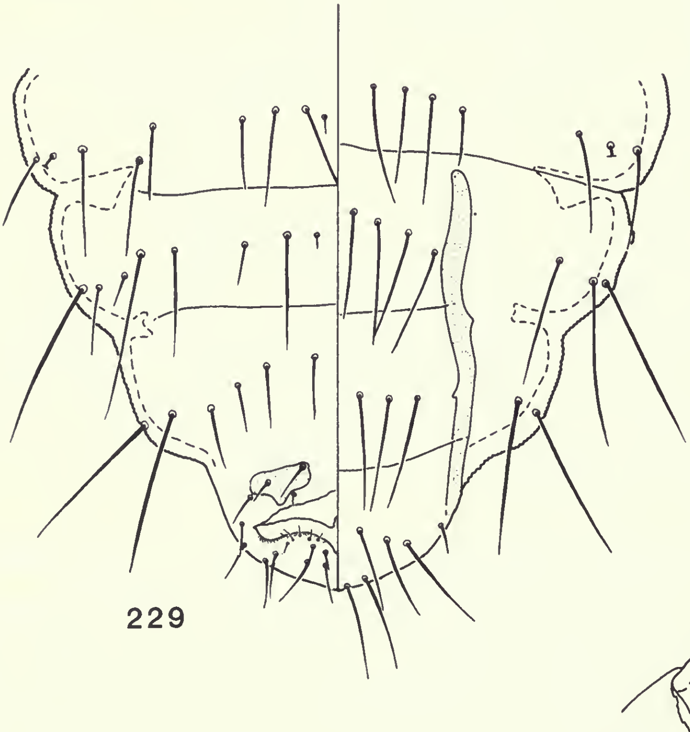

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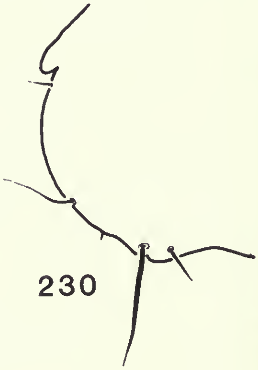

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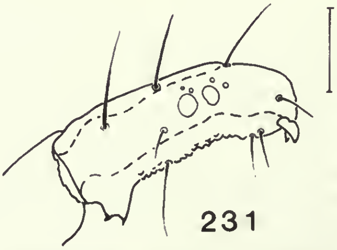

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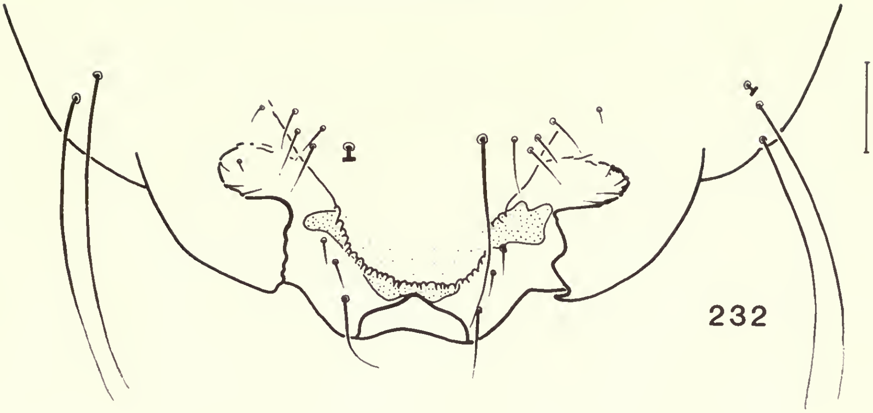
Figs 227–231 *Neotrichodectes* species. 227, *N. barbarae*, ♂ anterior abdominal segments, dorsal. 228, *N. mephitidis*, ♀ abdominal pleura II and III, dorsal. 229, *N. mephitidis*, ♂ terminalia. 230, *N. barbarae*, ♂ temple margin. 231, *N. semistriatus*, ♂ flagellum.

Description. Anterior of head with osculum present, sometimes very shallow*; dorsal preantennal sulcus present, not always clear; clypeal marginal carina broadened medially into dorsal sclerite of variable form* which is always more heavily sclerotised laterally (dorsal to margin of clypeus and pulvinus) than medially; antero-lateral margin of head convex, straight or sinuate*; preantennal portion of head short or longer, sometimes as long as postantennal portion*, outline broadly rounded or triangular*. Temple margin broadly convex. Male scape expanded, with longitudinal setal row present and comprising at least four setae; flagellomeres fused in males and females; male flagellum with two or more basally-articulated 'teeth'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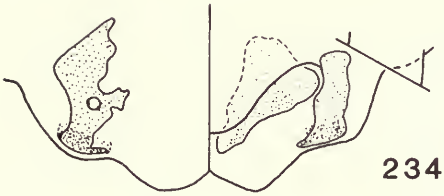
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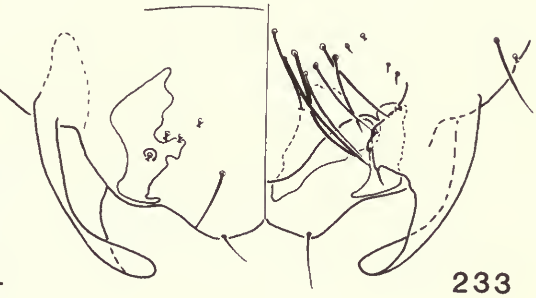
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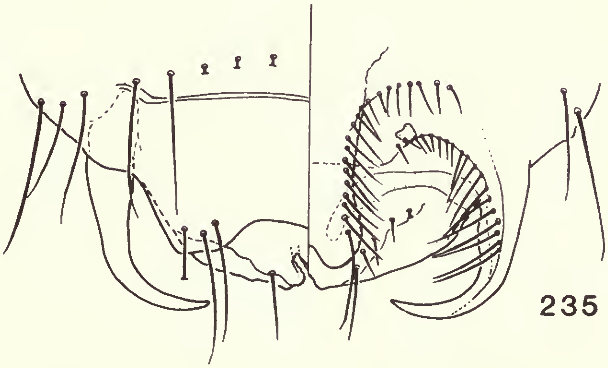
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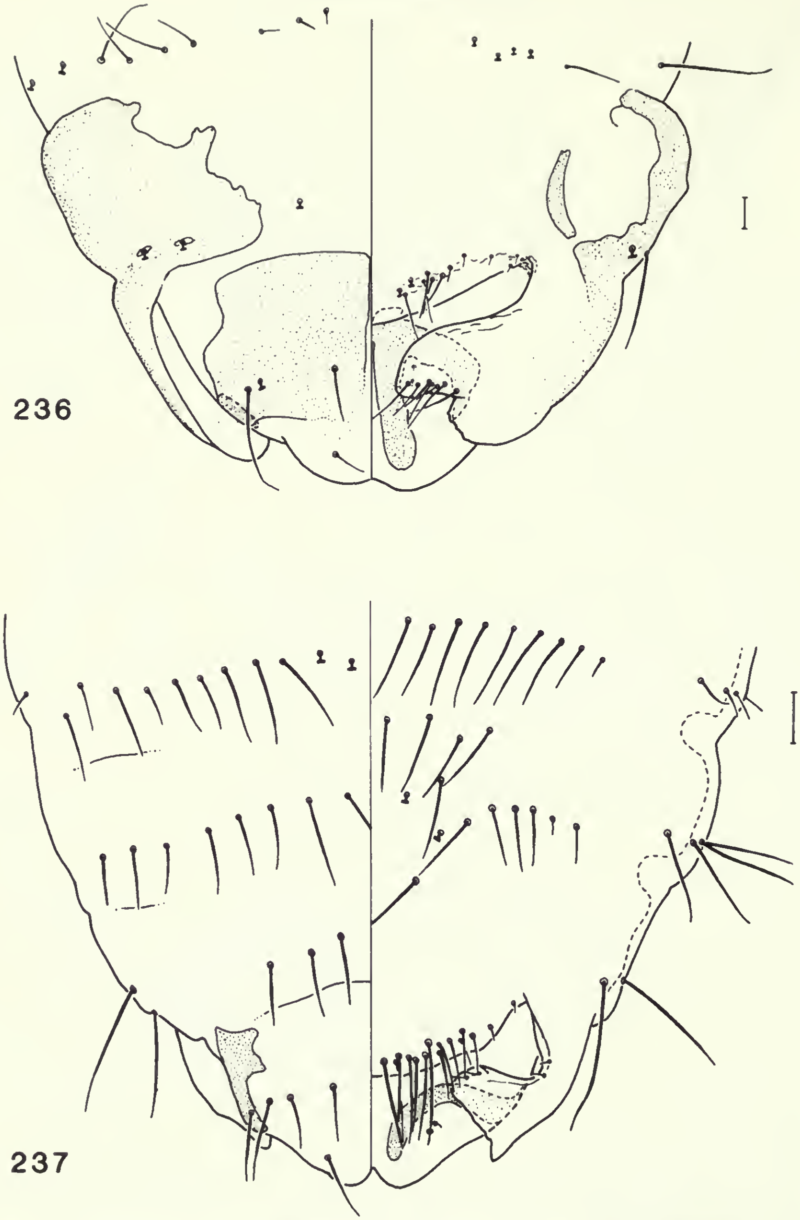
Figs 232–235 *Neotrichodectes* species, ♀ terminalia. 232, *N. mephitidis*, ventral. 233, *N. chilensis*, showing setal distribution. 234, *N. chilensis*, showing sclerites. 235, *N. barbarae*.

distally, and with basal toothed or rough projection sometimes present* (Fig. 231); female pedicel lacking membranous projection. Dorsum of head with most setae short or of moderate length, more or less sparse, sometimes with long seta on posterior margin of temple* (Fig. 230). Sitophore sclerite unmodified.

Thorax with dorsal setae long or of moderate length* though frequently short and spine-like on postero-lateral angles of prothorax and pterothorax; posterior margin of pronotum with four setae and wide median gap, posterior of pterothorax dorsally with setae more abundant, marginal or submarginal, median gap present or absent.

Abdomen broadly rounded, not greatly projecting posteriad in male (Fig. 229). Abdominal spiracles absent. Abdominal setae grenerally abundant, as long as segment or sparse, shorter, with long setae present only on posterior pleura*; terga, especially of males, with median and lateral setal groups distinct, though median groups generally united; male terga II–VI with median two setae much smaller than other setae in the row, sometimes separated by one or more longer setae (Fig. 229); anterior setae present on



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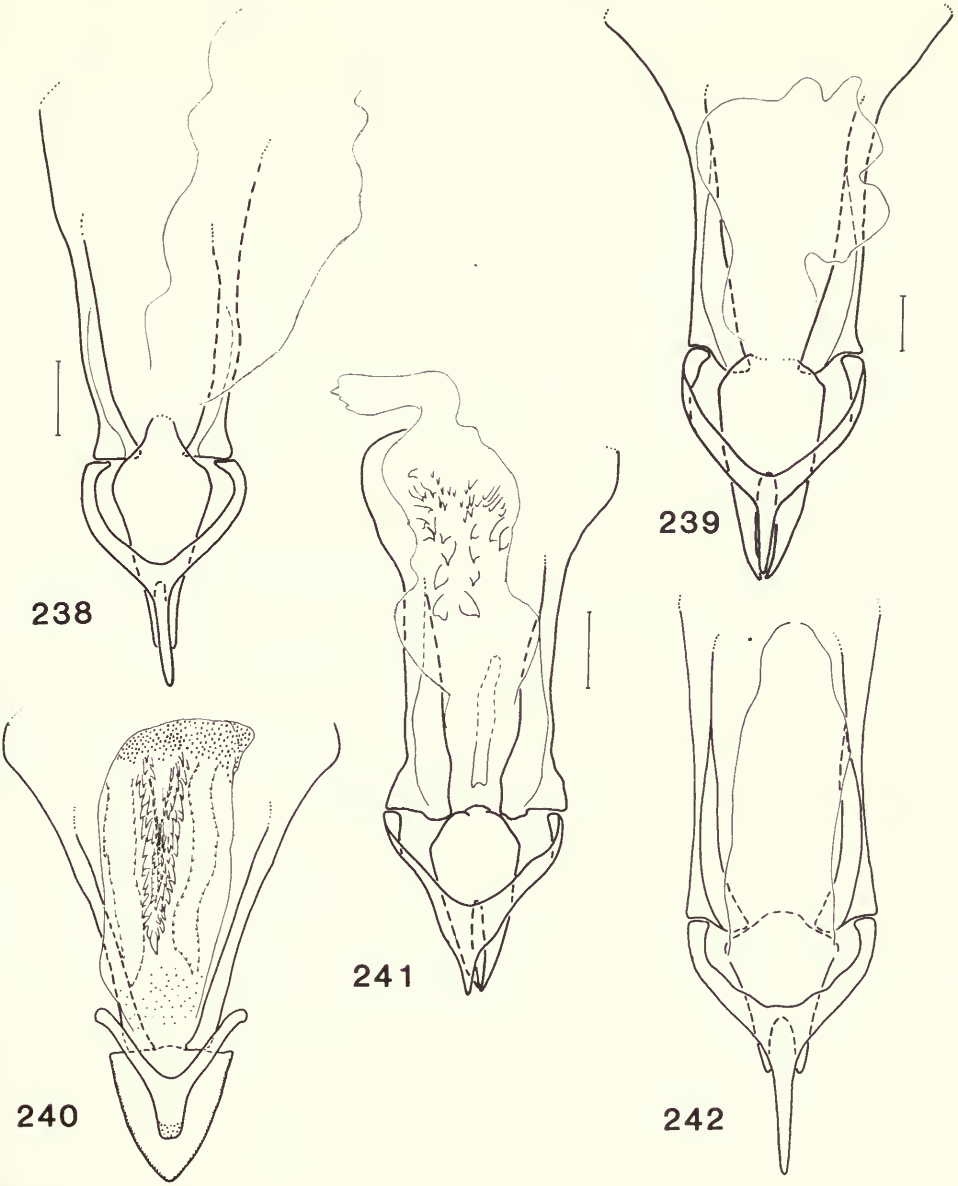
Figs 236, 237 *Neotrichodectes* species, ♀ terminalia. 236, *N. gastrodes*. 237, *N. pallidus*.

pleura II and III only; postero-lateral setae presumed absent, though possibly present as the most lateral seta of lateral group, which is frequently situated more posteriorly than other setae. Abdominal pleura lacking projections, except for small sclerotised or unsclerotised projection dorsally on pleurum III of female *N. mephitidis*. Abdominal terga and sterna lacking sclerites, except for lateral rods of subgenital plate in male and, sometimes, tergite IX in female; abdominal pleura usually unsclerotised, sometimes with sclerites on pleura II, III, IV and, in females, VIII*.

Gonapophyses with or without lobe on ventral margin, very variable*. Gonapophyses meet ventral vulval margin smoothly or acutely, but not linked by sclerotised band. Ventral vulval margin not sclerotised; generally convex medially*, subgenital lobe present or absent*. Common oviduct not notably striate (cf. *Geomydoecus*).

Male subgenital plate with only s.g.p.r. present (Fig. 229). Pseudostyli absent. Male genital opening



Figs 238–242 *Neotrichodectes* species, ♂ genitalia. 238, *N. (Neotrichodectes) mephitidis*. 239, *N. (Nasuicola) pallidus*. 240, *N. (Trigonodectes) barbarae*. 241, *N. (Lakshminarayanella) gastrodes*. 242, *N. (Conepaticola) chilensis*.

dorsal. Parameres fused to form single plate with apex pointed or bifid*. Basiparameral sclerites absent. Mesomeres fused apically; mesomeral arch with median extension*; mesomeres basally abut postero-lateral projections of b.a.l.s. but do not contact parameral plate (Fig. 242), or contact neither b.a.l.s. nor parameral plate (Fig. 240).

Hosts. Mustelidae and Procyonidae (Carnivora) and Bradypodidae (Edentata).

Comments. *Neotrichodectes* has been considered a synonym and a subgenus of *Trichodectes* (by Hopkins, 1942 and Hopkins, 1949 respectively); a more complete history of the variations in status of *Neotrichodectes* is presented in Table 4.

Subgenus *NEOTRICHODECTES* Ewing

(Figs 228, 229, 232, 238)

Neotrichodectes Ewing, 1929: 194. Type-species: *Goniodes mephitidis* Packard, by original designation.

DESCRIPTION. Anterior of head with clypeal marginal carina broadened into dorsal sclerite which is more or less convex posteriorly, sometimes almost circular; preantennal portion of head sometimes as long as postantennal portion. Male flagellum with two basally-articulated 'teeth' distally, and with toothed projection sometimes present basally (Fig. 231). Temple with long seta present on posterior margin.

Thoracic and abdominal setae long, abundant. Abdominal pleura lacking projections, except for small sclerotised or unsclerotised projection dorsally on pleurum III of female *N. mephitidis* (Fig. 228). Abdomen lacking sternal, tergal and pleural sclerites, except for lateral rods of male subgenital plate.

Gonapophyses broad, membranous, with ventral marginal setae absent or, if present, basal only (Fig. 232); ventral lobe absent. Ventral vulval margin with lobe present though difficult to see; lobe serrate, at least along posterior margin (Fig. 232). Female genital chamber with dorsal wall bearing slanting scales laterally, lightly sclerotised and lacking scales or other decoration medially (anteriorly).

Parameral plate slender, apically bifid, with median basal extension reaching anteriorly between b.a.l.s. Mesomeral arch with median extension pointed; mesomeres basally abut postero-lateral extensions of b.a.l.s. Male genitalia depicted in Fig. 238.

HOSTS. Mustelidae and Procyonidae (Carnivora).

COMMENTS. *Neotrichodectes* s. str. is most readily distinguished from other subgenera of *Neotrichodectes* by characters of the female terminalia: the retention of the plesiomorphic form of the gonapophyses (found also in *Geomydoecus*) and the apomorphic development of a membranous subgenital lobe (cf. the very different structure in *N. (Trigonodectes)*). Assignment of male insects to the subgenus relies on absence of the basal flagellar projection (a character-state reversal not undergone by the type-species of the subgenus), the presence of an anterior development of the parameral plate between the b.a.l.s., and the slenderness of that parameral plate in relation to its length. *Neotrichodectes wolffhuegeli* (Werneck) is known only from the male, although Werneck (1948) predicted that the female would be very similar to that of *N. chilensis* (placed in *N. (Conepaticola)* in this study), and so must be assigned to subgenus on the basis of male characters. *N. wolffhuegeli* does have a toothed projection on the base of the male flagellum, although, as indicated above, cannot be eliminated from *Neotrichodectes* s. str. on that basis. The form of the parameral plate of *N. wolffhuegeli* is much the same as members of *Neotrichodectes* s. str. and on this evidence the species is placed in the subgenus. Emerson (pers. comm.), however, suggests that the male genitalia of *N. wolffhuegeli* lie within the limits of permissible variation of *N. chilensis*, which he therefore considers as a junior synonym; *N. wolffhuegeli* and *N. chilensis* are found on the same host, although *N. chilensis* is also found on several other species of the host genus. All specimens identified as *N. wolffhuegeli* (by Werneck and in the present study) have a much narrower parameral plate than those identified as *N. chilensis*. However, the parameral plate, whilst not extending anteriad between the b.a.l.s. in most specimens of *N. chilensis*, does do so in some. In those specimens of *N. chilensis* where there is no anterior extension of the parameral plate the endophallus lacks large, heavily-sclerotised teeth, or such teeth are few in number; in those where the extension is present the teeth are correspondingly more developed. The degree of development of the endophallus teeth seems to be proportional to the degree of development of the anterior margin of the parameral plate in *N. chilensis* and such teeth are present and well developed in *N. wolffhuegeli*. The sample of specimens of both species was too small to permit any correlations of genitalia type with host species or geographical distribution, though within *N. chilensis* specimens exhibiting both extremes were found from the same host in the same area. For the purposes of this study, the two species are treated as separate, *N. wolffhuegeli* is assigned to *Neotrichodectes* s. str., and *N. chilensis* is assigned to *Neotrichodectes (Conepaticola)*. This conclusion is regarded as the most satisfactory for the data presently available, but further collecting from species of the host genus (*Conepatus*) is needed to clarify the situation.

The original spelling of the species name *wolffhügeli* is emended here to *wolffhuegeli* in accordance with Article 32 (d)(i) of the *International Code of Zoological Nomenclature* (1984).

SPECIES INCLUDED

mephitidis (Packard, 1873) (*c.*50 ♂, *c.*100 ♀)
minutus (Paine, 1912) (64 ♂, 76 ♀)
osborni Kéler, 1944 (16 ♂, 21 ♀)
thoracicus (Osborn, 1902) (11 ♂, 9 ♀)
wolffhuegeli (Werneck, 1936) (1 ♂)

Subgenus *TRIGONODECTES* Kéler **gen. rev., stat. n.**

(Figs 227, 230, 235, 240)

Trigonodectes Kéler, 1944: 179, 185. Type-species: *Trichodectes barbarae* Neumann, by original designation.

DESCRIPTION. Anterior of head with osculum very shallow; clypeal marginal carina broadened medially into dorsal U-shaped sclerite with median posterior process; anterolateral margin of head convex; preantennal portion of head with outline rounded. Male flagellum with two basally-articulated 'teeth' distally, and with toothed projection present basally. Temple with long seta present on posterior margin.

Thoracic and abdominal setae long, abundant. Abdominal pleura lacking projections. Abdomen lacking sternal, tergal and pleural sclerites, except for lateral rods of male subgenital plate.

Gonapophyses slender, apically acute, sclerotised, with strong setae present along ventral margin; ventral lobe absent. Gonapophyses meet ventral vulval margin acutely. Ventral vulval margin with median lobulate projection, with margin not serrate, and submarginal setal row present (Fig. 235). Female genital chamber lacking lateral slanting scales and anterior sclerotised area on dorsal wall, but both ventral and dorsal walls bearing numerous scales with posterior spinules.

Parameral plate triangular or shield-shaped, pointed apically. Mesomeral arch with median extension rounded, covered in small tubercles; mesomeres extend basally anterior to ends of b.a.l.s., and do not contact b.a.l.s. or parameral plate. Basal apodeme lacking postero-lateral projections on b.a.l.s. Male genitalia depicted in Fig. 240.

HOSTS. Mustelinae (Carnivora: Mustelidae).

COMMENTS. *Trigonodectes* has been treated as a synonym and a subgenus of *Trichodectes* (by Werneck, 1948 and Hopkins, 1949 respectively); in this study it is raised from synonymy with *Trichodectes* and *barbarae* is placed for the first time in *Neotrichodectes*. A more complete history of the varying status accorded to *Trigonodectes* is presented in Table 4.

SPECIES INCLUDED

barbarae (Neumann, 1913) **comb. n.** from *Trichodectes* (13 ♂, 13 ♀)

Subgenus *NASUICOLA* **subgen. n.**

(Figs 237, 239)

Type-species: *Trichodectes pallidus* Piaget.

DESCRIPTION. Anterior of head with osculum shallow; clypeal marginal carina broadened into dorsal rectangular sclerite; antero-lateral margin of head convex; preantennal portion of head not as long as postantennal portion, outline broadly rounded. Male flagellum with two basally-articulated 'teeth' distally, and with toothed projection present basally. Temple with long seta present on posterior margin.

Thoracic and abdominal setae long, abundant. Abdominal pleura lacking projections. Abdomen lacking sternal, tergal and pleural sclerites, except for lateral rods of male subgenital plate.

Gonapophyses with rounded ventral lobe with submarginal setae; spur distal to lobe very short. Gonapophyses meet ventral vulval margin acutely. Ventral vulval margin convex, but subgenital lobe or lobulate process not present. Female terminalia depicted in Fig. 237. Female genital chamber with dorsal wall bearing slanting scales laterally, spines medially (spines most apparent anteriorly, though may be obscured).

Parameral plate apically bifid, lacking median basal extension reaching anteriorly between b.a.l.s. Mesomeral arch with median extension pointed; mesomeres basally abut postero-lateral extensions of b.a.l.s. Male genitalia depicted in Fig. 239.

HOSTS. Procyonidae (Carnivora).

SPECIES INCLUDED

pallidus (Piaget, 1880) [treated by previous authors as *Neotrichodectes* s. str.] (65 ♂, 75 ♀)

Subgenus *LAKSHMINARAYANELLA* Eichler **stat. n.**

(Figs 236, 241)

Lymeon Eichler, 1940: 158. Type-species: *Trichodectes gastrodes* Cummings, by monotypy. [Homonym of *Lymeon* Foerster, 1868: 176.]

Lakshminarayanella Eichler, 1982: 83. [Replacement name for *Lymeon* Eichler.]

Description. Anterior of head with osculum present, deep; clypeal marginal carina broadened medially into posteriorly convex bar, parallel to curvature of osculum; antero-lateral margin of head straight or slightly sinuate; preantennal portion of head short in male, longer in female; outline broadly triangular. Male flagellum with seven basally-articulated 'teeth' distally, and with roughened projection present basally. Temple with no long setae present on posterior margin.

Thorax with dorsal setae of moderate length, longest on postero-lateral angle of pterothorax; pterothorax with setae sparse along posterior dorsal margin.

Abdominal setae of moderate length, not as long as segment except on posterior pleura; terga with lateral and median setal groups not clearly distinct, median gap sometimes pronounced. Abdominal pleura lacking projections. Abdomen lacking tergal and sternal sclerites except for lateral rods of male subgenital plate and tergite IX of female; abdominal pleura II, III, IV and, in female, VIII, with sclerites, though that of IV sometimes very small.

Gonapophyses broad, very thick; ventral lobe present, thick, with setae along posterior margin; spur distal to lobe not short, rounded apically (Fig. 236). Gonapophyses meet ventral vulval margin acutely. Ventral vulval margin convex, but subgenital lobe or lobulate process not present. Female genital chamber with dorsal wall bearing slanting scales laterally, spines medially (spines most apparent anteriorly).

Parameral plate apically bifid, sometimes projecting slightly anteriad between b.a.l.s. Mesomeral arch with median extension pointed, broad basally; mesomeres basally abut postero-lateral extensions of b.a.l.s. Male genitalia depicted in Fig. 241.

Hosts. Bradypodidae (Edentata).

Species included
cummingsi (Eichler, 1943) **comb. n.** from *Lakshminarayanella*
gastrodes (Cummings, 1916) **comb. n.** from *Lakshminarayanella* (4 ♂, 6 ♀, 4 nymphs)

Subgenus ***CONEPATICOLA*** subgen. n.

(Figs 231, 233, 234, 242)

Type-species: *Neotrichodectes semistriatus* Emerson & Price.

Description. Anterior of head with clypeal marginal carina broadened medially into dorsal U-shaped sclerite with median posterior process; antero-lateral margin of head convex or sinuate; preantennal portion of head not as long as postantennal portion, outline broadly rounded. Male flagellum with two basally-articulated 'teeth' distally, and with toothed projection basally. Temple with long seta present on posterior margin.

Thoracic and abdominal setae long, abundant. Abdominal pleura lacking projections. Abdomen lacking sternal and tergal sclerites, except for sternal rods of male subgenital plate and tergite IX of female; abdominal pleura II, III and VIII in female sometimes with sclerites, though that of III may be very small.

Gonapophyses with ventral lobe present, large, apparently comprising fused setal tubercles, with setae along posterior margin and anterior margin, the latter frequently directed posteriad; spur distal to lobe present, not short, frequently obtuse apically. Gonapophyses meet ventral vulval margin acutely. Ventral vulval margin convex, but subgenital lobe or lobulate process not present. Female terminalia depicted in Figs 233, 234. Female genital chamber with dorsal wall bearing slanting scales laterally, spines medially, sometimes lightly sclerotised and lacking scales, spines or other decoration antero-medially.

Parameral plate apically bifid, sometimes projecting slightly anteriad between b.a.l.s. Mesomeral arch with median extension pointed; mesomeres basally abut postero-lateral extension of b.a.l.s. Male genitalia depicted in Fig. 242.

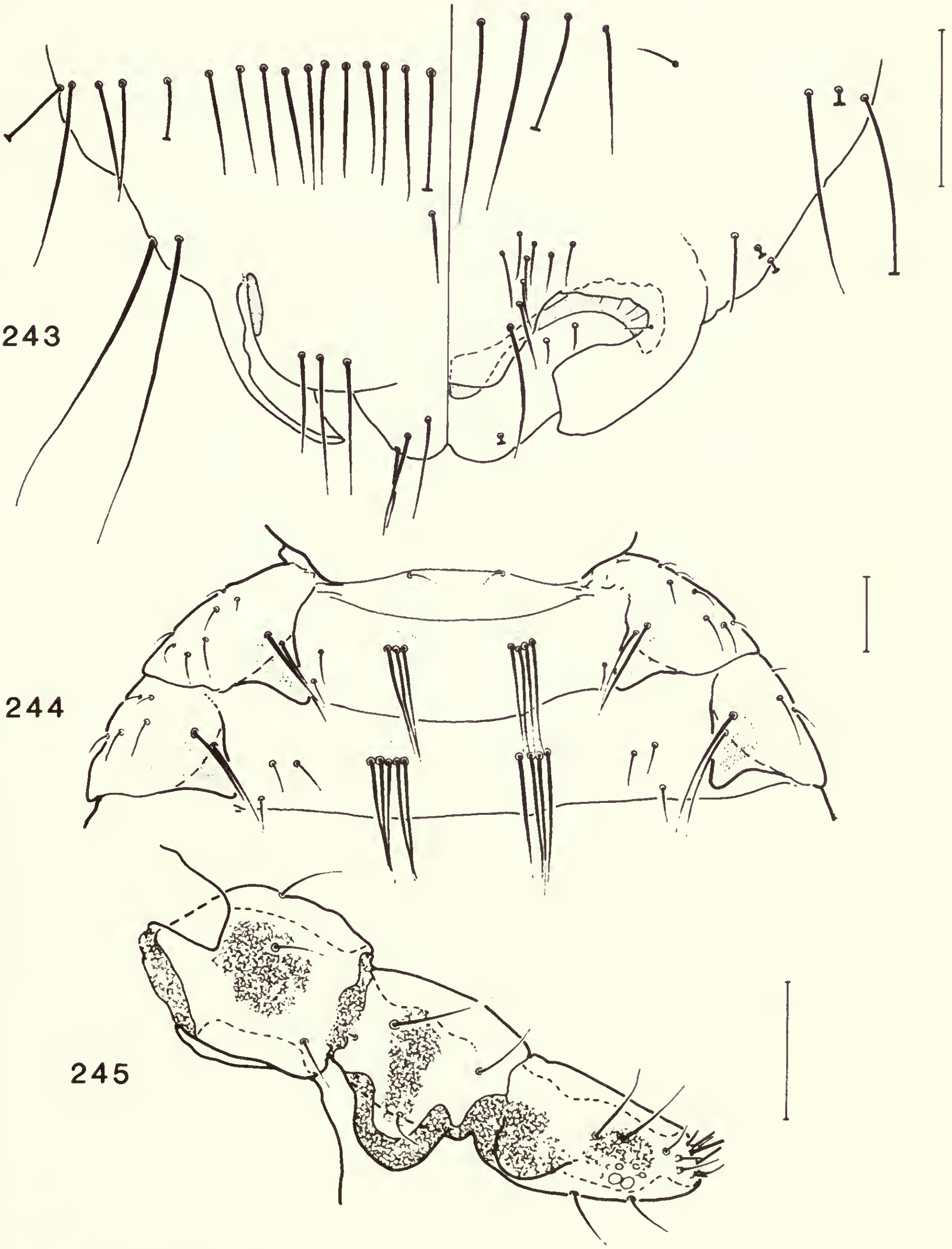
Hosts. Mustelinae and Mephitinae (Carnivora: Mustelidae).

Species included
arizonae Werneck, 1948 (18 ♂, 39 ♀)
chilensis Werneck, 1948 (*c*.50 ♂, *c*.50 ♀)
interruptofasciatus (Kellogg & Ferris, 1915) (27 ♂, 46 ♀)
semistriatus Emerson & Price, 1976 (5 ♂, 5 ♀)
All the above species have been treated previously as *Neotrichodectes* s. str.

Genus ***GEOMYDOECUS*** Ewing

The genus *Geomydoecus* comprises two subgenera.

DESCRIPTION. Anterior of head with osculum present; dorsal preantennal sulcus present; clypeal marginal carina broadened medially into posteriorly convex bar; antero-lateral margin of head convex or sinuate; preantennal portion of head not long, outline broadly triangular or rounded. Temple margin broadly convex. Male scape expanded; longitudinal setal row present and comprising at least three setae; male scape sometimes with median posterior projection; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth'; female pedicel with membranous postero-ventral projection (Fig. 245), sometimes obscure. Dorsum of head with setae short or of moderate length, more or less sparse; temple margin sometimes with specialised long, fine or short and stout latero-posterior setae*. Sitophore sclerite unmodified.



Figs 243–245 *Geomydoecus* species. 243, *G. (G.) californicus*, ♀ terminalia. 244, *G. (Thomomydoecus) asymmetricus*, ♂ anterior of abdomen, dorsal. 245, *G. (T.) pattoni*, ♀ antenna.

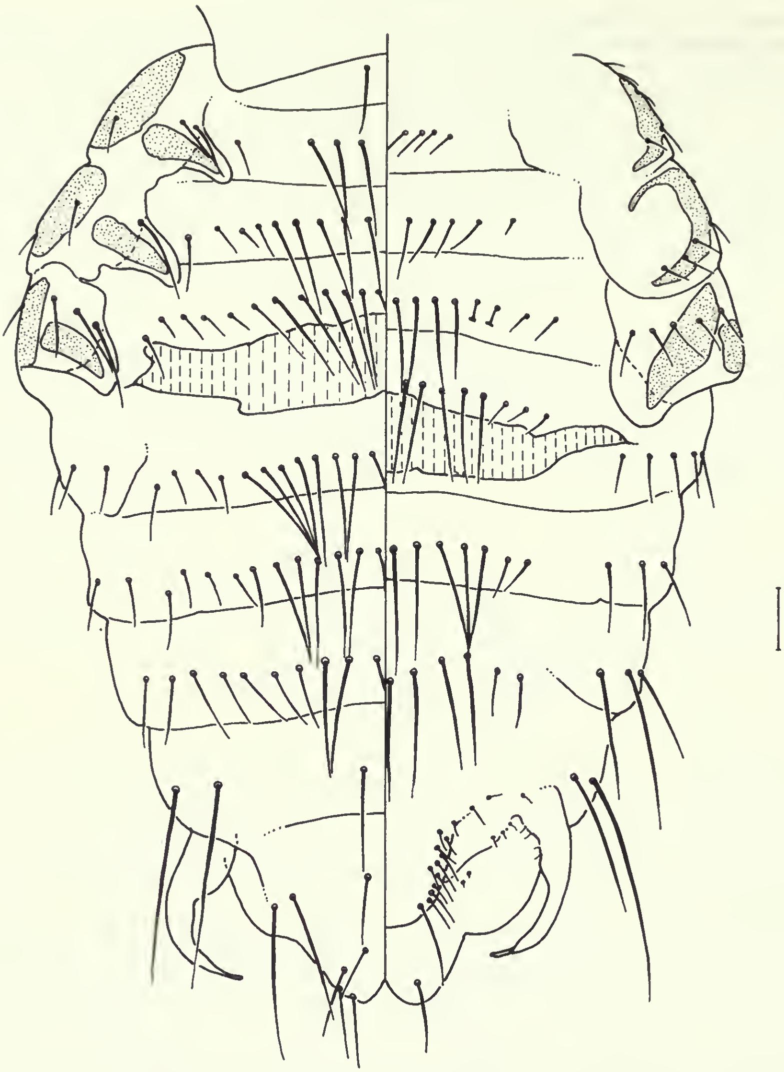
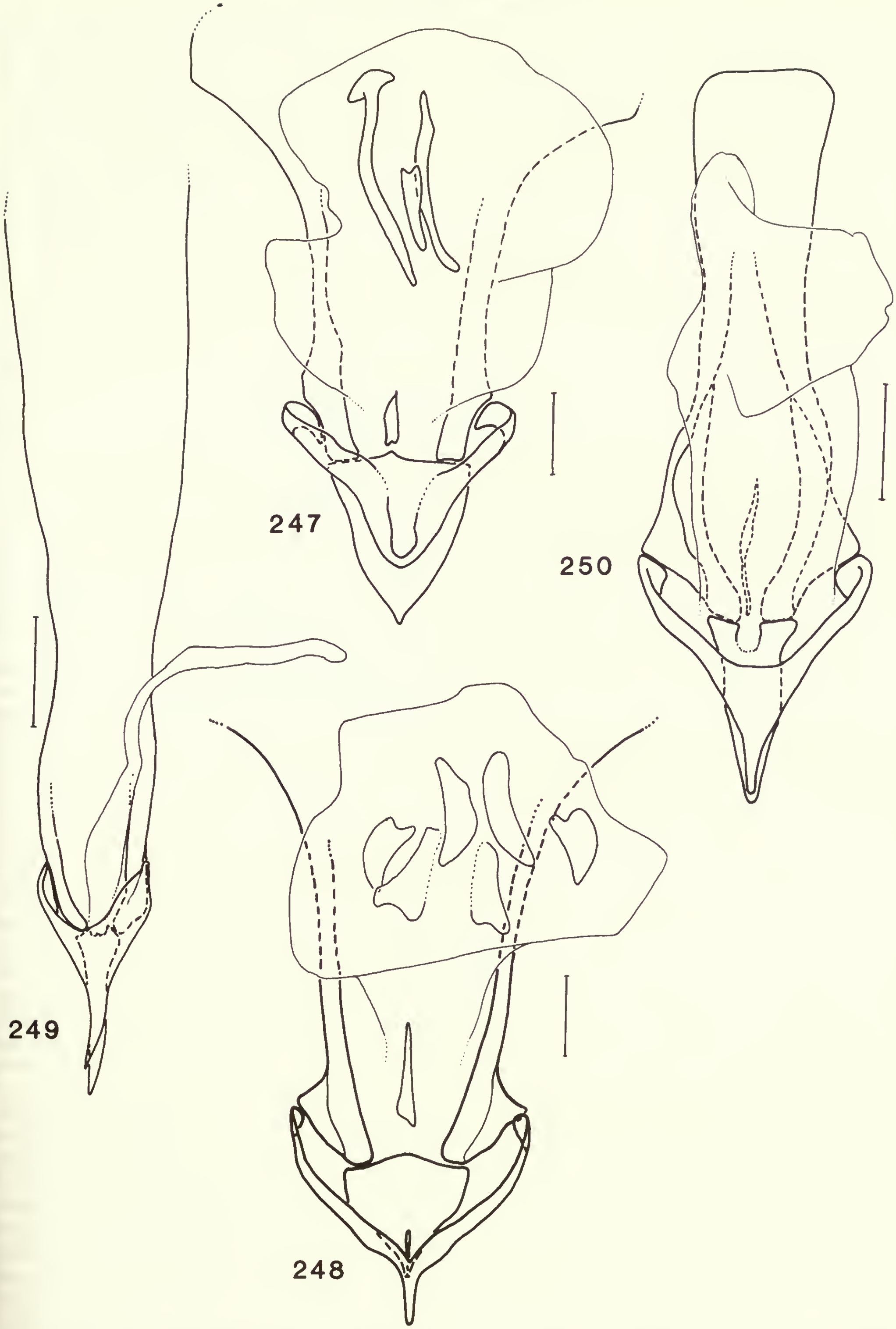


Fig. 246 *Geomydoecus (Thomomydoecus) minor*, ♀ abdomen. Hatched areas indicate damage to specimen.

Thorax with dorsal setae long or of moderate length; posterior margin of pronotum with four setae and wide median gap, posterior margin of pterothorax dorsally with varying number of marginal or submarginal setae.

Abdomen broadly rounded or more elongate and tapered, particularly in male. Abdominal spiracles absent. Abdomen with at least some setae as long as segment; setae generally abundant; terga, especially of males, with median and lateral setal groups distinct, though median groups generally united; male terga II–VI without median setae shorter than others; male terga II and III sometimes with median group comprising exceptionally long, stout setae* (Fig. 244); anterior setae present on pleura II and III only; postero-lateral setae sometimes clearly present (Fig. 244), otherwise obscured, though may be present as most lateral seta of lateral group, which is frequently situated more posteriorly than other setae. Abdominal pleura with projections dorsally on pleura II, III, IV and, at least in female, ventrally on IV, sclerotised (Fig. 246) or unsclerotised*; projections generally more apparent in females than males. Abdominal terga and sterna lacking sclerites, except for lateral rods of male subgenital plate and, sometimes, terga II–IV of male*; abdominal pleura II and sometimes III and IV sclerotised, at least in female; other pleura unsclerotised.



Figs 247–250 *Geomydoecus* species, ♂ genitalia. 247, *G. (G.) thomomyus*. 248, *G. (G.) actuosi*. 249, *G. (Thomomydoecus) minor*. 250, *G. (T.) wardi*.

Gonapophyses broad, membranous, with ventral marginal setae, if present, generally basal only; ventral lobe absent (Figs 243, 246). Gonapophyses meet ventral vulval margin smoothly or acutely, but not linked by sclerotised band. Ventral vulval margin not sclerotised; generally convex or very convex medially; subgenital lobe not present. Female genital chamber with dorsal wall bearing slanting scales laterally, lightly sclerotised and lacking scales or other decoration antero-medially. Common oviduct generally with distinct striae.

Male subgenital plate with only s.g.p.r. present. Pseudostyli absent. Male genital opening dorsal. Parameres fused to form single plate with apex pointed or bifid*. Basiparameral sclerites absent. Mesomeres fused apically; mesomeral arch with or without median extension; mesomeres basally abut b.a.l.s., which sometimes have postero-lateral extensions; mesomeres do not contact parameral plate. Male genitalia depicted in Figs 247–250.

HOSTS. Geomyidae (Rodentia).

COMMENTS. A few of the species are parthenogenetic.

No more than 25 specimens of most species were examined during the course of this study, though in many cases large numbers were available.

Detailed descriptions of all species of *Geomydoecus* s.l. and a phenetic treatment of the genus may be found in Hellenthal & Price (1976, 1980), Price (1974, 1975), Price & Emerson (1971, 1972), Price & Hellenthal (1975*a*, 1975*b*, 1976, 1979, 1980*a*, 1980*b*, 1980*c*, 1981*a*, 1981*b*), Price & Timm (1979), Timm & Price (1979, 1980).

Subgenus *GEOMYDOECUS* Ewing

(Figs 243, 247, 248)

Geomydoecus Ewing, 1929: 193. Type-species: *Trichodectes geomydis* Osborn, by original designation.

DESCRIPTION. Temple margin sometimes with two short, stout setae latero-posteriorly, or single long, fine seta latero-posteriorly.

Male abdominal terga II and III only rarely with median setal group comprising exceptionally long, stout setae (*G. copei*). Pleural projections rarely sclerotised. Male terga II–IV not sclerotised.

Male genitalia not asymmetric. Parameral plate apically pointed or bifid. Male genitalia depicted in Figs 247, 248.

HOSTS. Geomyidae (Rodentia).

SPECIES INCLUDED

actuosi Price & Hellenthal, 1981 (25 ♂, 25 ♀)
albati Price & Hellenthal, 1981 (25 ♂, 25 ♀)
alcorni Price & Emerson, 1971 (6 ♂, 6 ♀)
alleni Price & Emerson, 1971 (2 ♂, 6 ♀)
angularis Price & Hellenthal, 1981 (25 ♂, 25 ♀)
aurei aurei Price & Hellenthal, 1981 (25 ♂, 25 ♀)
aurei grahamensis Price & Hellenthal, 1981 (25 ♂, 25 ♀)
bajaiensis Price & Hellenthal, 1981 (25 ♂, 25 ♀)
bulleri Price & Emerson, 1971 (25 ♂, 25 ♀)
californicus (Chapman, 1897) (25 ♂, 25 ♀)
centralis Price & Hellenthal, 1981 (25 ♂, 25 ♀)
chapini Werneck, 1945 (12 ♂, 16 ♀)
cherriei Price, 1974
chiapensis Price & Emerson, 1971 (18 ♂, 20 ♀)
chihuahuae chihuahuae Price & Hellenthal, 1979 (25 ♂, 25 ♀)
chihuahuae emersoni Price & Hellenthal, 1979 (25 ♂, 17 ♀)
clausonae Price & Hellenthal, 1981 (25 ♂, 25 ♀)
cliftoni Price & Hellenthal, 1981 (25 ♂, 25 ♀)
copei Werneck, 1945 (25 ♂, 25 ♀)
coronadoi Barrera, 1961 (25 ♂, 25 ♀)
costaricensis Price & Emerson, 1971 (7 ♂, 7 ♀)
crovelloi Price & Hellenthal, 1981 (25 ♂, 25 ♀)
dakotensis Price & Emerson, 1971 (25 ♂, 25 ♀)
dalgleishi Timm & Price, 1979 (2 ♂, 2 ♀)

dariensis Price & Emerson, 1971 (10 ♂, 14 ♀)
duchesnensis Price & Emerson, 1971 (5 ♂, 8 ♀)
ewingi Price & Emerson, 1971 (25 ♂, 25 ♀)
expansus (Duges, 1902) (25 ♂, 25 ♀)
extimi Price & Hellenthal, 1981 (26 ♂, 25 ♀)
fulvescens Price & Emerson, 1971 (25 ♂, 25 ♀)
fulvi Price & Hellenthal, 1979 (25 ♂, 25 ♀)
geomydis (Osborn, 1891) (25 ♂, 25 ♀)
guadalupensis Hellenthal & Price, 1980 (25 ♂, 25 ♀)
heaneyi Timm & Price, 1980 (25 ♂, 25 ♀)
hoffmanni Price & Hellenthal, 1976 (25 ♂, 25 ♀)
hueyi Price & Hellenthal, 1980 (25 ♂, 25 ♀)
idahoensis Price & Emerson, 1971 (25 ♂, 25 ♀)
illinoensis Price & Emerson, 1971 (25 ♂, 25 ♀)
jaliscoensis Price & Hellenthal, 1981 (25 ♂, 25 ♀)
jonesi Price & Emerson, 1971 (4 ♂, 5 ♀)
limitaris limitaris Price & Hellenthal, 1981 (25 ♂, 25 ♀)
limitaris bakeri Price & Hellenthal, 1981 (25 ♂, 25 ♀)
limitaris halli Price & Hellenthal, 1981 (25 ♂, 25 ♀)
limitaris tolteci Price & Hellenthal, 1981 (25 ♂, 25 ♀)
martini Price & Hellenthal, 1975 (25 ♂, 25 ♀)
mcgregori Price & Emerson, 1971 (25 ♂, 25 ♀)
merriami Price & Emerson, 1971 (25 ♂, 25 ♀)
mexicanus Price & Emerson, 1971 (25 ♂, 25 ♀)
mobilensis Price, 1975 (25 ♀)
musculi Price & Hellenthal, 1981 (25 ♂, 25 ♀)
nayaritensis Price & Hellenthal, 1981 (16 ♂, 25 ♀)
nebrathkensis Timm & Price, 1980 (25 ♂, 25 ♀)
oklahomensis Price & Emerson, 1971 (25 ♂, 25 ♀)
oregonus Price & Emerson, 1971 (25 ♂, 25 ♀)
panamensis Price & Emerson, 1971 (23 ♂, 22 ♀)
pattoni Price & Hellenthal, 1979 (12 ♂, 8 ♀)
perotensis perotensis Price & Emerson, 1971 (25 ♂, 25 ♀)
perotensis irolonis Price & Emerson, 1971 (25 ♂, 25 ♀)
polydentatus Price & Emerson, 1971 (25 ♂, 25 ♀)
quadridentatus Price & Emerson, 1971 (25 ♂, 25 ♀)
scleritus (McGregor, 1917) (3 ♂, 25 ♀)
setzeri Price, 1974 (6 ♂, 8 ♀)
shastensis Price & Hellenthal, 1980 (25 ♂, 25 ♀)
sinaloae Price & Hellenthal, 1981 (25 ♂, 25 ♀)
spickai Timm & Price, 1980 (25 ♂, 25 ♀)
subcalifornicus Price & Emerson, 1971 (25 ♂, 25 ♀)
subgeomydis Price & Emerson, 1971 (25 ♂, 25 ♀)
subnubili Price & Hellenthal, 1975 (25 ♂, 25 ♀)
tamaulipensis Price & Hellenthal, 1975 (3 ♂, 25 ♀)
texanus texanus Ewing, 1936 (25 ♂, 25 ♀)
texanus tropicalis Price & Hellenthal, 1975 (25 ♂, 25 ♀)
thomomyus (McGregor, 1917) (25 ♂, 25 ♀)
tolucae Price & Emerson, 1971 (25 ♂, 25 ♀)
traubi Price & Emerson, 1971 (25 ♂, 25 ♀)
trichopi Price & Emerson, 1971 (25 ♂, 25 ♀)
truncatus Werneck, 1950 (25 ♂, 25 ♀)
umbrini Price & Emerson, 1971 (25 ♂, 25 ♀)
ustulati ustulati Price & Hellenthal, 1975 (25 ♂, 25 ♀)
ustulati clarkii Price & Hellenthal, 1975 (25 ♂, 25 ♀)
veracruzensis Price & Emerson, 1971 (25 ♂, 25 ♀)
warmanae Price & Hellenthal, 1981 (25 ♂, 25 ♀)
welleri welleri Price & Hellenthal, 1981 (25 ♂, 25 ♀)
welleri multilineatus Price & Hellenthal, 1981 (25 ♂, 25 ♀)

wernecki Price & Emerson, 1971 (25 ♂, 25 ♀)
yucatanensis Price & Emerson, 1971 (25 ♂, 25 ♀)

Subgenus ***THOMOMYDOECUS*** Price & Emerson

(Figs 244–246, 249, 250)

Thomomydoecus Price & Emerson, 1972: 464 [as subgenus of *Geomydoecus* Ewing]. Type-species: *Geomydoecus (Thomomydoecus) jamesbeeri* Price & Emerson, by original designation.

DESCRIPTION. Temple margin with single stout seta and finer, shorter adjacent setae latero-posteriorly.

Male abdominal terga II and III with median setal group comprising exceptionally long, stout setae. Pleural projections sclerotised, at least in female (Fig. 246). Male terga II–IV sometimes with sclerites.

Gonapophyses meet vulval margin smoothly.

Male genitalia symmetric (Fig. 250) or asymmetric (Fig. 249). Parameral plate apically pointed.

HOSTS. *Thomomyus* spp. (Rodentia: Geomyidae).

COMMENTS. As discussed on p. 232, the subgenus *Geomydoecus* is probably paraphyletic and *Thomomydoecus* paraphyletic or even polyphyletic. *Geomydoecus (Thomomydoecus)* was raised to generic status by Hellenthal & Price (1984), on the basis that there are 'sufficient' morphological differences between it and *Geomydoecus* s. str. This action, reversed here, is consistent with the purely phenetic approach employed by the authors, but cannot be reconciled with the cladistic methods used in this study. The division of *Geomydoecus* into subgenera is retained, even though neither of the two subgenera is 'natural' (i.e. holophyletic), because insufficient work has been done to resolve the relationships properly, and the independent unit of the classification, the genus *Geomydoecus*, is holophyletic. Raising *Thomomydoecus* to generic status, however, would produce two independent units in the classification (*Geomydoecus* and *Thomomydoecus*) that differ from all the others in not being holophyletic.

Geomydoecus (T.) byersi (Hellenthal & Price) was described after the completion of this manuscript and has not been included in the cladistic analysis.

SPECIES INCLUDED
asymmetricus Price & Hellenthal, 1980 (25 ♂, 25 ♀)
birneyi Price & Hellenthal, 1980 (25 ♂, 25 ♀)
byersi (Hellenthal & Price, 1984) **comb. n.** from *Thomomydoecus*
dickermani Price & Emerson, 1972 (25 ♂, 25 ♀)
genowaysi Price & Emerson, 1972 (25 ♂, 25 ♀)
greeri Price & Hellenthal, 1980 (2 ♂)
jamesbeeri Price & Emerson, 1972 (8 ♂, 10 ♀)
johnhafneri Price & Hellenthal, 1980 (25 ♂, 25 ♀)
markhafneri Price & Hellenthal, 1980 (25 ♂, 25 ♀)
minor Werneck, 1950 (25 ♂, 25 ♀)
neocopei Price & Emerson, 1971 (2 ♂, 1 ♀)
orizabae Price & Hellenthal, 1980 (10 ♂, 26 ♀)
peregrini Price & Hellenthal, 1980 (4 ♂, 4 ♀)
potteri Price & Hellenthal, 1980 (16 ♂, 25 ♀)
timmi Price & Hellenthal, 1980 (25 ♂, 25 ♀)
wardi Price & Emerson, 1971 (25 ♂, 25 ♀)
williamsi Price & Hellenthal, 1980 (8 ♂, 16 ♀)
zacatecae Price & Hellenthal, 1980 (25 ♂, 25 ♀)

Keys to Trichodectidae

Two keys are provided: a key to subfamilies and a key to genera and subgenera. The latter key contains all genera and subgenera, and it is not necessary to use the subfamily key as an introduction to it.

The subfamily key is included because of the formal requirement that any newly described taxon must be accompanied by some form of description in order to make the name available. The key to the five subfamilies of Trichodectidae therefore serves to distinguish Neotrichodectinae subfam. n. from all others.

Key to subfamilies

1 No abdominal spiracles present; majority of tergal and sternal setae at least two-thirds length of segment or, if not, median setal group on tergum II comprising at least three setae (and, frequently, median groups running together). New World **NEOTRICHODECTINAE** subfam. n. (p. 321)

– At least one pair of abdominal spiracles present or, if not, majority of abdominal sternal and tergal setae less than two-thirds length of segment or median setal group on tergum II comprising only one seta. Old and New World 2

2 Female subgenital lobe present, frequently with serrate margin, at least posteriorly; if margin of subgenital lobe smooth, gonapophyses meet vulval margin smoothly (Fig. 153); female flagellomeres fused; abdominal spiracles numbering six or fewer pairs. Parasitic on Carnivora and Primates. Old and New World .... **TRICHODECTINAE** Kellogg, 1896 (p. 286)

– Female subgenital lobe absent or, if present, not marginally serrate and gonapophyses meet vulval margin acutely; female flagellomeres fused or unfused; abdominal spiracles numbering six pairs, though spiracles on segment VIII may be very small and inconspicuous, possibly non-functional (some species of *Procaviphilus (Meganarionoides)*). Not parasitic on Carnivora. Old and New World 3

3 Dorsal or ventral projection present on abdominal pleurum IV; mesomeral arch generally produced basally between b.a.l.s.; female antennal flagellomeres generally not fused, or only partially fused; parasitic on hyraxes and primates. Old and New World **DASYONYGINAE** Kéler, 1938 (p. 267)

– Pleurum IV lacking any projection; mesomeral arch rarely produced basally between b.a.l.s.; female flagellomeres generally fused or, if not, then female with long setal tufts on abdominal pleura VIII and IX; not parasitic on hyraxes or primates 4

4 Posterior margin of temple generally produced, very convex; (Fig. 87); very long setae present on at least pleurum VIII, sometimes also on pleura VII (male) or IX (female); basiparameral sclerites present; mesomeral arch lacking extension if complete, otherwise tripartite, median part sometimes obscure (Figs 91, 93); if mesomeral arch entire, male genitalia as in Fig. 89, temple margins not greatly produced, and female with two flagellomeres; parasitic on New World porcupines (Erethizontidae) .... **EUTRICHOPHILINAE** Kéler, 1938 (p. 265)

– Temples not so developed; setae on pleurum VIII not exceptionally long; basiparameral sclerite present or absent; mesomeral arch, if present, with or without extension, but arch never tripartite; female flagellomeres fused; pseudostyli frequently present; parasitic on Artiodactyla and Perissodactyla. Old and New World .... **BOVICOLINAE** Kéler, 1938 (p. 247)

Key to genera and subgenera

1 No abdominal spiracles present; majority of tergal and sternal setae at least two-thirds length of segment or, if not, median setal group on tergum II comprising at least three setae (and, frequently, median groups running together). New World 2

– At least one pair of abdominal spiracles present or, if not, majority of abdominal sternal and tergal setae less than two-thirds length of segment or median setal group on tergum II comprising only one seta. Old and New World 8

2 Abdominal pleura II–IV with dorsal projections (Fig. 246), though most apparent in females and sometimes very inconspicuous; male lacking tergocentral microsetae; latero-posterior corner of temple margin frequently with single long fine seta or one or two shorter, stout setae; female pedicel with dorsal membranous projection (Fig. 245) (sometimes obscure). [Geomyidae] (***GEOMYDOECUS*** s.l., p. 328) 3

– Abdominal pleura lacking dorsal projections, or single membranous projection present on pleurum IV only (Fig. 228); male with tergocentral microsetae on abdominal terga II–VI (Fig. 227): long seta frequently present on temple margin but shorter stout seta not developed; female pedicel lacking any projection. (***NEOTRICHODECTES*** s.l., p. 321) 4

3 Pleural projections on pleurum II sclerotised; temple margin with single stout seta and associated smaller finer setae; male abdominal terga II and III with rows of enlarged setae (Fig. 244); parameral plate with single apical point; male genitalia symmetric or asymmetric ***GEOMYDOECUS (THOMOMYDOECUS)*** (p. 334)

– Pleural projection on pleurum II unsclerotised or, if sclerotised, posterolateral temple margin with single long fine seta and associated smaller setae; temple margin with or without specialised setae but not with single stout seta; male abdominal terga II and III rarely with rows of specialised setae (*G. copei* only); parameral plate with single apical point or apically bifid; male genitalia symmetric .... ***GEOMYDOECUS (GEOMYDOECUS)*** (p. 332)

4 Female subgenital lobe present, with serrate margins; female genital chamber with clear, flat dorsal region but lacking single scattered spines; gonapophyses broad, membranous, lacking lobe; parameral plate slender, with basal projection between b.a.l.s. (Fig. 238). [Mustelidae and Procyonidae] .... ***NEOTRICHODECTES (NEOTRICHODECTES)*** (p. 326)

– Female subgenital lobe absent or, if present, lobe with smooth margins and longitudinal setal rows (Fig. 235); female genital chamber, if with clear flat dorsal area, then with single spines scattered over it; gonapophyses not broad and membranous, frequently with lobe; parameral plate broad, with very limited projection between b.a.l.s. 5

5 Ventral vulval margin with lobulate process with smooth margins and longitudinal rows of setae (Fig. 235); gonapophyses slender, sclerotised, lacking lobe; parameral plate with single apical point; mesomeral arch extension broad, clubbed (Fig. 240). [Mustelidae] ***NEOTRICHODECTES (TRIGONODECTES)*** (p. 327)

– Ventral vulval margin convex, but not produced; gonapophyses not slender, lobe present; parameral plate with apex bifid; mesomeral arch with pointed extension 6

6 Large species, over 2·75 mm long; male flagellum with 7 articulated 'teeth'; female gonapophyses thick, with lobe and spur (Fig. 236); female pleurum VIII sclerotised; abdominal setae relatively small, not attaining following setal row. [Bradypodidae] ***NEOTRICHODECTES (LAKSHMINARAYANELLA)*** (p. 327)

– Smaller species, under 2·25 mm long; male flagellum with 2 articulated 'teeth'; female gonapophyses otherwise; female pleurum VIII not sclerotised; abdominal setae long, attaining or nearly attaining setal bases of following setal row. [Carnivora] 7

7 Gonapophyses with flat lobe and small spur (Fig. 237); male mesomeral arch extension attaining end of parameral plate (Fig. 239) [Procyonidae] ***NEOTRICHODECTES (NASUICOLA)*** (p. 327)

– Gonapophyses with lobe comprising fused setal tubercles, long spur present (Fig. 233); male mesomeral arch extension reaching beyond apex of parameral plate (Fig. 242). [Mustelidae] ***NEOTRICHODECTES (CONEPATICOLA)*** (p. 328)

8 Five pairs of abdominal spiracles present; vulval margin sclerotised, with or without setal tubercles, and meeting gonapophyses smoothly; subgenital lobe present; parameres not fused to b.a.l.s.; mesomeres absent; postcoxale absent; abdominal segments II–V with median setal group present, comprising at least three setae. [Mustelidae] ***TRICHODECTES (PARATRICHODECTES)*** (p. 300)

– Other than five pairs of abdominal spiracles present, though spiracles on segment VIII may be very small, inconspicuous and possibly non-functional (some species of *Procaviphilus (Meganarionoides)* as described in key couplet 26, and some species of *Trichodectes (Stachiella)*, as described in key couplet 14)... 9

9 Abdominal pleura V–VI (at least) lacking setae 10

– Abdominal pleura III–VIII (at least) with posterior setal row and, sometimes, anterior setae ... 12

10 Abdominal tergal setae on segments I–VI less than half length of segment, shorter than postero-lateral setae; pleura V–VI lacking setae (Fig. 159); male flagellum with two basally-articulated 'teeth'; mesomeres present, unfused; parameres fused, with distinct inturned apices arising from plate (Fig. 171); subgenital lobe bifurcate, with long basal lateral processes (Fig. 149). [Mustelidae] ***TRICHODECTES (TRICHODECTES)*** (in part) (p. 299)

– At least some setae on abdominal terga I–III as long or longer than segment and postero-lateral seta, and postero-lateral setae sometimes absent; pleura IV–VII (at least) lacking setae (Fig. 141); male flagellum lacking 'teeth'; mesomeres absent; parameres unfused or united at base only; subgenital lobe not bifurcate or only slightly so; basal processes of subgenital lobe absent or, if present, not long (Fig. 146). [Lutrinae] 11

11 Posterior setal row present on pleurum III; parameres slender, rod-like, fused basally (Figs 144, 145); subgenital lobe lacking basal lateral processes; gonapophyses lacking setal tubercles (Fig. 143) .... ***LUTRIDIA*** (p. 288)

– Posterior setal row not present on pleurum III; parameres broad, not fused to each other (Fig.

147); subgenital lobe with basal lateral processes; gonapophyses with setal tubercles (Fig. 146) .... ***NEOLUTRIDIA*** (p. 289)

12 Ventral vulval margin meets gonapophyses smoothly, joined by sclerotised band; subgenital lobe present, frequently with basal lateral processes; sternal setae on at least segments III–VI attaining or nearly attaining base of following setal row; dorsum of head with setae sparse; male scape expanded or, if not, parameres fused to b.a.l.s. 13

– Ventral vulval margin meets gonapophyses acutely or, if meeting smoothly, not joined by sclerotised band; subgenital lobe present or absent, but, if present, never with basal lateral processes (except *Damalinia (Tricholipeurus) elongata*; see Fig. 65); sternal setae on segments III–VI not attaining base of following setal row, usually less than three-quarters length of segment or, if longer, either female genitalia not as described and dorsum of head with dense setal covering (*Bovicola (Holakartikos)* and *B. (Spinibovicola)*) or male scape not expanded and parameres not fused to b.a.l.s. 15

13 Pleurum IV with dorsal projection; anterior setae present on abdominal terga and sterna. [Ursidae]... ***WERNECKODECTES*** (p. 290)

– Pleurum IV without dorsal projection; anterior setae not present on abdominal terga and sterna 14

14 Male abdominal terga II–IV (at least) with median setal group reduced to one seta (Fig. 164); parameres fused to b.a.l.s. (Figs 172, 174) or characteristically asymmetric (Fig. 173); female abdominal terga III–VII (at least) with median setal group reduced to one seta or absent. [Mustelidae and Procyonidae] .... ***TRICHODECTES (STACHIELLA)*** (p. 301)

– Tergal setae of both sexes more abundant, with at least two setae in median setal group; parameres not fused to b.a.l.s. [Canidae, Viverridae, Ursidae and Mustelidae]
TRICHODECTES (TRICHODECTES) (in part) (p. 299)

15 Posterior setal row of pleurum III with setae stouter than those of p.s.r. of pleurum V (Figs 182, 188) or, if not, species with four pairs of abdominal spiracles; otherwise species with 0, 1, 2, 3, 4 or 6 pairs of abdominal spiracles; subgenital lobe present; gonapophyses with lobe present 16

– Posterior setal row of pleurum III with setae not stouter than those of p.s.r. of pleurum V; six pairs of abdominal spiracles present, if gonapophyses with lobe, then subgenital lobe absent 19

16 Abdominal spiracles numbering 6, 4 or 0 pairs; if no abdominal spiracles present, then female with gonopore surrounded by spicular refringent patch, or gonapophysis lobe comprising two fused tubercles, or antennal sensilla in pit with peripheral tongue-like projections; female subgenital lobe frequently with overlapping scales or spines; male mesomeral arch always present, with median extension or two apical nipples; mesomeres produced basally between b.a.l.s. or, if not, antennal sensilla as described above; parameres usually broad, contacting mesomeres only, not b.a.l.s.; male abdominal tergum II lacking specialised setae of median group. (***LORISICOLA*** s.l., p. 312) 17

– Abdominal spiracles numbering 3, 2, 1 or 0 pairs; if no abdominal spiracles present, then female gonopore not surrounded by spicular refringent patch, gonapophysis lobe not comprising two fused setal tubercles; antennal sensilla of male and female never in pit with peripheral tongue-like projections; female subgenital lobe never with overlapping scales or spines; male mesomeres fused, unfused or absent; if mesomeres fused, mesomeral arch never with median extension or apical nipples; parameres frequently narrow, rod-like, contacting mesomeres, b.a.l.s. or both; male abdominal tergum II frequently with long, specialised setae (Figs 179, 180, 187–189). (***FELICOLA*** s.l., p. 302) 18

17 Male antennal flagellum with 'teeth' on projection; six pairs of abdominal spiracles present or abdominal spiracles absent, in which case antennal sensilla in pit with peripheral tongue-like projections. [Felidae, Viverridae and Lorisidae] .... ***LORISICOLA (LORISICOLA)*** (p. 316)

– Male antennal flagellum with 'teeth' not on projection, or, if projection present, mesomeral arch lacking extension; four pairs of abdominal spiracles present or abdominal spiracles absent, in which case male gonopore surrounded by spicular patch (Fig. 225). [Viverridae and Herpestidae] .... ***LORISICOLA (PARADOXUROECUS)*** (p. 318)

18 Male antennal flagellum with one or three basally-articulated 'teeth', or 'teeth' absent, in which case male abdominal tergum III with median setal group reduced to one seta of similar size to those on tergum II, which are not greatly enlarged, and parameres not fused; female gonapophysis with lobe and spur present, lobe rounded or rectangular and formed of fused tubercles; subgenital lobe bifid or not; if subgenital lobe bifid, lobes pointed, rounded or with

rectangularly obtuse posterior margins (Fig. 176); everted portion of male endophallus never sclerotised; abdominal spiracles numbering 0, 1 or 3 pairs. [Herpestidae and Canidae] ***FELICOLA (SURICATOECUS)***(p. 312)

– Male antennal flagellum with one, two, three or four nonarticulated 'teeth', or 'teeth' absent, in which case male abdominal tergum III with median setal group reduced to one seta much smaller than those on tergum II, which are greatly enlarged, and parameres fused, at least basally; female with gonapophysis lobe rounded, with or without spur, but lobe never rectangular; subgenital lobe bifid or not; if subgenital lobe bifid, lobes of various shapes, but never with rectangularly obtuse posterior margins; everted portion of male endophallus frequently thinly sclerotised (Figs 190, 196); abdominal spiracles numbering 0, 2 or 3 pairs. [Herpestidae, Viverridae and Felidae] .... ***FELICOLA (FELICOLA)***(p. 302)

19 Dorsal or ventral projection present on abdominal pleurum IV (Fig. 105); mesomeral arch generally produced basally between b.a.l.s.; female antennal flagellomeres generally not fused, or only partially fused. [Procaviidae and Primates].. 20

– Pleurum IV lacking any projection; mesomeral arch rarely produced basally between b.a.l.s.; female flagellomeres generally fused or, if not, then female with long setal tufts on abdominal pleura VIII and IX (see couplet 27); not parasitic on hyraxes or primates 27

20 Sitophore sclerite modified, with posterior arms extended (Fig. 12) (sclerite difficult to see) 21

– Sitophore sclerite unmodified (Fig. 11) (not, generally, difficult to see) 23

21 Tarsal claws with ventral teeth or spines; temple margin with or without small rounded projection; pleural projection on abdominal pleurum IV not elongate. [Procaviidae] (***DASYONYX*** s.l., p. 279) 22

– Tarsal claws lacking ventral teeth or spines; temple margin with long, broad, triangular projection (Fig. 138); pleural projection on abdominal pleurum IV long (Fig. 136). [Procaviidae] .... ***EURYTRICHODECTES***(p. 284)

22 Tarsal claws with sharp, fine spines (Fig. 14)........................ ***DASYONYX (DASYONYX)***(p. 282)

– Tarsal claws with broad, saw-like teeth (Fig. 15)........... ***DASYONYX (NEODASYONYX)***(p. 284)

23 Abdominal sternum II with broad, heavily-sclerotised band articulated with abdominal pleurum II (Fig. 105); setal row of male scape comprising only two setae; basiparameral sclerites present. [Procaviidae] (***PROCAVICOLA*** s.l., p. 270) 24

– Abdominal sternum II lacking sclerotised band or, if sclerotised band present, this is fused to abdominal pleurum II or medially broken; setal row of male scape numbering more than two setae; basiparameral sclerites absent or, if present, thoracic spiracle with tubular atrium and female flagellomeres fused 25

24 Posterior angle of temple with small projection; mesomeral arch with lateral double flexion and median extension; endophallus with large hook-like spines (Fig. 107) ***PROCAVICOLA (CONDYLOCEPHALUS)***(p. 274)

– Posterior angle of temple lacking projection; mesomeres unfused and lacking lateral double flexion and median extension; endophallus lacking large hook-like spines (Fig. 109) ***PROCAVICOLA (PROCAVICOLA)***(p. 270)

25 Atrium of thoracic spiracle spherical; mesomeral arch with median extension and lateral desclerotisations; gonapophyses with setal tubercles or, if not, postcoxale greatly developed and fused to abdominal pleurum II. [Procaviidae and Cercopithecidae] (***PROCAVIPHILUS*** s.l., p. 274) 26

– Atrium of thoracic spiracle tubular; mesomeral arch lacking median extension and not desclerotised laterally; gonapophyses lacking setal tubercles; postcoxale not greatly developed and fused to abdominal pleurum II. [Cebidae]....................... ***CEBIDICOLA*** (p. 267)

26 Parameres with basal flange, sometimes fused faintly; perisetal gap of male subgenital plate absent; postcoxale not fused to abdominal pleurum II; setal tubercles of gonapophyses not fused characteristically. [Procaviidae] .... ***PROCAVIPHILUS (PROCAVIPHILUS)***(p. 278)

– Parameres usually lacking basal flange; perisetal gap of male subgenital plate present or, if absent, parameres fused together and articulated with mesomeral arch as in Fig. 120, and mesomeral arch produced basally along b.a.l.s. (Fig. 121); postcoxale fused to abdominal pleurum II, at least in females; setal tubercles of gonapophyses fused characteristically (Fig. 111) or, if not, ventral vulval margin as in Fig. 113. [Procaviidae and Cercopithecidae] ***PROCAVIPHILUS (MEGANARIONOIDES)***(p. 278)

27 Posterior margins of temple generally produced, very convex (Fig. 87); very long setae present on at least pleurum VIII (Figs 88, 90), sometimes also on pleurum VII (males) or IX (female); basiparameral sclerites present; mesomeral arch lacking extension if complete, otherwise tripartite, median part sometimes obscure (Figs 101, 102); if mesomeral arch entire, male genitalia as in Fig. 100, temples not greatly produced, and female with two flagellomeres, otherwise female flagellomeres fused. [Erethizontidae] ***EUTRICHOPHILUS*** (p. 265)

– Temples not so developed; setae on pleurum VIII not exceptionally long; basiparameral sclerites present or absent; mesomeral arch, if present, with or without extension, but never tripartite; female flagellomeres fused 28

28 Parameres narrow, rod-like and fused basally; mesomeral arch with broad lobe-like extension; b.a.l.s. widely divergent anteriorly (Fig. 139); gonapophyses with setal tubercles; pseudostyli absent. [Protelidae and Hyaenidae] .... ***PROTELICOLA*** (p. 286)

– Parameres not narrow and fused basally or, if so, then b.a.l.s. not widely divergent anteriorly; mesomeral arch without broad lobulate extension; gonapophyses lacking setal tubercles; pseudostyli frequently present 29

29 Subgenital lobe present; endophallus with dense patch of regularly-arranged spicules or, if not, parameral plate with single apex (Fig. 81); mesomeral arch entire, with abrupt bend to enable bases to meet parameres (Figs 81, 82), or mesomeres unfused and b.a.l.s. with anteposterior spur (Fig. 83); interior face of male flagellum serrate (Fig. 13); abdominal sterna never with anterior setae; long, slender species. [Bovidae and Cervidae] ***DAMALINIA (TRICHOLIPEURUS)*** (p. 264)

– Subgenital lobe absent or, if present, as small flap (Fig. 42) and species with anterior setae on abdominal sterna (*Bovicola jellisoni*); sternum VII sometimes developed posteriorly into two projecting spikes (*Damalinia theileri, neotheileri* and *semitheileri*, Fig. 73); endophallus lacking spicular patch; parameres with apices free; mesomeres apically fused, unfused or absent, but abrupt bend not present; b.a.l.s. lacking anteposterior spur; interior face of male flagellum without serrations; broader species 30

30 Dorsal face of vulva with pointed scales; gonapophyses hook-shaped (Fig. 66); common oviduct, at branching point, with folded and more or less apparent collar, sometimes partially sclerotised and refracting transmitted light; mesomeres unfused; abdominal pleurum never extending ventrally onto abdominal sternum II; interior face of male flagellum serrate. [Bovidae and Cervidae] .... ***DAMALINIA (CERVICOLA)*** (p. 263)

– Dorsal face of vulva lacking pointed scales; gonapophyses not hook-shaped or, if they are, then abdominal pleurum II extending onto sternum II (Fig. 68); common oviduct lacking 'collar' as described above; mesomeres fused, unfused or absent; interior face of male flagellum with or without serrations 31

31 Abdominal pleurum II with sclerite extending onto sternum II and occasionally tergum II, sometimes at the expense of sternite or tergite (Fig. 68); mesomeres unfused, may be fused to parameres and apparently absent; pseudostyli absent or, if present, broad or narrow (Figs 68, 71, 72); interior face of male flagellum serrate. [Bovidae] .... ***DAMALINIA (DAMALINIA)*** (p. 260)

– Abdominal pleurum II not extending onto sternum II; mesomeres fused, unfused or absent; pseudostyli, if present, not as figured above; interior face of male flagellum lacking serrations 32

32 Atria of abdominal spiracles large, clear; mesomeral arch fused to b.a.l.s.; parameres broad, asymmetrically deflected (Fig. 64); thorax with setae sparse dorsally in female, but male with median patch of setae on prothorax; head elongate, trapezoid, with deep osculum present (Fig. 63) [Tragulidae] .... ***TRAGULICOLA*** (p. 255)

– Atria of abdominal spiracles not large; mesomeral arch not fused to b.a.l.s. or, if it is, parameres and mesomeres also fused (Fig. 60); parameres not broad or asymmetrically deflected; thoracic setae less sparse but male thorax lacking central setal patch; head not elongate but rounded, osculum absent or, if present, not deep (Fig. 3) 33

33 Parameres fused to mesomeres (Fig. 60); pseudostyli present, apically angular (Fig. 59); gonapophyses broad, truncate (Fig. 58); osculum absent, but anterior margin of head slightly flattened or concave medially, with hyaline border where pulvinus attains margin. [Bovidae] ***BISONICOLA*** (p. 253)

– Parameres not fused to mesomeres; pseudostyli, if present, apically rounded; gonapophyses not broad, and with lobe variably apparent, or, if gonapophyses broad and truncate (*Werneckiella*), then pulvinus not attaining anterior margin of head, which is smoothly rounded and lacks a median hyaline border 34

34 Gonapophyses broad, truncate; mesomeres of characteristic pentagonal form (Fig. 62). [Equidae and Bovidae] .... ***WERNECKIELLA*** (p. 255)

– Gonapophyses with more or less discrete lobe (Figs 42, 43); mesomeres, if present, not pentagonal; base of parameres frequently heavily block-like. [Bovidae, Cervidae and Camelidae] (***BOVICOLA*** s.l., p. 247) 35

35 Species with more or less dense covering of long setae; anterior setae present on abdominal terga, sterna and pleura, slightly shorter than setae of posterior setal rows on these elements (Fig. 47); gonapophyses with very limited lobe formation (Fig. 44) 36

– Species with shorter setae or, if setae long, then sparsely distributed and anterior setae not present on abdominal terga and sterna; gonapophyses generally with more developed lobe (Figs 43, 45) 37

36 Sitophore sclerite with posterior arms extended (Fig. 12); male with specialised setae on abdominal tergum II (Fig. 41); mesomeres absent (Fig. 56); female lacks spinose patch on postgenital pleural area .... ***BOVICOLA (SPINIBOVICOLA)*** (p. 253)

– Sitophore sclerite with posterior arms not extended; male lacking specialised setae on abdominal tergum II; mesomeres present, fused apically, with median extension (Fig. 57); female with spinose setal patch on postgenital pleural area ***BOVICOLA (HOLAKARTIKOS)*** (p. 251)

37 Setae on head long, fine; osculum absent; preantennal sulcus absent; gonapophyses with very distinct lobe of characteristic form (Fig. 43); male genitalia with mesomeres not fused, bipartite (Fig. 55) .... ***BOVICOLA (LEPIKENTRON)*** (p. 252)

– Setae on head not long and fine; osculum present or absent; preantennal sulcus present or absent; gonapophyses with less distinct lobe, of different form (Figs 42, 45); male genitalia of different form, mesomeres never bipartite .... ***BOVICOLA (BOVICOLA)*** (p. 251)

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Synonyms are in *italics*; original generic combinations are indicated for identical specific epithets.

British Museum (Natural History)

An introduction to the Ichneumonidae of Australia

I. D. Gauld

In the important field of biological and integrated control of pests the parasitic Hymenoptera are of particular significance, and this work considers one of the largest families of Parasitica, the Ichneumonidae. The group has received little attention in Australia – though it has already been utilized successfully in curtailing the ravages caused by accidentally introduced pests. For selective control programmes to be effective, however, a sound knowledge of the biology of both the pest and its parasites is essential – and a sound taxonomic base is vital for the development of such knowledge.

Ironically, considering the group's economic importance, the parasitic Hymenoptera is amongst the least studied of any group of living organisms, and taxonomic difficulties have presented major problems to many entomologists working with the Parasitica. **An Introduction to the Ichneumonidae of Australia** will go a long way towards rectifying this situation, being a taxonomic treatment, by genus, of the Australian ichneumonids, a comprehensive illustrated identification guide, and a summary of all available information on the group. It will also serve as an introduction to the biology and distribution of Australian ichneumonids, and provide a check-list of the described species and an index to their known hosts. It provides an important revision of ichneumonid nomenclature in order to bring the group into line with the generally accepted principles of zoological nomenclature.

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D. J. Williams

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The British and some other European Eriococcidae (Homoptera: Coccoidea)

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Synopsis

Eleven of the 12 indigenous British Eriococcidae, *Cryptococcus fagisuga* Lindinger, *Eriococcus devoniensis* (Green), *E. glyceriae* Green, *E. greeni* Newstead, *E. inermis* Green, *E. insignis* Newstead, *E. munroi* (Boratynski), *E. placidus* Green, *E. pseudinsignis* Green, *E. spurius* (Modeer) and *Pseudochermes fraxini* (Kaltenbach), are redescribed; the twelfth species, *E. cantium*, is described as new. Four introduced species, *E. lagerstroemiae* Kuwana, *Kuwanina parva* (Maskell), *Noteococcus hoheriae* (Maskell) and *Ovaticoccus agavium* (Douglas), are discussed. *Coccus buxi* Fonscolombe, the type-species of *Eriococcus* Targioni Tozzetti, is redescribed, as are *Coccus spurius* Modeer, *Acanthococcus aceris* Signoret and *Rhizococcus gnidii* Signoret, the type-species of *Gossyparia* Signoret, *Acanthococcus* Signoret and *Rhizococcus* Signoret respectively.

In agreement with some earlier works, these three genera remain synonyms of *Eriococcus* but *Greenisca* Borchsenius and *Kaweckia* Koteja & Żak-Ogaza are newly synonymised with *Eriococcus*. *R. gnidii* is newly synonymised with *E. thymi* (Schrank). An unnamed species of *Eriococcus* near *E. buxi*, occurring in the U.S.S.R. and Turkey, is also discussed and lectotypes of the British species are designated, where appropriate. There are sections also on morphology, biology and economic importance.

Introduction

The family Eriococcidae has been formerly associated with the Pseudococcidae, or mealybugs, but the two are now considered to be distinct, and Afifi (1968) has given good characters to separate the adult males of both families. Ferris (1957*a*, 1957*b*) discussed numerous genera, based on the female, that might be included in the Eriococcidae, and defined the family, mainly on negative characters or without certain characters normally found in other families of scale insects. Many genera that have been included in the family have never been studied critically and their affinities may lie elsewhere.

In order to establish the true relationships and possible phylogeny of the Eriococcidae, Dr J. M. Cox, British Museum (Natural History), and the present writer are currently studying the group on a world basis, and it is hoped to publish on these aspects later. In the meantime this

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paper has been written to facilitate identification of the British species currently assigned to the family, and to discuss some European genera, the type-species of which are not British although such genera have been recorded from Britain.

Williams (1984) discussed briefly the distribution of the family and commented on its possible origins in Gondwanaland. It is poorly represented in the tropics and much speciation has taken place in the more temperate areas. The North American fauna was described by Ferris (1955) (under the name Dactylopiidae) and by Miller & McKenzie (1967). Much of the Palaearctic fauna has been discussed in recent years by Borchsenius (1949), Danzig (1962, 1980), Dziedicka & Koteja (1971) and Tereznikova (1981). Some interesting species from South America have been described by Miller & González (1975) and a thorough study of the 75 New Zealand species was made by Hoy (1962). The British species were listed by Boratynski & Williams (1964). Of the 481 species included by Hoy (1963) in his catalogue of world species, almost 150 are known from Australia. It is doubtful, however, if more than one or two Australian species can be identified from the present literature and, because the Australian Region probably includes some of the most interesting and bizarre species, it is clear that a definition of the family and its limits can only be made after the Australian species have been studied adequately. Species from the Oriental Region, although at present rather few, are virtually unrecognisable from the literature and need revising.

Acknowledgements and depositories

The writer is much indebted to Dr A. Kaltenbach, Naturhistorisches Museum, Vienna, who has kindly supplied for study specimens from V. Signoret's collection mentioned in the text. Mrs D. Matile-Ferrero, Muséum National d'Histoire Naturelle, Paris, has sent for study valuable material of *Rhizococcus gnidii* and *Eriococcus thymi* collected in France, for which the writer extends his sincere thanks. Dr J. M. Cox, British Museum (Natural History), has given much help in discussions during the preparation of the manuscript.

Most of the material studied is deposited in the British Museum (Natural History) (BMNH) but other depositories of original material mentioned are the Imperial Agricultural Experiment Station, Tokyo (IAES) and the New Zealand Arthropod Collection, Auckland (NZAC).

Morphology

Many of the characters of the North American species were discussed by Ferris (1955) and by Miller & McKenzie (1967), resulting in definitions of the family for this area. The morphology has also been discussed by Danzig (1980) and Hoy (1962) and a study of the labium was made by Koteja (1974*a*). Present studies of the British and other genera have revealed characters that have not normally been used to separate species or genera and these characters are discussed briefly here.

There is no generally accepted common name for the family but the names 'felted scale insects' or 'felted coccids' have gained some acceptance and the former name could easily be used. The name refers to the ovisac produced by most species from the dorsum and the ventral margins. This ovisac, secreted from ducts, has a felted texture and completely covers the top of the insect except for a hole at the posterior end, allowing first instars to escape. The felted sac combines with mealy secretion on the venter, but on the dorsum rods of wax that seem to be produced from the dorsal setae are also present. Many slide preparations show these rods attached to the enlarged setae.

Body shape and segmentation. The shape of the body varies from globular to broadly-oval and elongate, and although species may be found on leaves, stems and roots, the elongate species are usually found on grasses. In many species the body is strongly nodulose and when this takes up stain, it often masks minute characters. Numbering of the segments follows that given by Miller (1984) for Eriococcidae and by Williams (1985*a*) for Pseudococcidae. In this system the vulva is situated between the 7th and 8th abdominal segments, so that the first abdominal segment on the venter is represented by areas lateral to the 3rd coxae and the 2nd abdominal segment is complete after the metathorax. On the dorsum the 1st abdominal segment is complete, but because the segment containing the anal lobes is probably complex, it is here regarded as the 8th or anal lobe segment.

Anal area. In many genera of Eriococcidae the posterior end of the body is produced into two prominent anal lobes, each usually sclerotised and often conical with a long apical seta. Dorsally there are frequently enlarged setae, varying in number, but in most species there are two such setae on the inner edge and one on the outer edge, although this may be reduced to a much smaller seta. Ventrally there are flagellate setae, often numbering 1–3, and near the inner corner of each lobe there is a seta that Hoy (1962) named the suranal seta. This is usually slender but in some genera it is flat or spatulate. In all the species discussed here the suranal setae are slender. Sometimes the inner edges of the lobes are so strongly nodulose and sclerotised that they appear to be toothed or serrate. When there are no definite anal lobes present the suranal setae are represented by a pair just anterior to the anal ring on the venter. Species with anal lobes often have a small dorsal lobe or plate projecting between the base of the lobes. It varies from being only a slight prominence to triangular, well developed and nodulose. In some species it is heavily sclerotised in the form of a definite plate, as in *Eriococcus phyllanthi* Ferris, and this led Ferris (1957*b*) to refer to it as a cauda. It is not certain whether this plate is homologous with the cauda of the Aphidoidea and it is here called a dorsal plate no matter what the extent of its development is. The anal ring, in species with well-developed anal lobes, is normally situated vertically to the body between the dorsal plate and the apical margin of the venter between the suranal setae. When prepared on microscope slides it often becomes distorted or is pushed inwards, lying neither on the dorsum nor venter. Although the shape varies considerably, and this is mentioned in the text when appropriate, a normal anal ring usually has 8 setae and a single row of pores, except laterally, where there are a few pores forming a double row.

Antennae. These vary from being normal with 6 or 7 segments, to small stubs with 1 or 2 segments. A normal antenna appears to taper, with the terminal segment usually one of the shortest and not wider than the previous segments.

Frontal lobes and frontal tubercles. Often just antero-medially to each basal antennal segment there is a lobe-like structure that varies in size and length. They are much more pronounced in distorted specimens when they can be observed to stick out from the surface. Normally they are membranous but sometimes, as in *Eriococcus buxi* and its relative herein described, they tend to be sclerotised. Their function is unknown. Signoret (1875) mentioned these lobes when describing *Acanthococcus aceris*. Boratynski described them as eversible membranous tubercles in *A. munroi* but there is no evidence that they are eversible. They were mentioned also by Dziedicka & Koteja (1971) when describing *Rhizococcus palustris*. These structures seem to have been ignored in most other works but Dr J. M. Cox and the present writer have observed them in numerous species from all the zoogeographical regions. In at least one species from Australia these lobes extend around and posterior to the basal antennal segment; for this reason a more appropriate term would be frontal lobes and this term is used throughout this work.

Frontal tubercles are minute raised spots situated antero-medially to each antennal base. They are difficult to see but once their normal position is located their presence or absence can be noted. Again, their function is unknown but they seem to be homologous with the 'conical disc pores' mentioned by Ben-Dov *et al.* (1975) in *Protopulvinaria mangiferae* (Green), and to the 'preantennal spots' discussed by Ben-Dov (1979) in species of *Kilifia*. The species in these genera belong to the family Coccidae and the presence of these tubercles may be much more common throughout the group. They are certainly present in many species of Eriococcidae and may have some taxonomic significance. In all species studied so far, frontal lobes and frontal tubercles never occur together and one may have been derived from the other. *Pseudochermes fraxini*, herein described, possesses frontal tubercles in all instars and this may be normal, but some species have neither frontal lobes nor frontal tubercles.

Legs. Unlike species of Pseudococcidae, most of which have the tibia longer than the tarsus, the tarsus in the Eriococcidae is often longer than the tibia. Also the trochanter pores in the

Eriococcidae form a line from the anterior lateral corner to about half-way along the posterior edge, more or less dividing the trochanter into two equal parts. In the Pseudococcidae the trochanter pores are situated towards the distal end.

Labium. The basal segment often has 2 pairs of setae but in some genera these are reduced to a single pair. In *Cryptococcus fagisuga*, herein described, they are absent except in the first instar when a single pair is present.

Setae. On the dorsum and ventral edges, there are often enlarged setae that are spine-like, conical, pointed, blunt or truncate, but sometimes they are cylindrical, lanceolate or even bulbous. Sometimes they are interspersed by quite slender setae. In some species, enlarged setae are confined to the anal lobes or they are absent entirely, but usually the dorsal setae, which may be minute, show some signs of being stiff and not flagellate. When the dorsal setae tend to be small and slender in the adult, there are usually thicker setae in at least the first instar. On the median part of the venter, what are here referred to as normal setae are flagellate setae found in many groups of the Coccoidea. Laterally there are often other setae which, although slender, are nevertheless stiff.

Macroducts. These have been discussed by Ferris (1955), Miller & McKenzie (1967), Miller (1984) and by many other workers. They normally have the inner end reflexed in the form of a cup and, although found in some other families, they represent one of the most important characters of the Eriococcidae, although sometimes they are absent entirely.

Microducts. The significance of these minute ducts has been little understood but their structure may indicate affinities and evolutionary paths. They have been discussed in some detail by Goux (1948). Normally the inner end is bulbous, and the term ampulla is here adopted for it. It usually bears a minute filament arising from the inner end. Between the ampulla and the external orifice there is a tube varying from filamentous and slender to short and bulbous at the inner end, and situated internally just next to the orifice there is a structure often wing-nut-shaped in profile but which is here called a collar. Sometimes the orifice is bifid, as shown already by Miller & González (1975) in *Eriococcus araucariae* Maskell. The bifid orifice is external and may be seen on microducts at the edge of the body where the bifid part protrudes from the surface of the integument. They are not internal as shown by Hoy (1962) for *E. araucariae*. It is still not clear whether the shape and type of the microduct has generic significance. *Cryptococcus fagisuga* herein described possess microducts in the form of a double tube.

Enlarged ducts. These are illustrated here in *E. buxi* and *E.* sp. near *buxi*. They are usually larger than the macroducts but differ in having a flat or slightly rounded inner end, instead of being reflexed into a cup. Because *Eriococcus* possesses these ducts, Borchsenius (1949) separated this genus from all others. The significance of these special ducts is still not clear because Miller & González (1975) discussed them in *Exallococcus laureliae* Miller & González. Furthermore, some Australian species currently assigned to *Eriococcus* also have them.

Pores. Although the disc pores are usually quinquelocular, there are often pores with up to 9 loculi. They are usually on the ventral surface but when present on the dorsum they have sometimes been given generic significance. Cruciform pores are usually oval with a central slit in the form of a cross. When present they are usually found on the venter but their presence on the dorsum has been given generic importance by Koteja & Żag-Ogaza (1981) when describing *Kaweckia*.

Biology and economic importance

Little work has been done on the biology of the British Eriococcidae, but Newstead (1903) has given useful field notes on some species. Gullan (1984) included the specialised gall-forming genus *Apiomorpha* in the family and has given important information on gall formation. Normally British species are univoltine but Patel (1971), discussing *Eriococcus coriaceus* Maskell from South Australia, has stated that it has five generations a year there.

British species are oviparous but whether this is true for all Eriococcidae is not clear from the literature. So far as is known, there are always three instars in the female and five in the male when present. Koteja (1983) has discussed an additional moult in *Acanthococcus greeni* (Newstead) after the adult female had formed, but this was probably caused by parasitism. In Pseudococcidae there are normally four female instars.

The ovisac in the indigenous British species is felted but, apart from the gall-forming species, it is not clear how the covering of many is formed. In *Ovaticoccus agavium* it is described by Boratynski (1958) as loosely felted. The ovisac of *Eriococcus spurius* in mature adults is present only around the margins, but this is because there are no macroducts in the median areas. The insect is, therefore, easily recognisable and is specific to elms.

Most of the British species feed on grasses but it is not known if they cause damage. *Eriococcus devoniensis* is always found on *Erica tetralix* in Britain, causing the stems to turn a complete circle enclosing the insect and ovisac in the bend. Large areas of the plant can be killed and this led Warburton (1937) to recommend burning to destroy the insect. *Pseudochermes fraxini* is found in enormous numbers in the crevices of bark of ash trees and often causes concern, but so far there are no records of mortality of trees. By far the most important insect is *Cryptococcus fagisuga*, found in the crevices of bark of beech trees. It is particularly prevalent in older trees (Wainhouse, 1980, states that trees around 25 years of age are particularly susceptible) and the species is probably found throughout Britain wherever beech is grown. Parker (1975) has stated that beech planted in southern England 1951–60 will be susceptible during the 1980s. The insect is probably the only parthenogenetic species of Eriococcidae in Britain and is often present in enormous numbers producing what has been termed fluffy white wool, so that trunks appear to be completely white. Despite the large numbers, the insects themselves apparently do not cause damage. But, associated with the insect is an ascomycete fungus, *Nectria* sp., known as 'beech bark disease', a name coined by Ehrlich (1934) in a comprehensive account of the disease and insect in Canada and U.S.A. The fungus causes considerable damage resulting in mortality of the tree, and is dependent on the insect for providing an entry wound at the point of feeding. Parker (1975) showed that *Nectria* infected the bark only following wounding, but as Lonsdale (1980) has shown, heavy infestations of the insect induce a lowering of resistance to fungal invasion within bark tissue.

In the Old World the insect is distributed throughout Europe, with incursions into Turkey and Iran. Covassi (1975) stated that Sicily is the southern limit, and the Commonwealth Institute of Entomology (1979) has produced a map showing the world distribution. Thomsen *et al.* (1949) gave a full and important account of the insect and fungus in Denmark. In Britain the insect has been made the subject of a Forestry Commission Leaflet (Hussey, 1956). Wainhouse (1979) showed that the larvae are dispersed passively by wind and a small percentage are carried above the canopy. Some trees are more susceptible than others (Wainhouse & Howell, 1983) and, although there is possible intraspecific variation within populations of the beech scale, there is no evidence of adaptation of the scale to particular trees.

It was reported by Elliott (1933) that, in Suffolk, this species was devoured by a small beetle, *Enicmus* [now *Lathridius*] *minutus* (L.), but this was unlikely because the beetle is normally a fungus-feeder.

ERIOCOCCIDAE Cockerell

Acanthococcites Signoret, 1875: 16. Type-genus: *Acanthococcus* Signoret. [Placed on Official List of Family-Group Names in Zoology (Name Number 535) with an endorsement that it is not to be given priority over Eriococcini Cockerell, 1899 whenever both names are held to denote a single taxon (Melville, 1982: 96).]

Acanthococcidae Signoret; Maskell, 1887: 47.

Eriococcini Cockerell, 1899*a*: 389. Type-genus: *Eriococcus* Targioni Tozzetti. [Placed on Official List of Family-Group Names in Zoology (Name Number 534) with an endorsement that it is to be given precedence over Acanthococcidae Signoret, 1875 whenever both names are held to denote a single taxon (Melville, 1982: 96).]

Eriococcidae Cockerell; Brues & Melander, 1932: 134.

Cryptococcidae Kosztarab, 1968*b*: 12. Type-genus: *Cryptococcus* Douglas. [Synonymised with Eriococcidae by Danzig, 1980: 58.]

Until all genera are studied, including the peculiar gall-producing forms, it is impossible to define the family on a world basis. The following definition is based only on species that have been studied in some detail.

ADULT FEMALES. Body elongate, broadly oval or globular, usually membranous but often strongly nodulose. Segmentation usually distinct in the oval and elongate forms, obscure in the globular forms. Anal lobes often well developed, conical and sclerotised; when present usually with a dorsal plate between and with suranal setae at inner ventral bases. Anal ring often with 8 setae and pores, sometimes reduced, without pores. Antennae, when normal, with 6 or 7 segments, the apical segment usually narrower than preceding segments, sometimes segments reduced to one or two. Frontal lobes or frontal tubercles sometimes present. Legs present or absent; when absent sometimes third pair represented by minute flaps; when present and normal, tibia frequently longer than tarsus, trochanter pores in a line almost dividing trochanter into two equal parts. Labium usually with 1 or 2 pairs of setae on basal segment, rarely absent entirely. Dorsal setae often enlarged, conical, bulbous or cylindrical, if small, remaining spine-like or stiff. Disc pores, when present, usually quinquelocular, but sometimes with up to 9 loculi, frequently on venter and sometimes on dorsum. Macroducts normally present, at least on dorsum, sometimes absent. Microducts usually present. Cruciform pores often present on venter, rarely on dorsum.

Key to genera of British Eriococcidae

Adult females

1 Legs absent except for third pair replaced by small leg flaps 2
– Legs present 3
2 Macroducts present on dorsum .... ***CRYPTOCOCCUS*** Douglas (p. 352)
– Macroducts absent on dorsum, replaced by large invaginated quinquelocular pores ***KUWANINA*** Cockerell (p. 384)
3 Anal lobes present, sclerotised 4
– Anal lobes absent 5
4 Anal lobes with a series of about 12 enlarged setae on dorsum. Segmentation absent between trochanter and femur and between tibia and tarsus .... ***NOTEOCOCCUS*** Hoy (p. 384)
– Anal lobes with at most 4 enlarged setae on dorsum. Segmentation distinct between trochanter and femur and between tibia and tarsus .... ***ERIOCOCCUS*** Targioni Tozzetti (p. 356)
5 Anal ring crescentic, containing pores and setae. Cruciform pores absent ***PSEUDOCHERMES*** Nitsche (p. 385)
– Anal ring not as above, without pores. Cruciform pores present ...... ***OVATICOCCUS*** Kloet (p. 384)

CRYPTOCOCCUS Douglas

Cryptococcus Douglas, 1890: 155. Type-species: *Coccus fagi* Baerensprung [= *Cryptococcus fagisuga* Lindinger], by original designation.

The type-species is now known to occur on *Fagus* spp. throughout Europe and the eastern part of the U.S.A. *C. aceris* Borchsenius is known from Georgia and Azerbaizhan in U.S.S.R. and from Germany on *Acer*. Another species on *Acer* was described as *C. williamsi* Kosztarab from eastern U.S.A., and *C. integricornis* Danzig is known from the Primorsky region in the far east of U.S.S.R. on *Tilia amurensis*. Kosztarab (1968*a*) gave a key to the species known at the time.

All four species are without legs in the adult female, but the hind pair are replaced by small flaps. In the type-species these are simple, each with at most a single seta, but in the other species the flaps are either reticulate or they possess minute pores. When viewed at the edge of the body these structures are flap-like and protrude. They are not plates on the surface of the body or pore plates, as has been suggested; because they are always in the positions of the third legs and probably emit pheromones they are here referred to as leg flaps. *C. integricornis* possesses also spine-like remains of the first and second pairs of legs. All four species have 2–5 segmented antennae that are stub-like, and macroducts each with a cup-shaped inner end on the dorsum and at least the ventral margins. Microducts are present. In the type-species they are in the form of double tubes, the ampulla of each being expanded, with a filament between. The microducts of the other species need more critical study. Quinquelocular pores are present and the anal ring is simple, square or oval with 4–6 setae and a few pores. In *C. fagisuga* the basal segment of the labium is without setae but there is a single pair present in the first instar. Specimens of *C. fagisuga, C. aceris* and *C. williamsi* examined possess neither frontal lobes nor frontal tubercles.

Hoy (1962) accepted *C. nudatus* Brittin in the genus. The species was described from New Zealand on *Hoheria* spp., but because it lacks macroducts it may belong to another genus, although it is very close. *Kuwanina parva* (Maskell), described from Japan and recorded from Britain on *Prunus*, has at one time been assigned to *Cryptococcus*, but the genus *Kuwanina* is here accepted as distinct because it lacks macroducts. These are replaced by large invaginated quinquelocular pores.

Cryptococcus is represented by *C. fagisuga* only in Britain, where it is sometimes injurious to beech.

Cryptococcus fagisuga Lindinger

(Figs 1, 2)

Coccus fagi Baerensprung, 1849: 174. Syntypes ♀, Germany: Berlin (probably lost). [Junior homonym of *Coccus fagi* Sulzer, 1776.]
Coccus fagi Walker, 1852: 1086. LECTOTYPE ♀, England (BMNH), here designated [examined]. [Junior homonym of *Coccus fagi* Sulzer, 1776.]
Pseudococcus fagi (Baerensprung) Douglas, 1886: 152.
Cryptococcus fagi (Baerensprung) Douglas, 1890: 155; Newstead, 1903: 215; Schmutterer, 1952: 417; Ferris, 1955: 83; Tereznikova, 1981: 46.
Cryptococcus fagisuga Lindinger, 1936: 444; Borchsenius, 1949: 37; Hoy, 1963: 54; Danzig, 1964: 634. [Replacement name for *Coccus fagi* Baerensprung.]

Description. Adult female (Fig. 1) in life, globular, bright to lemon yellow, completely covered in a white ovisac. On the slide, rotund, membranous, nodulose, largest about 0·6 μm in diameter, often wider than long, anal lobes not developed, their positions removed to ventral surface of body. Antennae reduced, with 1–2 segments. Legs absent but position of each third leg represented by a small flap often containing a single seta. Labium 48 μm long, often wider than long, shorter than clypeolabral shield, basal segment without setae. Spiracles often triangular, sclerotised. Anal ring at apex of venter, sclerotised, almost quadrate, with 4 short setae 12 μm long occupying corners, a few minute pores on posterior margin or morphologically anterior margin.

Dorsal surface with small setae that are pointed and stiff, 5 μm long, in more or less single rows across the segments. Macroducts in single rows across the segments, each about 8 μm long, with the cup wider than a dorsal setal base. Microducts in moderate numbers, each about 6 μm long, in the form of a double tube tapering towards double orifice, each tube with inner end swollen into an ampulla with a filament between.

Ventral surface with setae about same size as dorsal setae except on anal lobe segment where the suranal setae, and one or two near margins, are larger and conical, about 10 μm long and usually a pair of slightly longer setae near anterolateral corners of anal ring, probably the anal lobe setae. Macroducts of two types. A large type, similar to those on dorsum, few, around margins and sometimes in submarginal areas of thorax and anterior abdominal segments. A small type, not much larger than a microduct, arranged singly in submedian areas of third to fifth abdominal segments and on metathorax anterior to leg-flaps, each duct with a shallow cup. Microducts, same as on dorsum, sparse, present in median areas as well as margins. Quinquelocular pores, about same diameter as the cup of a large macroduct, in more or less single rows on posterior abdominal segments, there being also one or two near each spiracular opening and one or two between clypeolabral shield and labium.

Second instar female (Fig. 2B) broadly oval, smaller than adult female. Antennae near margins, 2-segmented, reduced. Legs absent but position of each third leg represented by a minute sclerotised point. Labium 36 μm long, smaller than clypeolabral shield, basal segment without setae. Anal ring on venter at apex of abdomen, similar to that of adult but smaller. Dorsal surface with small pointed but stiff setae, each 4 μm long, many not much longer than a setal base. Macroducts smaller than in adult female, present in single transverse rows on most segments. Microducts, as in adult, bitubular, represented by one or two only. Ventral surface with setae as on dorsum except for larger conical setae lateral to anal ring, a pair of which longer than others and probably apical setae. Suranal setae small. Macroducts same as on dorsum, occasionally on margins only. Microducts represented by one or two on margins only. Quinquelocular pores arranged singly next to spiracular openings only.

First instar (Fig. 2A), oval, the smallest 300 μm long, 180 μm wide. Anal ring displaced to apex of venter, as in later instars but smaller. Antennae 65 μm long, with 5 segments. Legs normal, hind trochanter + femur 40 μm long, hind tibia 16 μm long, hind tarsus 16 μm long, claw slender, without a denticle, 16 μm long. Labium 32 μm long, basal segment with a pair of minute setae. Dorsal surface with short pointed and stiff setae, 4–5 μm long, but some on head longer and flagellate. Macroducts absent. Microducts

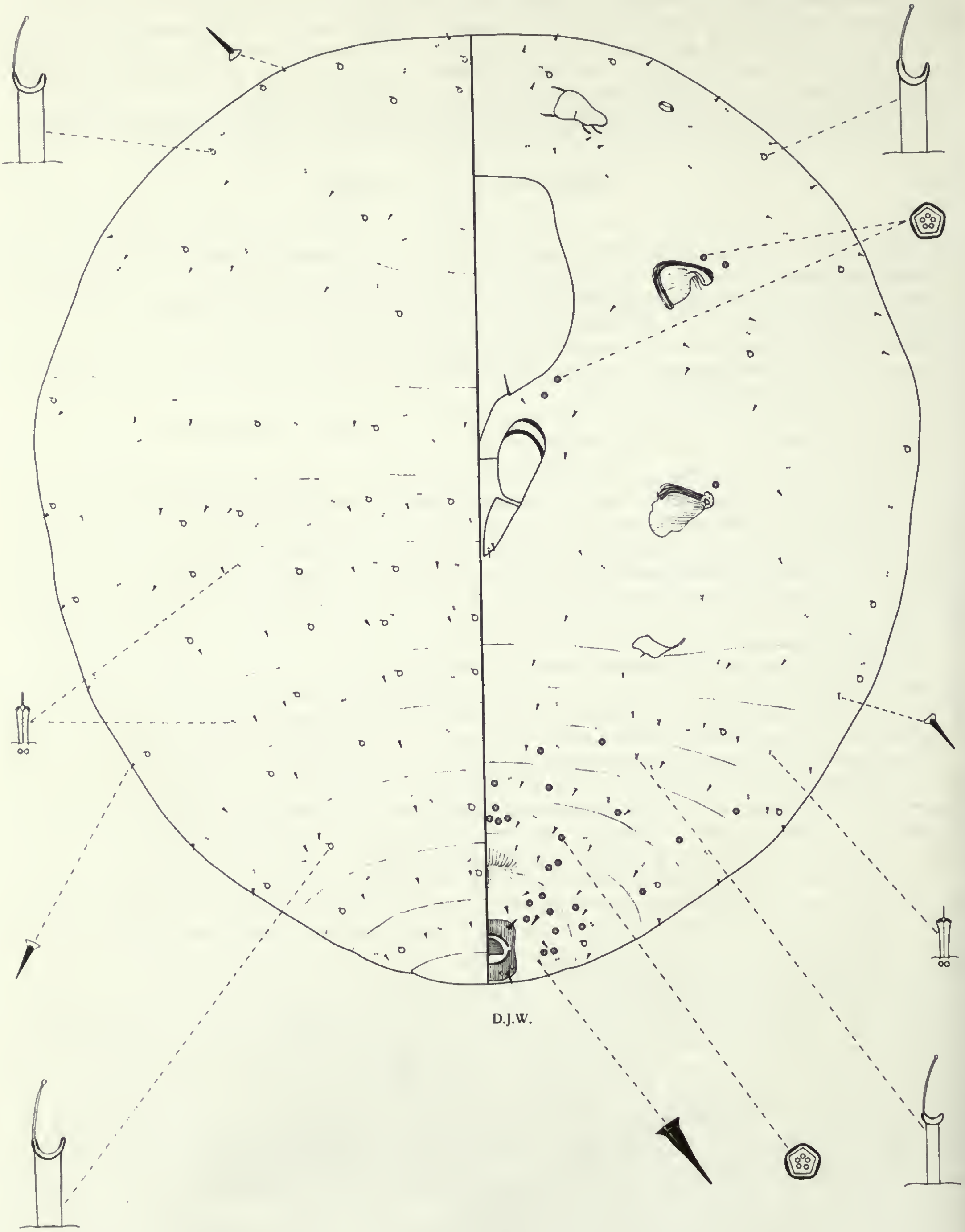

Fig. 1 *Cryptococcus fagisuga* Lindinger. England, Buckinghamshire, Burnham Beeches, on *Fagus sylvatica*.

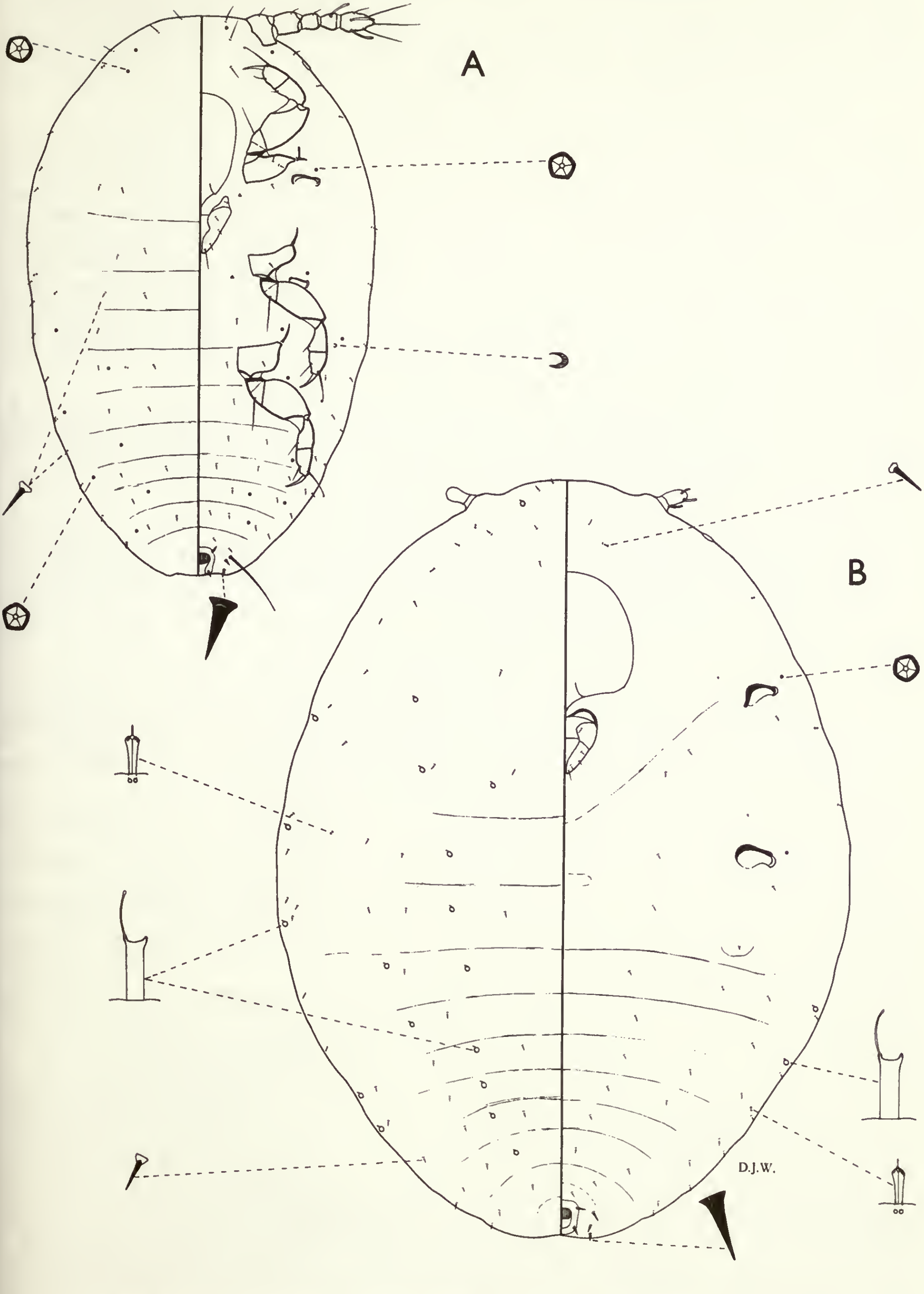

Fig. 2 *Cryptococcus fagisuga* Lindinger. (A) First instar. (B) Second instar.

represented at most by one or two varying in position. Quinquelocular disc pores sparse, rarely more than 2 on any segment. Ventral surface with short setae similar to dorsal setae except for apical setae each 40 μm long, larger conical setae lateral to anal lobes, and longer flagellate setae on head. Suranal setae small. Macroducts and microducts absent. Quinquelocular pores few in submarginal areas of abdomen and head and singly near spiracular openings. One or two pores medially to first and second coxa often trilocular, but this condition not constant. A minute indefinite scar present lateral to third coxae.

MATERIAL EXAMINED (all on *Fagus sylvatica* unless stated otherwise)

England: Berkshire, Silwood Park, 5.v.1948, 17.iii.1950, 29.v.1959 (*K. L. Boratynski*), Cookham, 4.iv.1973, 11.viii.1983 (*D. J. Williams*); Buckinghamshire, Burnham Beeches, 18.iii.1973, 1, 4, 15, 23.iv.1973 (*D. J. Williams*); Cheshire, nr Chester, 1890 (*R. Newstead*), Ince, xi.1895 (*R. Newstead*); Hampshire, Bolderwood, 29.iii.1975 (*J. H. Martin*); Kent, Malling, ix.1895 (*E. E. Green*), Bearsted, 27.vii.1913 (*E. E. Green*), nr Canterbury, 19.v.1973 (*L. M. Hanford*); London, Buckingham Palace Gardens, 8.x.1963 (*K. L. Boratynski*); Northumberland, Riding Mill, 8.x.1950 (*D. J. Williams*); Shropshire, 1.xi.1933 (*E. E. Edwards*); Suffolk, xi.1970; Surrey, Camberley, 25.v.1920, 10.iv.1930 (*E. E. Green*), Wisley, 4.vii.1954 (*D. J. Williams*); Yorkshire, Bingley, 10.x.1933 (*G. Fox-Wilson*), Hardcastle Crags, 22.viii.1961 (*D. J. Williams*). **Scotland:** Aberdeen, iv.1924 (*G. D. Morison*). **Luxembourg:** Beaufort, 29.vi.1961 (*K. L. Boratynski*). **Hungary:** Nagymilis Laszlotanya, 12.viii.1980 (*F. Kozár & M. Kosztarab*). **U.S.A.:** Vermont, on *F. grandifolia*, 8.v.1975.

DISCUSSION. When discussing the homonymy of *Coccus fagi*, Lindinger (1936) referred to Roemer (1789) who gave an illustration. The first 32 plates of this work are a re-issue of those in Sulzer (1776) where on Plate XI, fig. 11 there is an illustration in colour of *C. fagi*. This seems to be *Eulecanium tiliae* (L.) as present understood.

C. fagisuga is always parthenogenetic insofar as males have never been found.

Although Walker made numerous slide preparations of aphids, there is no evidence that he made any slide preparations of the scale insects that he described. A batch of dry material mounted on a card labelled *Coccus fagi* in Walker's handwriting is present in BMNH. This is here regarded as Walker's original material and among 9 specimens prepared on separate microscope slides one has been selected as lectotype. The other 8 are labelled paralectotypes.

ERIOCOCCUS Targioni Tozzetti

Eriococcus Targioni Tozzetti, 1868: 726. Type-species: *Coccus buxi* Fonscolombe, by subsequent designation (Signoret, 1872: 429) and by Opinion 1203 (Melville, 1982: 95).

Gossyparia Signoret, 1875: 20. Type-species: *Coccus ulmi* Linnaeus sensu Linnaeus, 1766 [= *Coccus spurius* Modeer, 1778.], by original designation. [Synonymised by Ferris, 1955: 94.]

Acanthococcus Signoret, 1875: 35. Type-species: *Acanthococcus aceris* Signoret, by monotypy and by Opinion 1203 (Melville, 1982: 95). [Synonymised by Ferris, 1955: 94.]

Rhizococcus Signoret, 1875: 36. Type-species: *Rhizococcus gnidii* Signoret, by monotypy. [Synonymised by Ferris, 1955: 94.]

Greenisca Borchsenius, 1948: 502. Type-species: *Eriococcus inermis* Green, by original designation. **Syn. n.**

Anophococcus Balachowsky, 1954: 61. Type-species: *Eriococcus inermis* Green, by original designation. [Synonymised with *Acanthococcus* Signoret by Danzig, 1980: 205.]

Kaweckia Koteja & Żak-Ogaza, 1981: 501. Type-species: *Eriococcus glyceriae* Green, by original designation. **Syn. n.**

Eriococcus Targioni Tozzetti; Melville, 1982: 95. [Addition to Official List, Name Number 2153.]

Acanthococcus Signoret; Melville, 1982: 95. [Addition to Official List, Name Number 2154.]

Although in time it may be necessary to recognise some of the genera synonymised above, they are here regarded as components of *Eriococcus* pending further research on the family and until the characters of microducts, frontal lobes and tubercles can be assessed on a world basis. As Ferris (1955) has mentioned, division of the group seems undesirable (except for extreme forms) until comprehensive studies have been made, especially of the Australian fauna. Some reasons for the synonymy need explanation, however.

Eriococcus. This genus was separated by Borchsenius (1948, 1949) because the type-species possesses enlarged ducts. As already stated, some Australian species possess these ducts and their true significance is not yet known. The type-species also has well-developed frontal lobes, slender microducts with bifid orifice and only a single ventral seta on the anal lobes. Borchsenius based his interpretation of the type-species on Russian specimens which do not appear to be identical with specimens from the type-locality in France.

Acanthococcus. The most important characters separating the type-species from *Eriococcus* are the absence of enlarged ducts and the presence of 2 ventral setae instead of one on the anal lobes and 2 pairs of setae on the basal segment of the labium instead of a single pair. Frontal lobes are well developed and the microducts are slender with bifid orifice. At present there seems to be no reason for recognising the genus.

Gossyparia. Based on the type-species, this is almost a replica of *Acanthococcus* but lacks dorsal macroducts in the median areas of the dorsum, regarded here as nothing more than a specific character. There are well-developed frontal lobes and the microducts are slender with bifid orifice.

Rhizococcus. The genus was separated from *Acanthococcus* originally because, in the type-species, the antennae had 7 segments instead of 6 and because the body was presumed to be naked. It is now known that a normal ovisac is produced and the antennae may have either 6 or 7 segments. Other characters present are frontal tubercles instead of frontal lobes and slender microducts with bifid orifice. With our present knowledge the genus is not distinctive enough from *Eriococcus.*

Greenisca. There are nomenclatural problems concerning the type-species. According to Danzig (1962) the species on which Borchsenius (1948) based *Greenisca* was not *E. inermis* Green but another species, which Danzig (1980) stated, was later described as *Anophococcus gouxi* Balachowsky; the type-species, therefore, of *Greenisca* should be *A. gouxi* Balachowsky, 1954 = *E. inermis* Green sensu Borchsenius 1948. Article 70 of the *International Code of Zoological Nomenclature* states that 'if a zoologist considers that a type-species designated for a new genus has been misidentified, then that person should refer the case to the Commission to designate as the type-species whichever species will in its judgement best serve stability and uniformity of nomenclature . . .' Furthermore, the anal lobes of *G. gouxi* illustrated by Danzig (1980) have three enlarged setae but the same species illustrated by Balachowsky (1954) has the outer seta much reduced in size. *E. inermis* Green has a minute outer seta on the anal lobes, frontal tubercles and microducts without bifid orifice. Based on this type-species the genus *Greenisca* is here regarded as a component of *Eriococcus.* If *Anophococcus gouxi* is accepted as the type-species, a species with dorsal disc pores, there may be some justification for recognising the genus but until the significance of dorsal disc pores is better understood, the species is here regarded as belonging to *Eriococcus.*

Kaweckia. The type-species has numerous cruciform pores and disc pores on the dorsum and the numbers of dorsal enlarged setae are restricted to the margins of the posterior abdominal segments. Other characters are frontal tubercles and microducts without a bifid orifice. At present there seems to be little justification for accepting this genus and it is here regarded as a component of *Eriococcus.*

Although the type-species of *Eriococcus, Acanthococcus* and *Rhizococcus* are not British species they are described here to help facilitate identification and to assess the characters. The following key is presented to separate the British indigenous and introduced species.

Key to British species of *Eriococcus*

1 Enlarged setae on abdomen confined to inner edges of dorsum of anal lobes only. Outer dorsal setae on anal lobes much smaller 2
– Enlarged setae on abdomen on at least a few segments anterior to anal lobes. Outer dorsal setae on anal lobes same type as inner setae 3
2 Disc pores of quinquelocular type present on dorsum of body. Enlarged setae present on head margins .... **placidus** Green (p. 376)
– Disc pores on dorsum absent. Enlarged setae absent on head margins .... **inermis** Green (p. 370)
3 Enlarged setae in bands across head, thoracic and most abdominal segments 4
– Enlarged setae on margins only except for a few occasionally on head 9
4 Anal lobes with 4 enlarged setae .... **cantium** sp. n. (p. 363)
– Anal lobes with 3 enlarged setae 5
5 Enlarged setae in median areas of posterior abdominal segments much smaller than others on dorsum .... **munroi** (Boratynski) (p. 374)
– Enlarged setae in median areas of posterior abdominal segments same size as others on dorsum 6
6 Dorsal macroducts in bands across segments 7
– Dorsal macroducts absent in mid-regions of thorax and abdomen .... **spurius** (Modeer) (p. 380)
7 With at least 2 setae in mid-dorsal area of anal lobe segment .... **lagerstroemiae** Kuwana (p. 374)
– Without setae in mid-dorsal area of anal lobe segment 8
8 Body elongate-oval. Dorsal setae sharply pointed. Frontal tubercles present **greeni** Newstead (p. 367)
– Body broadly oval. Dorsal setae truncate. Frontal lobes present .... **devoniensis** (Green) (p. 365)

9 Dorsal enlarged setae truncate, with almost parallel sides, on margins only of 7th and two or three preceding segments, in addition to anal lobe setae. Dorsal disc pores present. Dorsal cruciform pores present .... ***glyceriae*** Green (p. 367)

– Dorsal enlarged setae conical, either truncate or bluntly pointed, in a continuous row around margins. Dorsal disc pores absent. Dorsal cruciform pores absent 10

10 Margins of 7th abdominal segment each with 4 enlarged marginal setae. All dorsal setae except marginal, minute and about same length .... ***insignis*** Newstead (p. 372)

– Margins of 7th abdominal segment each with 3 enlarged marginal setae. Dorsal setae, excluding marginal, noticeably longer on head and thorax than on posterior abdominal segments .... ***pseudinsignis*** Green (p. 378)

Eriococcus aceris (Signoret)

(Fig. 3)

Acanthococcus aceris Signoret, 1875: 35; Borchsenius, 1949: 347; Danzig, 1964: 632; Tereznikova, 1981: 15. Syntypes ♀, Savoie and Austria: on *Acer campestre* (probably lost).
Eriococcus aceris (Signoret) Cockerell, 1896: 323; Schmutterer, 1952: 406.
Nidularia aceris (Signoret) Lindinger, 1933: 108.

Description. Adult female on slide broadly oval, largest specimens 3·75 mm long, 2·2 mm wide. Surface of body strongly nodulose. Anal lobes protruding, about twice as long as wide, apically rounded, moderately sclerotised with inner margins conspicuously nodulose, each lobe with apical seta 200 μm long, two inner dorsal enlarged setae and one outer enlarged seta situated towards mid-dorsum; ventral setae flagellate, one subapical, one at outer base and suranal seta longest but shorter than anal ring setae. Dorsal plate triangular, lightly sclerotised, strongly nodulose. Antennae 6- or 7-segmented, 250–330 μm long. Frontal lobes developed but smaller than basal antennal segment. Legs normal, well developed. Trochanter + femur 180–220 μm long, tibia 110–140 μm long, tarsus about 150 μm long, the tibia + tarsus always longer than trochanter + femur, claw 35 μm long, stout and curved with denticle near apex. Coxa without translucent pores but with spicules. Labium 160–170 μm long, shorter than clypeolabral shield, basal segment with 2 pairs of setae. Anal ring with 8 setae, each about 150 μm long.

Dorsal surface with numerous enlarged setae of two main sizes, but all with more or less straight sides tapering gradually to a truncate tip, in profile curved and bluntly thorn-like. The largest setae 50 μm long on margins of posterior segments, the shortest, which are the most numerous, about 28 μm long. Macrotubular ducts of one size, 30 μm long, tapering to orifice, the cup wider than base of a dorsal seta, evenly distributed. Microducts about 10 μm long, elongate, each with orifice bifid, evenly distributed.

Ventral surface with normal flagellate setae in median areas, short, slender but stiff in lateral areas. Macrotubular ducts of three sizes. A large type similar to dorsal ducts on margins of abdomen. A smaller type about half width of large type, not numerous, in more or less single rows on abdominal segments and around submargins to head. A small type about half as wide again as the medium-sized ducts in small numbers across abdominal segments. Microducts absent. Disc pores predominantly quinquelocular but occasional pores present that have 6 or 7 loculi; in bands across the abdominal segments, around margins to head and on mid-venter. Cruciform pores present in a wide submarginal band from head to about fourth abdominal segment.

Material examined

Austria: Weidling, on *Acer campestre.* **Germany:** Baden, on *A. campestre,* 24.v.1916 (*H. Wünn*); Munich, on *A. platanoides,* 26.v.1951 (*H. Schmutterer*), Erlangen, 6.vi.1949 (*H. Schmutterer*). **Switzerland:** Valais, on *A. campestre*, 20.viii.1906.

Discussion. No original material has been traced. The specimens from Austria, one of the type-localities, are from the Naturhistorisches Museum, Vienna, identified by F. Löw, and the specimens from Switzerland are from the collection of P. Marchal. There seems to be no doubt about the identity of the species now recognised as such by many modern workers.

Eriococcus buxi (Fonscolombe)

(Fig. 4)

Coccus buxi Fonscolombe, 1834: 218. Syntypes ♀, France: Aix[-en-Provence] (probably lost).
Eriococcus buxi (Fonscolombe) Targioni Tozzetti, 1868: 726; Fernald, 1903: 72.
Nidularia buxi (Fonscolombe) Lindinger, 1933: 108.

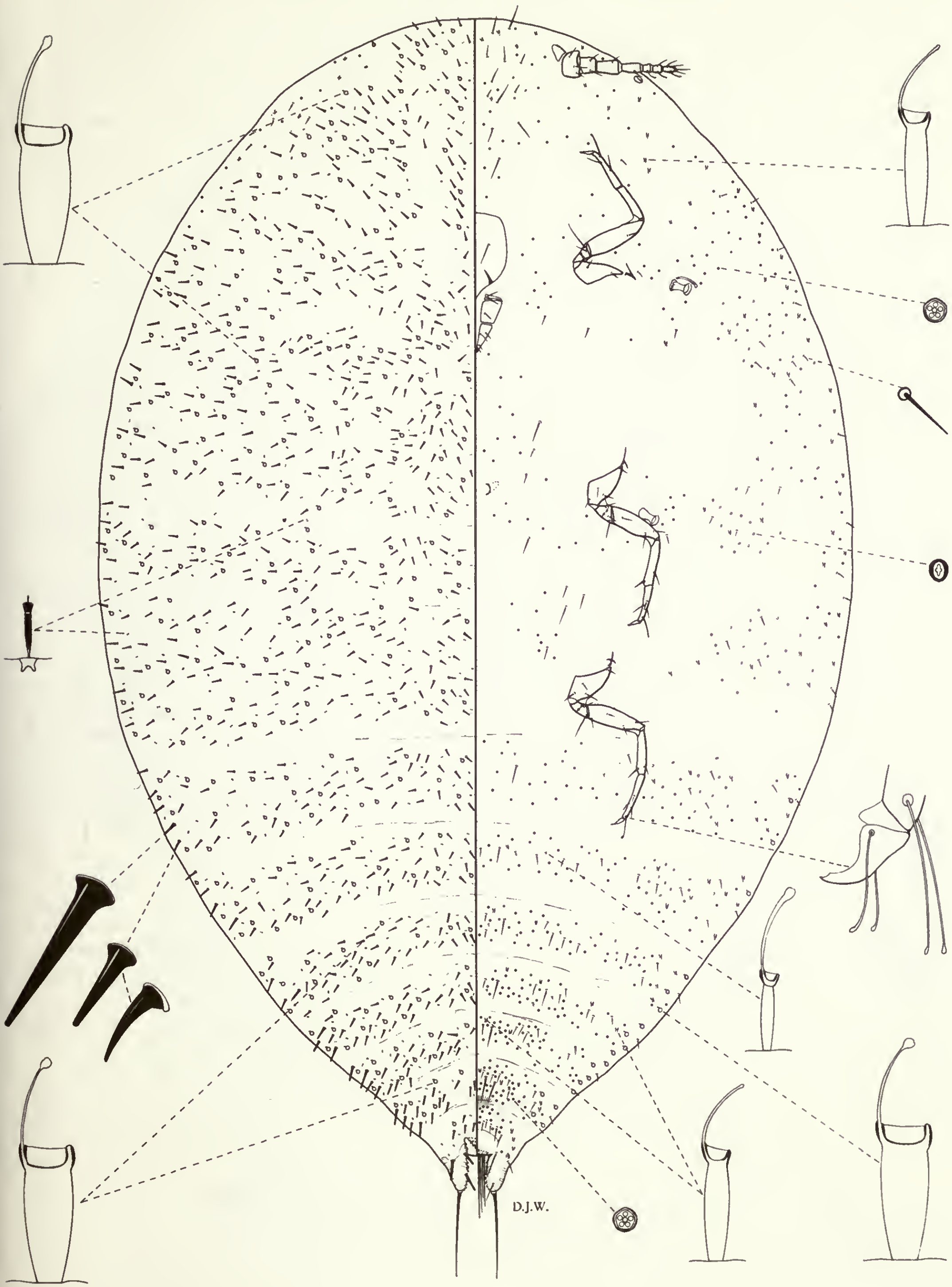

Fig. 3 *Eriococcus aceris* Signoret. Germany, Erlangen.

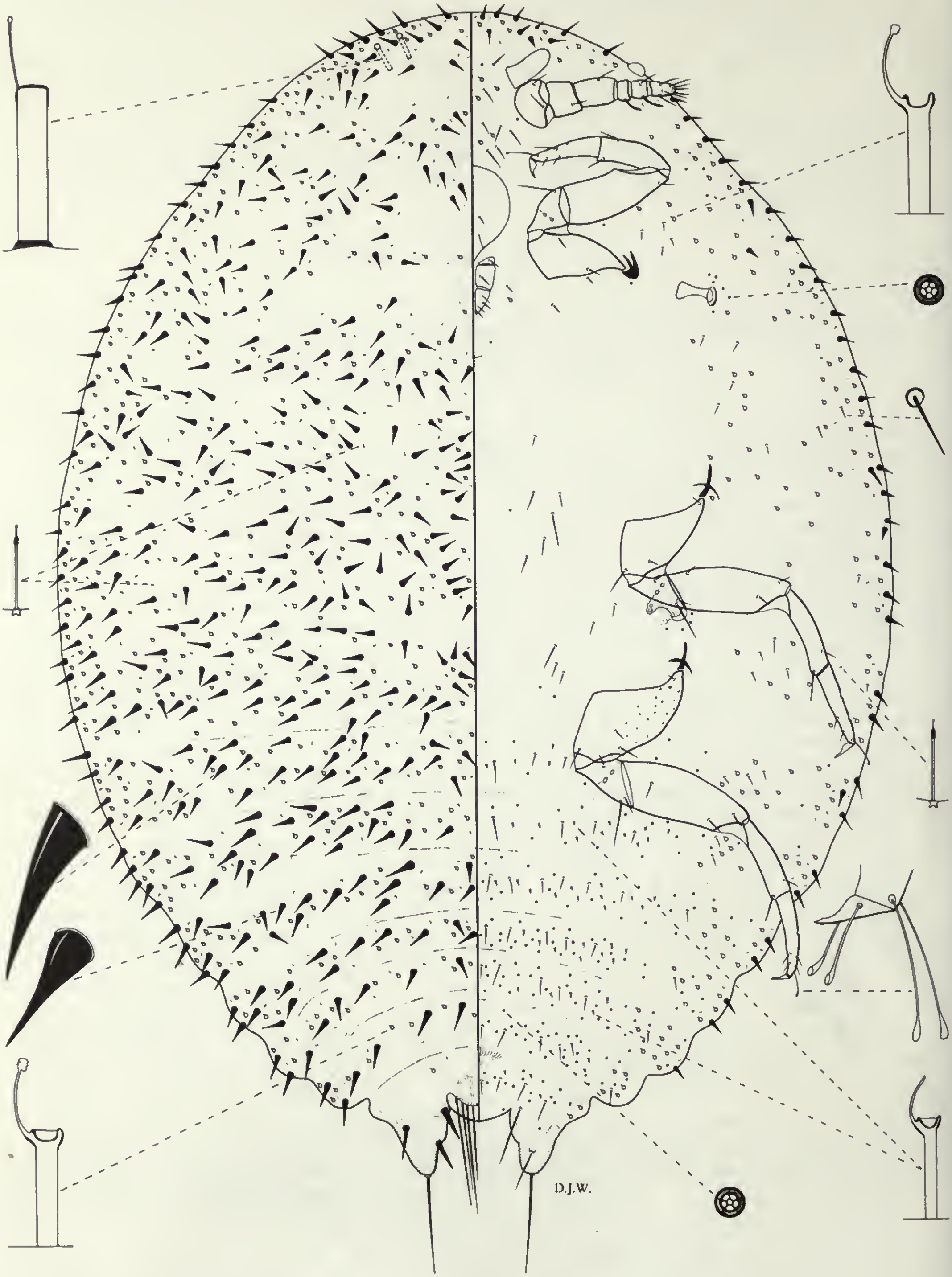

Fig. 4 *Eriococcus buxi* (Fonscolombe). France, Orange, on *Buxus sempervirens*.

Description. Adult female broadly oval, largest specimens 1·9 mm long, 1·35 mm wide, not nodulose. Anal lobes about twice as long as wide, conical, each lobe with an apical seta 140 μm long. Dorsally with an outer enlarged conical seta situated submarginally rather than on edge, and 2 inner enlarged setae. Ventrally with a single slender seta and a suranal seta shorter than anal ring setae. Dorsal plate only lightly sclerotised, rounded. Anal ring with 8 setae, each about 110 μm long. Antennae 160–175 μm long, with 6 segments. Frontal lobes well developed, about as long as width of basal antennal segment. Legs robust, hind trochanter + femur 170–190 μm long, hind tibia 80–90 μm long, hind tarsus 80–90 μm long, the tibia + tarsus either same length as trochanter + femur or slightly shorter, claw 25 μm long, straight, with a minute denticle near apex. Hind coxa with a few small translucent pores. Labium 80 μm long, shorter than clypeolabral shield, basal segment with a single pair of setae.

Dorsal surface densely covered with enlarged setae, lanceolate, 32–52 μm long, pointed, the sides concave but curved in profile and thorn-like. Macroducts of one size, evenly distributed, each about 20 μm long, the cup about two-thirds width of diameter of setal base of a dorsal seta, the inner end of filament small and barely perceptible. Enlarged ducts present, each 35 μm long, the sides almost parallel, with inner end flat and rim of orifice sclerotised, but in profile thicker towards one side; present either singly or sometimes in pairs on head margin where there are 2–4 present at most. Microducts in a regular arrangement, each about 12 μm long, very slender, the sides parallel, with orifice widely bifid.

Ventral surface with normal slender setae in median areas. In submarginal areas the setae are shorter, stiff and blunt. Enlarged setae, same as on dorsum, around margins only. Macroducts of two sizes. A larger type, same as dorsal macroducts, numerous in a wide zone around margins and submargins, on thorax reaching to spiracles, and on head occupying area between clypeolabral shield and antennal bases. A narrower type on abdomen only, in transverse rows or bands across median areas of segments. Microducts, same as on dorsum, around margins only. Cruciform pores absent. Disc pores of quinquelocular type, numerous across abdominal segments almost to margins, occasional pores present in median areas of thorax and head and around spiracular openings.

Material examined (all on *Buxus sempervirens*)

France: 'south' (det. Signoret); Lyons, 20.vi.1932 (*L. Goux*); Orange, 15.iv.1978 (*D. Matile-Ferrero & D. J. Williams*). **Switzerland:** Rolle, ix.1906 (*P. Marchal*), others labelled ex coll. P. Marchal.

Discussion. The most important characters are the dorsal setae 32–52 μm long, the dorsal macroducts about half width of setal base of dorsal seta, the enlarged ducts on head only and the lateral enlarged seta on anal lobes submarginal.

There seems to be no doubt about the identity of this species, even though the original material cannot be traced. The species was described from Aix-en-Provence and the specimens at hand collected in Orange, and from Lyons not far from the type-locality, are considered by French workers to be this species. A further specimen is available from material collected in the south of France and this was identified by V. Signoret as *E. buxi*.

Eriococcus sp. near ***buxi*** (Fonscolombe)

(Fig. 5)

Description. Body of adult female on slide, broadly oval, membranous, not nodulose, largest specimens 2·3 mm long, 1·3 mm wide. Anal lobes sclerotised, conical, pointed, about twice as long as wide at base, each lobe with an apical seta 180 μm long; dorsally with 1 outer enlarged seta on groove on edge and 2 lateral enlarged setae; ventrally with 1 slender seta and a suranal seta shorter than anal ring setae. Dorsal plate projecting slightly, rounded. Anal ring with 8 setae, each about 185 μm long. Antennae 150–210 μm long, 6-segmented. Frontal lobes lightly sclerotised at tip, elongate, sometimes twice as long as width of basal antennal segment. Legs well developed, hind trochanter + femur 160–190 μm long, hind tibia 80–95 μm long, hind tarsus 80–95 μm long, the tibia + tarsus either same length as trochanter + femur, or slightly longer, claw straight, 25 μm long, with a minute denticle, near apex. Hind coxa with a few translucent pores. Labium 80–95 μm long, shorter than clypeolabral shield, basal segment with 1 pair of setae.

Dorsal surface with numerous enlarged setae, evenly distributed, each seta broadly lanceolate, pointed, 25–45 μm long, curved in profile. Groups of these setae usually present submarginally on mid-head region, behind eyes, on prothorax, 1st and 7th abdominal segments, each group associated with a single enlarged duct or sometimes 2, each duct 40 μm long with inner end flat and with sclerotised rim raised from surrounding integument. Other enlarged ducts sometimes present on submargins without the groups of setae, up to 17 marginal ducts present in some specimens and others present on midline, varying in number but there is usually one on mesothorax and another on 1st abdominal segment. Macroducts of one size, numerous, evenly distributed each duct about 25 μm long, with a clear circular rim surrounding orifice, the

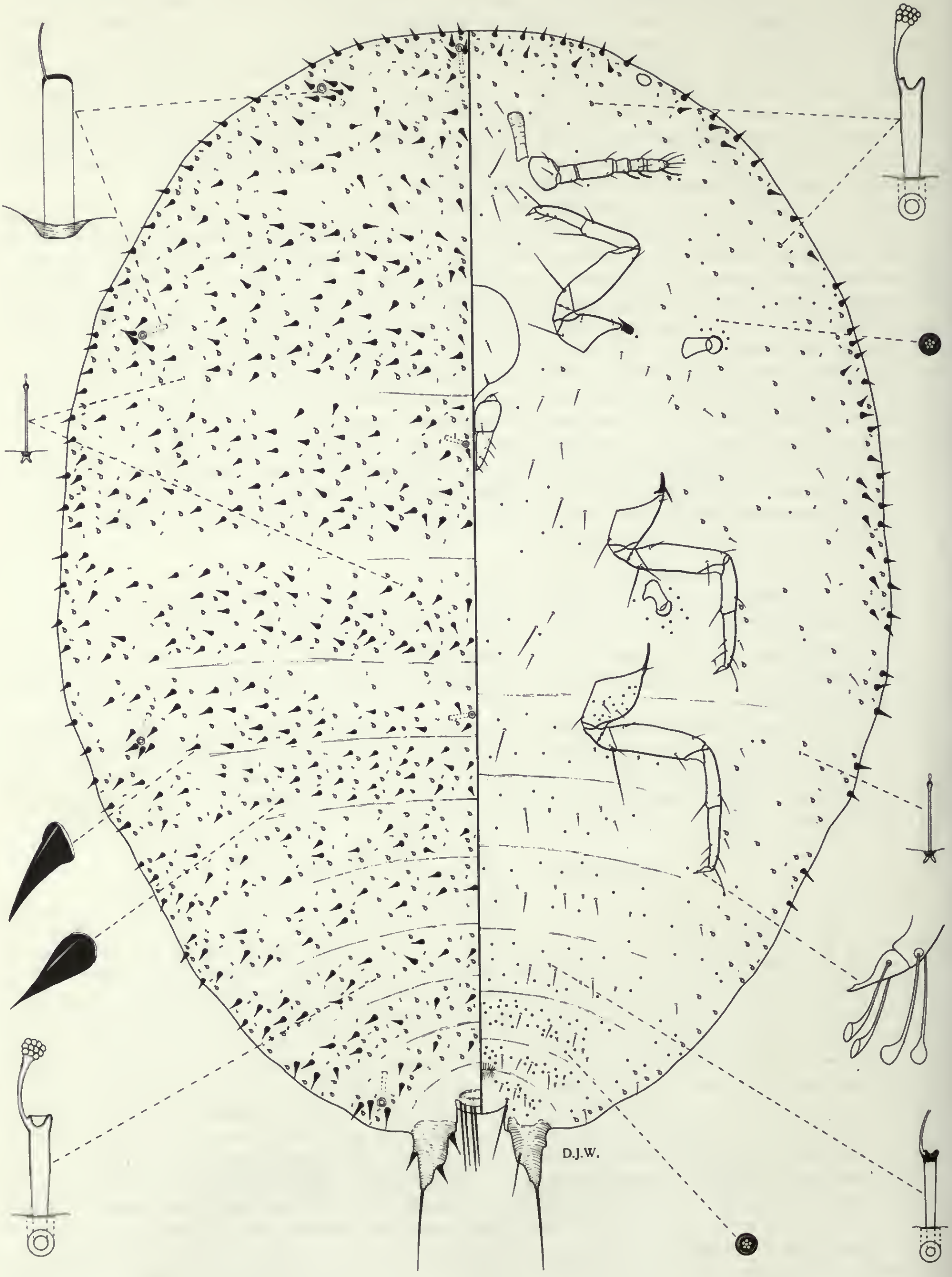

Fig. 5 *Eriococcus* sp. near *buxi* (Fonscolombe). U.S.S.R., Crimea, on *Buxus* sp.

cup about half width of setal base of a dorsal seta, the inner end of filament resembling a bunch of grapes. Microducts numerous, each about 12 μm long, slender, with parallel sides and with orifice widely bifid.

Ventral surface with normal slender setae in median areas and laterally towards margins. Enlarged setae same as on dorsum, around margins. Macroducts of two sizes. A large type, same size as dorsal ducts, present around margins and submargins, reaching to spiracles. A narrower type, not numerous in median areas of abdomen only, each duct with a distinct rim around orifice. Microducts on margins, same shape as on dorsum. Quinquelocular pores numerous on abdomen where they almost reach margins; others present in median areas of head and thorax and around spiracular openings, those next to first spiracle extending to margin. Cruciform pores absent.

MATERIAL EXAMINED

U.S.S.R.: Crimea, Massandra, on *Buxus* sp., 24.vii.1951 (*T. Bustchik*). **Turkey:** Gerede, on *B. sempervirens*, 13.vii.1970.

DISCUSSION. The large number of submarginal enlarged ducts, many surrounded by groups of setae, and other ducts on the midline, easily distinguish this species from *E. buxi*. Specimens from Crimea have the dorsal setae 25–40 μm long and noticeably shorter than those in *E. buxi*; in Turkish specimens, although 28–45 μm long, these setae are still shorter than in *E. buxi*. The position of the lateral enlarged seta on each anal lobe is always marginal, whereas in *E. buxi* this seta is displaced slightly to dorsum. Another main difference is the size of a dorsal macroduct, which in this species has the cup about half the width of a setal base, but in *E. buxi* it is about two-thirds the width. Furthermore, the dorsal ducts have a conspicuous rim around the orifice.

There is every indication that this species is new but for the moment it is left un-named pending further research by workers in U.S.S.R. It seems certain that it is the same as that described by Borchsenius (1949) and Tereznikova (1981) as *E. buxi*.

Eriococcus cantium sp. n.

(Fig. 6)

DESCRIPTION. Adult female, when prepared on microscope slides, elongate-oval with almost parallel sides, 2·6 mm long and 1·00 mm wide, nodulose. Anal lobes about twice as long as wide, moderately sclerotised. Each lobe with an apical seta 300 μm long, dorsally with 1 inner and 3 outer enlarged setae and ventrally with 2 slender setae and a slender suranal seta shorter than anal ring setae. Dorsal plate not prominent, rounded, nodulose. Antennae 7-segmented, 300 μm long. Frontal tubercle present, just anterior to basal antennal segment. Legs well developed, hind trochanter + femur 250 μm long, hind tibia 150 μm long, hind tarsus 160 μm long, claw curved 40 μm long, with a denticle near apex. Hind coxa with minute translucent pores on outer half and hind femur with a small group on mid-anterior margin. Labium 100 μm long, slightly shorter than clypeolabral shield and basal segment with 2 pairs of setae. Anal ring with 8 setae.

Dorsal surface with enlarged conical setae, pointed, 35–75 μm long, in bands across the segments. On 7th segment medially a group of 4–5 present and on 6th segment a similar group present but this merging with lateral setae. Macroducts of one size, about 25 μm long, the cup narrower than setal bases of largest setae, fairly evenly distributed across segments. Microducts not numerous, each about 4 μm long, with short collar, ampulla and swollen inner end to tube.

Ventral surface with normal slender setae in median areas. Enlarged setae, same as on dorsum, on margins of head, thorax and anterior abdominal segments, but submarginally a few setae that are more slender but stiff. Macroducts of two sizes; a larger type, same size as on dorsum, around margins and a narrower type in transverse rows on abdominal segments, and in median to submarginal areas of thorax and head. Microducts in small numbers on margins. Disc pores of quinquelocular type numerous across abdominal segments, in median areas of thorax and head and near spiracles. Cruciform pores present in small numbers in a narrow submarginal zone from about 5th abdominal segment forward to head.

Holotype ♀, **England:** Kent, Bearsted, on *Brachypodium sylvaticum* (Poaceae), 30.vii.1925 (*E. E. Green*) (BMNH).

Paratype. **England:** 1 ♀, same data as holotype (BMNH).

DISCUSSION. This species is close to *E. greeni* in having a similar distribution of enlarged dorsal setae. It differs, however, in possessing groups of 4–6 setae in the median areas of the seventh and sixth segments whereas in *E. greeni* these groups usually possess only 2 or at most 3 setae. The median group of setae on the sixth segment of *E. cantium* is not so differentiated and is almost continuous with the lateral setae. Furthermore there are three lateral setae on each anal lobe whereas in *E. greeni* there are only two.

The name is the Latin word for the county of Kent, and is used as a noun in apposition.

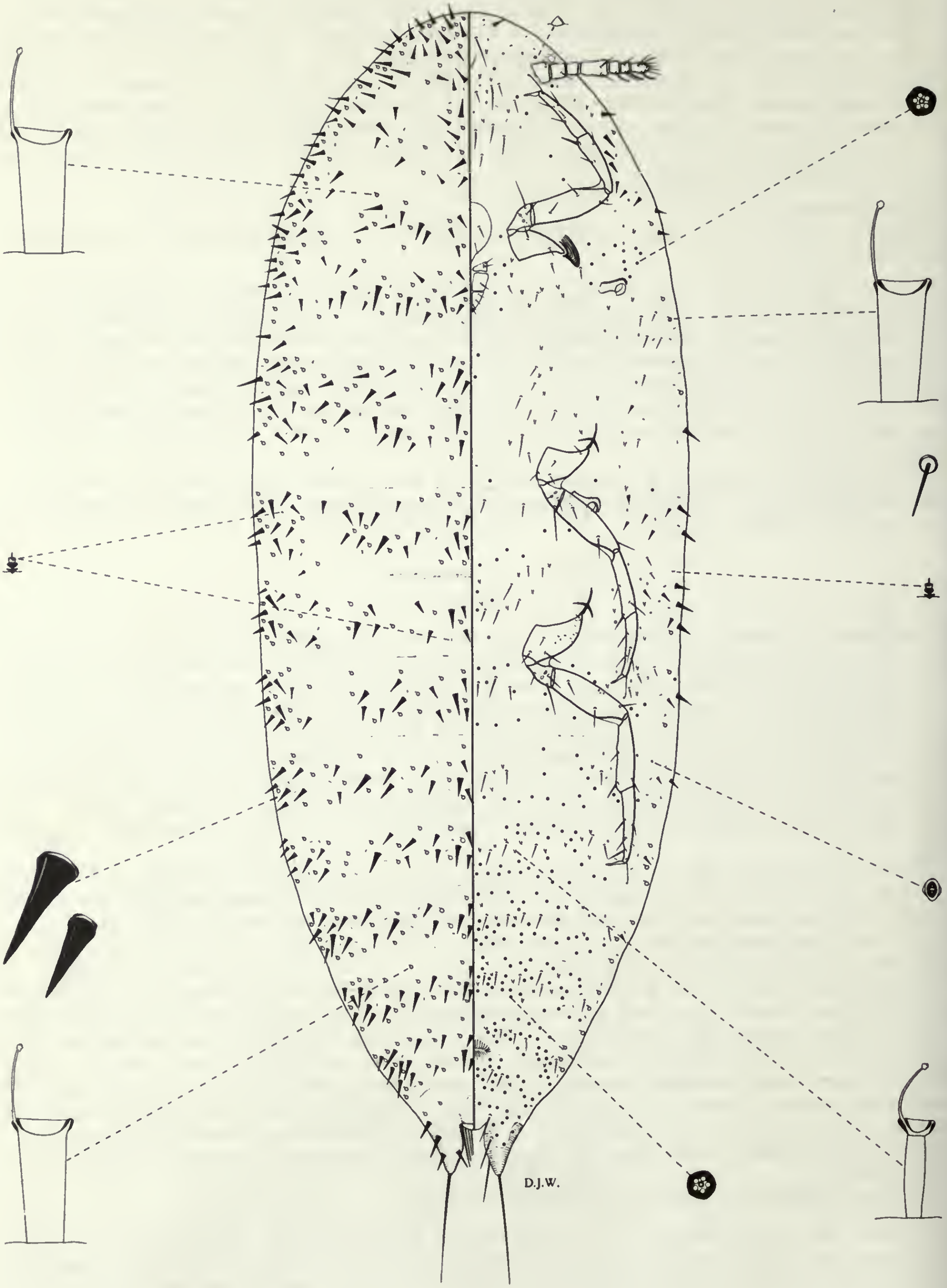

Fig. 6 *Eriococcus cantium* sp. n. England, Kent, Bearsted, on *Brachypodium sylvaticum*.

Eriococcus devoniensis (Green) comb. rev.

(Fig. 7)

Rhizococcus devoniensis Green, 1896: 260. LECTOTYPE ♀, England (BMNH), here designated [examined].
Eriococcus devoniensis (Green) Cockerell, 1897: 589; Newstead, 1903: 201; Schmutterer, 1952: 413.
Acanthococcus devoniensis (Green) Borchsenius, 1949: 337.

Description. A broadly oval species, attaining a length of 2·0 mm and a width of 1·3 mm, body nodulose. Anal lobes sclerotised, rather wide and pointed, triangular, about as wide as long at base in older specimens, but conical and rounded in young specimens. Each lobe with an apical seta 180 μm long and dorsally 2 inner submarginal enlarged setae and 1 outer marginal seta. Ventrally each lobe with 2 slender setae and a suranal seta shorter than anal ring setae. Dorsal plate poorly developed, rounded. Anal ring with 8 setae, each 100 μm long. Antennae 190–210 μm long, 7-segmented. Frontal lobes conspicuous and larger than a basal antennal segment. Legs well developed. Hind trochanter + femur 180–200 μm long, hind tibia 100–115 μm long, hind tarsus 110–120 μm long, the tibia + tarsus longer than trochanter + femur, claw stout and curved, 30 μm long, with a denticle near apex. Hind coxa with a few noticeable translucent pores and hind femur with a few on anterior edge. Labium 130–150 μm long, usually slightly shorter than clypeolabral shield, basal segment with 2 pairs of setae.

Dorsal surface with an even distribution of enlarged setae of various sizes, 28–40 μm long, each truncate, the sides straight or only slightly concave, and tapering gradually. Macroducts of one size, about 20 μm long, the cup about same size or smaller than diameter of setal base of largest setae, fairly numerous. Microducts each about 4 μm long, with ampulla, inner end of tube swollen, but without internal collar, opening to exterior with minute orifice, in moderate numbers over entire surface.

Ventral surface with normal slender setae in median areas and enlarged setae similar to those on dorsum, in a marginal zone, on thorax, reaching almost to spiracles. Macroducts of two sizes. A large type, same as those on dorsum, in a marginal zone, interspersed with the enlarged setae. A narrower type present across median areas of abdominal segments and in groups in median areas of thorax and head. Microducts few, on margins only. Disc pores predominantly quinquelocular, numerous on abdomen and present in median areas of thorax and around spiracles. Cruciform pores few, in submargins of head and thorax.

Material examined (all on *Erica tetralix* unless stated otherwise)

England: Devon, Budleigh Salterton, ix.1896 (lectotype), 20.ix.1896 (*E. E. Green*), Sherbrook, 18.viii.1896; Surrey, Camberley, 11.iv.1922, vii.1914, ix.1914, xi.1929 (*E. E. Green*), 10.vi.1959 (*D. J. Williams*); Durham, Waldridge Fell, vi.1950, 16.viii.1960 (*D. J. Williams*); Yorkshire, Hawkesworth, 12.viii.1960, Levisham, 27.viii.1959, Goathland, 25.viii.1959 (all *D. J. Williams*), Ickornshaw Moor, 29.viii.1948 (*A. Smith*), Shipley Glen, 25.viii.1984 (*N. B. Pungerl*). **Ireland:** Kerry, Mt Mangerton, in sphagnum, viii.1943 (*R. S. Bagnall*). **Austria:** Lunz, on *E. carnea*. **Germany:** Ratzeburg. **Corsica:** Vizzavone Forest, on *E. arborea*, 1.xi.1930 (*A. Balachowsky*).

Discussion. Green's original slide contains three specimens, and the lectotype selected is clearly marked. The two other specimens are here designated paralectotypes.

Although Green described this insect originally on *Erica cinerea* he (Green, 1917) corrected the misidentification of the host-plant to *E. tetralix* and the insect seems to be restricted to this plant in Britain, even when other species of *Erica* are growing next to it. It distorts the stems at the point of feeding, so much so that stems may curl in a circle enclosing the insect in the middle as illustrated in colour by Newstead (1903). Specimens are at hand from Corsica collected on *E. arborea* and the record led Green (1931) to correct an early impression that *E. tetralix* was the only host-plant. There are unconfirmed records on *E. cinerea* and *Calluna* by Goux (1934) and on *C. vulgaris* by Balachowsky (1937).

Apart from the British records already listed, Harrison (1916*a*, 1916*b*, 1918, 1948, 1949) has recorded it from Northumberland, Durham and Yorkshire, and from western Scotland including the Isle of Rhum and Benbecula, Ronay and Grimsay in the Outer Hebrides. Other records include those of Green (1917) from Cheshire and Green (1923) from Aberdeenshire, while Killington (1936) recorded it from Hampshire.

The species is found throughout Europe as far north as Sweden and may be present throughout the Palaearctic region wherever *E. tetralix* is found.

Fig. 7 *Eriococcus devoniensis* (Green). England, Durham, Waldridge Fell, on *Erica tetralix*.

Eriococcus glyceriae Green **comb. rev.**

(Fig. 8)

Eriococcus glyceriae Green, 1921: 146; Schmutterer, 1952: 410. LECTOTYPE ♀, England (BMNH), here designated [examined].
Nidularia glyceriae (Green) Lindinger, 1933: 116.
Greenisca glyceriae (Green) Borchsenius, 1949: 368; Danzig, 1964: 634; Danzig, 1980: 228; Tereznikova, 1981: 52.
Kaweckia glyceriae (Green) Koteja & Żak-Ogaza, 1981: 506.

Description. Body elongate-oval, largest specimens 3·4 mm long, 1·7 mm wide, membranous throughout, not nodulose. Anal lobes either membranous or faintly sclerotised, each lobe about as long as wide, with an apical seta 140 μm long and dorsally 2 inner and 1 outer truncate setae and one ventral seta that is flagellate and situated towards outer margin. Suranal setae slender and flagellate, shorter than anal ring setae. Antennae 7-segmented, 220–230 μm long. Frontal tubercle present just anterior to each basal antennal segment. Legs well developed, hind trochanter + femur 180 μm long, hind tibia 110 μm long, hind tarsus 110–120 μm long, the tibia + tarsus always longer than trochanter + femur, claw 35 μm long, curved with minute denticle near apex. Hind coxa with proximal edge indistinct, translucent pores numerous, a few extending on to surrounding integument at base. Labium 85–100 μm long, shorter than clypeolabral shield, basal segment with 2 pairs of setae. Spiracles heavily sclerotised, this sclerotisation completely surrounding atrium. Dorsal plate membranous in form of a narrow rounded lobe.

Dorsal surface with enlarged setae on 5th and posterior segments only except for an occasional seta on 4th segment, few, on margins, each seta with almost parallel sides, truncate, 15–25 μm long. Other dorsal setae slender, often curved but stiff, with blunt tip 12–20 μm long. Macroducts of two sizes, the largest about 16–20 μm long with the cup about same diameter as an enlarged setal base, in bands across the segments except on anal lobe segment where they are replaced by a narrower type. Microducts minute, about 6 μm long, with ampulla, swollen inner end to tube and an inner collar, few, across the posterior abdominal segments and around the margins to head. Disc pores, usually with 7 loculi, in more or less single rows at anterior edges of segments. Cruciform pores present in wide bands across median areas of second abdominal segment and forward to mesothorax; a few others present in lateral areas of these segments, on third abdominal segment and on prothorax.

Ventral surface with normal setae in median areas, replaced by shorter stiff setae, similar to those on dorsum, around margins of thorax and anterior abdominal segments. Macroducts, of the large type, similar to those on dorsum, on margins only. A narrower type in moderate numbers across abdominal segments, in median areas of thorax and head and reaching to submargins of thorax. Microducts as on dorsum, few, on margins. Cruciform pores restricted to a few only on margins of prothorax and head. Disc pores, usually with 7 loculi, but occasionally with more or fewer loculi at anterior and posterior edges of 5th and posterior segments, at anterior edges of anterior abdominal segments, in median area of thorax and in a zone around thoracic margins to head.

Material examined

England: Norfolk, Blakeney Point, on *Glyceria maritima* (now *Puccinellia maritima*), vii.1920 (*E. E. Green*) (lectotype), ix.1920 (*N. E. Brenchley*). **Hungary:** Zicsiujfalu, on *Agropyron* sp., 8.ix.1981 (*F. Kozár*). **U.S.S.R.:** Odessa, on *A. repens (A. Kiritshenko)*.

Discussion. The lectotype is here designated from three specimens on the same slide and clearly indicated. The two other specimens are labelled paralectotypes.

Although this species has concentrations of cruciform pores on the mid-dorsum and rather heavily sclerotised spiracles, these characters are probably of specific significance only and the species seems to be congeneric with the type-species. Specimens available from eastern Europe tend to have the enlarged setae with slightly concave sides.

Eriococcus greeni Newstead **comb. rev.**

(Fig. 9)

Eriococcus greeni Newstead, 1898: 96; Newstead, 1903: 200. LECTOTYPE ♀, England (BMNH), here designated [examined].
Acanthococcus greeni (Newstead) Borchsenius, 1949: 340; Danzig, 1975: 71; 1980: 212; Tereznikova, 1981: 27.

Description. An elongate-oval species, attaining a length of 3·0 mm and a width of 1·6 mm, body

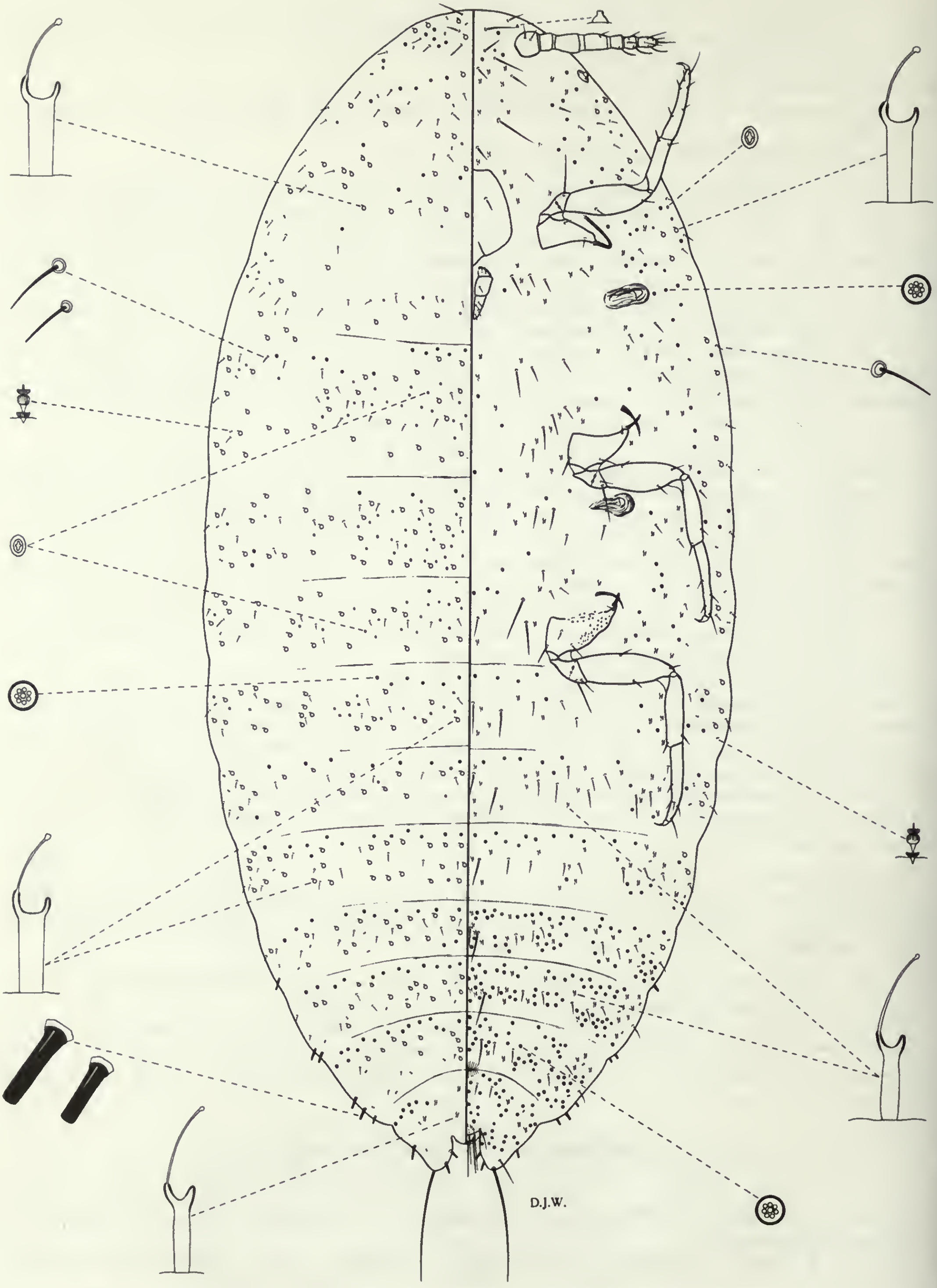

Fig. 8 *Eriococcus glyceriae* Green. England, Norfolk, Blakeney Point, on *Puccinellia maritima*.

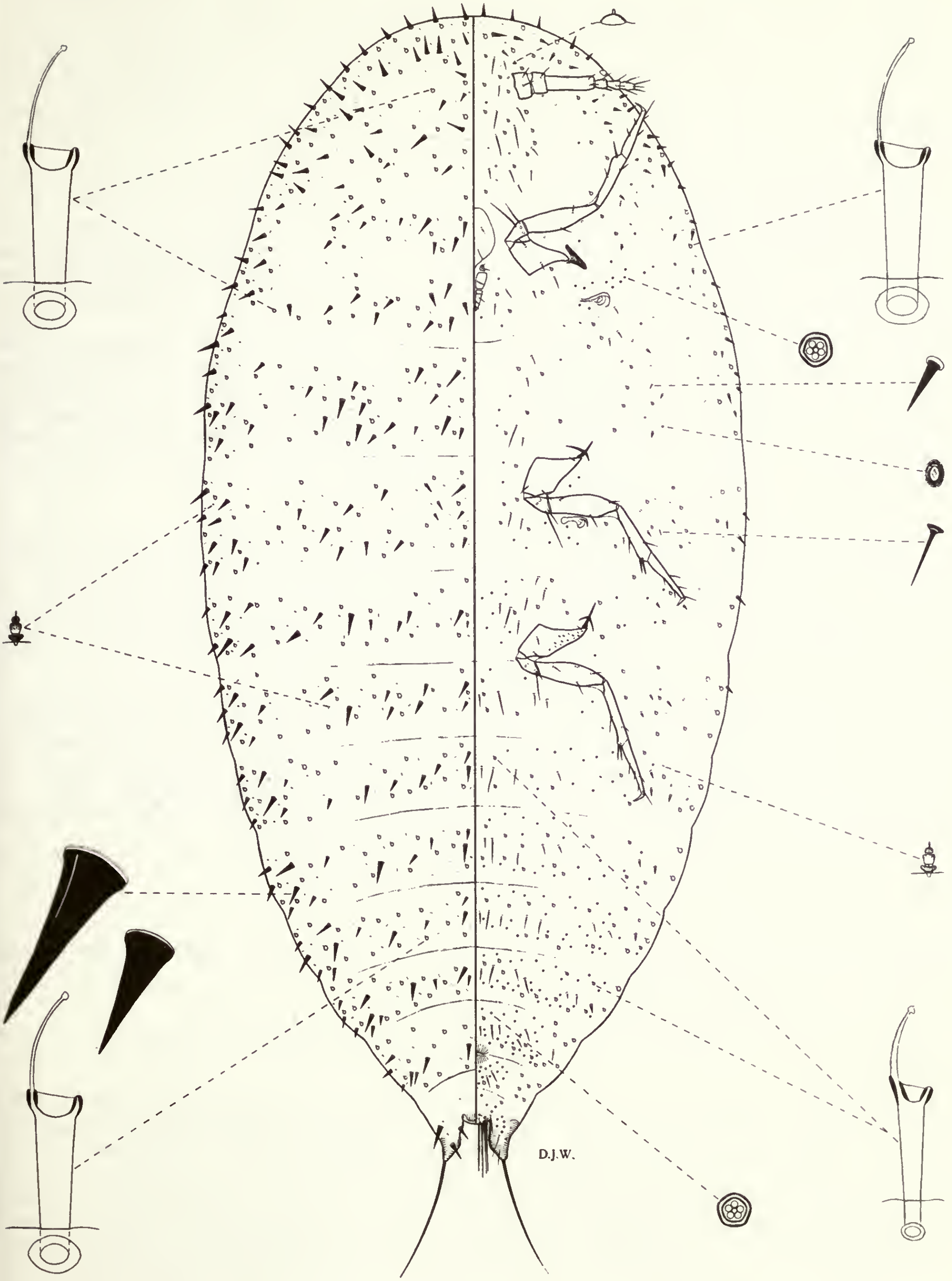

Fig. 9 *Eriococcus greeni* Newstead. England, Surrey, Camberley, on grass.

nodulose. Anal lobes about twice as long as wide, conical, tending to be pointed, moderately sclerotised. Each lobe with an apical seta 380 μm long and dorsally with 1 outer and 2 inner enlarged setae and ventrally with 2 slender setae and a slender suranal seta much shorter than anal ring setae. Dorsal plate sclerotised, moderately developed, rounded but nodulose. Anal ring with 8 setae each about 140 μm long. Antennae 280–300 μm long, with 6 or 7 segments. Frontal tubercle present just anterior to basal segment. Legs well developed. Hind trochanter + femur 240–270 μm long, hind tibia 150–170 μm long, hind tarsus 150–170 μm long, tibia + tarsus always longer than trochanter + femur. Claw curved, 35 μm long, with a minute denticle near apex. Hind coxa with translucent pores on outer half and hind femur with a small group on mid-anterior edge. Labium 110–120 μm long, shorter than clypeolabral shield.

Dorsal surface with pointed conical setae 30–70 μm long, the sizes in a haphazard arrangement but there are always some of the longest in the marginal groups. On the mid-dorsum of 7th abdominal segment, there is usually a group of 2 such setae, rarely 3, and a similar group is present on the mid-dorsum of 6th abdominal segment. Macroducts in a regular distribution, of one type, about 25 μm long, the cup smaller than diameter of setal base of largest setae, tapering gradually, the orifice usually surrounded by a pale oval area. Microducts about 4 μm long, each with ampulla, swollen inner end to tube and an internal collar, evenly distributed.

Ventral surface with normal slender setae in median areas, marginally with a few enlarged setae similar to dorsal setae, submarginally with more slender but stiff setae. Macroducts of two sizes. A large type, same as on dorsum, in small numbers around margins. A narrower type in bands across abdominal segments, in median areas of thorax and head, extending in submargins almost to marginal macroducts. Microducts not numerous, in a marginal zone from anterior abdominal segments to head. Quinquelocular pores numerous on abdomen, in median areas of thorax and around spiracles. Cruciform pores few, in submarginal areas only of head, thorax and first few abdominal segments.

MATERIAL EXAMINED

England: Devon, Budleigh Salterton, on grass, 20.ix.1896 (*E. E. Green*) (lectotype); Somerset, Minehead, on grass, ix.1920 (*E. E. Green*), Cheddar, vii.1926 (*E. E. Green*); Surrey, Camberley, 31.viii.1914, ix.1914, 25.ix.1934, Hog's Back, 21.vii.1922, on grass (all *E. E. Green*); Kent, Thurnham, on grass, 15.ix.1926 (*E. E. Green*); Berkshire, Silwood Park, on *Festuca* sp., *Deschampsia caespitosa*, 27.x.1948, on grass 19.viii.1948 (all *K. L. Boratynski*); Yorkshire, Hawkesworth, on grass, 20.viii.1961 (*D. J. Williams*). **Scotland:** E. Lothian, Gullane, on grass, viii.1925 (*E. E. Green*).

DISCUSSION. The lectotype designated is the only original specimen seen. In all specimens there is always a group of 2 large setae on the mid-dorsum of the 7th abdominal segment or rarely with a small seta forming a group of 3. Furthermore, there is always a median group of setae on the 6th segment. These characters separate it from *R. cantium* herein described as new, a species that has a group of 4 on the mid-dorsum of the 7th segment and with the setae on the mid-dorsum of 6th segment not forming a distinct group.

Green (1923, 1926, 1928) recorded this species also from Sea View, Isle of Wight; Bearsted, Kent; Yately, Hampshire; and from Monument Hill in East Lothian (Haddington).

Eriococcus inermis Green **comb. rev.**

(Fig. 10)

Eriococcus inermis Green, 1915: 176. LECTOTYPE ♀, ENGLAND (BMNH), here designated [examined].
Nidularia inermis (Green) Lindinger, 1933: 116.
Greenisca inermis (Green) Borchsenius, 1948: 502; 1949: 367.
Anophococcus inermis (Green) Balachowsky, 1954: 61.
Rhizococcus inermis (Green) Danzig, 1962: 854; 1964: 634; Dziedicka & Koteja, 1971: 576.
Acanthococcus inermis (Green) Danzig, 1975: 64; 1980: 226.

DESCRIPTION. Body of adult female not nodulose, elongate-oval, anterior end rounded, sides at times subparallel, largest specimens 2·5 mm long, 1·5 mm wide. Anal lobes about twice as long as wide, pointed. Each lobe with an apical seta 180 μm long, dorsally with 2 inner enlarged conical setae, the anterior usually the larger, about 28 μm long, the posterior about 24 μm long, and a minute outer seta near base; ventrally with 2 slender setae and a suranal seta shorter than anal ring setae. Dorsal plate rounded, lightly sclerotised. Anal ring with 8 setae each 130 μm long. Antennae 150–210 μm long, 6-segmented. Frontal tubercle present just anterior to basal antennal segment. Legs well developed, hind trochanter + femur 140–170 μm long, hind tibia 90–110 μm long, hind tarsus 110–130 μm long, the tibia + tarsus conspicuously longer than trochanter + femur, claw curved, 30 μm long, with a denticle near apex. Hind coxa with a few large translucent pores on outer half and hind femur sometimes with one or two on anterior edge. Labium 95–110 μm long, shorter than clypeolabral shield, basal segment with 2 pairs of setae.

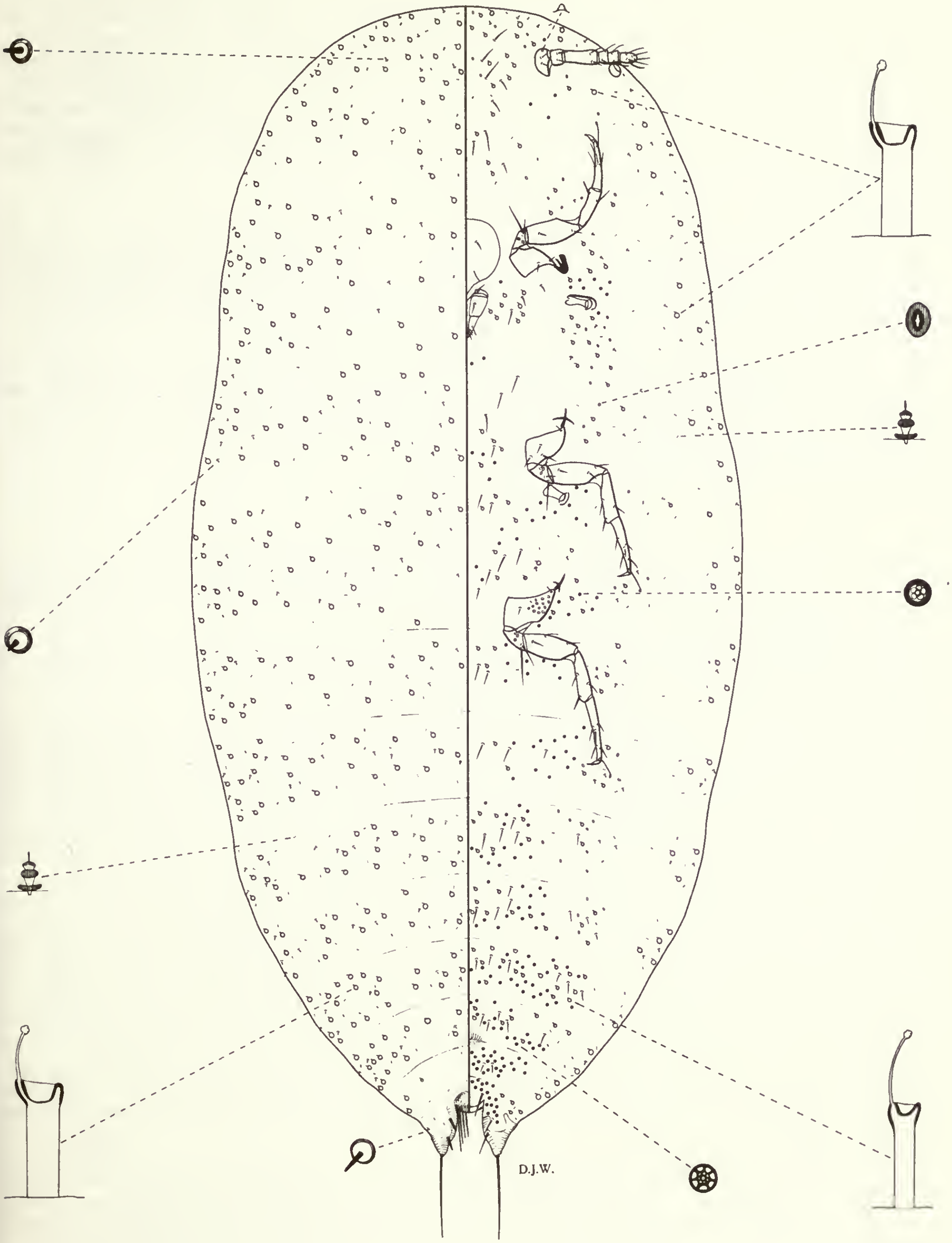

Fig. 10 *Eriococcus inermis* Green. England, Surrey, Camberley, on grass.

Dorsal surface with minute bluntly pointed setae, most scarcely longer than diameter of setal base and some appreciably shorter, in moderate numbers across segments. Macroducts evenly distributed, each about 20 µm long with cup nearly twice diameter of a dorsal setal base. Microducts each about 4 µm long, with ampulla, tube with inner end swollen, and an internal collar, in moderate numbers over surface.

Ventral surface with slender setae in median areas and minute setae, similar to those on dorsum, around margins and submargins. Macroducts of two sizes. A larger type, the same as dorsal ducts, on margins only. A narrower type in median areas as far forward as head margins. Disc pores varying in size, numerous on abdomen where, on the posterior segments, many have 7 or occasionally more loculi but anteriorly on the abdomen, the median area of thorax and around the spiracles, they are quinquelocular. Cruciform pores present in a submedian zone from head to about 5th abdominal segment.

MATERIAL EXAMINED

England: Surrey; Camberley, on grass, ix.1914 (*E. E. Green*) (lectotype, paralectotypes), 15.iv.1922, 1.x.1925, on *Festuca ovina*, ix.1929 (*E. E. Green*); Somerset, Cheddar, viii.1926 on *F. ovina* (*E. E. Green*); Berkshire, Silwood Park, on *F. ovina, Deschampsia flexuosa* 1948–1956 (various dates) (*K. L. Boratynski*); Yorkshire, Steeton Moor, 29.viii.1948 (*A. Smith*), Hawkesworth, on grass, 20.viii.1961 (*D. J. Williams*); Durham, Waldridge Fell, on grass, 17.vii.1960 (*D. J. Williams*).

DISCUSSION. The original material comprises 12 specimens, six on each of two slides, one labelled 'type' and the other labelled 'co-type'. The lectotype has been selected from the slide labelled 'type' and is clearly marked, the remaining 11 specimens are labelled paralectotypes.

The distribution at present also includes France, western U.S.S.R. and the far eastern area of U.S.S.R. It will probably be found throughout the Palaearctic Region.

Eriococcus insignis Newstead **comb. rev.**

(Fig. 11)

Eriococcus insignis Newstead, 1891: 164; 1903: 198. LECTOTYPE ♀, ENGLAND (BMNH), here designated [examined].

Nidularia insignis (Newstead) Lindinger, 1933: 116.

Rhizococcus insignis (Newstead) Borchsenius, 1949: 357; Danzig, 1962: 841; 1964: 633; Dziedicka & Koteja, 1971: 561.

Acanthococcus insignis (Newstead) Danzig, 1975: 64; Tereznikova, 1981: 29.

DESCRIPTION. Body of adult female elongate-oval, the sides often subparallel, nodulose, largest specimens 2·9 mm long and 1·2 mm wide. Anal lobes conical, pointed, about twice as long as wide, moderately sclerotised. Each lobe with an apical seta 280–320 µm long, on the dorsum 1 outer and 2 inner enlarged setae, on the venter 2 slender setae and a suranal setae shorter than anal ring setae. Dorsal plate rounded, narrow, sometimes nodulose and lightly sclerotised. Anal ring with 8 setae, each 135 µm long. Antennae 200–270 µm long with 7 segments. Legs well developed, hind trochanter + femur 200–250 µm long, hind tibia 120–160 µm long, hind tarsus 130–150 µm long, the tibia + tarsus always longer than trochanter + femur, claw curved, 35 µm long, with a denticle near apex. Hind coxa with conspicuous translucent pores on outer half. Labium 100 µm long, shorter than clypeolabral shield, basal segment with 2 pairs of setae.

Dorsal surface with a marginal row of enlarged setae 40–65 µm long, each with slightly concave sides. On segments 5–7 these setae are truncate, but anteriorly they are bluntly pointed and on head they extend to submarginal area near midline. The setae on the 7th abdominal segment always number 4. Elsewhere on the dorsum there are small setae in moderate numbers, 6–8 µm long. These vary in thickness on different specimens, even from the same batch, sometimes being quite slender but usually they are slightly conical and often they are thicker on the head and thorax. Despite these differences they vary little in length. Macroducts of one size, evenly distributed, about 25 µm long, cup narrower than a setal base of a marginal seta. Microducts in an even distribution, each about 4 µm long with ampulla, tube with swollen inner end, and an internal collar.

Ventral surface with normal slender setae in median areas, a few enlarged setae on head margin and stiff setae in a marginal zone from head to anterior abdominal segments, these setae usually larger than the small dorsal setae but smaller than dorsal marginal setae. Macroducts of two sizes. A larger type, same as on dorsum around margins, and a narrower type in median areas, extending laterally almost to marginal macroducts. Microducts few, around margins only. Disc pores usually with 7 loculi, fairly numerous across abdominal segments, but not reaching margins, also present in median areas of thorax and head and around spiracular openings. Cruciform pores in a narrow submarginal zone around entire body, not numerous.

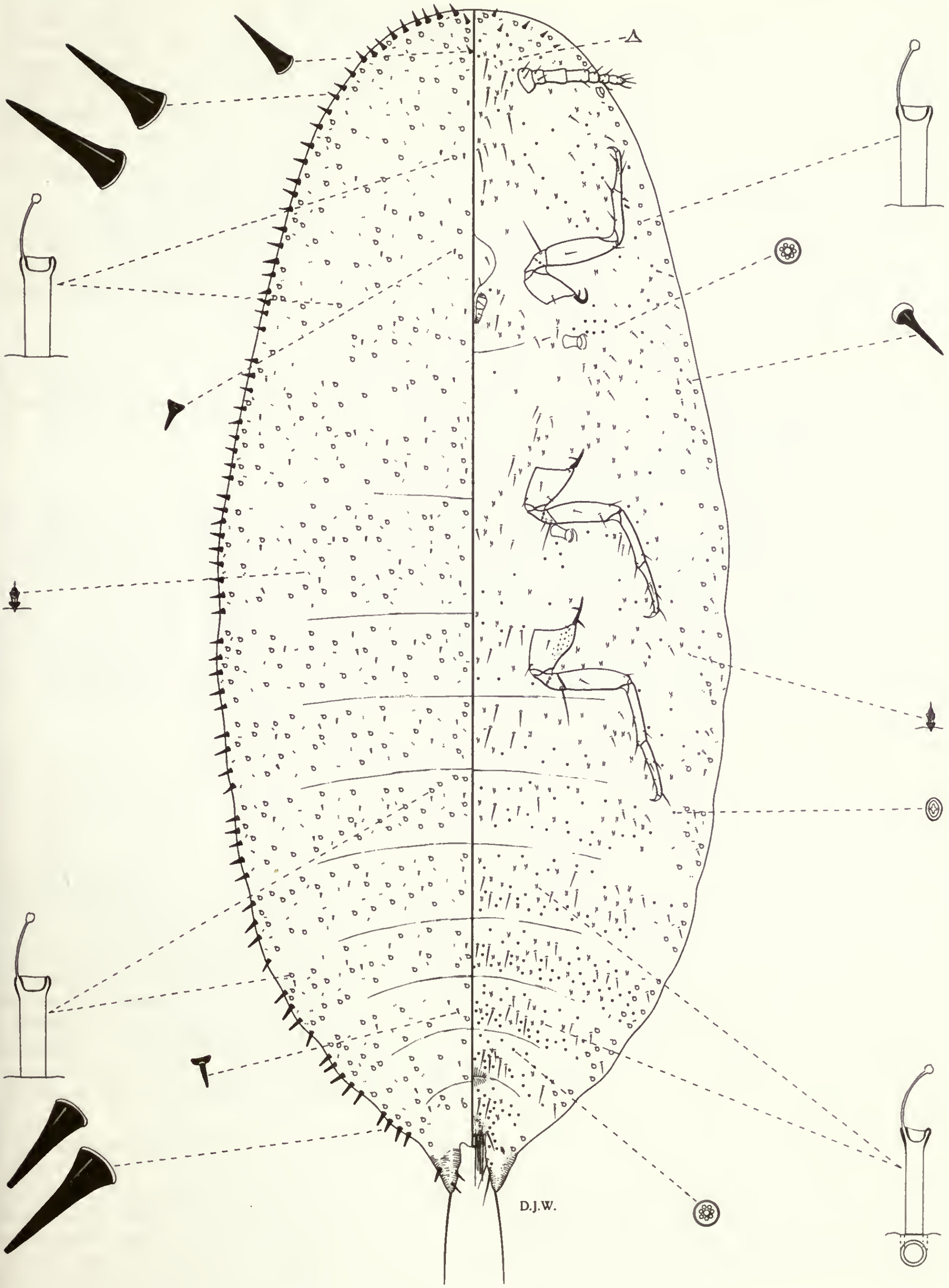

Fig. 11 *Eriococcus insignis* Newstead. England, Surrey, Camberley, on grass.

MATERIAL EXAMINED

England: Cheshire, Ince, on *Agrostis* sp., 1890 (lectotype, paralectotypes); Surrey, Camberley, 1914–1934 (various dates), on *Hypericum* sp., ix.1923, Wisley, ix.1915, Box Hill, 26.ix.1921; Sussex, Arundel, ix.1914; Kent, Thurnham, 15.ix.1926; Somerset, Cheddar, viii.1926, on *Brachypodium sylvaticum*, viii.1926, Minehead, ix.1920; Warwickshire, Morton Paddocks, 14.viii.1920 (*R. Newstead*); Devon, Budleigh Salterton, 10, 20.ix.1896; Yorkshire, Goathland, 25.viii.1959 (*D. J. Williams*). **Scotland:** E. Lothian, Gullane, vii.1925; Argyllshire, Skye, Uig, on grass, 8.ix.1973 (*D. J. Williams*). **Channel Is:** Guernsey, Houmet Homtolle, 9.ix.24; Herm, 13.ix.1924, all on grasses (all *E. E. Green*).

DISCUSSION. The lectotype has been selected and clearly marked, from four specimens on a single slide labelled 'Cotype ♀♀' by Newstead. The three other specimens are labelled paralectotypes.

A discussion of the similarities between this species and *E. pseudinsignis* is given under the latter. At present *E. insignis* may be identified by the presence of 4 marginal setae on each side of the seventh abdominal segment instead of 3 in *E. pseudinsignis*.

Literature records for Britain include those of Green (1915, 1925*b*, 1926, 1928) for Camberley, the Channel Is, Wales (Breconshire) and Cheddar.

Eriococcus lagerstroemiae Kuwana **comb. rev.**

Eriococcus lagerstroemiae Kuwana, 1907: 182; Boratynski & Williams, 1964: 91. Syntypes ♀, JAPAN: Ichijiku and Sarusuberi (IAES).
Nidularia lagerstroemiae (Kuwana) Lindinger, 1933: 116.
Acanthococcus lagerstroemiae (Kuwana) Borchsenius, 1960: 214.

This species was recorded from England by Green (1915) from specimens collected in a nursery garden at St. Albans on *Lagerstroemia* sp., growing in the open. It is not clear if the insects were destroyed at the time. The species has not been recorded from Britain since, but it has been found also in India and China.

No authentic material has been studied for this work, although some specimens are at hand from Japan, Tokyo, on *L. indica* sent by Kuwana to Green. The species is in great need of further study.

Material shows that the species possesses frontal lobes, numerous slender microducts with bifid orifice, and a small group of setae on mid-dorsum of the anal lobe segment. It comes close to *E. aceris* but differs in having the marginal setae, especially those on the posterior segments, not appreciably longer than those on the mid-dorsum. In *E. aceris* the marginal setae are about twice the length of the mid-dorsal setae.

Eriococcus munroi (Boratynski) **comb. n.**

(Fig. 12)

Acanthococcus munroi Boratynski, 1962: 56; Danzig, 1975: 71; 1980: 218; Tereznikova, 1981: 32. Holotype ♀, ENGLAND (BMNH) [examined].

DESCRIPTION. Body of adult female nodulose, elongate-oval, widest at mesothorax, largest specimens 2·1 mm long and 1·5 mm wide. Anal lobes about twice as long as wide, almost conical, sclerotised, each with apical setae up to 300 μm long. Dorsal surface of each lobe with 2 inner enlarged conical setae, the subapical longer than inner and with an outer enlarged seta, the longest, situated slightly on dorsum towards base. Dorsal plate sclerotised, narrow and rounded, the posterior edge with 'teeth' because of the nodulosity. Anal ring with 8 setae each about 125 μm long. Antennae usually 7-segmented, 250–300 μm long. Frontal lobes present just anterior to basal segment. Legs normal, well developed, hind trochanter + femur 220–230 μm long, hind tibia 130–150 μm long, hind tarsus 140–150 μm long, the tibia + tarsus always longer than trochanter + femur, claw curved, 30 μm long with denticle near apex. Hind coxa with a few conspicuous translucent pores. Labium 120 μm long, shorter than clypeolabral shield, basal segment with 2 pairs of setae.

Dorsal surface with enlarged setae, each conical with almost straight sides and with blunt tip, arranged in transverse bands across the segments but absent in the submarginal areas. These setae of various sizes, 30–60 μm long but always with one or two of the large type present in any marginal group. On the median areas of 4th and 5th abdominal segments the conical setae tend to be shorter but the normal conical setae are replaced on the median areas of 6th and 7th abdominal segments by minute conical setae about 6 μm long and rarely longer than the diameter of a setal base, there being usually 4 across the middle of each segment. Macroducts of one size, each about 20 μm long with almost straight sides and with cup narrower than a setal base of an enlarged seta, fairly numerous in wide bands across the segments. Microducts each about 4 μm long with inner end of tube swollen, ampulla and a saucer-shaped inner collar, evenly distributed.

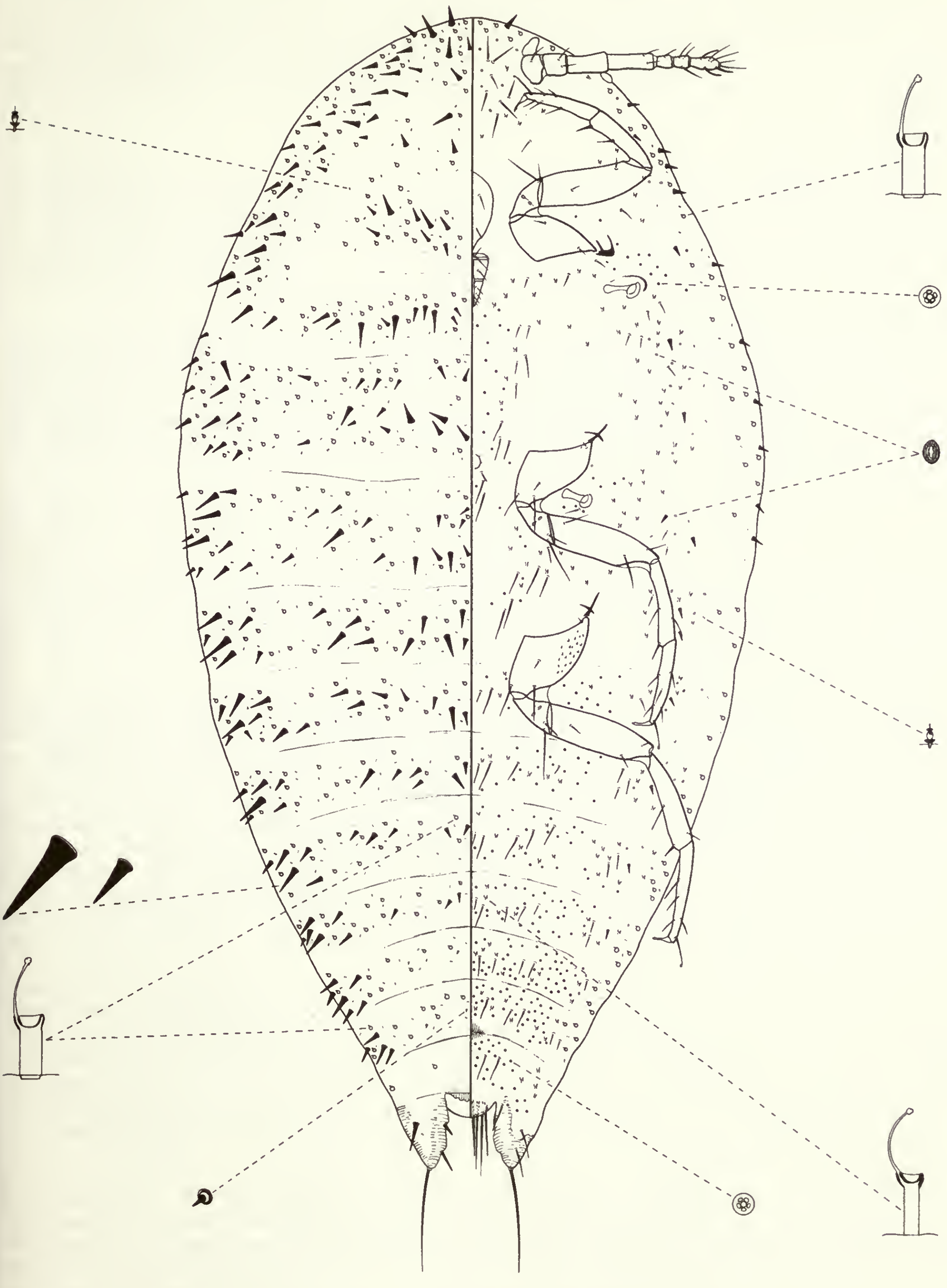

Fig. 12 *Eriococcus munroi* (Boratynski). England, Berkshire, Silwood Park, on *Veronica chamaedrys*.

Ventral surface with normal slender setae in median areas and a few enlarged conical setae on margins and submargins. Macroducts of two sizes. A larger type, similar to dorsal ducts, around margins and a narrower duct in transverse rows on abdominal segments, in median and submarginal areas of thorax and head. Microducts few, around margins only. Cruciform pores not numerous, in submarginal areas of 6th abdominal segment and forward to head. Disc pores, usually quinquelocular, numerous in bands across abdominal segments but not reaching margins, present also in median areas of thorax and around the spiracles.

MATERIAL EXAMINED

England: Berkshire, Silwood Park, on *Achillea millefolium* (Asteraceae), 7.ix.1948 (holotype) and subsequent specimens collected on the same host plant, on *Veronica chamaedrys* (Scrophulariaceae), 1948, 1949 (various dates), on *Deschampsia caespitosa* (Poaceae), 1949, *Chrysanthemum leucanthemum*, 21.vi.1949 and on 'thistle' (Asteraceae), 7.ix.1949 (all *K. L. Boratynski*); Surrey, Camberley, on grass, ix.1914 (*E. E. Green*); Somerset, Cheddar, on *Teucrium scorodoniae* (Lamiaceae); Isle of Man, Port Erin, 27.ix.1918.

DISCUSSION. Boratynski (1962) has given an extended description and an account of the biology of this species. He has also discussed some specimens available labelled ex coll. Manchester Museum, without locality data. These have the enlarged setae wider, shorter and more rounded or almost truncate at the posterior end of body. The single specimen available on *Teucrium scorodonia* has the minute setae on the sixth segment replaced by enlarged setae, and the posterior marginal setae are conspicuously rounded. The extent of variation is still not clear. Since its description the species has been found throughout Europe and the far east of U.S.S.R.

Eriococcus placidus Green comb. rev.

(Fig. 13)

Eriococcus placidus Green, 1915: 148. LECTOTYPE ♀, ENGLAND (BMNH), here designated [examined].
Nidularia placida (Green) Lindinger, 1933: 116.
Greenisca placida (Green) Rasina, 1955: 69; Danzig, 1964: 634.

DESCRIPTION. Body of adult female elongate-oval, not nodulose, largest specimens 3·5 mm long, 1·7 mm wide. Anal lobes conical, pointed, about twice as long as wide, moderately sclerotised, each lobe with an apical seta 220–300 μm long, the dorsum with 2 inner enlarged conical setae, the anterior 36–50 μm long, the posterior usually shorter, 32–40 μm long, and an outer minute seta situated, in most specimens, towards centre. Ventral surface of lobe with 2 slender setae and a slender suranal seta. Dorsal plate moderately developed, lightly sclerotised, outer edge rounded, often nodulose. Anal ring with 8 setae each 145 μm long. Antennae 280–300 μm long, with 7 segments. Frontal tubercles present, minute, just anterior to each basal antennal segment. Labium 100–120 μm long, shorter than clypeolabral shield, basal segment with 2 pairs of setae. Legs well developed, slender, hind trochanter + femur 230–240 μm long, hind tibia 140–150 μm long, hind tarsus 160–170 μm long, claw slightly curved, slender, 40 μm long, with a minute denticle near apex. Hind coxa with conspicuous translucent pores on outer half, hind femur with a small group at mid-anterior margin.

Dorsal surface with two types of setae. Apart from the enlarged setae on anal lobes there are others present about 30 μm long, on head margin in varying numbers but there are usually one or two present. Occasionally these are replaced by slender setae. Elsewhere the dorsum is beset with minute pointed setae scarcely more than 20 μm long, but often shorter, rarely more than twice as long as diameter of a setal base. Macroducts fairly evenly distributed, each about 25 μm long, the cup about 2–3 times as wide as diameter of setal base of a small seta. Microducts in a regular arrangement, each about 6 μm long, with ampulla, tube with inner end swollen, and inner collar. Quinquelocular pores present in single to double rows mainly at anterior and posterior edges of segments, each pore with wide sclerotised rim and about half width of a diameter of cup of macroduct.

Ventral surface with normal slender setae of various sizes. Short stiff setae present, often longer than small dorsal setae, on margins of head, thorax and anterior abdominal segments. Macroducts of two sizes. A larger type, same as on dorsum, around margins. A narrower type present in median to submarginal areas. Microducts apparently absent. Disc pores always smaller than dorsal pores, fairly numerous on abdomen, where on the posterior segments they have usually 7 loculi, but on the anterior abdominal segments, thorax and head they are quinquelocular. Cruciform pores not numerous, in a narrow submarginal zone from about 5th abdominal segment forward to head.

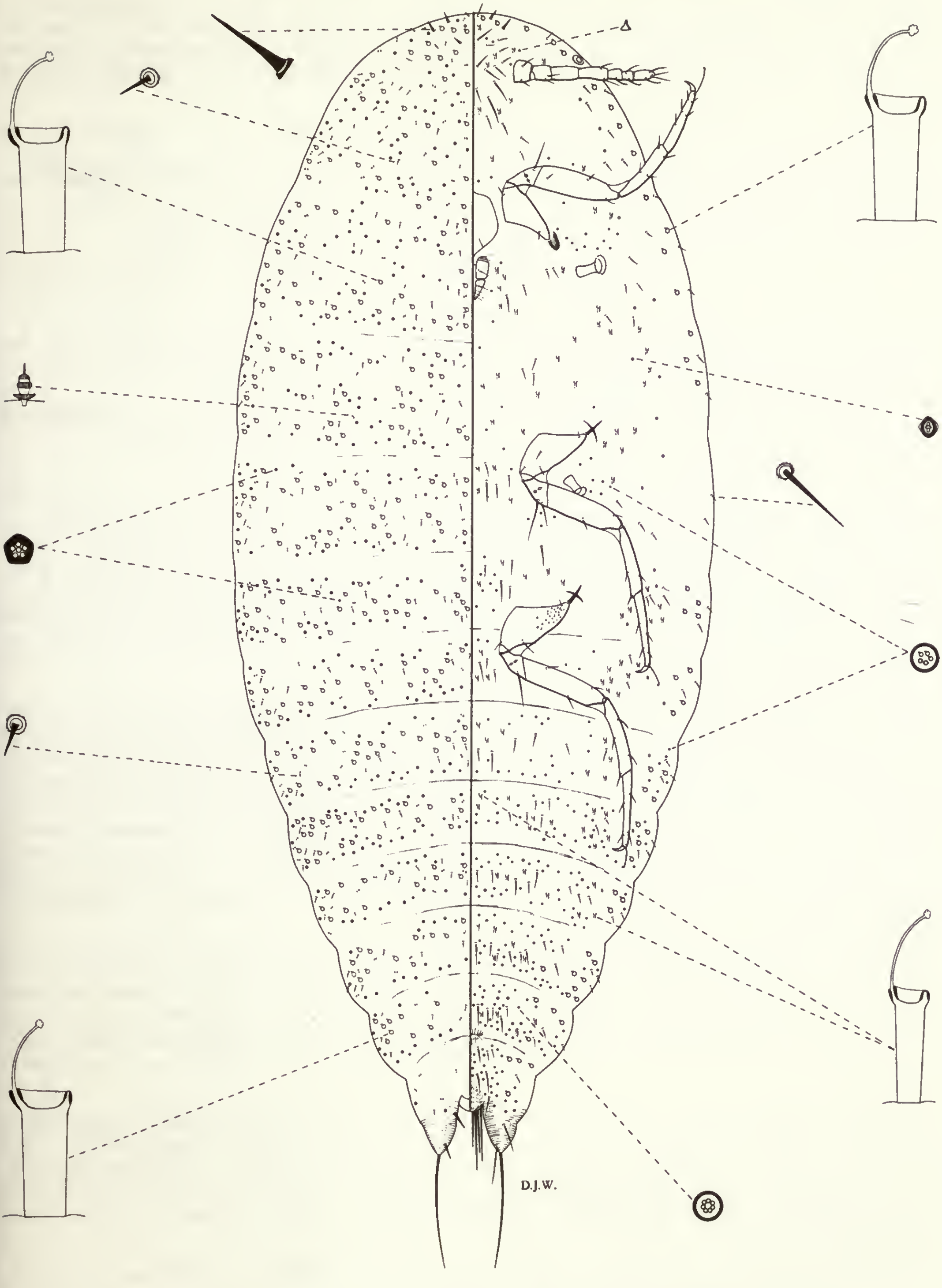

Fig. 13 *Eriococcus placidus* Green, England, Kent, Thurnham, on *Avena flavescens*.

MATERIAL EXAMINED

England: Kent, Thurnham, on ?*Festuca* sp., 8.ix.1920 (*E. E. Green*) (lectotype, paralectotypes), on *Avena flavescens, Brachypodium sylvaticum*, 13.vii.1921 (*E. E. Green*), Bearsted, on *B. sylvaticum*, 30.vii.1925 (*E. E. Green*); Isle of Wight, on *B. sylvaticum*, 3.ix.1921 (*E. E. Green*); Berkshire, Wytham, on *B. pinnatum*, 24.viii.1966, 30.viii.1968 (*G. Varley*), x.1969 (*D. Manawadu*). **Germany:** Ebernburg, on *B. pinnatum*, 16.ix.1928 (*H. Wünn*).

DISCUSSION. The original slide contains four specimens and the specimen selected as lectotype is clearly marked, the other three specimens are labelled paralectotypes.

This species is easily recognisable by the dorsal quinquelocular pores that have wide rims and are always larger than the ventral disc pores.

Green (1923) recorded the species from the Isle of Wight and from Box Hill in Surrey.

Eriococcus pseudinsignis Green **comb. rev.**

(Fig. 14)

Eriococcus pseudinsignis Green, 1921: 149; Schmutterer, 1952: 407. LECTOTYPE ♀, ENGLAND (BMNH), here designated [examined].

Nidularia pseudinsignis (Green) Lindinger, 1933: 116.

Rhizococcus pseudinsignis (Green) Borchsenius, 1949: 354; Danzig, 1962: 845; 1964: 633; Dziedicka & Koteja, 1971.

Acanthococcus pseudinsignis (Green) Tereznikova, 1981: 35.

DESCRIPTION. Slide-mounted specimens, elongate-oval, the largest 2·8 mm long and 1·4 mm wide, nodulose. Anal lobes conical, about twice as long as wide, sclerotised. Each lobe with an apical seta 280 μm long; dorsally 1 outer and 2 inner enlarged setae and ventrally 2 slender setae and a suranal seta shorter than anal ring setae. Dorsal plate lightly sclerotised, narrow, rounded and slightly nodulose. Anal ring with 8 setae each about 140 μm long. Antennae 250–300 μm long with 7 segments. Frontal tubercle present just anterior to basal segment. Legs well developed, slender, hind trochanter + femur 230–260 μm long, hind tibia 130–150 μm long, hind tarsus 150–160 μm long, claw 35 μm long, curved, with a small denticle near apex. Coxa with a few translucent pores on outer half. Labium 100–120 μm long, shorter than clypeolabral shield, basal segment with 2 pairs of setae.

Dorsal surface with a single row of enlarged marginal setae, 28–60 μm long, those on head extending to submarginal areas. Each seta almost conical but inner edges sometimes slightly concave or convex. On the posterior abdominal segments these setae are bluntly pointed, tending to be truncate, but anteriorly they are more sharply pointed. Margins of 7th abdominal segment always with 3 setae varying little in length. Elsewhere on the dorsum the setae on the head and thorax are conical, often curved, sometimes only slightly smaller than the enlarged setae on head, but usually 12–15 μm long. On the posterior abdominal segments the setae become shorter and more slender, 6–8 μm long. Macroducts of one size in moderate numbers, fairly evenly distributed, about 25 μm long, the cup only a little narrower than diameter of a setal base of marginal seta. Microducts not numerous, about 4 μm long, with inner end of tube swollen, ampulla and internal collar.

Ventral setae normal in median areas but laterally towards margins they are conical and thick but not so large as dorsal marginal setae. Macroducts of two sizes. A larger type, similar to dorsal ducts, around margins only. A narrower type in bands across abdominal segments in median areas of head and thorax, extending to submargins. Microducts around margins only. Cruciform pores in a narrow submarginal zone and in area between clypeolabral shield and antennae. Disc pores, usually with 7 loculi, numerous on abdominal segments but not reaching margins, present also in median areas of thorax and around spiracles.

MATERIAL EXAMINED

England: Kent, Thurnham, on *Festuca* sp., 9.ix.1920 (*E. E. Green*) (lectotype, paralectotypes); Surrey, Hog's Back, on *Brachypodium sylvaticum*, 21.vii.1922 (*E. E. Green*); Isle of Wight, Seaview, on *B. sylvaticum*, 3.ix.1921, Alum Bay, on grass, vii.1927 (*E. E. Green*); Berkshire, on *Achillea millefolium, Veronica chamaedrys, Alopecurus pratensis, Agrostis* sp., *Holcus mollis, Deschampsia caespitosa*, 1948 (various dates) (*K. Boratynski*); Yorkshire, Ickornshaw Moor, x.1958 (*A. Smith*), Steeton Moor, 29.viii.1948 (*A. Smith*).

DISCUSSION. Green's original slide contains three specimens, one of which is selected as lectotype and clearly marked, the other two are labelled paralectotypes.

It is sometimes difficult to distinguish this species from *R. insignis*. At present the main differences are the 3 marginal setae on the 7th abdominal segment in *R. pseudinsignis* compared with 4 in *R. insignis*. The

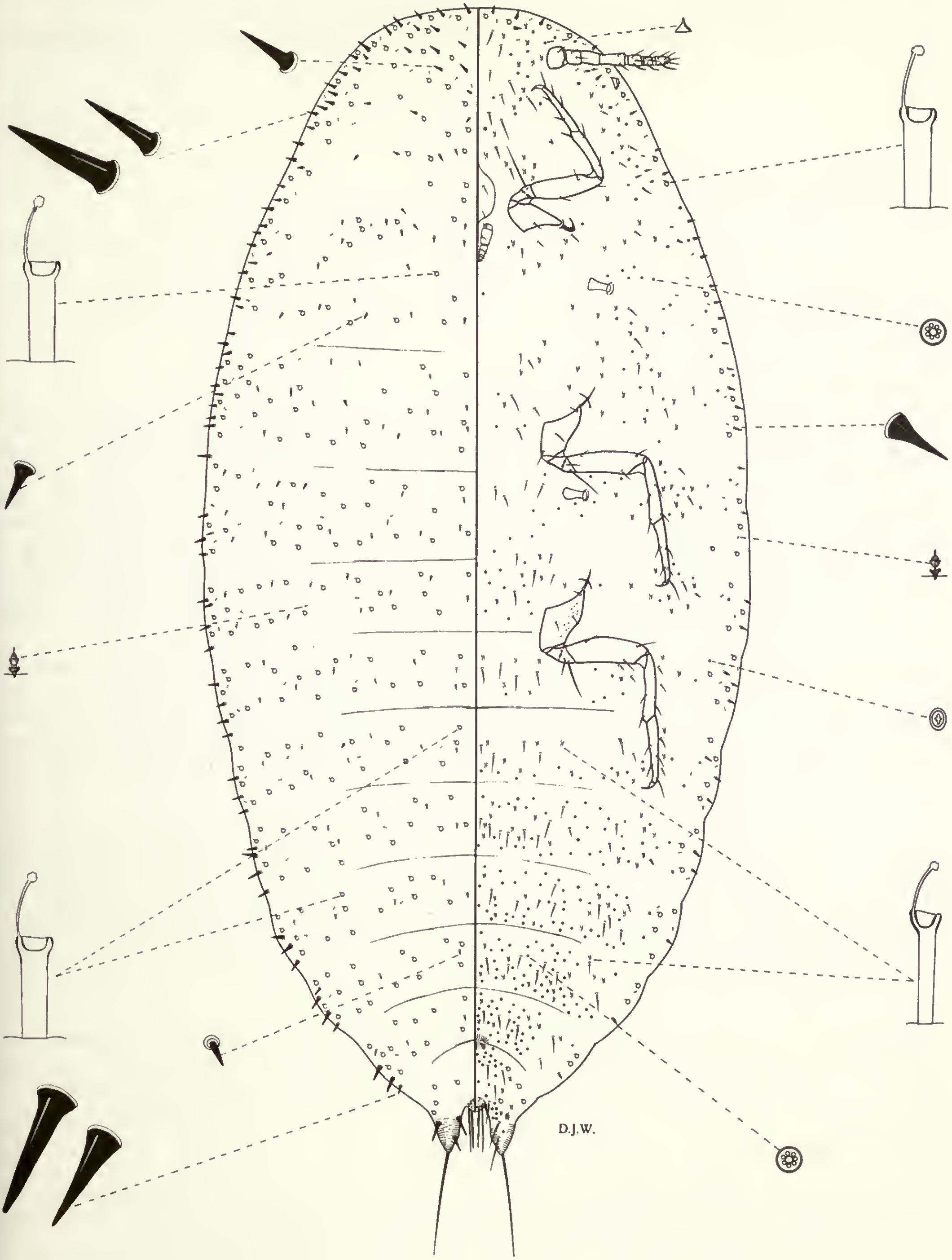

Fig. 14 *Eriococcus pseudinsignis* Green. England, Yorkshire, Ickornshaw Moor, on grass.

dorsal setae on the head and thorax of *R. pseudinsignis* are quite robust and are much longer than the setae on the posterior abdominal setae, whereas all the dorsal setae in *R. insignis* are short and usually slender, although those on the head and thorax are often wider than the abdominal setae.

At present both species are here regarded as distinct but intermediates may be found to warrant further research.

Eriococcus spurius (Modeer)

(Fig. 15)

Coccus ulmi Linnaeus, 1758: 455 (in part).
[*Coccus ulmi* Linnaeus sensu Linnaeus, 1766: 740. Misidentification.]
Coccus spurius Modeer, 1778: 43. Syntypes ♀, Europe (probably lost).
[*Gossyparia ulmi* (Linnaeus) sensu Linnaeus, 1766; Signoret, 1875: 21; Schmutterer, 1952: 416. Misidentifications.]
Gossyparia spuria (Modeer) Cockerell, 1899*b*: 268; Fernald, 1903: 68; Borchsenius, 1949: 330; Danzig, 1964: 632; Tereznikova, 1981: 50.
Nidularia spuria (Modeer) Lindinger, 1933: 108.
Eriococcus spurius (Modeer) Ferris, 1955: 164.

Description. Adult female, when prepared on slides, broadly oval, strongly nodulose, 3·0 mm long and 1·8 mm wide. Anal lobes well developed, protruding, about twice as long as wide, rounded at apex, moderately sclerotised, strongly nodulose with sclerotised teeth, especially on inner margins. Each lobe with an apical seta 250 μm long, dorsally with 2 inner and 1 outer enlarged setae, ventrally with 2 slender setae and a pointed suranal seta. Antennae 230–300 μm long, with 7 segments. Frontal lobes present, just anterior to basal segment. Legs normal, well developed. Hind trochanter + femur 160–190 μm long, hind tibia 100–110 μm long, hind tarsus 130–150 μm long, the tibia + tarsus always longer than trochanter + femur, claw 40 μm long, curved, with a denticle near apex. Hind coxa without translucent pores but with numerous spicules. Labium 150 μm long, shorter than clypeolabral shield, basal segment with 2 pairs of setae. Dorsal plate well developed, triangular, lightly sclerotised and strongly nodulose. Anal ring with 8 setae, each about 150 μm long.

Dorsal surface with numerous setae, in a regular distribution except on the intersegmental areas of thorax where they are absent, but present on mid-line. Setae long and slender with almost straight sides, tapering gradually to a blunt point, the largest 60 μm long around posterior margins, the smallest about 25 μm long. Macrotubular ducts, each about 20 μm long, tapering slightly to orifice, cup wider than a setal base, present around margins and submargins, rarely extending to submedian areas, absent entirely on median area. Microtubular ducts slender, about 10 μm long, with the orifice widely bifid, in an even distribution over entire dorsum.

Ventral surface with normal slender setae in median areas, a few enlarged setae the same as on dorsum, around margins, and a few short setae that are slender and stiff on submargins. Macroducts of two main sizes. A large duct, same size as on dorsum, on margins, and a narrower duct in transverse rows on abdomen and in submedian areas of thorax and head. Microtubular ducts absent. Quinquelocular disc pores present across median areas of abdominal segments, on metathorax and near spiracles and in an area between antennae and clypeolabral shield. Cruciform pores in submedian zone between first spiracles and anterior abdominal segments.

Material examined

England: Surrey, Camberley, on *Ulmus angustifolia*, iv–vii.1916, 18.iv.1922 (*E. E. Green*); Farnham, on *U. angustifolia*, x.1915 (*C. J. F. Fryer*); Woking, on *Ulmus* sp., vi.1918 (*G. C. Gough*). **France:** (ex coll. P. Marchal). **Germany:** Hanover, on *U. procera (U. campestris)*, vii.1893. **Austria:** 'Donau-Auen', on *U. procera*. **Czechoslovakia:** 'Bohemia', on *Ulmus* sp. (ex coll. K. Šulc). **Turkey:** Istanbul, on *U. 'campestris* var. *pyramidalis*.'

In addition numerous specimens have been examined from U.S.A.

Discussion. Linnaeus (1758) cited Réaumur (1738) but unfortunately referred to two distinct species that Réaumur had figured and described. The first refers to pl. 5, figs 5, 6 and this is undoubtedly an armoured scale insect discussed on p. 78 as found on a branch of elm. This species is accepted at present as *Lepidosaphes ulmi* (L.). The second species referred to by Linnaeus is illustrated on pl. 7, figs 1–10 and discussed by Réaumur on p. 119 as found on a branch of elm. There is no doubt from Réaumur's illustrations that this is the species under discussion here. Linnaeus (1766) realising his mistake in 1758, listed *C. ulmi* but referred to Linnaeus (1761) where only the name is mentioned and to Geoffroy (1762) (a work not consistently binominal but nevertheless vital) who, apart from giving a short description, refers to

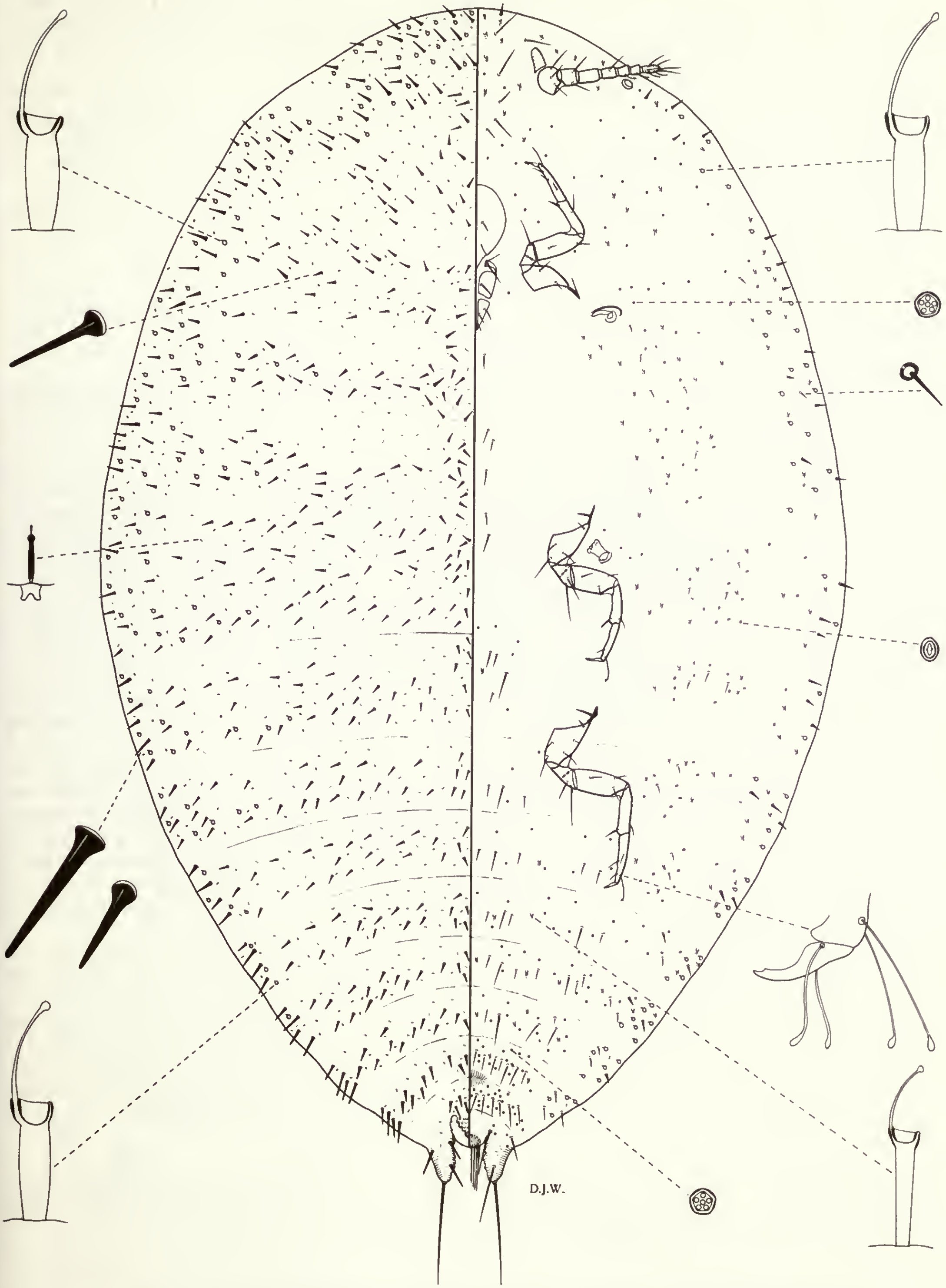

Fig. 15 *Eriococcus spurius* (Modeer). England, Surrey, Camberley, on *Ulmus angustifolia*.

the second of Réaumur's species mentioned by Linnaeus (1758). Clearly the listing by Linnaeus (1766) is based on a misidentification of the species listed by Linnaeus (1758). All subsequent references to *'ulmi'* the eriococcid, from Fabricius to the present day must refer to 'sensu Linnaeus, 1766'. Modeer (1778) described *Coccus spurius* and referred to the excellent illustrations of Réaumur (1738: pl. 7, figs 1–10). Modeer's name is accepted by all modern workers.

Records from England, listed above, were discussed by Green (1916, 1917) when there were outbreaks in Surrey. The insect has not been found since and it is not clear if it has become established but its external appearance is so distinctive that it should be easily recognised. Since it was introduced to the U.S.A., probably in the last century, it has caused concern by its frequent large aggregations on elms. The species seems to be confined to the genus *Ulmus*.

Macropterous and brachypterous males have been recorded and both forms have been described by Afifi (1968).

Eriococcus thymi (Schrank) **comb. rev.**

(Fig. 16)

Coccus thymi Schrank, 1801: 146. Syntypes ♀, GERMANY: Kehlheim (probably lost).
Eriococcus thymi (Schrank) Signoret, 1875: 32; Fernald, 1903: 79.
Rhizococcus gnidii Signoret, 1875: 37; Fernald, 1903: 66. Syntypes ♀, FRANCE: Estrelle Mts, nr Cannes (probably lost). **Syn. n.**
Nidularia gnidii (Signoret) Lindinger, 1933: 116.
Nidularia thymi (Schrank) Lindinger, 1957: 548.

DESCRIPTION. Body of adult female broadly oval, nodulose, largest specimens 1·9 mm long, 1·35 mm wide. Anal lobes well developed, conical, about twice as long as wide at base, heavily sclerotised on venter, lightly sclerotised on dorsum. Each lobe with apical seta 280 μm long, dorsal surface with 3 enlarged setae, ventral surface with 2 slender seta and a suranal seta much shorter than anal ring setae. Dorsal plate membranous, rounded, narrow, margin irregular, nodulose. Anal ring with 8 setae each 120 μm long. Antennae 170–250 μm long, with 6 or 7 segments, the 3rd segment often divided. Frontal tubercle present, seta-like, just anterior to each basal antennal segment. Legs well developed. Hind trochanter + femur 140–190 μm long, hind tibia 70–100 μm long, hind tarsus 110–130 μm long, claw 30 μm long, stout, curved with a denticle near apex. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 1·18–1·30. Hind coxa with a few translucent pores. Labium 130–160 μm long, slightly shorter than clypeolabral shield, basal segment with 2 pairs of setae. Spiracles heavily sclerotised, the sclerotisation continuing around the atrium in varying degrees.

Dorsal surface with enlarged setae of different sizes. The largest around margins 28–55 μm long, each seta blunt, with sides slightly concave but curved in profile, these setae tending to be longest on posterior abdominal segments. Remaining dorsal setae shorter, 12–28 μm long on the head, thorax and anterior abdominal segments, sometimes approaching in length the shorter marginal setae, becoming short, 8 μm long on the 6th and 7th segments, each seta blunt and curved in profile. Macroducts of one size, each about 25 μm long, the cup narrower than a setal base of an enlarged seta. Usually a single pair of smaller ducts on anal lobe segment. Microducts in moderate numbers, each about 8 μm long, with inner sclerotised ampulla, sclerotised tube and collar and with bifid orifice.

Ventral surface with normal flagellate setae in median areas. Enlarged setae, similar to dorsal setae on margins and submargins, varying in size but not as long as dorsal marginal setae. Slender but stiff setae also present in a submarginal zone. Macroducts of three sizes. A large type, similar to dorsal ducts, present around margins only. An intermediate type, only slightly narrower than the large type, in transverse rows on abdominal segments and in median areas of thorax and head. A small type sparse, present singly in submedian areas of most abdominal segments. Microducts few, in marginal and submarginal areas. Quinquelocular disc pores in transverse bands on abdominal segments but not reaching margins, in median areas of thorax and head and around spiracles. Cruciform pores few, in submarginal areas of anterior abdominal segments and thorax, and in median areas of thorax and head.

MATERIAL EXAMINED

France: Montpellier, on *Thymus vulgaris* (Lamiaceae) (det. as *E. thymi* by V. Signoret), Cannes, on *Daphne gnidium* (Thymelaeaceae) (det. as *R. gnidii* by V. Signoret), Var, Agay, on *D. gnidium*, 4.v.1908 (*P. Marchal*), Bouc-Bel-Air, on *T. vulgaris*, v.1932 (*L. Goux*).

DISCUSSION. Although there is no original material available, there seems to be no doubt that the specimens examined and identified by Signoret and others identified by Marchal and Goux represent the species described by Schrank on *Thymus* as *C. thymi* and on *Daphne gnidium* as *R. gnidii*. The characters

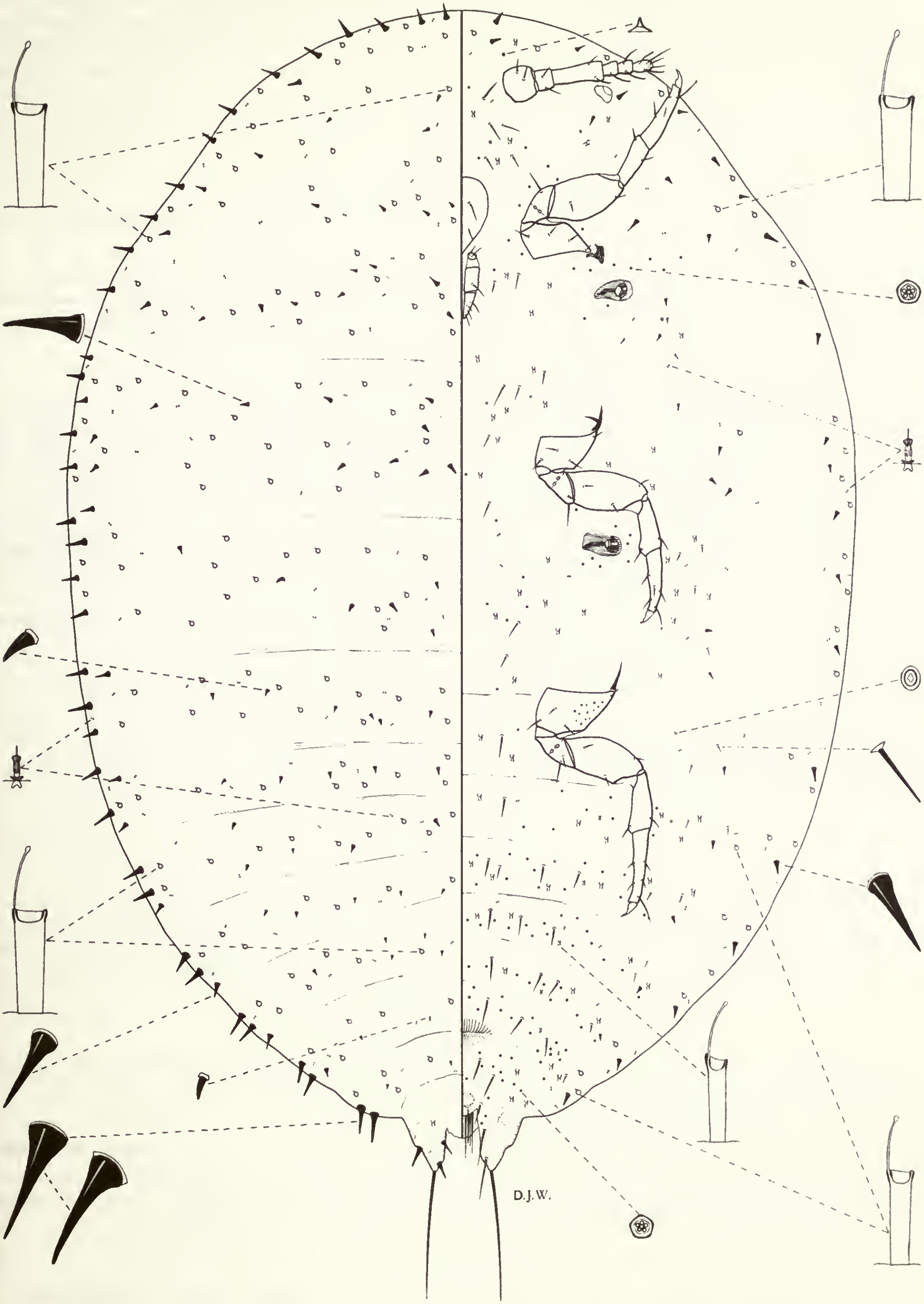

Fig. 16 *Eriococcus thymi* (Schrank). France, Montpellier, on *Thymus vulgaris*.

on some specimens of *D. gnidium* tend to be larger but the specimens themselves are larger and all represent the same species. In well-stained specimens the microducts clearly show the bifid orifice but this character is difficult to see in some specimens. The illustration is based on specimens from France on *Thymus vulgaris*, identified as *E. thymi* by Signoret. Further collecting may show a much wider host-plant range.

A record by Hardy (1876) from Watch Law in the north of Northumberland, England, on the roots of *Thymus serpyllum* (probably *T. drucei*), has never been substantiated.

KUWANINA Cockerell

Kuwanina Cockerell, *in* Fernald, 1903: 121. Type-species: *Sphaerococcus parvus* Maskell, by original designation.

Cockerell intimated that this genus differed from *Antonina* by the larva having 3 or 4 jointed antennae. *Antonina* belongs to the family Pseudococcidae but *Kuwanina* clearly belongs to the family Eriococcidae where it was accepted by Hoy (1963). Another species, *K. hilli* Laing, was shown by Williams (1985*a*) to be identical with *Chaetococcus australis* Froggatt, a mealybug in the family Pseudococcidae.

The type-species is in need of critical study, outside the scope of this work because the species is not native to Britain, having been found only once on imported cherry trees from Japan.

The genus, as represented by specimens at hand from Japan and Britain, seems to be related to *Cryptococcus* in lacking legs and having the third pair replaced by pore-bearing leg-flaps. It differs, however, in lacking macroducts. These are replaced by quite large invaginated quinquelocular pores on the dorsum and ventral margins. In addition there are smaller quinquelocular pores of two distinct sizes on the venter. Microducts are present.

Kosztarab (1968*b*) placed *Kuwanina* in the Cryptococcidae and Koteja (1974*b*), although agreeing that the genus was closely related to *Cryptococcus*, believed that the '*Kuwanina* group' may form a distinct family. The genus is here regarded as a normal component of the Eriococcidae.

Kuwanina parva (Maskell)

Sphaerococcus parvus Maskell, 1897: 244. Syntypes ♀, JAPAN: on cherry (NZAC).
Kuwanina parva (Maskell) Cockerell, *in* Fernald, 1903: 121; Hoy, 1963: 165.

MATERIAL EXAMINED

England: Hertfordshire, St Albans, on dwarf *Prunus* sp., imported from Japan, 1914 (*C. J. F. Fryer*).

DISCUSSION. Green stated that examples were found on gnarled branches in a nursery garden where they were able to thrive and exist. It is doubtful if the species now exists in Britain.

NOTEOCOCCUS Hoy

Noteococcus Hoy, 1962: 164. Type-species: *Eriococcus hoheriae* Maskell, by original designation.

Hoy erected this genus to accommodate *E. hoheriae* from New Zealand, a species with large sclerotised anal lobes, each with 12 small enlarged setae on the dorsum in addition to the normal pair on the inner margins, and with an irregular series of teeth on the venter. Furthermore, apart from the strongly nodulose posterior abdominal segments, there is a large rugose plate anterior to the anal lobes on the dorsum. The legs are much reduced with the trochanter + femur and the tibia + tarsus fused.

Noteococcus hoheriae (Maskell)

Eriococcus hoheriae Maskell, 1880: 298. Lectotype ♀, NEW ZEALAND: Lyttelton (NZAC), designated by Deitz & Tocker (1980: 47).
Noteococcus hoheriae (Maskell) Hoy, 1962: 164.

Specimens are at hand recorded by Green (1925*a*) from Cornwall, Isles of Scilly, Tresco, on *Hoheria populnea*, iii.1924 (*J. C. F. Fryer*), living in the open. Williams (1985*b*), reporting on scale insects collected at Tresco, stated that the species has not been found since, but in common with other exotic species that have been introduced to Tresco, on plant material, the insect may still occur there.

OVATICOCCUS Kloet

Gymnococcus Douglas, 1888: 150. Type-species: *Coccus agavium* Douglas, by original designation (see below). [Homonym of *Gymnococcus* Zopf, 1887: 126.]
Ovaticoccus Kloet, 1944: 86. [Replacement name for *Gymnococcus* Douglas.]

This genus has been revised by Miller & McKenzie (1967) who included nine North American species, but at least two others described from elsewhere have been listed by Boratynski (1958) and accepted by Hoy (1963). In a description of the genus, Miller & McKenzie (1967) stated that the anal lobes are absent and that the anal ring is without pores, usually in the form of a modified circle with usually 3 pairs of setae. Enlarged dorsal setae are present in some species, as are macroducts, microducts and cruciform pores.

The type-species has been redescribed and illustrated by Boratynski (1958) and by Miller & McKenzie (1967). An examination of numerous specimens shows that well-developed frontal tubercles are present. The genus is closely related to *Pseudochermes* but differs in possessing an anal ring without pores and in possessing cruciform pores.

Although *O. agavium* is not a native British species, it is included here because it was described from the Royal Botanic Gardens, Kew (under glass) in 1888 on *Agave*, and Boratynski (1958) has indicated that he had no trouble finding it again in 1956 and 1957. This species is easily separated from *Pseudochermes fraxini* by the presence of numerous enlarged setae in addition to slender lanceolate setae on the dorsum.

Douglas (1888) proposed *Gymnococcus* conditionally when describing *C. agavium* and according to the *International Code of Zoological Nomenclature* the name is available from that date.

Ovaticoccus agavium (Douglas)

Coccus agavium Douglas, 1888: 150. Syntypes ♀, ENGLAND: Kew (probably lost, but see below).
Gymnococcus agavium (Douglas) Cockerell, 1893: 1049; Newstead, 1903: 204; Fernald, 1903: 79; Borchsenius, 1949: 370; Tereznikova, 1981: 57.
Ripersia agavium (Douglas) Newstead, 1897: 12.
Ovaticoccus agavium (Douglas) Kloet, 1944: 86; Boratynski, 1958: 175; Danzig, 1964: 634; Miller & McKenzie, 1967: 509.

MATERIAL EXAMINED

England: Surrey, Royal Botanic Gardens (under glass), ii.1888, on leaves of *Agave* sp. (original material), 1956, 1957 (various dates) on *A. decipiens, A. francescini, A. parryi* (*K. L. Boratynski*), on *A. francescini*, 26.v.1964 (*S. A. Afifi*).

DISCUSSION. Boratynski (1958) has indicated that he designated a lectotype from a slide containing type-material and that this is in the British Museum (Natural History). This slide is not present in the collections and it is doubtful if Boratynski could have done so. There are numerous unmounted specimens from Douglas' collection on cards numbered 1052 and 1056. These numbers agree with the information in his collection data books and three of these specimens were prepared on a slide by F. Laing. Douglas also sent specimens to Newstead who labelled four slides 'Type lot ex coll. J. W. Douglas'. None of these slides represents the original specimens used by Douglas in his description, although they are authentic enough. There is no doubt about the identity of the species.

Afifi (1968) has described and illustrated the alate male.

PSEUDOCHERMES Nitsche

Pseudochermes Nitsche, *in* Judeich & Nitsche, 1895: 1249. Type-species: *Chermes ? fraxini* Kaltenbach, by original designation.
Apterococcus Newstead, 1898: 97 [as subgenus of *Ripersia* Signoret]. Type-species: *Eriococcus fraxini* Newstead, by original designation [cited as *Ripersia fraxini*]. [Synonymised by Cockerell, 1899*b*: 264 (see below).]

This genus is now widely recognised, even though for many years most workers accepted the synonymy, by Cockerell (1899*b*), with *Fonscolombia* Lichtenstein. Cockerell synonymised both *Pseudochermes* and *Apterococcus* with *Fonscolombia* but *Fonscolombia* is now regarded as an unrecognisable genus in the Pseudococcidae, even so the synonymy of *Apterococcus* with *Pseudochermes* still stands. *Pseudochermes* has remained monotypic.

DESCRIPTION. Adult female oval to almost circular, posterior end rounded without recognisable anal lobes but with normal apical setae. Anal ring crescentic with 6 setae and pores. Suranal setae normal. Antennae 6-segmented. Frontal tubercles present. Legs normal, claw with denticle. Labium short, basal segment with a single pair of setae. Dorsal setae short, narrow but spine-like. Macroducts present, each with inner end cupped, on dorsum and venter. Microducts slender, elongate, with simple orifice. Disc pores quinquelocular, on dorsum and venter. Cruciform pores absent.

First and second instars with normal legs. Antennae 6-segmented, basal segment with a pair of setae. Frontal tubercles present. Anal ring as in adult female but smaller.

Discussion. The genus has affinities with *Ovaticoccus* but differs in possessing an anal ring containing a crescentic plate with 6 setae and pores. In *Ovaticoccus* the anal ring is always without pores. Furthermore cruciform pores are present in *Ovaticoccus*, usually in large numbers, but are absent completely in *Pseudochermes*.

Koteja (1974*a*) allied this genus to *Cryptococcus* and included both in the family Cryptococcidae. There seems to be no reason for accepting this action.

Pseudochermes fraxini (Kaltenbach)

(Figs 17, 18)

Chermes (?) *fraxini* Kaltenbach, 1860: 259; 1974: 433. Syntypes ♀, Germany (probably lost).
Eriococcus fraxini Newstead, 1891: 165. LECTOTYPE ♀, England (BMNH), here designated [examined]. [Synonymised by Judeich & Nitsche, 1895: 1249.]
Ripersia fraxini (Newstead) Newstead, 1892: 147.
Coccus fraxini (Kaltenbach) Judeich & Nitsche, 1895: 1247.
Pseudochermes fraxini (Kaltenbach) Judeich & Nitsche, 1895: 1249; Borchsenius, 1949: 365; Danzig, 1964: 634; Tereznikova, 1981: 59.
Fonscolombia fraxini (Kaltenbach) Cockerell, 1899*b*: 264; Fernald, 1903: 114; Schmutterer, 1952: 418.
Ripersia (Apterococcus) fraxini (Newstead) Newstead, 1898: 97.
Apterococcus fraxini (Newstead) Newstead, 1903: 210.

Description. Young adult female (Fig. 17) on microscope slide oval, 1·15 mm long, 0·9 mm wide, but mature adult female sometimes almost circular, membranous, posterior end rounded, anal lobes not developed but position of each lobe with an apical seta 60 μm long. Anal ring in form of crescentic sclerotised plate 30 μm wide, with a few pores and 6 setae, each about 30 μm long, blunt and stiff, situated on ventral surface even in young adult females. Suranal setae present just anterior to anal ring, shorter than anal ring setae. Antennae 100–110 μm long, with 6 segments. Frontal tubercles present just anterior to basal antennal segment. Legs small but well developed. Hind trochanter + femur 70–75 μm long, hind tibia 35–40 μm long, hind tarsus 30–35 μm long, claw 16 μm long, curved, with a denticle near apex. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0·90–1·05. Hind coxa noticeably larger than anterior coxae, with a few large translucent pores. Labium 50–60 μm long, much smaller than clypeolabral shield; basal segment with a single pair of minute setae.

Dorsal surface with narrow conical setae on 7th and anal lobe segments, each about 20 μm long and usually shorter than anal ring setae. Anteriorly the setae are shorter and more slender, but stiff, 8 μm long. Macroducts fairly numerous, in an even distribution, each about 20 μm long, tapering to narrow orifice, the cup wider than a setal base of largest setae. Microducts present, not numerous, tending to be in rows across the segments, each duct filiform, about 4 μm long with a small sclerotised ampulla. Quinquelocular disc pores present in more or less single rows at posterior edges of segments.

Ventral surface with slender setae only slightly longer than dorsal setae, except on head where they are much longer. Macroducts of two sizes. A larger type, same as on dorsum, around margins only except on thorax near spiracles where they also occupy the submarginal areas. A narrower duct each with sclerotised cup and filiform tube, tapering to a minute orifice, sparse, on abdominal segments only. Microducts, same as on dorsum, few, on margins. Quinquelocular disc pores not numerous on head and thorax but more numerous on abdomen.

Second instar female (Fig. 18B), oval, similar in shape to young adult female but smaller. Anal lobes only slightly produced, each with an apical seta 40 μm long, and suranal setae minute. Anal ring 20 μm wide, crescentic, as in adult female situated at apex on venter, with 6 setae. Antennae 6-segmented, 75 μm long. Frontal tubercles present. Legs similar in shape to those of adult female but all coxae approximately same size. Hind trochanter + femur 48 μm long, hind tibia 25 μm long, hind tarsus 25 μm long, claw 12 μm long. Labium 45 μm long, basal segment with a single pair of setae. Dorsal surface with thick truncate setae, 12 μm long, on posterior segments, these longer than anal ring setae. Anteriorly the setae become shorter and more slender, but remain stiff. Macroducts in more or less single rows across the segments, each duct similar in shape to those of adult female but the cup narrower. Microducts as in adult, not numerous. Quinquelocular pores smaller than in adult, in single rows at posterior edges of segments.

Ventral surface with slender setae, usually shorter than on dorsum except for a few long setae on head. Macroducts of one size as on dorsum, on head and thoracic margins and extending almost to spiracles. Microducts few on margins only. Quinquelocular disc pores not numerous, in single rows on abdominal segments and present on head and thorax but absent in median area of thorax.

First instar (Fig. 18A) oval, 300 μm long, 180 μm wide, abdomen tapering. Anal lobes poorly developed, each with an apical seta 35 μm long. Anal ring as in second instar and adult female but 16 μm wide, with 6

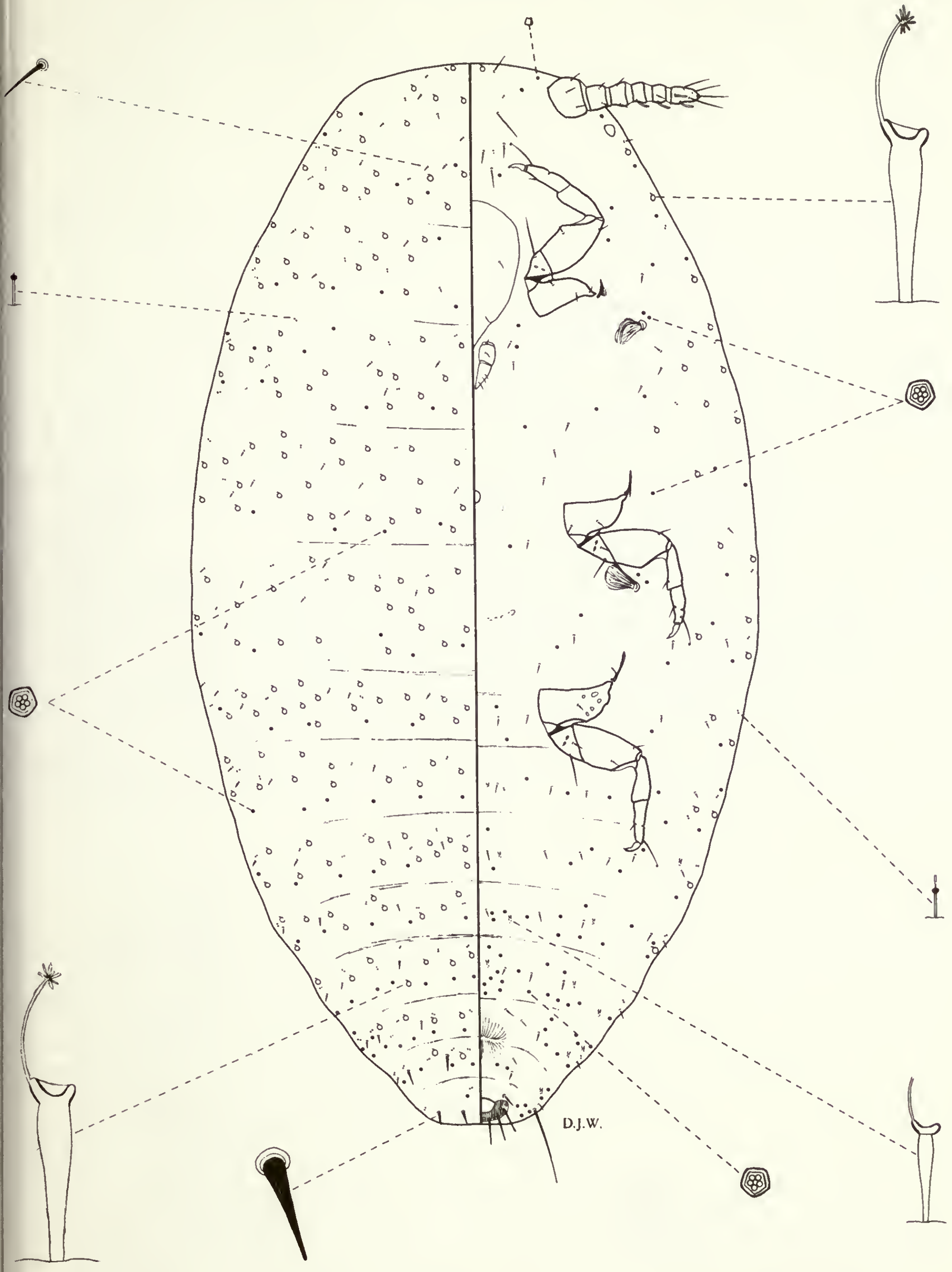

Fig. 17 *Pseudochermes fraxini* (Kaltenbach). Berkshire, Cookham, on *Fraxinus excelsior.*

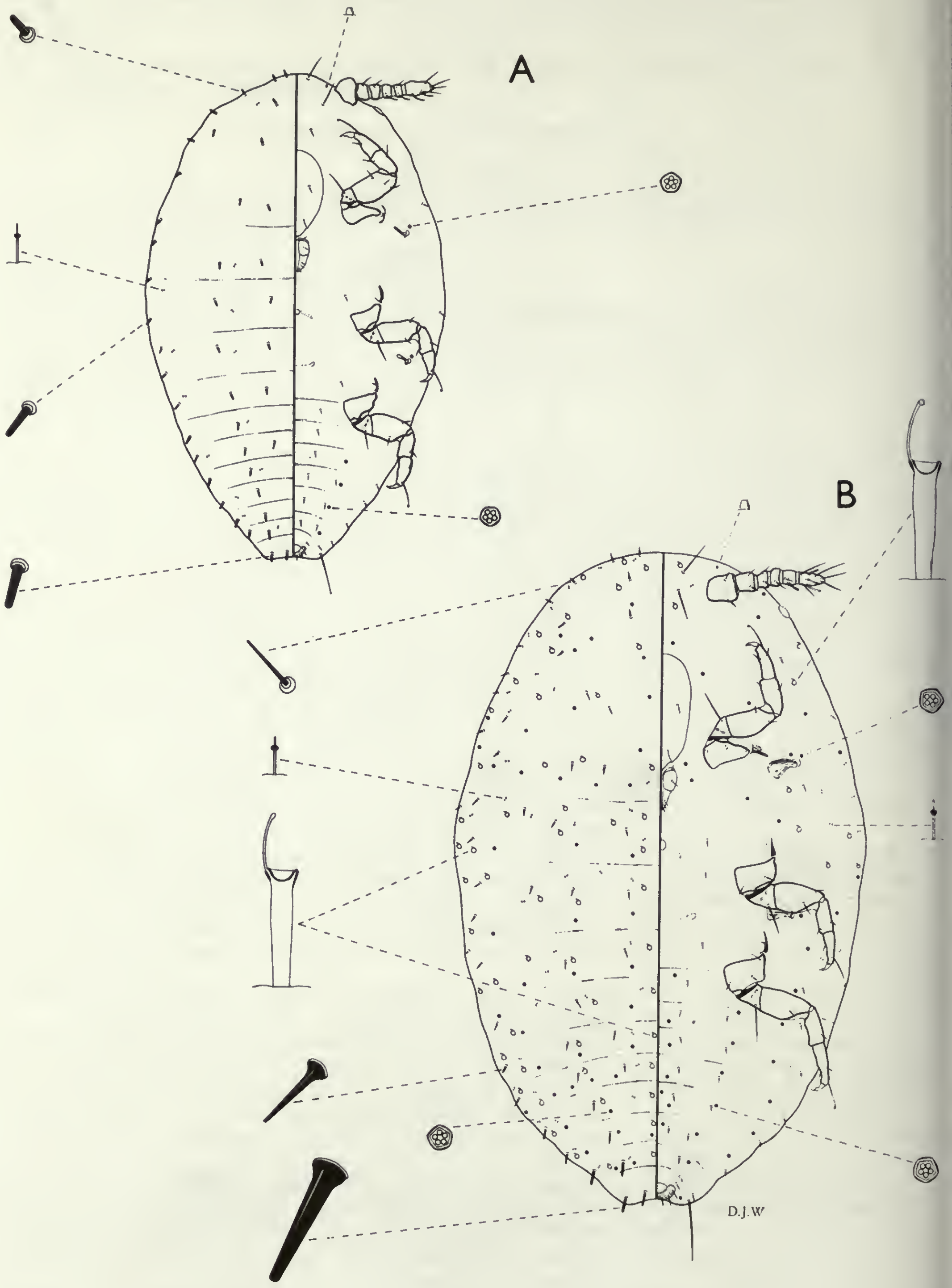

Fig. 18 *Pseudochermes fraxini* (Kaltenbach). (A) First instar. (B) Second instar female.

setae. Antennae 65 μm long, with 6 segments. Frontal tubercles present. Legs normal, hind trochanter + femur 35 μm long, hind tibia 35 μm long, hind tarsus 20 μm long. Claw curved, 10 μm long, with a minute denticle near apex. Labium 30 μm long, basal segment with a pair of setae. Dorsal surface with short truncate setae, tending to be cylindrical, tapering only slightly, those on abdomen the largest and thickest, about 8 μm long, becoming shorter anteriorly to head where they are 5 μm long, all setae thicker than anal ring setae. Microducts sparse, as in later instars. Ventral surface with slender setae, shorter than dorsal setae except for a few long setae on head. Ventral ducts absent. Quinquelocular pores smaller than in later instars, represented usually by a pair on each of 4th to 7th segments and singly next to openings of spiracles.

MATERIAL EXAMINED (all on *Fraxinus excelsior* unless stated otherwise)

England: Berkshire, Silwood Park, *F. excelsior* and *Populus tremula* (Salicaceae), 29.vi.1966 (*K. L. Boratynski*), Cookham, 5.viii.1972, 8.ix.1972, 11.iii.1973, 11.viii.1983 (*D. J. Williams*); Cheshire, Ince, viii.1890 (*R. Newstead*) (lectotype, paralectotypes), Chester, 1895, 11.xi.1895 (*R. Newstead*); Devon, Sidmouth, 26.vi.1963; Gloucestershire, Cheltenham, viii.1973 (*D. J. Williams*); Hampshire, Bentley, 18.iv.1969 (*C. I. Carter*), Exbury, viii.1974; Kent, Bearsted, vii.1913 (*E. E. Green*); Leicestershire, Loughborough, 8.xi.1938 (*A. Roebuck*); London, Buckingham Palace Gardens, 11.x.1963 (*K. L. Boratynski*); Northumberland, Riding Mill, 8.x.1950 (*D. J. Williams*); Oxfordshire, Goring, 25.ii.1914 (*E. E. Green*); Somerset, Bath, Ashrey Gullywood, 24.ii.1978; Surrey, Frimley, 23.v.1921 (*E. E. Green*), Wisley, on *Syringa* sp., 1958, 6.vii.1983 (*D. J. Williams*), Woking, 1914, vii.1915 (*E. E. Green*); Yorkshire, Adel, 2.vii.1963 (*D. J. Williams*). **Wales** (N.): 1976. **Belgium:** intercepted in England, 31.i.1967 (*S. H. Blore*). **Hungary:** Galgamocsa, 26.iv.1981 (*Nagy*).

DISCUSSION. Newstead's single original slide of *Eriococcus fraxini* contains nine whole specimens and a few pieces. The lectotype selected is clearly marked and the remaining eight whole specimens are labelled paralectotypes.

Afifi (1968) has described and illustrated the adult male of this species. It is always minute, wingless and degenerate.

Apart from incursions into Iran, this species is European where its favourite host-plant is *Fraxinus excelsior*, but it is known on other species of *Fraxinus*. It is often found in enormous numbers in the crevices of the bark. The record on *Syringa* is not surprising because this genus and *Fraxinus* both belong to the family Oleaceae. Furthermore, *Syringa* has been mentioned from Germany by Lindinger (1938) who also listed *Sorbus* sp. *S. aucuparia* (as *Pirus aucuparia*) was previously listed by Lindinger (1912). The record on *Populus tremula* is based on specimens collected at the same time as others on *F. excelsior*. There seems to be every reason that the insects were feeding on *Populus* and that *P. fraxini* may yet be found on other host-plants.

The species is probably widespread in Britain on ash. Harrison (1944) recorded it from Inverarish in the Isle of Raasay, Scotland.

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