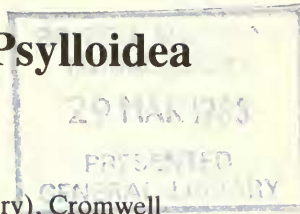


Nymphal taxonomy and systematics of the Psylloidea (Homoptera)



I. M. White

Commonwealth Institute of Entomology, c/o British Museum (Natural History), Cromwell Road, London SW7 5BD

I. D. Hodkinson

Department of Biology, Liverpool Polytechnic, Byrom Street, Liverpool L3 3AF

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Synopsis

The objectives of this study are to form a phenetic classification of Psylloidea using nymphal characters; to compare phenetic relationships suggested by nymphs with relationships suggested by adults; to combine nymphal data with existing adult data and produce a new classification; to devise keys based upon nymphal characters; to produce a predictive model (a cladogram) which describes the probable evolutionary history of the Psylloidea.

Nymphs of 303 species belonging to 94 genera were examined: these represented every existing psyllid family and included material from all zoogeographic regions.

Phenetic analyses were carried out using cluster analysis and ordination. A summary phenetic classification of nymphs is presented which defines four major groups: species with sectasetae (mainly Triozidae); species with lanceolate setae (mainly Aphalaridae); species with capitate setae (most Psyllidae); species without sectasetae, lanceolate setae or capitate setae (some species of each family).

Construction of an evolutionary ground plan for the Psylloidea was aided by the phenetic analyses. A cladogram of 106 psyllid genera and subgenera, based on this ground plan and using adult nymphal characters, is presented. Host-plant and zoogeographic evidence in association with the cladogram suggest that the modern psyllids evolved from an ancestor associated with the plant order Rutales in Gondwanaland.

General trends in the cladogram indicate that the following six families derived from an extinct ancestral group: Triozidae; Carsidaridae; Homotomidae (= Carsidaridae auct., partim); Phacopteronidae (= Carsidaridae auct., partim); Calophyidae (= Carsidaridae auct., partim); Aphalaridae. The Spondyliaspidae and Psyllidae appear to have evolved from a common aphalarid ancestor.

The main contributions made to psyllid systematics are: phenetic groups of nymphs are defined more precisely than they were previously; phenetic and cladistic studies indicate characters of especial value in forming psyllid taxa of rank above the generic category, e.g. tarsal arolium structure; a theory of the origin and evolution of psyllids is proposed incorporating information on nymphal and adult characters plus host-plant and zoogeographic data; a revised classification based on a cladogram incorporating taxa from all zoogeographic regions is presented; keys to genera are produced based on nymphal characters; at the theoretical level the method of cladogram construction is an advancement on that of Hennig (1966); nine new family group taxa are proposed.

Introduction

Psyllids or jumping plant-lice (Homoptera, Sternorrhyncha, Psylloidea) are small (1–5 mm long) phloem-sucking insects which breed almost exclusively upon perennial dicotyledonous plants (Eastop, 1972; Hodkinson, 1974). A review of psyllid biology is given by Hodkinson (1974).

Nomenclatural history

The first psyllid described was *Chermes alni* Linnaeus, 1758 (= *Psylla alni*), the type-species of the group. Four years later Geoffroy described *Psylla*, which is the type-genus, *Chermes* Linnaeus, 1758 having been suppressed and *P. alni* designated as the type-species by the International Commission on Zoological Nomenclature (Eastop, 1963 and Opinion 731, *Bull. zool. Nom.* 22: 86–87, 1965). The first major contribution to psyllid systematics was by Förster (1848) who described the genera *Aphalara*, *Euphyllura*, *Rhinocola*, *Spanioneura* and *Trioza*.

Löw (1879) produced the first formalized classification of the psyllids which he regarded as one family, the Psyllidae, comprised of four defined subfamilies: Liviinae (containing the genus *Livia*), Aphalarinae (containing the genera *Aphalara*, *Euphyllura*, *Psyllopsis* and *Rhinocola*), Psyllinae (*Alloeoneura*, *Amblyrhina*, *Arytaina*, *Calophya*, *Diaphorina*, *Floria*, *Homotoma*, *Psylla* and *Spanioneura*) and Triozinae (*Bactericera* and *Trioza*). Subsequently, Scott (1882) erected the subfamily Livillinae (for which he only lists *Creiis*) and the family Prionocnemidae (*Carsidara* and *Tyora*) but neither of these are valid as they are not based on recognised genera. Löw's subfamilies were raised to family status by Edwards (1896) but this was not generally accepted for another 60 years.

Schwarz (1898) erected a further subfamily, the Spondyliaspininae, for the genus *Spondyliaspis*, and several genera, such as *Carsidara*, *Tyora* and *Ciriaceum*, were placed in the subfamily Ciriaceminae by Enderlein (1910). However, Crawford (1911) separated *Ciriaceum* from *Carsidara* and erected a new subfamily, the Carsidarinae, to include such genera as *Carsidara* and *Tyora*. Later, Aulmann (1913) listed six subfamilies: Psyllinae (e.g. *Calophya*, *Diaphorina*, *Mycopsylla*, *Pauropsylla* and *Psylla*), Triozinae (e.g. *Bactericera* and *Trioza*), Aphalarinae (e.g. *Aphalara*, *Cardiaspis* (= *Cardiaspina*), *Euphalerus*, *Euphyllura* and *Phytolyma*), Liviinae, Ciriaceminae (e.g. *Carsidara*, *Ciriaceum* and *Phacopteron*) and Spondyliaspininae.

The classification was further revised by Crawford (1914) who recognised six subfamilies: Liviinae (*Aphalara*, *Aphalaroida*, *Livia* and *Rhinocola*), Pauropsyllinae (*Calophya*, *Heteropsylla*, *Paurocephala* and *Pauropsylla*), Carsidarinae (*Carsidara*, *Epicarsa*, *Freysuila* sensu Schwarz (= *Mastigimas*) and *Rhinopsylla*), Ciriaceminae (*Ciriaceum* (= *Ciriaceum*)), Triozinae (e.g. *Trioza*) and Psyllinae (e.g. *Euphalerus*, *Euphyllura*, *Pachyopsylla* and *Psylla*). A similar

classification was presented by Pflugfelder (1941) except that Liviinae and Aphalarinae (including *Diaphorina* and *Psyllopsis*) were again separated.

The Spondyliaspinae was first properly defined by Heslop-Harrison who reviewed the subfamily groupings and separated the subfamilies Aphalarinae, Ciriacreminae (including *Bactericera*, *Carsidara*, *Ciriacremum* and *Pauropsylla*), Liviinae, Psyllinae, Spondyliaspinae, and Triozinae in a key (Heslop-Harrison 1949, 1951, 1954, 1958, 1959).

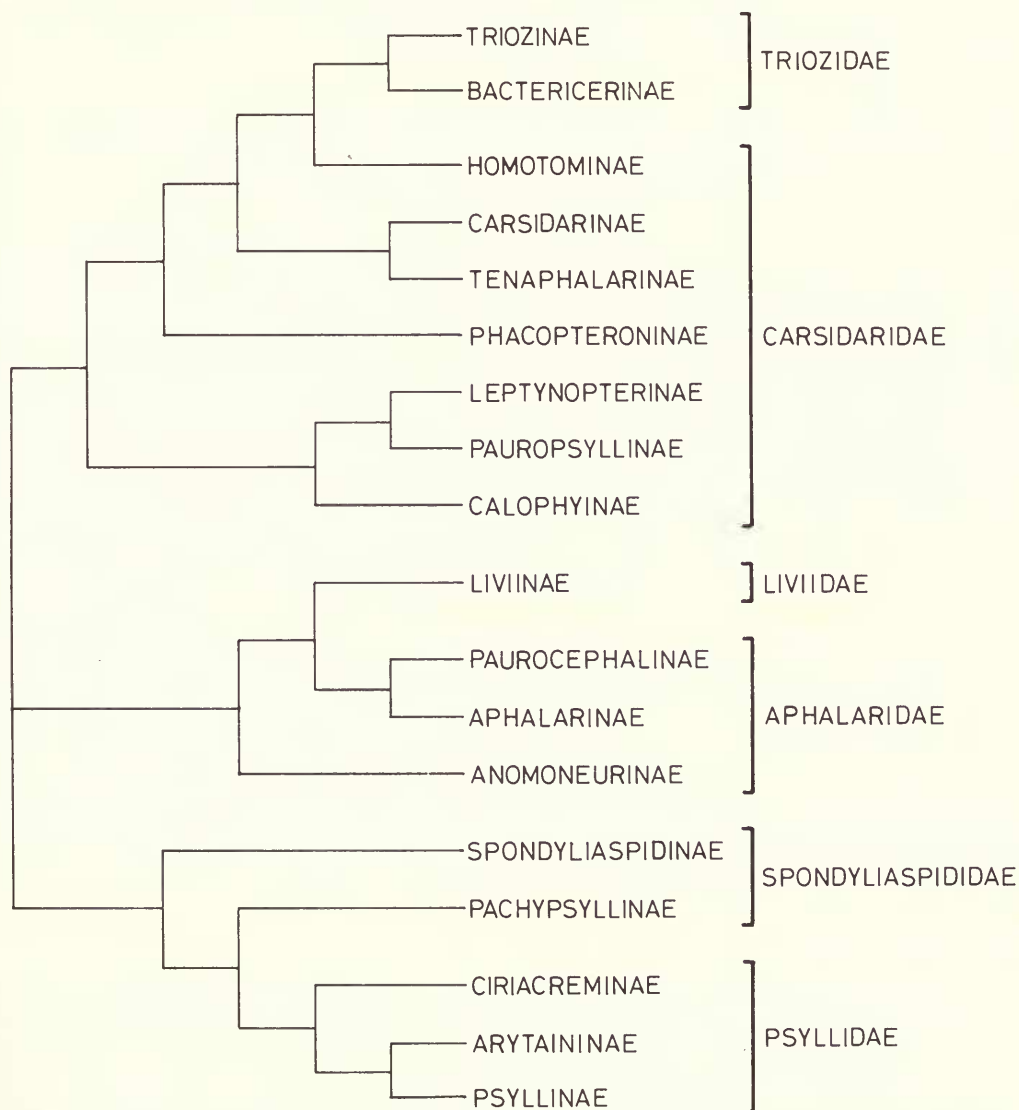


Fig. 1 Cladogram showing the relationships of subfamilies according to Becker-Migdisova (1973).

Superfamily status was given to the psyllids by Handlirsch (1903) and the subfamily units were again promoted to families by Vondracek (1957) who recognised the Aphalaridae (e.g. *Aphalara*, *Paurocephala* and *Pauropsylla*), Carsidaridae, Liviidae, Psyllidae (e.g. *Calophya*, *Ciriacremum*, *Diaphorina*, *Psylla* and *Psyllopsis*), Spondyliaspidae and Triozidae. Vondracek (1963) later replaced the Carsidaridae by the Ciriacremidae (which included *Bactericera*, *Ciriacremum*, *Syndesmophlebia* (= *Klienella*) and *Triozamia*) and expanded the content of Spondyliaspidae to include *Anomalopsylla*, *Phytolyma* and *Tainarys*.

The classification of Klimaszewski (1964) differed from that of Vondracek in certain respects: Bactericerinae (e.g. *Triozamia*) was moved to Triozidae, Anomalopsyllinae (e.g. *Phytolyma* and *Tainarys*) to the Aphalaridae, and *Ciriacremum* to the Psyllidae. Genera such as *Carsidara*, *Homotoma* and *Tenaphalara* were placed in the Carsidaridae. A similar classification for Palaearctic genera is given by Loginova (1964b).

The most recent comprehensive study of psyllid systematics was undertaken by Becker-Migdisova (1973), who produced a classification similar to that of Klimaszewski. Subsequently Loginova (1972, 1973, 1974a, 1974b, 1975, 1976a, 1976b, 1977) has revised several subfamilies and tribes and since completion of this work, has produced a paper on nymphal morphology (Loginova, 1982).

Recently Eastop (1978) presented a classification (attributed to D. Hollis) in which only two families, the Psyllidae (including *Aphalara*, *Calophya*, *Diaphorina*, *Livia*, *Psylla* and *Spondyliaspis*) and the Triozidae (including *Carsidara* and *Trioza*) were proposed.

Contemporary classifications of the Psylloidea (Vondracek, 1957; Klimaszewski, 1964; Becker-Migdisova, 1973) are based on suggested phyletic trees and a summary of the tree of Becker-Migdisova is given in Fig. 1. No attempt has been made to produce cladograms for the Psylloidea as a whole, but they have been constructed for a few genera and tribes, namely *Glycaspis* (Moore, 1970), *Psylla* (Burckhardt, 1979), *Strophingia* (Hodkinson, 1981) and Ciriacremeni (Hollis, 1976).

Comprehensive faunal surveys have been made for several temperate and subtropical regions. They include Alaska (Hodkinson, 1978), Australia (Tuthill & Taylor, 1955), central Europe (Haupt, 1935), Czechoslovakia (Vondracek, 1957), European U.S.S.R. (Loginova, 1964a), Great Britain (Hodkinson & White, 1979b; White & Hodkinson, 1982), Mallorca (Hodkinson & Hollis, 1981), New Zealand (Tuthill, 1952), North America (Crawford, 1914; Tuthill, 1943), Poland (Klimaszewski, 1969, 1975), Rumania (Dobreanu & Manolache, 1962), Spain (Gomez, 1956a, 1956b, 1960) and Switzerland (Schaefer, 1949). The only relatively complete faunal surveys of major tropical areas are for India (Mathur, 1975) and Taiwan (Yang, 1984).

Other substantial faunistic papers on psyllids cover Central Africa (Vondracek, 1963), South Africa (Pettey, 1924, 1925, 1933; Capener, 1968, 1970, 1973), Central America (Crawford, 1914; Caldwell, 1944a, 1944b; Tuthill, 1944, 1945, 1950), South America (Crawford, 1914, 1925; Lima, 1942; Tuthill, 1959, 1964a), Borneo (Crawford, 1920), Hawaii (Zimmerman, 1948), Japan (Miyatake, 1963, 1964), Micronesia (Tuthill, 1964b), Philippines (Uichanco, 1921; Miyatake, 1971, 1972) and Puerto Rico (Caldwell & Martorell, 1952). Comprehensive bibliographies of taxonomic literature are available for the Palaearctic (Klimaszewski, 1973) and Neotropical (Hodkinson & White, 1981) regions and the Austro-Oriental, Pacific and Hawaiian regions (Hodkinson, 1983).

Aims of present study

A classification such as that of Becker-Migdisova (1973) is adequate for studies on temperate psyllid faunas. However, an increasing knowledge of tropical psyllids has brought with it a realisation that a classification which has been largely based on a knowledge of north temperate psyllids is perhaps inappropriate when applied to tropical forms.

This problem cannot be resolved simply by defining more major groups; new information of a suitable nature for incorporation in a systematic study is required. A study of nymphal morphology is one possible source of such information.

The aims of this work were: to investigate the phenetic taxonomic relationships of psyllids as suggested by nymphal data; to compare phenetic relationships based upon nymphal or adult data; to pool nymphal data with existing adult data and produce a new predictive classification, i.e. a classification which has maximal likelihood of predicting unknown character states; to produce a predictive model (a cladogram) against which other forms of data can be compared, and to use this model to derive a theory as to the age, possible origin and ancestral host of the psyllids; to write provisional keys for the nymphs of psyllids.

Over 2000 species of Psylloidea have been described and for nymphal data to be of any value the nymphal stages of a few hundred species, representing as many genera as possible, had to be examined and described. This was facilitated by the use of numerical description and computerised data-handling techniques.

Use of numerical taxonomic methods

The use of phenetic methods indicates, within the bounds of the characters used, which taxa are most similar to other taxa, without any characters being empirically weighted. They can initiate new ideas, they are resistant to preconceived ideas, and they can help in deciding whether an attribute is ancestral or derived.

The first application of numerical techniques to psyllid taxonomy was a study, based upon inadequate data, of Polish *Triozza* adults (Klimaszewski, 1967). Recently, Hodkinson (1981) used principal component analysis in a study of *Strophingia* adults.

Previous studies of nymphal psyllids

Many descriptions of nymphal psyllids have been published and these are listed by White (1980). Prior to 1920 these were generally colour descriptions, such as those of Scott (1886a, 1886b, 1886c), although a few authors, such as Löw (1876, 1884, 1886), presented outline drawings. The first descriptions of any taxonomic value were those of Ferris (1923, 1924, 1925, 1926, 1928a, 1928b) who also presented a phenetic classification of the nymphs (Ferris, 1925) which was later expanded by Rahman (1932). There are only three keys to nymphal psyllids: Swedish species of *Psylla* (Ossiannilsson, 1970), subgenera of *Psylla* (Loginova, 1978) and the British Psylloidea (White & Hodkinson, 1982). Good nymphal descriptions of almost half the species known from the Indian subcontinent have been provided by Mathur (1975).

Methods of illustration

Nymphal morphology

In whole nymph drawings (Figs 2–4) and in most illustrations of anal pore fields (Figs 97–160) the dorsal view is shown to the left of the body mid-line and the ventral view to the right.

Minimum spanning networks (MSN)

MSN's use abbreviated generic names with numbers denoting species (Table 1). In Figs 178 and 182 a summary of each MSN is given in which species are only labelled with the initial letter of the family to which they belong in the classification of Becker-Migdisova (1973) (A – Aphalaridae, C – Carsidaridae, L – Liviidae, P – Psyllidae, S – Spondylaspididae, T – Triozidae).

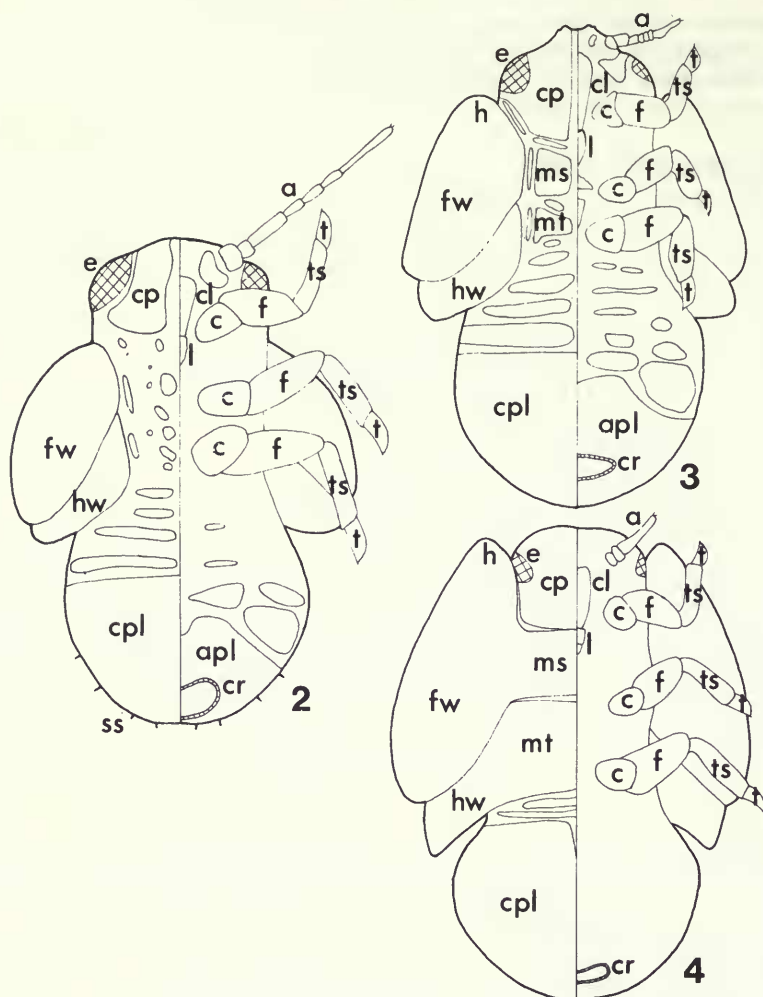
Phenograms

Phenograms are labelled with the full names of species. Species adjacent in the phenogram but belonging to different Becker-Migdisova families are spaced further apart than species of the same family so as to give a visual impression of which clusters are highly congruent with the families of Becker-Migdisova (congruent clusters appear more tightly packed than incongruent clusters). The initial letter of the family of Becker-Migdisova (1973) to which each species belongs is indicated in the phenogram.

Material examined

Taxonomic and zoogeographic coverage

The final instar nymphs of 301 species were examined (Table 1). Two species descriptions (*Tetragonocephala* sp. from Ferris, 1926 and *Togepssylla matsumurana* from Miyatake, 1970) were incorporated from the literature as they were considered valuable additions to the study.



Figs 2-4 Psylloidea nymphs, morphological features of the three types of nymph defined by Rahman (1932). 2, psylline type nymph; 3, pauropsylline type nymph; 4, triozine type nymph. (a - antenna; apl - anal plate; c - coxa; cl - clypeus; cp - cephaloprothorax; cpl - caudal plate; cr - circum-anal pore ring; e - eye; f - femur; fw - forewing-pad; h - humeral lobe; hw - hindwing-pad; l - labium; ms - mesothoracic sclerites; mt - metathoracic sclerites; ss - setae arranged 4 + 4 on abdomen margin; ts - tibiotarsus; t - tarsal segment II.) Modified from White & Hodkinson (1982).

This represents a total species coverage of approximately 15 per cent and a generic coverage of about 43 per cent.

For purposes of comparison the genera examined are fitted as closely as possible to the phylogenetic tree proposed by Becker-Migdisova (Fig. 1 and Table 1).

The generic and specific representation across each recognised family and each zoogeographic region are given in Tables 2 and 3. The absolute total number of genera and species is not given because taxonomic position and status of many groups is uncertain; the Liviidae, however, contains only one genus.

Recognition of final instar nymphs

In all cases where the life-cycle of a psyllid has been carefully studied five nymphal instars were recorded (e.g. Mathur, 1975). The most certain method of recognising a fifth instar nymphal

Table 1 Species examined listed according to the classification of Becker-Migdisova (1973). Type-species of genera and subgenera, when examined, are indicated by an asterisk. Genera not examined by Becker-Migdisova are indicated by †. Abbreviated generic and subgeneric names of up to eight small capital letters are given on the right of each generic and subgeneric name. These abbreviations are used in the minimum spanning network diagrams, in combination with the species numbers. Species numbers are given in parentheses on the right-hand side of the table.

Depositories of material are indicated after each species name. Locality data for each specimen are given by White (1980).

Abbreviations of depositories

BMAG	Bolton Museum and Art Gallery, Bolton, Lancs.
BMNH	British Museum (Natural History), London.
FRI	Forest Research Institute, Dehra Dun, India.
IDH	I. D. Hodkinson (private collection), Liverpool.
LC	Loyola College, Madras, India.
TRL	Tasmanian Regional Laboratory, Commonwealth Scientific and Industrial Research Organisation, Hobart, Tasmania, Australia.
UC	University of California, Davies, California, U.S.A.
USDAC	United States Department of Food and Agriculture (California), Sacramento, California, U.S.A.
USNM	United States National Museum of Natural History, Entomological Collection at the Systematic Entomology Laboratory, USDA, Beltsville, Maryland, U.S.A.

APHALARIDAE

Paurocephalinae

Rhinocolini

<i>Rhinocola</i> Förster, 1848	RHINCOL
* <i>aceris</i> (Linnaeus, 1758) [BMNH]	.
† <i>Leurolophus</i> Tuthill, 1942	LEUROLOP
* <i>vittatus</i> Tuthill, 1942 [USNM]	

Euphyllurini

<i>Euphyllura</i> Förster, 1848	EUPHYLLU
? <i>aethiopica</i> Silvestri, 1934 [BMNH]	(1)
<i>olivina</i> (Costa, 1939) [BMNH]	(2)
* <i>phillyreae</i> Förster, 1848 [BMNH]	(3)
† <i>Neophyllura</i> Loginova, 1973	NEOPHYLL
<i>Arbutophila</i> Loginova, 1973	
* <i>arbuti</i> (Schwarz, 1904) [USNM]	(1)
<i>Neophyllura</i> Loginova, 1973	
* <i>arctostaphyli</i> (Schwarz, 1904) [USNM]	(2)
<i>bicolor</i> (Martin, 1931) [USNM]	(3)

Paurocephalini

<i>Paurocephala</i> Crawford, 1914	PAUROCEP
<i>gossypii</i> Russell, 1943 [BMNH]	(1)
<i>urenae</i> Russell, 1946 [USNM]	(2)
<i>Strophingia</i> Enderlein, 1914	STROPHIN
<i>cinereae</i> Hodkinson, 1971 [BMNH]	(1)
* <i>ericae</i> (Curtis, 1835) [BMNH]	(2)
<i>Agonosцена</i> Enderlein, 1914	AGONOSCE
A. sp. (A) [USNM]	(1)
A. sp. (B) [BMNH]	(2)
A. sp. (C) [BMNH]	(3)
<i>Aphalaroida</i> Crawford, 1914 [USDAC]	APHROIDA
<i>inermis</i> Crawford, 1914 [USDAC]	(1)
?near <i>pithecolobia</i> Crawford, 1914 [USNM]	(2)
† <i>Camartoscena</i> Haupt, 1935	CAMAROTO
* <i>speciosa</i> (Flor, 1861) [BMNH]	(1)
?unicolor Loginova & Parfent'ev, 1958 [BMNH]	(2)
† <i>Moraniella</i> Loginova, 1972	MORANIEL
* <i>calodendri</i> (Moran, 1968) [BMNH]	

† <i>Paraphalaroida</i> Loginova, 1972	PARAPHAL
* <i>fremontiae</i> (Klyver, 1930) [USDAC]	
Aphalarinae	
Aphalarini	
<i>Aphalara</i> Förster, 1848	APHALARA
<i>curta</i> Caldwell, 1937 [USNM]	(1)
<i>exilis</i> (Weber & Mohr, 1804) [BMNH]	(2)
<i>monticola</i> Hodkinson, 1973 [IDH]	(3)
? <i>nubifera</i> Patch, 1912 [USNM]	(4)
<i>persicaria</i> Caldwell, 1937 [USNM]	(5)
<i>polygona</i> Förster, 1848 [BMNH]	(6)
<i>rumicis</i> Mally, 1894 [USNM]	(7)
<i>simila</i> Caldwell, 1937 [USNM]	(8)
<i>Craspedolepta</i> Enderlein, 1921	CRASPEDO
? <i>angustipennis</i> (Crawford, 1911) [USNM]	(1)
* <i>artemisiae</i> (Förster, 1848) [BMNH]	(2)
? <i>vancouverensis</i> (Klyver, 1931) [USNM]	(3)
? <i>constricta</i> (Caldwell, 1936) [USNM]	(4)
<i>furcata</i> (Caldwell, 1936) [USNM]	(5)
<i>minuta</i> (Caldwell, 1938) [USNM]	(6)
<i>minutissima</i> (Crawford, 1914) [USNM]	(7)
<i>nebulosa</i> (Zetterstedt, 1828) [IDH]	(8)
<i>nervosa</i> (Förster, 1848) [BMAG]	(9)
<i>sonchi</i> (Förster, 1848) [IDH]	(10)
<i>suaedae</i> (Crawford, 1914) [USNM]	(11)
<i>subpunctata</i> (Förster, 1848) [BMNH]	(12)
? <i>veaziei</i> (Patch, 1911) [USNM]	(13)
† <i>Gyropsylla</i> Bréthes, 1921	GYROPSYL
<i>ilicis</i> (Ashmead, 1881) [USNM]	(1)
<i>spgazziniana</i> (Lizer, 1917) [USNM]	(2)
Colposceniini	
<i>Colposcena</i> Enderlein, 1929	COLPOSCE
C. sp. [USNM]	
<i>Crastina</i> Loginova, 1964	CRASTINA
? <i>linavuorii</i> Loginova, 1974 [BMNH]	
Anomalopsyllinae	
Apsyllini	
<i>Apsylla</i> Crawford, 1912	APSYLLA
* <i>cistellata</i> (Buckton, 1896) [LC]	
Anomalopsyllini	
<i>Tainarys</i> Bréthes, 1920	TAINARYS
* <i>schini</i> Bréthes, 1920 [USNM]	
Phytolymini	
<i>Phytolyma</i> Scott, 1882	PHYTOLYM
<i>fusca</i> Alibert, 1947 [BMNH]	(1)
* <i>lata</i> (Walker, 1852) [BMNH]	(2)
<i>minuta</i> (Hollis, 1973) [BMNH]	(3)
CARSIDARIDAE	
Calophyinae	
<i>Calophya</i> Löw, 1878	CALOPHYA
? <i>californica</i> Schwarz, 1904 [USDAC]	(1)
<i>dubia</i> Crawford, 1914 [USNM]	(2)
<i>flavida</i> Schwarz, 1904 [USNM]	(3)
<i>nigripennis</i> Riley, 1883 [USNM]	(4)
* <i>rhois</i> (Löw, 1877) [IDH]	(5)
<i>schini</i> Tuthill, 1959 [USNM]	(6)
<i>triozomima</i> Schwarz, 1904 [USNM]	(7)
<i>rotundipennis</i> White & Hodkinson, 1980 [BMNH]	(8)

Pauropsyllinae		
Microceropsyllini		
<i>Microceropsylla</i> Boselli, 1930		MICROCER
<i>M. sp.</i> [BMNH]		
<i>Pelmatobrachia</i> Enderlein, 1921		PELMATOB
<i>P. sp.</i> [LC]		
Pauropsyllini		
<i>Pauropsylla</i> Rubsaamen, 1899		PAUROPSY
<i>beelsoni</i> Laing, 1930 [BMNH]		(1)
<i>depressa</i> Crawford, 1912 [LC]		(2)
<i>trichaeta</i> Pettey, 1924 [BMNH]		(3)
Leptynopterinae		
<i>Leptynoptera</i> Crawford, 1919		LEPTYNOP
* <i>sulfurea</i> Crawford, 1919 [BMNH]		
Phacopterinae		
Pseudophacopterini		
<i>Pseudophacopteron</i> Enderlein, 1921		PSEUDOPH
<i>floccosa</i> (Crawford, 1915) [USNM]		(1)
sp. (A) [BMNH]		(2)
sp. (B) [BMNH]		(3)
Phacopterini		
<i>Phacopteron</i> Buckton, 1894		PHACOPT
* <i>lentiginosum</i> Buckton, 1894 [USDAC]		
Tenaphalarinae		
Tenaphalarini		
<i>Protyora</i> Kieffer, 1906		PROTYORA
* <i>sterculiae</i> (Froggatt, 1901) [BMNH]		
<i>Tenaphalara</i> Kuwayama, 1907		TENAPHAL
? <i>acutipennis</i> Kuwayama, 1907 [BMNH]		(1)
<i>malayensis</i> Crawford, 1919 [BMNH]		(2)
sp. [BMNH]		(3)
Togepsyllini		
<i>Togepsylla</i> Kuwayama, 1931		TOGEPSYL
<i>matsumurana</i> Kuwayama, 1949		
[described from Miyatake, 1970]		
Diclidophlebiini		
<i>Diclidophlebia</i> Crawford, 1920		DICLIDOP
? <i>eastopi</i> Vondracek, 1963 [BMNH]		
Mastigmatini		
<i>Mastigimas</i> Enderlein, 1921		MASTIGIM
<i>cedrelae</i> (Schwarz, 1899) [BMNH]		(1)
sp. (A) [IDH]		(2)
sp. (B) [BMNH]		(3)
Carsidarinae		
Mesohomotomini		
<i>Epicarsa</i> Crawford, 1911		EPICARSA
<i>E. sp.</i> [USNM]		
<i>Mesohomotoma</i> Kuwayama, 1907		MESOHOMO
<i>hibisci</i> (Froggatt, 1901) [BMNH]		(1)
<i>tessmanni</i> (Aulmann, 1912) [BMNH]		(2)
<i>Paracarsidara</i> Heslop-Harrison, 1960		PARACARS
<i>dugesii</i> (Löw, 1886) [USNM]		(1)
<i>gigantea</i> (Crawford, 1911) [BMNH]		(2)
sp. [USNM]		(3)
Unplaced		
† <i>Bharatiana</i> Mathur, 1974		BHARATIA
* <i>octospinosa</i> Mathur, 1974 [BMNH]		

Homotominae		
Synoziini		
<i>Synoza</i> Enderlein, 1918		SYNOZA
<i>floccosa</i> Ferris, 1928 [UC]		(1)
sp. [USNM]		(2)
Dynopsyllini		
<i>Macrohomotoma</i> Kuwayama, 1907		MACROHOM
* <i>gladiatum</i> Kuwayama, 1907 [BMNH]		(1)
<i>striata</i> Crawford, 1925 [BMNH]		(2)
<i>Mycopsylla</i> Froggatt, 1901		MYCOPSYL
?* <i>fici</i> (Tryon, 1895) [BMNH]		(1)
<i>gardenensis</i> Bhanotar, Ghosh & Ghosh, 1972 [BMNH]		(2)
† <i>Pseudoeriopsylla</i> Newstead, 1911		PSEUDOER
<i>nyasae</i> Newstead, 1911 [BMNH]		
Homotomini		
<i>Homotoma</i> Guérin-Méneville, 1834		HOMOTOMA
* <i>ficus</i> (Linnaeus, 1767) [BMNH]		(1)
<i>indica</i> (Mathur, 1975) [FRI]		(2)

LIVIIDAE

<i>Livia</i> Latreille, 1804		LIVIA
<i>coloradensis</i> Crawford, 1914 [USNM]		(1)
<i>crefeldensis</i> (Mink, 1855) [BMNH]		(2)
* <i>juncorum</i> (Latreille, 1798) [IDH]		(3)
<i>maculipennis</i> (Fitch, 1857) [USNM]		(4)
<i>vernalis</i> Fitch, 1851 [USNM]		(5)

PSYLLIDAE

Ciriacreminae		
Ciriacremini		
<i>Ciriacremum</i> Enderlein, 1910		CIRIACRE
<i>capeneri</i> Hollis, 1976 [BMNH]		(1)
<i>capense</i> Enderlein, 1923 [BMNH]		(2)
<i>harteni</i> Hollis, 1976 [BMNH]		(3)
<i>julbernardioides</i> Hollis, 1976 [BMNH]		(4)
Anomoneurini		
<i>Anomoneura</i> Schwarz, 1896		ANOMONEU
* <i>mori</i> Schwarz, 1896 [USNM]		
Arytaininae		
Diaphorini		
<i>Diaphorina</i> Löw, 1879		DIAPHORI
<i>albomaculata</i> Capener, 1970 [BMNH]		(1)
<i>cardiae</i> Crawford, 1924 [BMNH]		(2)
<i>chobauti</i> Putton, 1898 [BMNH]		(3)
<i>citri</i> Kuwayama, 1907 [BMNH]		(4)
<i>clutiae</i> Capener, 1970 [IDH]		(5)
<i>florea</i> Capener, 1970 [IDH]		(6)
<i>punctulata</i> (Petty, 1924) [BMNH]		(7)
* <i>putonii</i> Löw, 1878 [USNM]		(8)
<i>solani</i> Capener, 1970 [IDH]		(9)
† <i>Pennavena</i> Capener, 1968		PENNAVEN
* <i>fabulosa</i> Capener, 1968 [IDH]		
Arytainini		
<i>Arytaina</i> Förster, 1848		ARYTAINA
* <i>genistae</i> (Latreille, 1804) [BMAG]		
† <i>Acizzia</i> Heslop-Harrison, 1961		ACIZZIA
<i>acaciae</i> (Maskell, 1894) [BMNH]		(1)
<i>acaciaebaileyanae</i> (Froggatt, 1901) [BMNH]		(2)

	<i>hakeae</i> (Tuthill, 1952) [BMNH]	(3)
	<i>russellae</i> Webb & Moran, 1974 [BMNH]	(4)
	<i>uncatoides</i> (Ferris & Klyver, 1932) [BMNH]	(5)
†	<i>Amorphicola</i> Heslop-Harrison, 1961	AMORPHIC
	* <i>amorphae</i> (Mally, 1894) [USNM]	
†	<i>Arytainilla</i> Loginova, 1972	ARYNILLA
	<i>cytisi</i> (Puton, 1873) [BMNH]	(1)
	<i>hakani</i> Loginova, 1972 [BMNH]	(2)
	<i>spartiicola</i> (Šulc, 1907) [BMNH]	(3)
	<i>spartiophila</i> (Förster, 1848) [BMNH]	(4)
†	<i>Ceanothia</i> Heslop-Harrison, 1961	CEANOTHI
	<i>aculeata</i> (Crawford, 1914) [USNM]	(1)
	* <i>ceanothi</i> (Crawford, 1914) [USNM]	(2)
†	<i>Euceropysylla</i> Boselli, 1929	EUCEROPS
	<i>cayeyensis</i> (Caldwell, 1942) [USNM]	(1)
	<i>minuticona</i> (Crawford, 1914) [USNM]	(2)
	* <i>russoi</i> Boselli, 1949 [USNM]	(3)
	sp. [USNM]	(4)
†	<i>Euglyptoneura</i> Heslop-Harrison, 1961	EUGLYPTO
	<i>fuscipennis</i> (Crawford, 1914) [USNM]	(1)
	<i>robusta</i> (Crawford, 1914) [USNM]	(2)
	sp. [USNM]	(3)
†	<i>Floria</i> Löw, 1879	FLORIA
	<i>variegata</i> Löw, 1881 [BMNH]	
†	<i>Insnesia</i> Tuthill, 1964	INSNESIA
	<i>glabruscuta</i> (Caldwell, 1942) [USNM]	
†	<i>Purshivora</i> Heslop-Harrison, 1961	PURSHIVO
	<i>chelifera</i> (Crawford, 1914) [USNM]	(1)
	<i>pubescens</i> (Crawford, 1914) [USNM]	(2)
Euphalerini		
	<i>Colophorina</i> Capener, 1973	COLOPHOR
	* <i>cassiae</i> Capener, 1973 [BMNH]	
	<i>Euphalerus</i> Schwarz, 1904	EUPHALER
	<i>gallicolus</i> Ferris, 1928 [UC]	(1)
	<i>jugovenosus</i> Tuthill, 1937 [USNM]	(2)
	<i>nidifex</i> Schwarz, 1904 [USNM]	(3)
	<i>rugipennis</i> Crawford, 1914 [USNM]	(4)
	<i>tanillus</i> Tuthill, 1937 [USNM]	(5)
	<i>vermiculosus</i> Crawford, 1914 [USNM]	(6)
	sp. (A) [BMNH]	(7)
	sp. (B) [BMNH]	(8)
	sp. (C) [LC]	(9)
	sp. (D) [BMNH]	(10)
Psyllopseini		
	<i>Psyllopsis</i> Löw, 1879	PSYLLOPS
	<i>fraxini</i> (Linnaeus, 1761) [BMAG]	(1)
	* <i>fraxinicola</i> (Förster, 1848) [BMNH]	(2)
Psyllinae		
	<i>Psylla</i> Geoffroy, 1862	
	<i>Asphagidella</i> Enderlein, 1921	P-ASPHAG
	* <i>buxi</i> (Linnaeus, 1758) [BMNH]	
	<i>Baeopelma</i> Enderlein, 1926	P-BAEOPE
	<i>foersteri</i> Flor, 1861 [BMNH]	
	<i>Cacopsylla</i> Ossiannilsson, 1970	P-CACOPS
	* <i>mali</i> (Schmidberger, 1836) [IDH]	(1)
	<i>peregrina</i> Förster, 1848 [BMNH]	(2)
	<i>sorbi</i> (Linnaeus, 1758) [IDH]	(3)
	<i>stricklandi</i> (Caldwell, 1939) [USNM]	(4)
	<i>ulmi</i> Förster, 1848 [BMNH]	(5)

<i>Hepatopsylla</i> Ossiannilsson, 1970	P-HEPATO
<i>albagena</i> (Caldwell, 1938) [USNM]	(1)
<i>ambigua</i> Förster, 1848 [IDH]	(2)
<i>brunneipennis</i> Edwards, 1896 [BMNH]	(3)
<i>moscovita</i> Andrianova, 1848 [BMNH]	(4)
<i>myrtilli</i> Wagner, 1847 [IDH]	(5)
* <i>nigrita</i> (Zetterstedt, 1828) [IDH]	(6)
? <i>parallela</i> Crawford, 1914 [USNM]	(7)
<i>palmeni</i> Löw, 1883 [IDH]	(8)
<i>pulchra</i> (Zetterstedt, 1840) [BMNH]	(9)
<i>pyri</i> (Linnaeus, 1758) [USNM]	(10)
<i>pyricola</i> Förster, 1848 [BMNH]	(11)
<i>saliceti</i> Förster, 1848 [BMNH]	(12)
<i>visci</i> Curtis, 1835 [BMNH]	(13)
? <i>Hepatopsylla</i> Ossiannilsson, 1970	
<i>alba</i> Crawford, 1914 [USNM]	(14)
<i>americana</i> Crawford, 1914 [USNM]	(15)
<i>annulata</i> Fitch, 1851 [USNM]	(16)
<i>brevistigmata</i> Patch, 1912 [USNM]	(17)
? <i>coryli</i> Patch, 1912 [USNM]	(18)
<i>hamata</i> Tuthill, 1944 [IDH]	(19)
<i>hirsuta</i> Tuthill, 1938 [USNM]	(20)
<i>magnicauda</i> Crawford, 1914 [USNM]	(21)
<i>minor</i> v. <i>flava</i> Crawford, 1914 [USNM]	(22)
<i>minuta</i> Crawford, 1914 [USNM]	(23)
<i>negundinis</i> Mally, 1895 [USNM]	(24)
<i>rhododendri</i> Puton, 1871 [USNM]	(25)
<i>sinuata</i> Crawford, 1914 [USNM]	(26)
<i>subspiculata</i> Hodkinson, 1976 [IDH]	(27)
<i>Osmopsylla</i> Loginova, 1978	P-OSMOPS
* <i>ribesiae</i> Crawford, 1911 [USNM]	
<i>Psylla</i> Geoffroy, 1862	O-PSYLLA
* <i>alni</i> Linnaeus, 1758 [BMNH]	(1)
<i>betulaenanae</i> Ossiannilsson, 1970 [IDH]	(2)
<i>carpinicola</i> Crawford, 1914 [USNM]	(3)
<i>floccosa</i> Patch, 1909 [USNM]	(4)
<i>galeaformis</i> Patch, 1911 [USNM]	(5)
<i>striata</i> Patch, 1911 [USNM]	(6)
<i>trimaculata</i> Crawford, 1911 [USNM]	(7)
<i>Thamnopsylla</i> Loginova, 1978	P-THAMNO
<i>melanoneura</i> Förster, 1848 [BMNH]	(1)
* <i>pyrisuga</i> Förster, 1848 [BMNH]	(2)
<i>rhamnicola</i> Scott, 1876 [BMAG]	(3)
? <i>Thamnopsylla</i> Loginova, 1978	
<i>magna</i> Crawford, 1914 [USNM]	(4)
<i>media</i> Tuthill, 1943 [USNM]	(5)
<i>pruni</i> (Scopoli, 1763) [IDH]	(6)
sp. near <i>simlae</i> Crawford, 1912 [BMNH]	(7)
subgenus not certain	PSYLLA
<i>phoradendrae</i> Tuthill, 1939 [USNM]	(1)
<i>pulchella</i> Löw, 1878 [BMNH]	(2)
† <i>Spanioneura</i> Förster, 1848	SPANIONE
* <i>fonscolombii</i> Förster, 1848 [BMNH]	
Unplaced	
† <i>Arepuna</i> Tuthill, 1959	AREPUNA
<i>A. sp.</i> [USNM]	
† <i>Epipsylla</i> Kuwayama, 1907	EPIPSYLL
<i>E. sp.</i> (A) [BMNH]	(1)
<i>E. sp.</i> (B) [BMNH]	(2)

† <i>Freysuila</i> Aleman, 1887	FREYSUIL
<i>F.</i> sp. [USNM]	
† <i>Heteropsylla</i> Crawford, 1914	HETEROPS
<i>incisa</i> (Šulc, 1914) [BMNH]	(1)
* <i>texana</i> Crawford, 1914 [USDAC]	(2)
† <i>Isogonoceraia</i> Tuthill, 1964	ISOGONOC
<i>divergipennis</i> White & Hodkinson, 1980 [BMNH]	
† <i>Mitropsylla</i> Crawford, 1914	MITRAPS
? <i>deserata</i> Caldwell, 1944 [USNM]	
† <i>Neopsyllia</i> Caldwell, 1947	NEOPSYLL
<i>erythrinae</i> (Lizer, 1918) [USNM]	(1)
sp. [USNM]	(2)
† <i>Pexopsylla</i> Jensen, 1957	PEXOPSYL
* <i>cercocarpi</i> Jensen, 1957 [USNM]	
† <i>Platycorypha</i> Tuthill, 1945	PLATYCOR
* <i>princeps</i> Tuthill, 1945 [USNM]	
† <i>Retroacizzia</i> Heslop-Harrison, 1961	RETACIZZ
* <i>antennata</i> Heslop-Harrison, 1961 [BMNH]	
† <i>Trigonon</i> Crawford, 1920	TRIGONON
* <i>longicornis</i> (Crawford, 1919) [USNM]	

SPONDYLIASPIDIDAE

Spondyliaspidinae

<i>Spondyliaspis</i> Signoret, 1879	SPONDYLI
<i>S.</i> sp. [BMNH]	
† <i>Cardiaspina</i> Crawford, 1911	CARDIASP
<i>albitextura</i> Taylor, 1962 [BMNH]	(1)
<i>densitexta</i> Taylor, 1962 [IDH]	(2)
<i>squamula</i> Taylor, 1962 [TRL]	(3)
sp. [TRL]	(4)
† <i>Creiis</i> Scott, 1882	CREIIS
<i>C.</i> sp. [TRL]	
† <i>Ctenarytaina</i> Ferris & Klyver, 1932	CTENARYT
* <i>eucalypti</i> (Maskell, 1890) [BMNH]	
† <i>Eucalyptolyma</i> Froggatt, 1901	EUCALYPT
<i>E.</i> sp. [BMNH]	
† <i>Glycaspis</i> Taylor 1960	GLYCASPI
<i>baileyi</i> Moore, 1961 [BMNH]	(1)
<i>imponens</i> Moore, 1961 [BMNH]	(2)
<i>rivalis</i> Moore, 1961 [BMNH]	(3)
<i>aggregata</i> Moore, 1961 [BMNH]	(4)
<i>conflecta</i> Moore, 1961 [BMNH]	(5)
<i>conserta</i> Moore, 1961 [BMNH]	(6)
<i>cyanoreios</i> Moore, 1961 [BMNH]	(7)
<i>orientalis</i> Moore, 1961 [BMNH]	(8)
<i>salebrosa</i> Moore, 1961 [BMNH]	(9)
† <i>Phellopsylla</i> Taylor 1960	PHELLOPS
<i>P.</i> sp. [TRL]	

Pachypsyllinae

<i>Pachypsylla</i> Riley, 1883	PACHYPSY
? <i>celtidisgemma</i> Riley, 1883 [USDAC]	(1)
<i>celtidismamma</i> (Riley, 1876) [USDAC]	(2)
<i>celtidisvesiculum</i> Riley, 1883 [USDAC]	(3)
<i>japonica</i> Miyatake, 1968 [USNM]	(4)
* <i>venusta</i> (Osten-Sacken, 1861) [USDAC]	(5)
<i>Tetragonocephala</i> Crawford, 1914	TETRAGON
<i>T.</i> sp. [described from Ferris, 1926]	

TRIOZIDAE

Bactericerinae	
Triozamiini	
<i>Triozamia</i> Vondracek, 1963	TRIOZAMI
* <i>lamborni</i> (Newstead, 1913) [BMNH]	
Unplaced	
<i>Neolithus</i> Scott, 1882	NEOLITHU
<i>N. sp.</i> [BMNH]	
Triozinae	
Eutriozini	
<i>Trichohermes</i> Kirkaldy, 1904	TRICHOCH
* <i>walkeri</i> (Förster, 1848) [BMNH]	
Paracomecini	
† <i>Leuronota</i> Crawford, 1914	LEURONOT
<i>michoacana</i> Ferris, 1828 [UC]	
Triozini	
<i>Egeirotrioza</i> Boselli, 1931	EGEIROTR
* <i>ceardi v. euphratica</i> Boselli, 1931 [BMNH]	(1)
<i>verucifica</i> Loginova, 1965 [BMNH]	(2)
sp. (A) [BMNH]	(3)
sp. (B) [BMNH]	(4)
<i>Paratrioza</i> Crawford, 1911	PARATRIO
<i>arbolensis</i> Crawford, 1910 [USNM]	(1)
<i>cockerelli</i> (Sülc, 1909) [USNM]	(2)
<i>lavatae</i> (Van Duzee, 1925) [USNM]	(3)
<i>maculipennis</i> (Crawford, 1910) [USNM]	(4)
<i>Trioza</i> Förster, 1848	
<i>Bactericera</i> Puton, 1876	T-BACTER
<i>crithmi</i> Löw, 1880 [BMAG]	(1)
? <i>curvatinerwis</i> Förster, 1848 [BMNH]	(2)
? <i>nigricornis</i> Förster, 1848 [USNM]	(3)
<i>salicivora</i> Reuter, 1876 [USNM]	(4)
? <i>Bactericera</i> Puton, 1876	
<i>atkasookensis</i> Hodkinson, 1978 [IDH]	(5)
<i>aylmeriae</i> Patch, 1912 [USNM]	(6)
<i>frontalis</i> Crawford, 1910 [USNM]	(7)
<i>obtusata</i> Patch, 1911 [IDH]	(8)
<i>tripunctata</i> (Fitch, 1851) [USNM]	(9)
<i>Heterotrioza</i> Dobreanu & Manolache, 1962	T-HETERO
<i>alacris</i> Flor, 1861 [BMNH]	(1)
<i>albiventris</i> Förster, 1848 [BMAG]	(2)
<i>remota</i> Förster, 1848 [IDH]	(3)
<i>chenopodii</i> Reuter, 1876 [BMNH]	(4)
? <i>Heterotrioza</i> Dobreanu & Manolache, 1962	
<i>lobata</i> Crawford, 1914 [USNM]	(5)
<i>magnoliae</i> (Ashmead, 1881) [USNM]	(6)
<i>minuta</i> Crawford, 1910 [USNM]	(7)
<i>obsoleta</i> (Buckton, 1900) [BMNH]	(8)
<i>litseae</i> ?Bordage, 1914 [BMNH]	(9)
<i>Megatrioza</i> Crawford, 1915	T-MEGATR
<i>diospyri</i> (Ashmead, 1881) [USNM]	(1)
<i>hirsuta</i> (Crawford, 1912) [BMNH]	(2)
<i>incidata</i> Tuthill, 1945 [USNM]	(3)
<i>palmicola</i> Crawford, 1918 [USNM]	(4)
<i>vitiensis</i> (Kirkaldy, 1907) [BMNH]	(5)
<i>Trioza</i> Förster, 1848	T-TRIOZA
<i>cinnamomi</i> (Boselli, 1930) [BMNH]	(1)
? <i>marginepunctata</i> Flor, 1861 [USNM]	(2)
* <i>urticae</i> (Linnaeus, 1758) [BMNH]	(3)

? <i>Trioza</i> Förster, 1848	
<i>albifrons</i> Crawford, 1910 [USNM]	(4)
<i>bakeri</i> Crawford, 1910 [USNM]	(5)
<i>beameri</i> Tuthill, 1939 [USNM]	(6)
<i>erytraea</i> (Del Guercio, 1918) [BMNH]	(7)
<i>falcata</i> (Ferris & Klyver, 1932) [BMNH]	(8)
<i>panacis</i> Maskell, 1890 [BMNH]	(9)
<i>phoradendrae</i> Tuthill, 1939 [USNM]	(10)
<i>quadripunctata</i> Crawford, 1910 [USNM]	(11)
<i>vitreoradiata</i> (Maskell, 1879) [BMNH]	(12)
subgenus not certain	TRIOZA
? <i>anceps</i> Tuthill, 1944 [USNM]	(1)
sp. [USNM]	(2)
† <i>Aacanthocnema</i> Tuthill & Taylor, 1955	AACANTHO
*? <i>casuarinae</i> (Froggatt, 1901) [IDH]	
† <i>Ceropsylla</i> Riley, 1884	CEROPSYL
? <i>martorelli</i> Caldwell, 1942 [USNM]	(1)
? <i>sideroxyli</i> Riley, 1883 [UC]	(2)
sp. [USNM]	(3)
† <i>Crawforda</i> Caldwell, 1940	CRAWFORD
<i>triopsyllina</i> Caldwell, 1940 [USNM]	
† <i>Hevaheva</i> Kirkaldy, 1902	HEVAHEVA
<i>swezeyi</i> Crawford, 1928 [USNM]	
† <i>Kuwayama</i> Crawford, 1911	KUWAYAMA
<i>pisonia</i> Caldwell, 1940 [USNM]	
† <i>Swezeyana</i> Caldwell, 1940	SWEZEYAN
<i>elongagena</i> Caldwell, 1940 [USNM]	
† <i>Triozoidea</i> Crawford, 1911	TRIOZOID
<i>silvestris</i> Tuthill, 1959 [USNM]	

Table 2 Numbers of genera and species examined in each psyllid family.

Family	Genera examined	Species examined
APHALARIDAE	19	51
CARSIDARIDAE	21	43
LIVIIDAE	1	5
PSYLLIDAE	30	119
SPONDYLIASPIDIDAE	9	24
TRIOZIDAE	14	61
TOTAL	94	303

skin was by the presence of a pharate adult within. Such specimens had at least one tarsal segment separate from the tibiotarsus of the hindleg (and usually the fore and midlegs as well). It was therefore assumed that the maximum differentiation of tarsi from the tibia occurred in the final instar. As a further check the size of the final instar nymph was compared with the adult of the same species. With experience the size of the wing-pads relative to the body proved to be a further confirmatory character.

Table 3 Numbers of species and genera, and total genera recorded from each zoogeographic region.

Region	Species examined	Genera examined	Total recorded genera
AUSTRALASIAN	21	12	27
AUSTRO-ORIENTAL	2	20*	34
ETHIOPIAN	31	28	36
HAWAIIAN	6	6	9
MALAGASIAN	1	4*	4
NEARCTIC	100	24	30
NEOTROPICAL	36	24	52
NEW ZEALAND	4	5	7
ORIENTAL	23	34*	50
PACIFIC	4	10*	17
PALAEARCTIC	75	29	59

*Figure includes species collected outside the region.

Morphology of final instar nymphs

Pflugfelder (1941) gives a general account of nymphal morphology. The following account is intended as an explanation of terminology, a discussion of possible homology and an indication of the taxonomic distribution of attributes within the superfamily Psylloidea. Major body parts are shown in Figures 2-4.

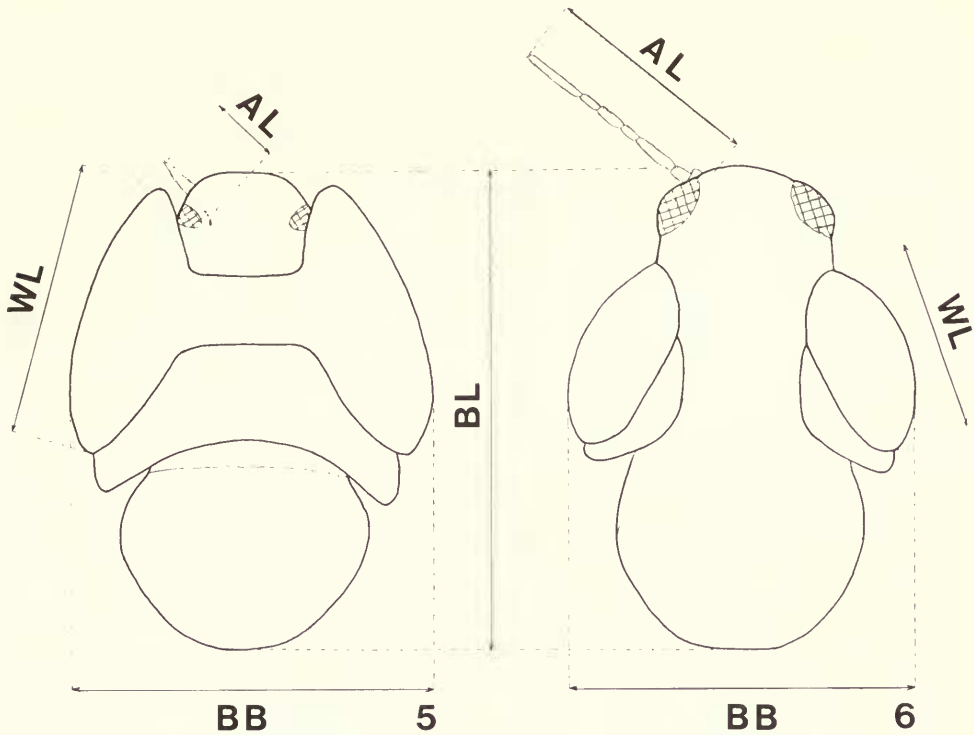
General form

Nymphal psyllids are generally dorso-ventrally flattened, a condition reaching its maximum expression in pit-gall inhabiting species, e.g. many *Trioza* spp. (Fig. 4). Ferris (1925) defined two morphological types of nymph, i.e. 'psylline' and 'triozine'. This division was made on the basis of wing-pad shape. The 'psylline' type (Fig. 2) does not have the forewing-pad produced anteriorly into a prominent humeral lobe and the apical extremity projects prominently from the contour of the body. In the 'triozine' type there is an anteriorly produced humeral lobe (Fig. 4) to the forewing-pad and the margins of the pads are confluent with the body margin. Rahman (1932) defined a third type of nymph in which the humeral lobe is present but not produced anteriorly and the forewing-pad margin is parallel to the general body contour. He termed this the 'pauropsylline' type (Fig. 3) and gave examples of each of the three nymphal forms, e.g. *Aphalara calthae* and *Pauropsylla depressa* ('pauropsylline'), *Paracarsidara gigantea* and *Psylla alni* ('psylline') plus *Diaphorina citri* and *Trioza urticae* ('triozine'). These descriptions of morphological types were found to be inadequate and emphasis was placed upon the characters described below.

Head

The main dorsal sclerite or pair of sclerites generally extend posteriorly so that the hind margin is posterior to the procoxae. This suggests that these sclerites are derived from a fusion of the vertex and part of the pronotum at least. This fusion is least expressed in the Spondyliaspidae, whereas complete fusion is observed in many Carsidaridae and Triozidae, especially those forming pit-galls.

The length, basal position and number of apparent segments of the antennae vary within the group. Free-living forms such as *Psylla alni* have long antennae with many apparent segments and the antennal base is on the margin of the head. Most Triozidae and *Calophya* spp. which inhabit pit-galls have short antennae, often with a total of only one apparent segment, and the



Figs 5, 6 Body measurements. 5, psylline type nymph; 6, triozine type nymph. (AL – antenna length; BB – body breadth; BL – body length; WL – forewing-pad length.) Modified from White & Hodkinson (1982).

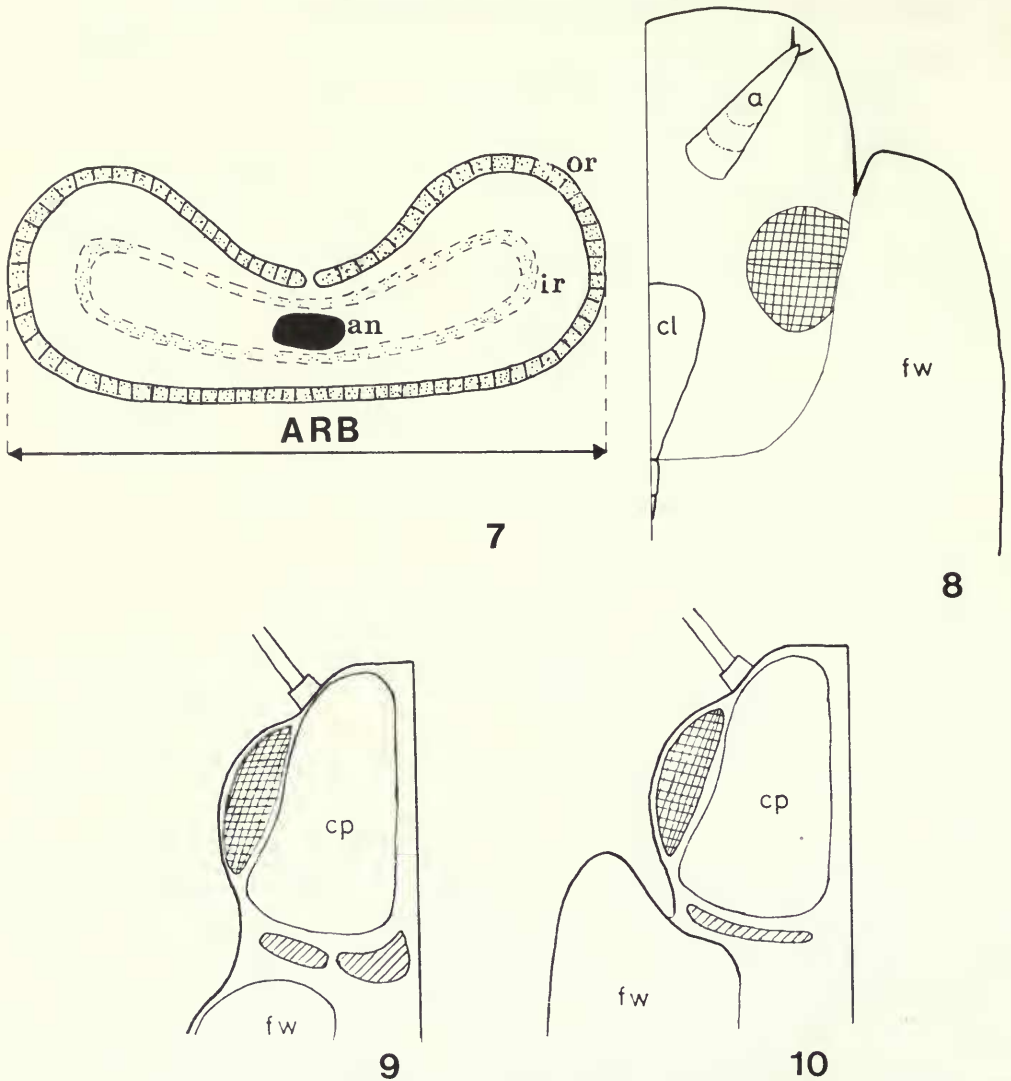
base is usually ventrally placed (Fig. 4). Adults normally have 10 antennal segments with rhinaria or antennal sensoria at the apices of segments IV, VI, VIII and IX. Most nymphs also have four rhinaria which, when 10 antennal segments are present, occur on segments IV, VI, VIII and IX. In those nymphs with fewer than 10 apparent segments fine sutures can sometimes be seen suggesting the positions where further division of the antennae will occur. However, to avoid implication of homology between nymphs and adults, the term ‘division’ will be used and the divisions will be numbered with arabic numerals. Rhinaria positions are assumed to be homologous with those of the adult and the first, second, third and fourth rhinaria are referred to as rhinaria IV, VI, VIII and IX respectively.

Some nymphal Carsidaridae (*Microceropsylla* sp. and *Calophya rotundipennis*) appear to have fewer than four rhinaria. Many adult Aphalaridae have six rhinaria placed singly at the apices of segments IV, V, VI, VII, VIII and IX. However, their nymphs have four, five or six rhinaria, e.g. the adults of *Craspedolepta artemisiae* and *C. angustipennis* have four and five respectively.

The mouthparts are of the normal sternorrhynchous type, i.e. the apex of the clypeus extends to the mesothorax. The labium is two-segmented.

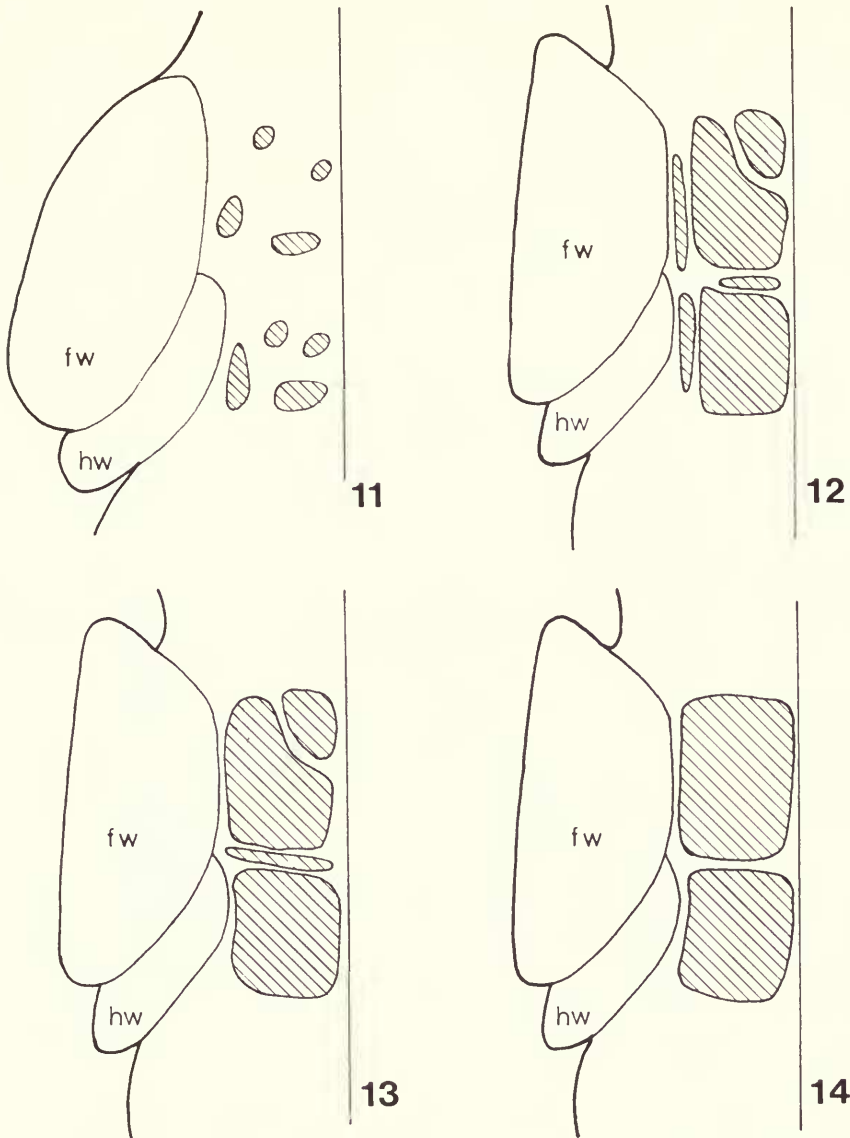
Thorax

The prothoracic tergum is assumed to be the area posterior to the eyes and anterior to the thoracic area which is continuous with the dorsal surface of the mesothoracic or forewing-pads. Most of the sclerites are generally fused with the head to form the ‘cephaloprothorax’. The Aphalaridae and Psyllidae normally have at least 2 + 2 sclerites between the mesothorax and cephaloprothorax (Fig. 9) whereas most Triozidae have 1 + 1 (Fig. 10) or no sclerites of the prothorax.



Figs 7-10 Circum-anal pore rings, antenna and prothorax forms. 7, circum-anal pore ring terminology and measurement; 8, antenna not extending beyond head margin, character N35; 9, 2 + 2 prothoracic sclerites (shaded), character N7; 10, 1 + 1 prothoracic sclerite (shaded), character N7. (a - antenna; an - anus; cl - clypeus; cp - cephaloprothorax; fw - forewing-pad; ir - inner circum-anal pore ring; or - outer circum-anal pore ring.) Fig. 7 from White & Hodkinson (1982).

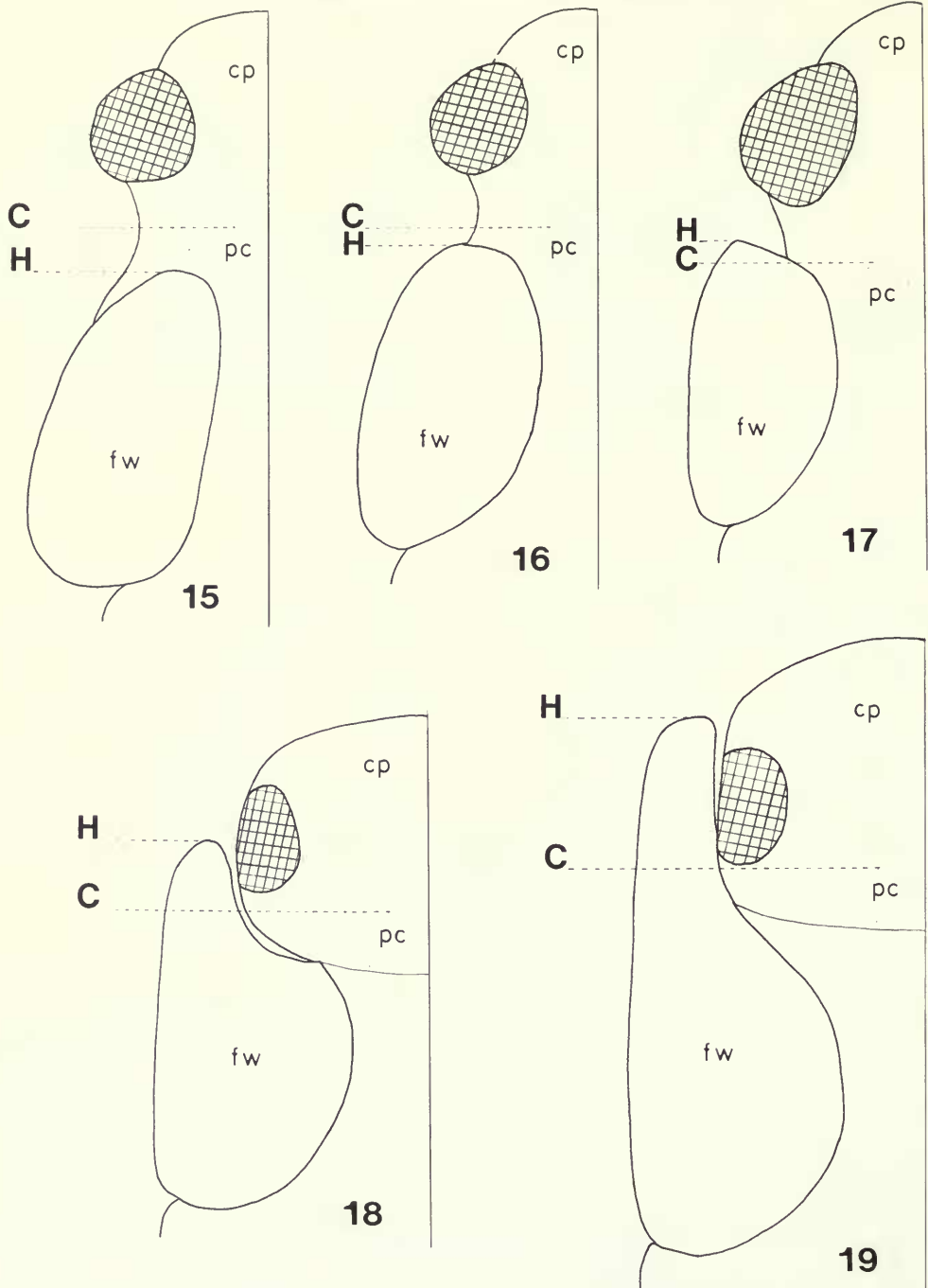
The mesothoracic tergum is taken to be the area between the lines of attachment of the forewing-pads with the body. The sclerites are completely fused in many Triozidae, especially those forming pit-galls. Some species of *Euphalerus* and *Pachypsylla* have large numbers of very small sclerites. In general the sclerites may be divided into laterals and medials. Nymphs of most Psyllidae and Spondylaspididae have small laterals and small medial sclerites (Fig. 11). The nymphs of *Aphalara* and *Diaphorina* have elongate small lateral sclerites and at least 2 + 2 enlarged medials (Fig. 12) and *Paurocephala* have no laterals but at least 2 + 2 large medials (Fig. 13). *Egeirotrioza* and *Homotoma* have 1 + 1 medial sclerites only (Fig. 14). The metathoracic tergum is assumed to be the area between the lines of attachment with the hindwing-pads with the body. The sclerites of the metathoracic tergum take the same form as those of the mesothoracic tergum.



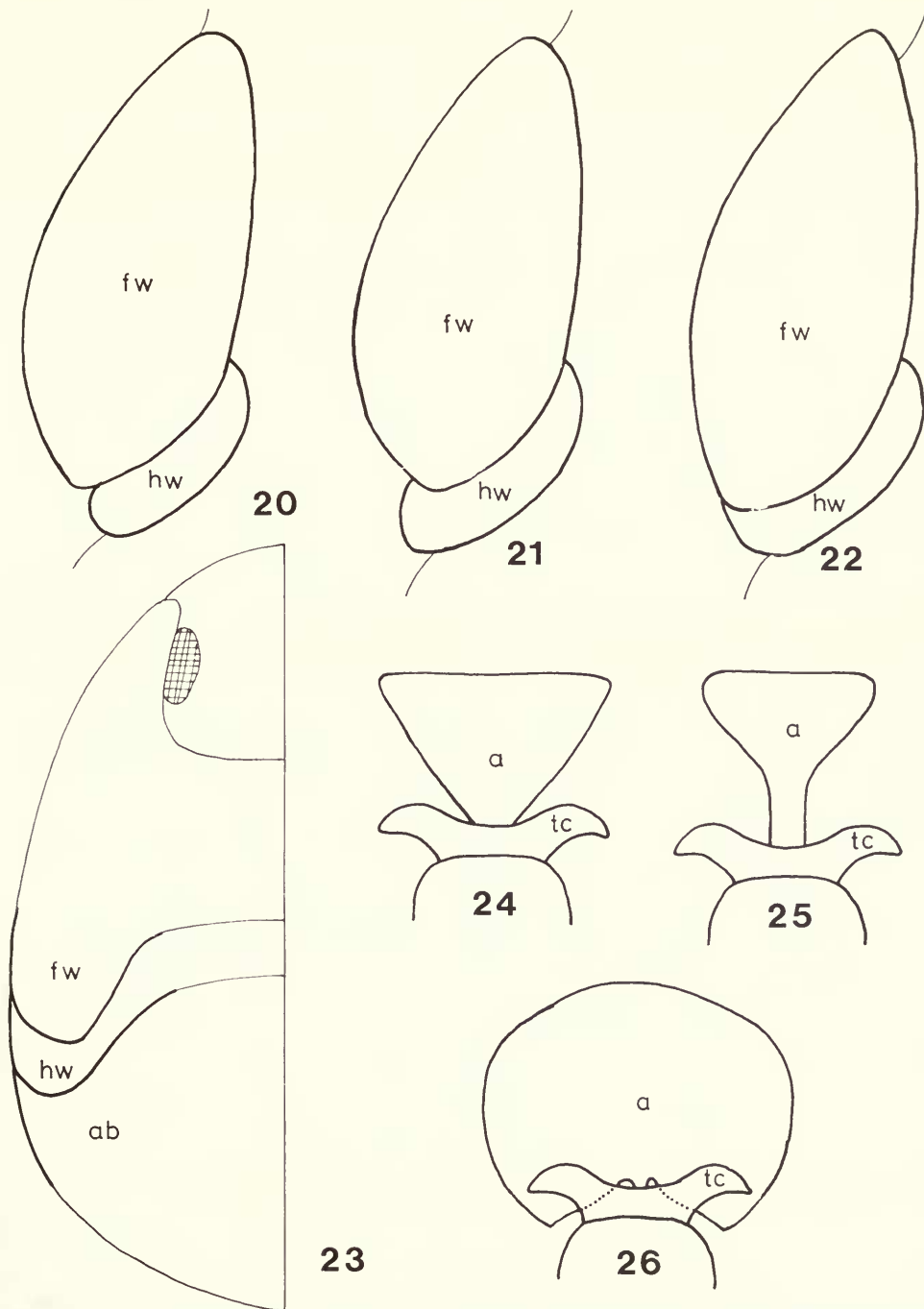
Figs 11–14 Thoracic morphology, character N8. 11, small lateral and small medial sclerites (shaded); 12, elongate lateral (adjacent to wing-pad) and 2 + 2 large medial sclerites on both meso- and metathorax; 13, no lateral and 2 + 2 large medial sclerites on both meso- and metathorax; 14, no lateral and 1 + 1 large medial sclerite on both meso- and metathorax. (fw – forewing-pad; hw – hindwing-pad.)

Many species have paired depressions on each thoracic tergite. These are very well developed on the meso- and metathoracic tergites of *Aacanthocnema casuarinae*. The dorsal thoracic and abdominal areas of some *Calophya* spp. are covered in long processes (Fig. 144) while other species of the genus have apparent ‘perforations’ in their dorsal sclerites.

The forewing-pad is extended anteriorly as a humeral lobe in many Aphalaridae, Carsidaridae, *Diaphorina* and Triozidae. In *Aphalara* and *Diaphorina* the humeral angle is normally placed away from the head margin (Fig. 17) while in Triozidae the humeral lobe may be adjacent to the eye (Fig. 19). In most species the apical (posterior) angle of the forewing-pad is adjacent or exterior to the margin of the hindwing-pad (Fig. 20). However, in some *Calophya* spp. and Triozidae the apical angle is interior to the hindwing-pad margin, and the margins of the



Figs 15–19 Humeral lobe development, character N1. 15, forewing-pad without a humeral lobe; 16, humeral lobe present, but not extending anterior to procoxa; 17, humeral lobe anterior to procoxa; 18, humeral lobe anterior to posterior margin of eye; 19, humeral lobe anterior to eye. (C – level of anterior margin of procoxa; cp – cephaloprothorax; fw – forewing-pad; H – level of humerus; pc – procoxa.)



Figs 20–26 Wing-pad and tarsal arolium forms. 20, apex of forewing-pad exterior to margin of hindwing-pad, character N2; 21, apex of forewing-pad interior to margin of hindwing-pad, but apex of hindwing-pad external to abdomen margin, characters N2 and N3; 22, apex of forewing-pad adjacent to margin of hindwing-pad and wing-pad margins confluent, character N2; 23, apex of forewing-pad interior to margin of hindwing-pad, apex of hindwing-pad interior to margin of abdomen and all margins confluent, characters N2 and N3; 24, triangular tarsal arolium, character N41; 25, triangular and petiolate arolium, character N4; 26, almost circular arolium, character N5. (a – arolium; ab – abdomen; fw – forewing-pad; hw – hindwing-pad; tc – tarsal claw.)

forewing-pad and hindwing-pad are confluent (Fig. 22). Furthermore, the hindwing-pad margin may also be confluent with the abdominal margin (Fig. 23). These features are especially well developed in species which form pit-galls. Adults of *Leptynoptera sulfurea* and *Trioza diospyri* have very reduced hindwings and thus the nymphs have reduced hindwing-pads (Fig. 48). Wing-pad tracheation is sometimes observed just before adult moult and Heslop-Harrison (1951) illustrates this for *Psylla* sp. and *Trioza* sp.

Psyllid nymphal legs lack such elaborate features as meracanthi, genual spurs, metatibial spines and metabasitarsal spines which are seen in the adult. Of the nymphs studies only two, i.e. *Paraphalaroida fremontiae* and *Togepssylla matsumurana*, appear to have articulate tarsi, as in the adult (Fig. 55). *Pachypsylla celtididisgemma* and *Pelmatobrachia* sp. also have two-segmented tarsi but they appear non articulate (Fig. 52). Most species have a single apparent tarsal segment on each leg. This appears to be homologous with segment II of the adult because the apparent 'tibia' is often constricted sub-apically at a point assumed to represent the division line between the tibia and segment I (Fig. 53). The division line is often marked by simple setae. Because this division line is not always visible the apparent tibia and tarsus will hereafter be called the tibiotarsus and the one apparent tarsal segment will be called a division. Most species have a pad between the tarsal claws. Ferris (1923, 1925, 1926), Ferris & Hyatt (1923) and Rahman (1932) term this a pulvillus. Ferris (1928*a*, 1928*b*) uses the word empodium and Lal (1937) was inconsistent. However, the correct term is arolium (Imms, 1957; Chapman, 1971). Arolia are very reduced, or absent, in some Carsidaridae, while in many Triozidae they are at least semicircular (Fig. 26) and in most Psyllidae the arolia are petiolate (Fig. 25).

Abdomen

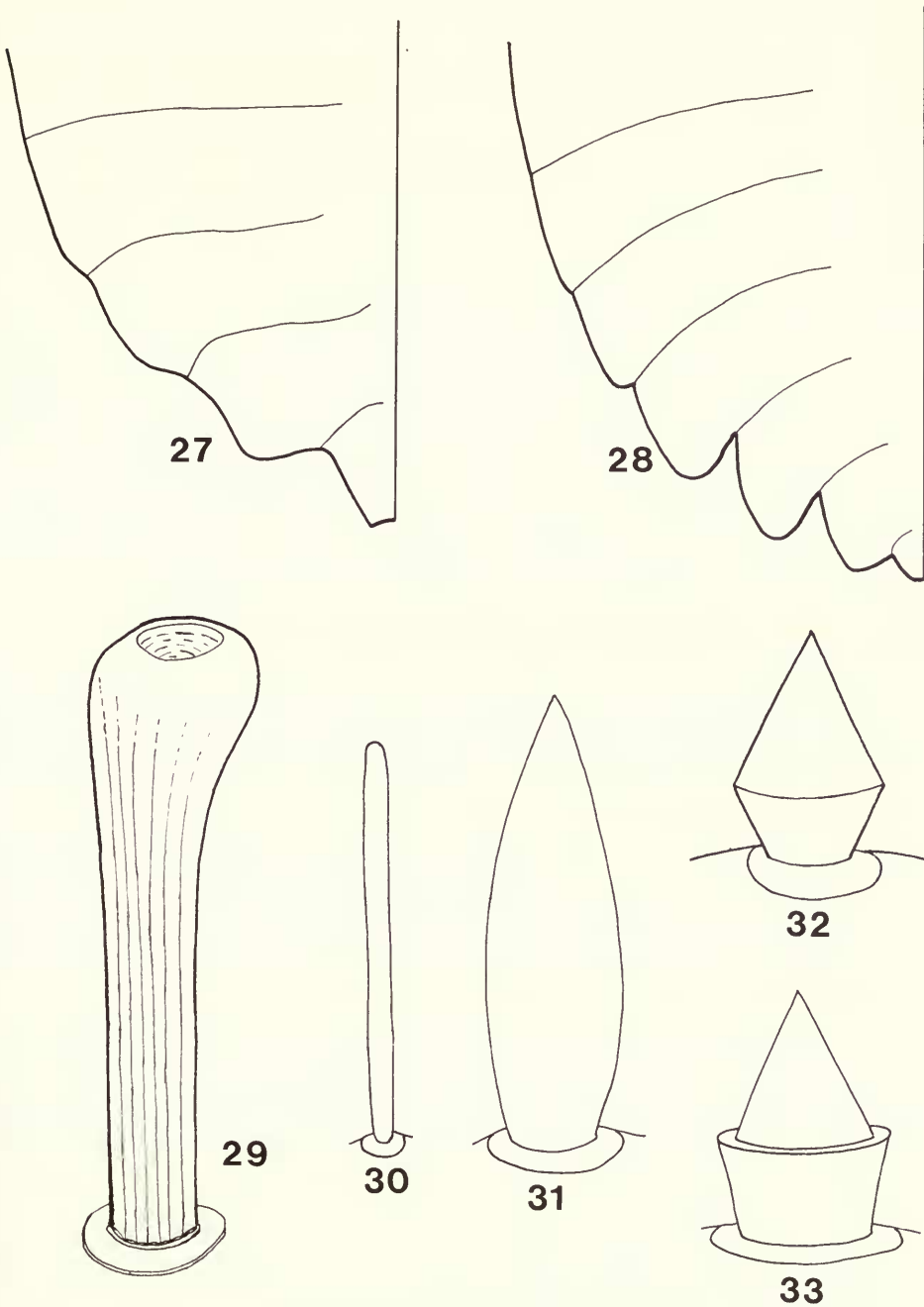
The abdomen is assumed to be any body part posterior to the join of the metathoracic tergum and hindwing-pads. Any short broad free sclerites near the base of the abdomen are discounted when describing the sclerites of the abdomen as they may equally well be of thoracic origin. In most species free sclerites and transverse rows of setae indicate the segments. In these species the sclerites are arranged at least 1 + 1 per segment but in the apical area the individual sclerites are often fused to form a caudal plate (Figs 2–4). Some Carsidaridae have completely membranous abdomens while in many Triozidae the caudal plate covers the whole abdomen (Fig. 4). With this confusing set of possibilities no attempt has been made to homologise the abdominal sclerites. The ventral abdominal surface of most species has 2 + 2 sclerites on each segment anterior to the anal plate. The anal plate is formed by a fusion of the individual sclerites in the apical area. The most lateral free sclerites surround the spiracles. Because the true base of the abdomen is poorly defined and spiracles can 'migrate' or 'float' (Heslop-Harrison, 1952*a*) or be reduced in number (Matsuda, 1976) the possible homology of the spiracles was not studied.

The abdomen of *Paurocephala* spp. has large apical tubercles (Fig. 114) and many Spondylaspidinae have lateral bulges, coincident with each apparent segment (Fig. 28). Some species have apical 'teeth' (Fig. 122). In most *Pachypsylla* spp. the central 'tooth' or 'teeth' are larger than the most lateral 'teeth' (Fig. 125) while in *Euphalerus gallicolus* the most lateral 'teeth' are enlarged (Fig. 120).

Some species of each family have the anal opening posterior (i.e. apical) while others have a ventral anal opening. In many species the sex of the final instar nymphs can be determined by the shape of the suture which extends anteriorly from the anus (Ball & Jensen, 1966; Ossiannilsson, 1970; Hodkinson, 1973).

Most species have an anal pore-field which usually surrounds the anus as a ring (Figs 7, 130–142). This ring, which is often double, is called the circum-anal pore ring by Ferris (1928*a*). The following types of anal pore-fields have been observed.

- (i) Circum-anal ring only (Fig. 111).
- (ii) Circum-anal ring plus two additional rings placed laterally to it (Fig. 110).
- (iii) Two rings each lateral to the anus and no circum-anal ring (Fig. 150).
- (iv) Four rings and no circum-anal ring (Fig. 120).



Figs 27–33 Abdomen shapes and setal types. 27, abdomen margin with lateral bulges, character N44; 28, abdomen margin serrate (typical of many Spondylaspididae), character N44; 29, capitata seta, showing hollow structure (as observed with a scanning electron microscope); 30, rod seta; 31, lanceolate seta; 32, sectaseta, pointed and without a ring; 33, sectaseta, pointed and with a ring.

- (v) Outer circum-anal ring broken at two or more places (Fig. 97).
- (vi) Circum-anal ring very small and remainder of pore-field arranged as bands (Fig. 155).
- (vii) Circum-anal ring absent – otherwise as (vi).
- (viii) Circum-anal ring plus round or ovoid groups of pores which are probably derived from an outer ring (Fig. 99).
- (ix) Small groups of pores (Fig. 154).
- (x) Individual or grouped pores arranged in rings (Fig. 123) or broken rings (Fig. 119).
- (xi) Small groups of pores dispersed in anal region, no circum-anal ring (Fig. 129).

Ferris (1928a) discussed the homology of the anal pore-field. He concluded that the pore rings of *Euphalerus gallicolus* (iv) were not homologous with the circum-anal ring. However, species were observed whose circum-anal rings were constricted, suggesting a tendency to break into separate rings, e.g. *Livia* spp. feeding on *Carex* (Fig. 111) and *Macrohomotoma gladiatum* (Fig. 148). This breakage of the circum-anal ring is complete in *Livia* spp. feeding on *Juncus* (Fig. 110) and in *M. striata* (Fig. 149). This suggests that the pore rings of *E. gallicolus* (Fig. 120) may be of similar origin, i.e. homologous with the circum-anal ring. Groups of pores (type x) may represent a reduction of pore rings (of type ii, iii or iv) as in *Eucalyptolyma* sp. (Fig. 119). Further breakdown may result in isolated pore groups (type xi) as in many Spondyliaspidiinae (Fig. 129). The homology of pore bands (type vi & vii), e.g. *Mesohomotoma hibisci* (Fig. 155), remains uncertain although they may derive from the outer circum-anal ring.

Setal types and chaetotaxy

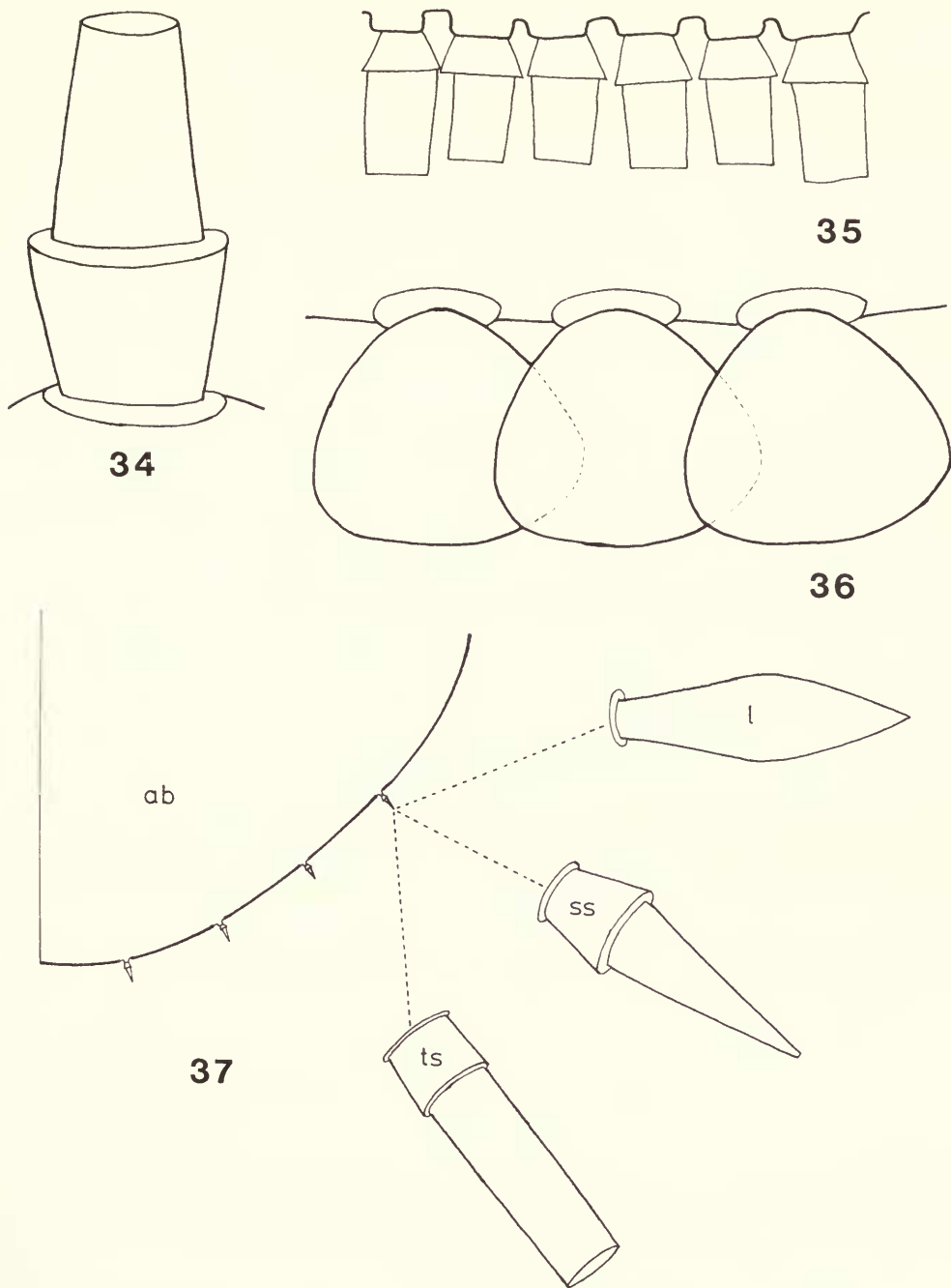
Simple setae, including the ring-based setae of Lal (1937), are simple articulated hairs showing a general distribution over many body parts in all major groups. It may be possible to homologue the positions of some of these setae within a few groups. Because this study is concerned with formation of, and the relationships between higher groups, these setae are not further considered.

Capitate setae (Ossiannilsson, 1970) or spatulate setae (Klyver, 1931; Lal, 1937) are defined as any seta which is apically dilated. Under the SEM the apex appears to be 'cup-like' (Fig. 29) and broken setae reveal a hollow structure. Capitate setae are found on the head, dorsal surface of the thorax, wing-pads, tibia and abdomen of many Psyllidae. These setae are also found singly or in pairs at the tarsal apices of many psyllids and they are best developed in most Spondyliaspidiinae (Fig. 38).

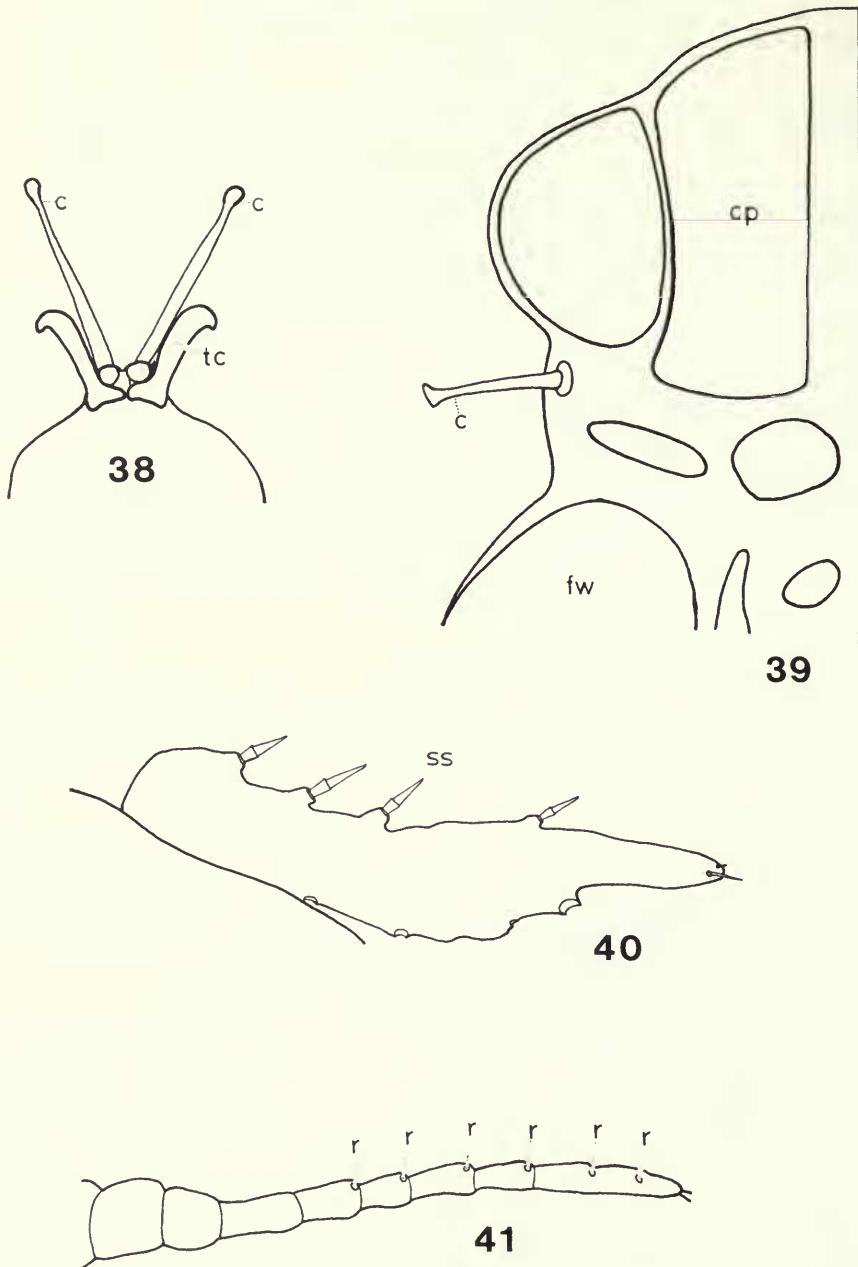
Clavate setae (Ferris, 1923) are very short setae with a narrow base broadening gradually to maximum breadth just prior to the blunt apex (Fig. 172). Clavate setae are observed in *Arepuna* sp., many *Diaphorina* spp. and some Triozidae. In some individual species of *Diaphorina* they occur together with lanceolate setae while in some Triozidae they occur together with sectasetae or scales. Clavate setae are very small and difficult to observe. In reality they may be modified lanceolate setae, sectasetae or scales.

Sectasetae (Ferris, 1923; Boselli, 1929; Lal, 1937). These include dagger-shaped and spear-shaped setae (Lal, 1937), and dagger-like setae (Klyver, 1931). Sectasetae are defined as setae having an angle (Fig. 32) or ring (Figs 33, 34), around their circumference, in the basal third which is visible under phase contrast. Sectasetae arranged in the 1 + 1, 2 + 2, 3 + 3 and 4 + 4 pattern, spaced from the next by more than their own length (Fig. 37), along the abdomen margin occur in two forms. In *Ciriactremum* spp., *Euceropysylla* spp., *Insnesia glabruscuta* and *Isogonoceraia divergipennis* they are tubular. However, these sectasetae are pointed in other Psyllidae. Species with this precise arrangement of abdomen margin sectasetae normally lack sectasetae on other body areas. The only exceptions are *Neopsyllia* spp. and *Platycorypha princeps* each of which have a single sectaseta on the hindwing-pad margin.

Pointed sectasetae (Figs 32–33) arranged in large numbers on many body areas are a feature of some Aphalaridae, some Carsidaridae and some Triozidae. However, on most Triozidae the



Figs 34–37 Setal types and chaetotactic arrangements. 34, sectaseta, truncate and with a ring; 35, truncate sectasetae on a body margin, adjacent to each other, character N25; 36, scales on a body margin (typical of many Hawaiian Triozidae); 37, the positions in which up to 4 + 4 setae are placed on the abdomen margin of many Psyllidae, and the three types of setae which occupy these positions, namely lanceolate (e.g. *Mitrapsylla deserata*), pointed sectaseta (e.g. many *Psylla* spp.) and the tubular shaped truncate sectaseta of *Ciriacrellum* spp. (ab – abdomen; l – lanceolate seta; ss – sectaseta; ts – tubular sectaseta).



Figs 38–41 Chaetotactic arrangements and antennae. 38, a pair of capitate setae at the apex of a tarsus (these setae are especially well developed in many Spondyliaspidae), characters N20–N22; 39, a capitate seta placed behind the eye, character N13. Antennae. 40, *Calophya californica*; 41, *Gyropsylla spegazziniana*. (c – capitate seta; cp – cephaloprothorax; fw – forewing-pad; r – rhinaria; ss – sectaseta; tc – tarsal claw.)

sectasetae are truncate (Fig. 34). Three distribution patterns of sectasetae could be recognised on the antennae. One row on the opposite side to the rhinaria occurs in many *Calophya* spp. (Fig. 40) while one row adjacent to the rhinaria occurs in *Diclidophlebia eastopi*. Species with more than one row (Fig. 45) are *Moraniella calodendri*, *Paraphalaroida fremontiae*, *Paurocephala* spp. and *Togepsylla matsumurana*.

Lanceolate setae (Ferris, 1923; Boselli, 1929; Rahman, 1932; Lal, 1937) are defined as stout setae with a convex profile and a constricted base (Fig. 31). The maximum breadth of the seta is normally in the basal two-thirds. Lanceolate setae are a feature of most Aphalaridae, Diaphorini and *Psyllopsis* spp. They are also observed in a few Carsidaridae (e.g. *Epicarsa* sp., *Mycopsylla fici* and *Pseudophacopteron floccosa*) and some Spondyliaspididae (*Ctenarytaina eucalypti*, *Eucalyptolyma* sp. and *Phellopsylla* sp.). *Homotoma ficus* has lanceolate setae based upon tall tubercles (Fig. 171).

Heteropsylla spp. have lanceolate setae arranged 3 + 3 in positions resembling the similarly placed sectasetae in many species of Psyllidae (Fig. 37). These lanceolate setae are treated as homologous with similarly placed sectasetae and not with other lanceolate setae.

Scales are defined as broad, apparently flat setae with a narrow base (Fig. 36) which are placed marginally on some New World and Hawaiian Triozidae.

Rod setae are long, parallel or subparallel-sided, with a constricted base (Fig. 30), and they are found covering the bodies of *Aphalaroida pithecolobia*, *Euglyptoneura robusta*, *Pexopsylla cercocarpi* and *Psylla ulmi*.

All attempts to recognise homology of setal positions across the whole of the Psylloidea failed except in one case, i.e. a single capitate seta placed laterally or sublaterally behind each eye (Fig. 39). In general the specialised setae occur in large numbers in any one body area. It is assumed that at least some of the setae in one body area of one species are homologous with some of the same type of seta in the same body area in any other species. The only exception to this rule is the sectasetae and lanceolate setae on the margin of the abdomen. Two arrangements of these setae were recognised: a set of one to four pairs spaced well apart (Fig. 37) and secondly much larger numbers with no obvious individual positions.

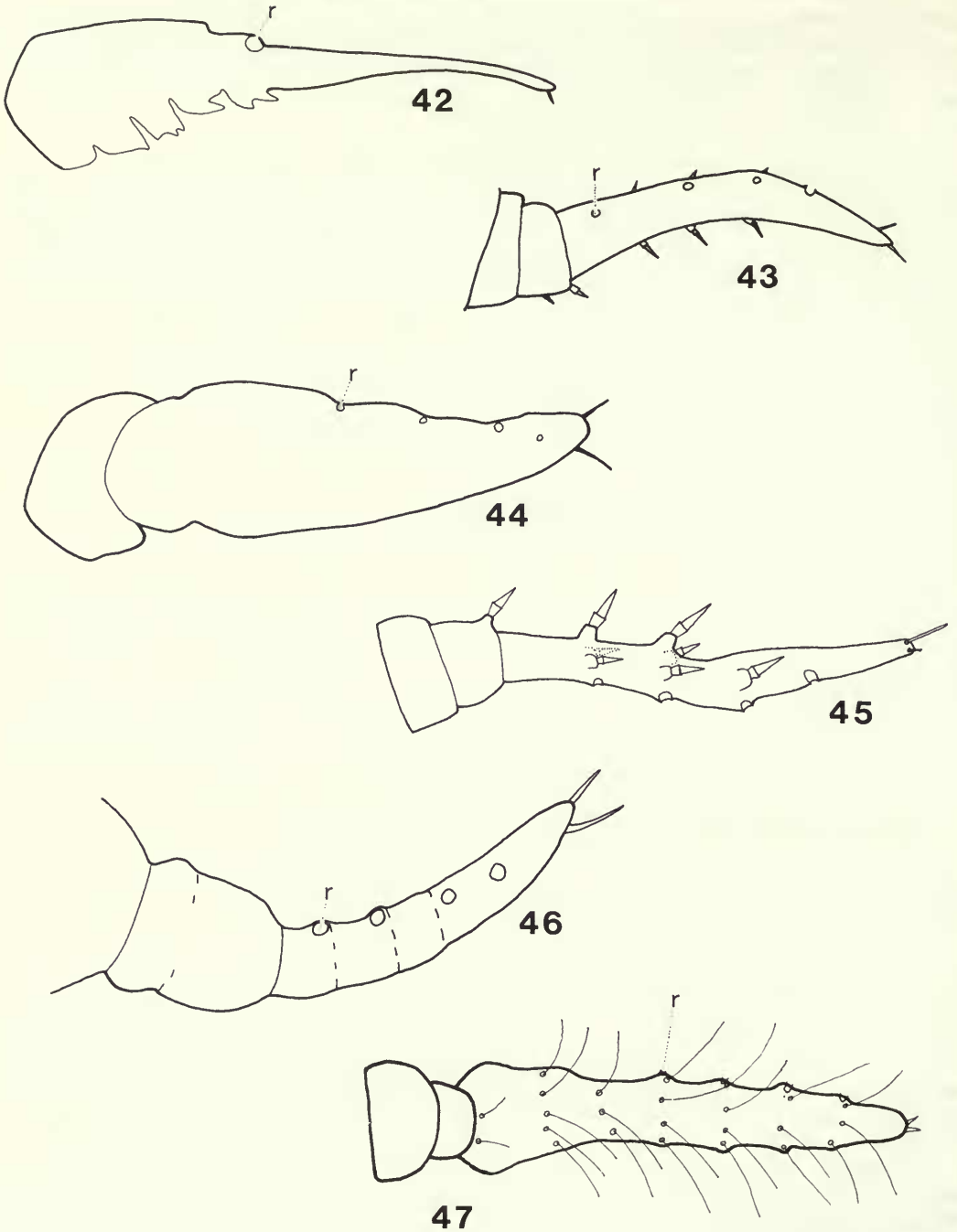
Selection of nymphal characters

A set of 88 ordered multistate and two-state characters were initially defined. From these characters those most likely to be of value in forming major groups were selected for a detailed series of analyses.

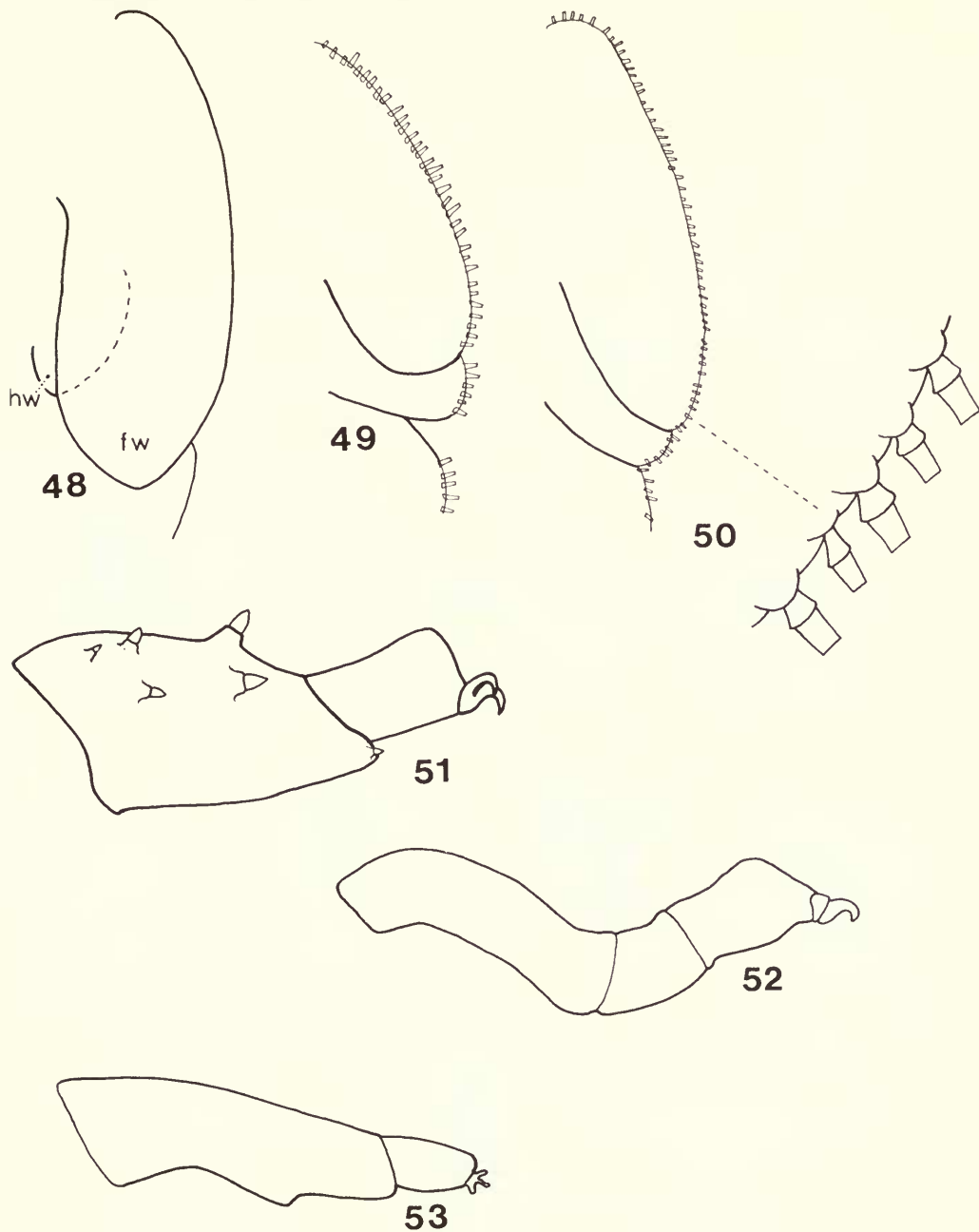
For character selection the ordered multistate characters were recoded into 120 additive two-state characters (Sneath & Sokal, 1973). Characters which correlated with large numbers of other characters were identified by the SUMRAT information statistic (Legendre & Rogers, 1972). Only those characters having a SUMRAT value in excess of the mean value were accepted (Baum, 1977). Characters selected by this method were almost identical with those selected by an examination of character eigenvector values in a principal component analysis, carried out on the original character covariance matrix (see Davies & Boratynski, 1979 for method).

After these initial analyses, 45 selected two-state characters remained and these were combined to form 34 ordered multistate and two-state characters (Table 4). Rejected characters are summarised in Table 5.

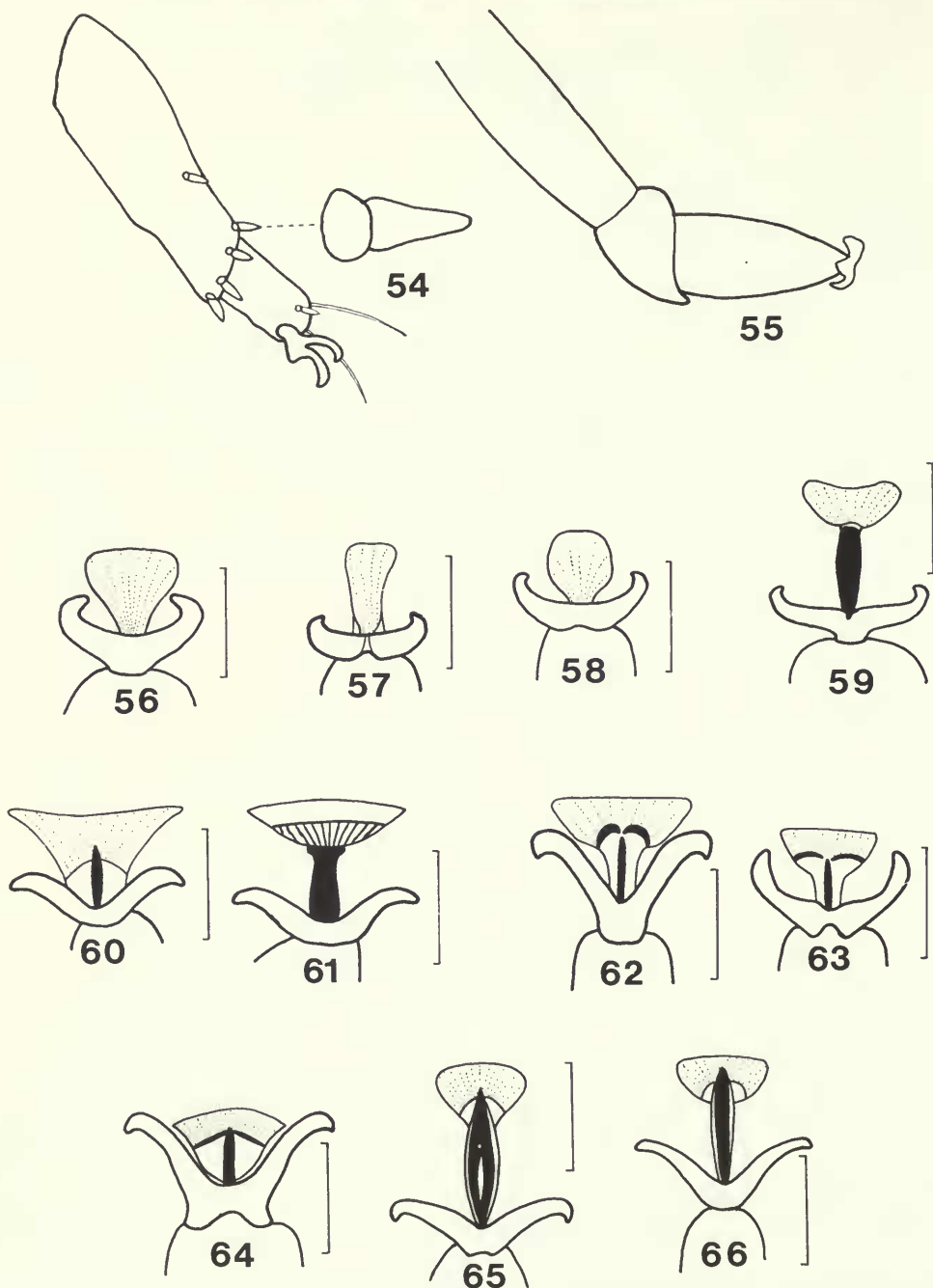
Once the number of characters has been reduced to 34, many species are identical as defined by the selected character set. Forty-eight species groups were formed, and one representative species was chosen from each (Table 6). The 134 species which remain distinct are also listed in Table 6, making a total of 182 selected species. All subsequent phenetic analyses are conducted using the 34 selected characters and the 182 selected species.



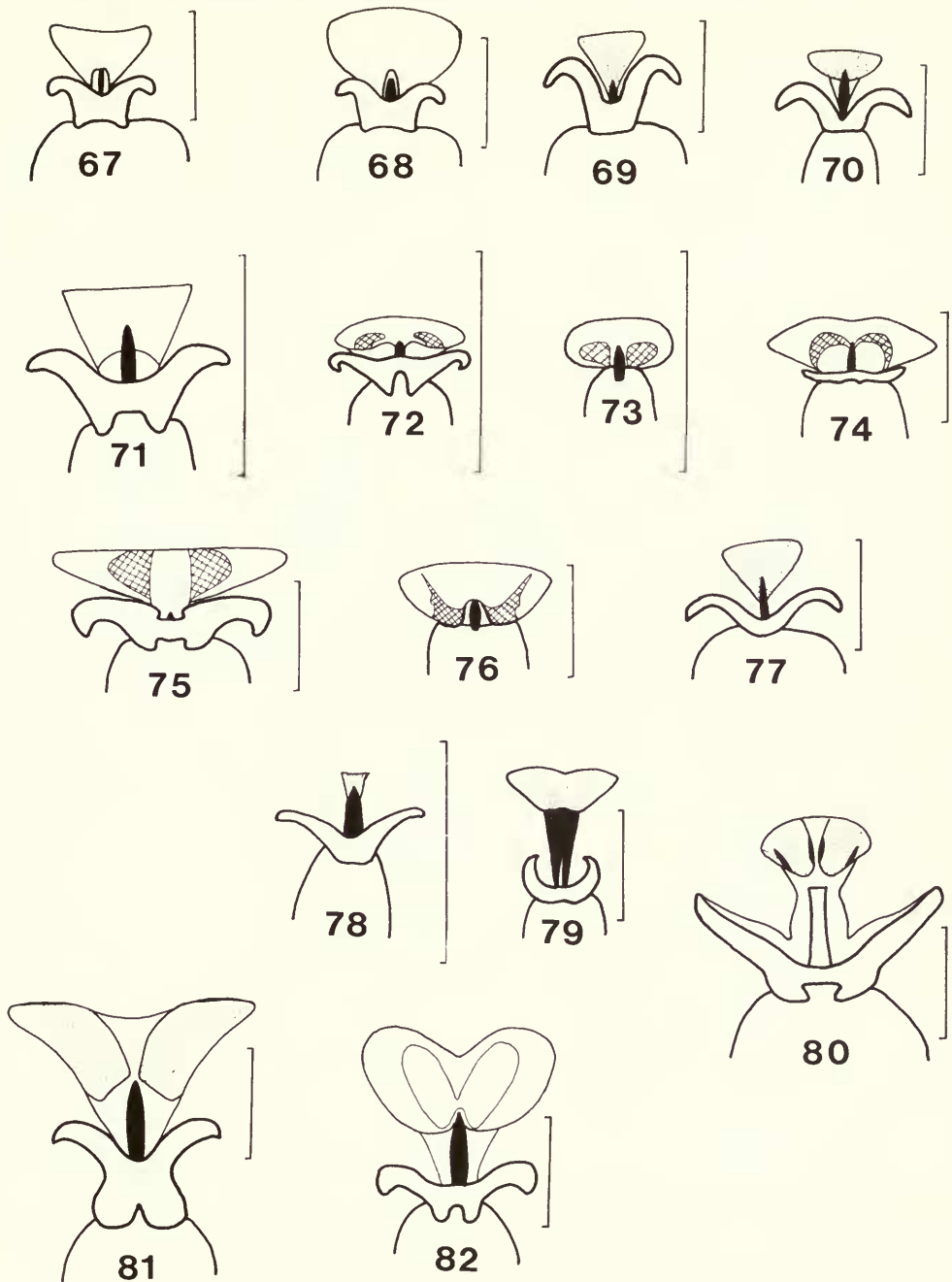
Figs 42-47 Antennae. 42, *Microceropsylla* sp.; 43, *Moraniella calodendri*; 44, *Mycopssylla gardenensis*; 45, *Paurocephala gossypii*; 46, *Pauropsylla depressa*; 47, *Phacopteron lentiginosum*. (r - rhinaria.)



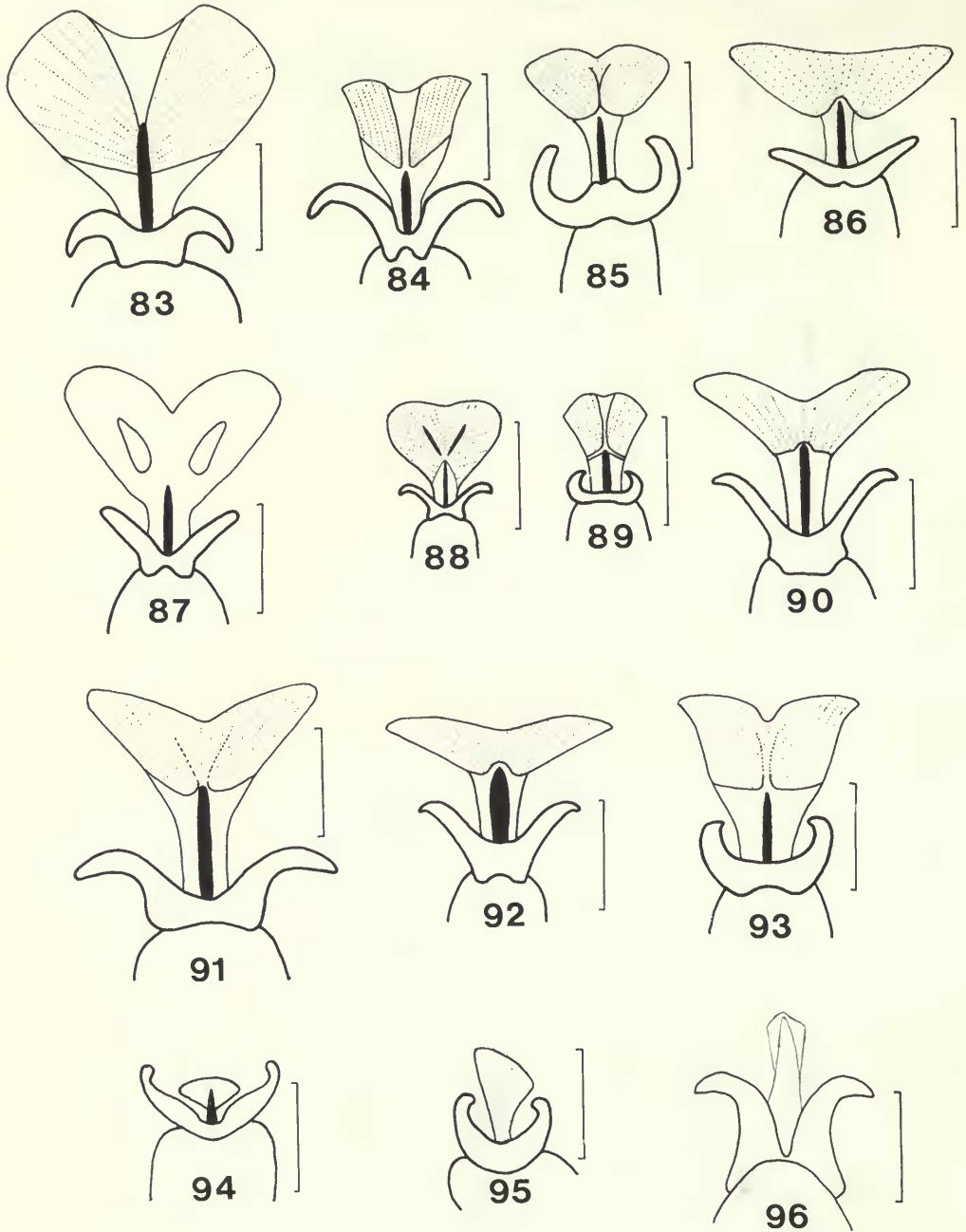
Figs 48–53 Wing-pads, hind tibia and tarsi. 48, *Leptynoptera sulfurea* wing pads, showing reduced hindwing-pad corresponding to the dipterous adult. Wing-pads and chaetotaxy, 49, *Pauropsylla trichaeta*; 50, *Trioza chenopodii*. Hind tibia and tarsi, 51, *Camarotoscena unicolor* showing tibiotarsus (tibia + tarsal segment I) and the differentiated tarsal segment II; 52, *Pelmatobrachia* sp. showing the tibia and both tarsal segments differentiated; 53, *Phytolyma fusca* showing tibiotarsus and tarsal segment II. (fw – forewing-pad; hw – hindwing-pad.)



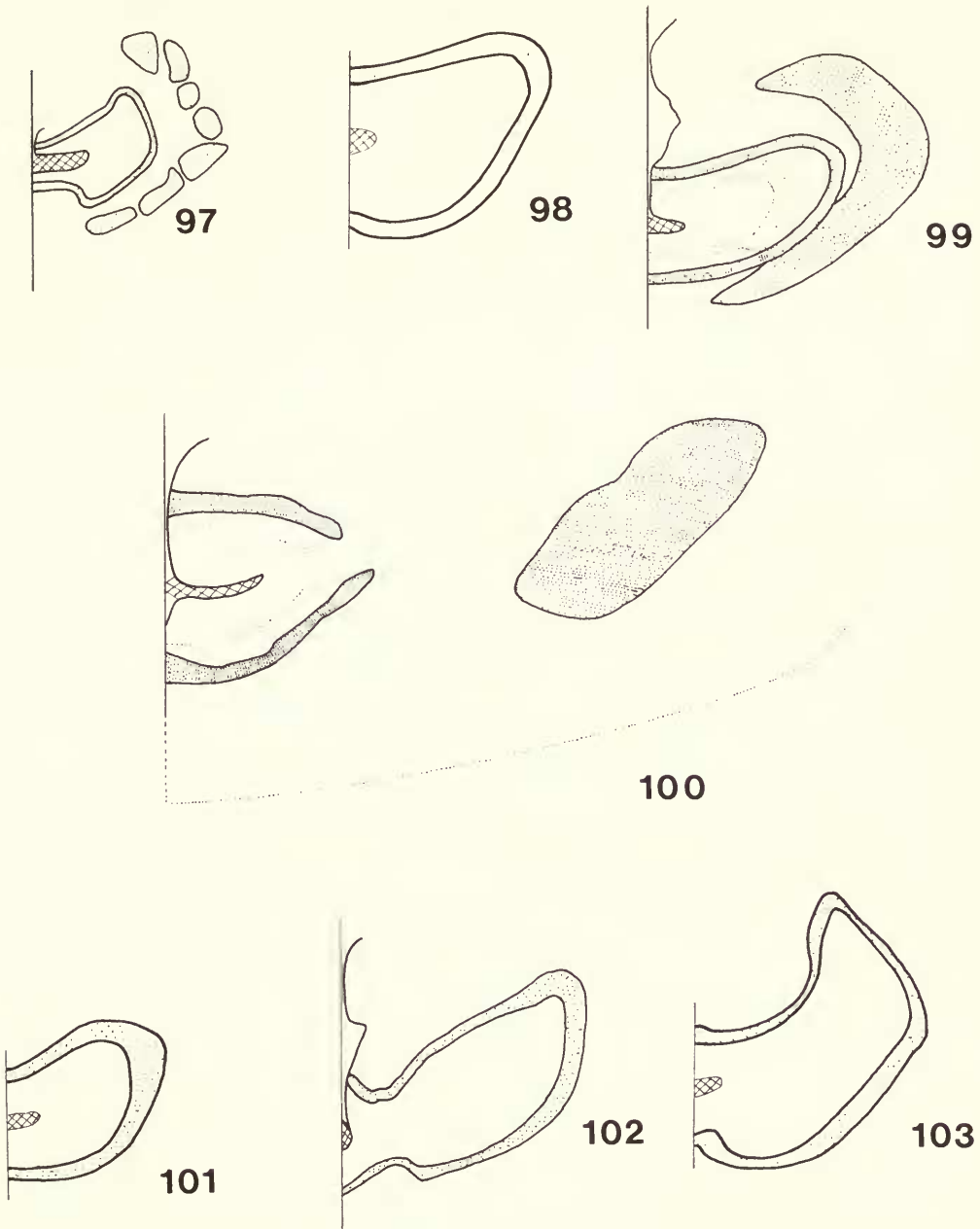
Figs 54–66 Hind tibia and tarsi, and tarsal arolia (uniguitractor shown in black). Hind tibia and tarsi, 54, *?Pseudophacopteron floccosa* (*?Chineura* sp.) showing tibiotarsus, tarsal segment II and associated setae; 55, *Togepepsylla* sp. showing both tarsal segments separate to tibia. Tarsal arolia of Aphalarinae: 56, *Aphalara persicaria*; 57, *Colposcena* sp.; 58, *Gyropsylla ilicis*. Tarsal arolium of Aphalaroidinae: 59, *Aphalaroida ? pithecolobia*. Tarsal arolium of Diaphorininae: 60, *Diaphorina solani*; 61, *Psyllopsis fraxinicola*. Tarsal arolium of Euphyllurini: 62, *Euphyllura ? aethiopica*; 63, *Neophyllura (Arbutophila) arbuti*; 64, *N. (N.) arctostaphyli*. Tarsal arolium of Paraphalaroidini: 65, *Diclidophlebia eastopi*; 66, *Paraphalaroida fremontiae*. Scale line represents 0.05 mm.



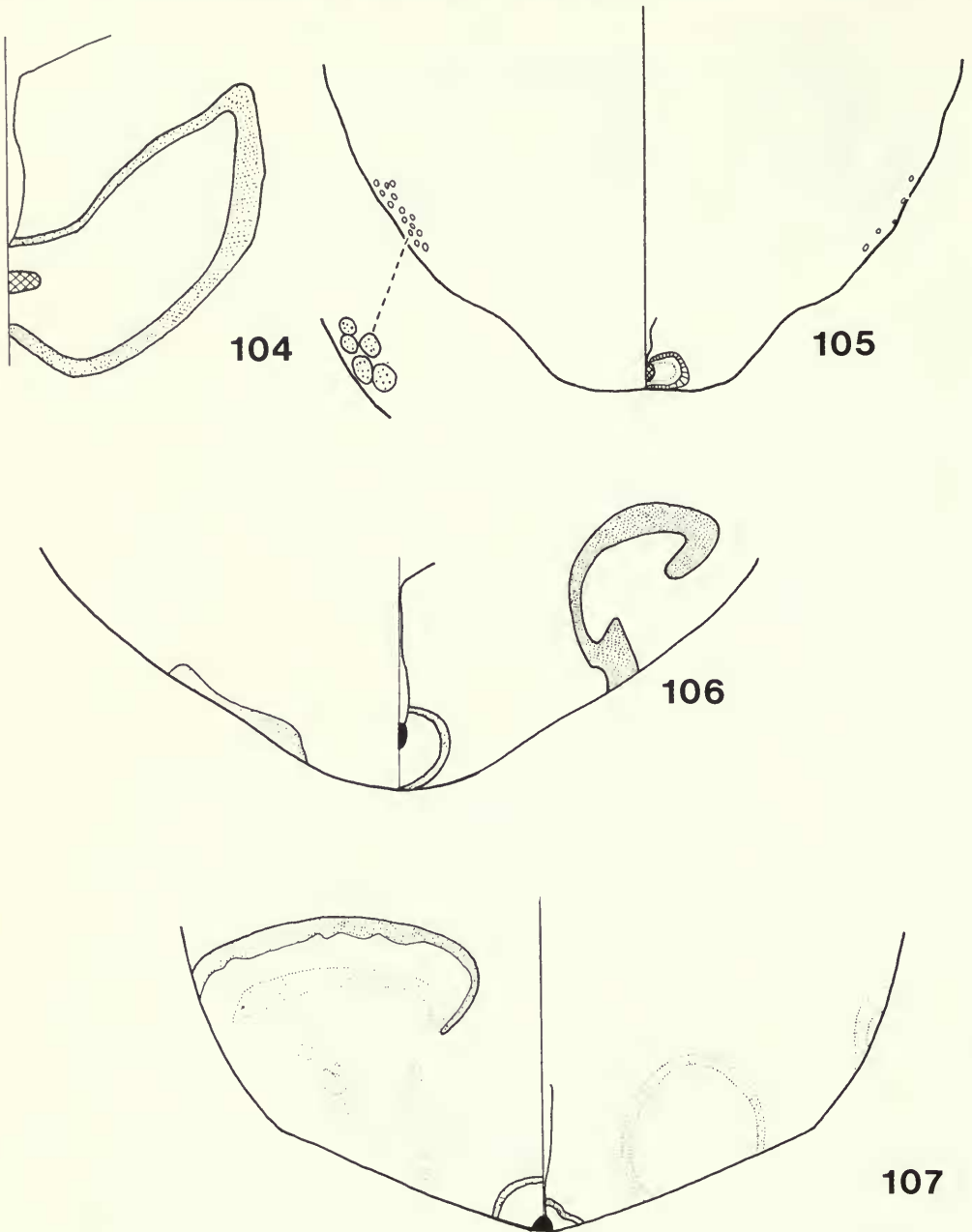
Figs 67–82 Tarsal arolia (unguitractor shown in black). Liviinae: 67, *Livia maculipennis*; 68, *L. vernalis*. Paurocephalinae: 69, *Camarotoscena unicolor*; 70, *Paurocephala urenae*. Strophingiinae: 71, *Strophingia ericae*. Rhinocolinae: 72, *Agonosцена sp. (A)*; 73, *Leurolophus vittatus*; 74, *Moraniella calodendri*; 75, *Rhinocola aceris*; 76, *Tainarys schini*. Euphalerinae: 77, *Euphalerus nidifex*; 78, *Retroacizzia antennata*. Psyllidae: 79, *Acizzia acaciaebaileyanae*; 80, *A. uncatoides*; 81, *Anomoneura mori*; 82, *Ciriactremum julbernardioides*. Scale line represents 0.05 mm.



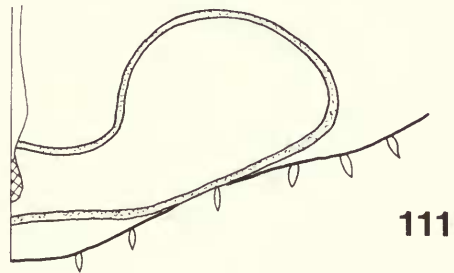
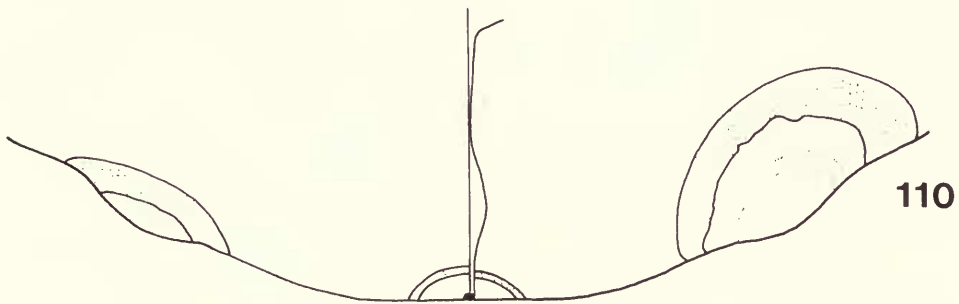
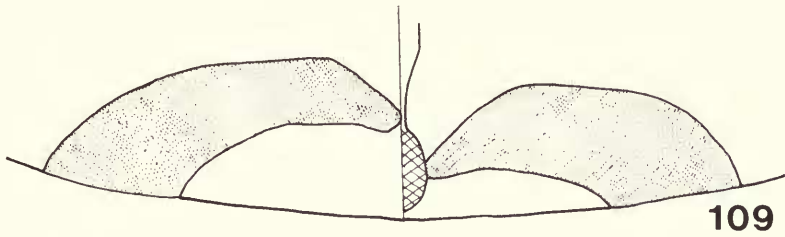
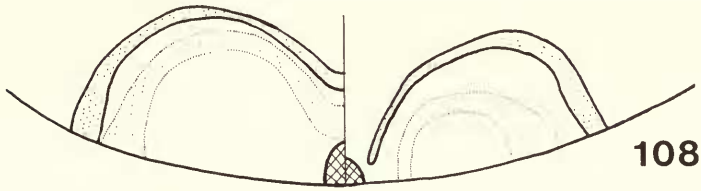
Figs 83–96 Tarsal arolia (uniguitractor shown in black). Psyllidae: 83, *Epipsylla* sp. (A); 84, *Epipsylla* sp. (B); 85, *Euceropsylla cayeyensis*; 86, *Freysuila* sp.; 87, *Insnesia disjuncta*; 88, *Isogonoceraia* sp.; 89, *Mitrapssylla deserata*; 90, *Neopsyllia erythinae*; 91, *Platycorypha princeps*; 92, *Psylla parallela*; 93, *Trigonon longicornis*. Phacopterionidae: 94, *Pseudophacopteron* sp. (A). Triozidae: 95, *Egeirotrioza* sp. (A); 96, *Trioza hirsuta*. Scale line represents 0.05 mm.



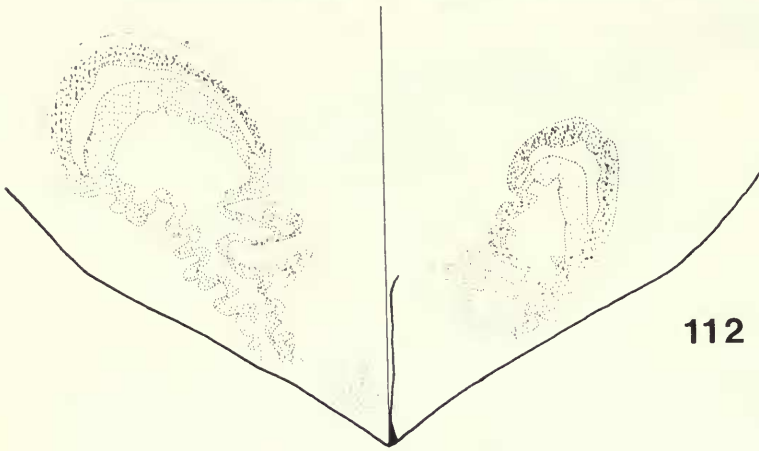
Figs 97-103 Anal pore-fields of Apalaridae. 97, *Agonoscena* sp. (A); 98, *Aphalara polygoni*; 99, *Camarotoscena speciosa*; 100, *C. unicolor* (broken line indicates position of abdomen margin); 101, *Craspedolepta nebulosa*; 102, *C. suaedae*; 103, *C. subpunctata*.



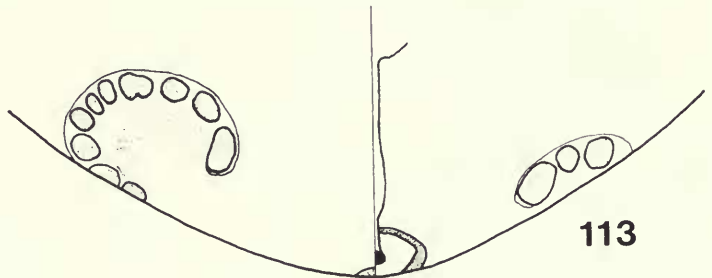
Figs 104–107 Anal pore-fields of Aphalaridae. 104, *Craspedolepta* ? *vancouverensis*; 105, *Ctenarytaina eucalypti* (inset shows detail of pore-field); 106, *Diclidophlebia* ? *eastopi*; 107, *Euphyllura* ? *aethiopica*.



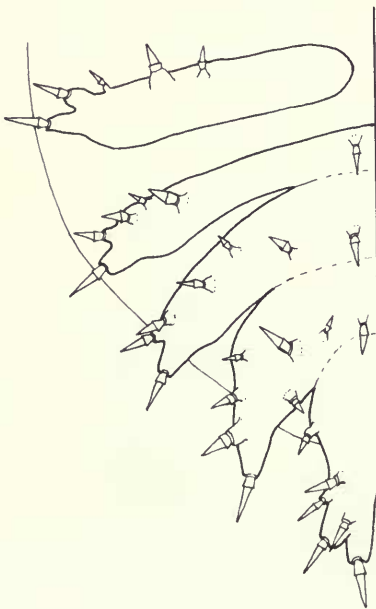
Figs 108–111 Anal pore-fields of Aphalaridae. 108, *Gyropsylla ilicis*; 109, *Leurolophus vittatus*; 110, *Livia maculipennis*; 111, *L. vernalis*.



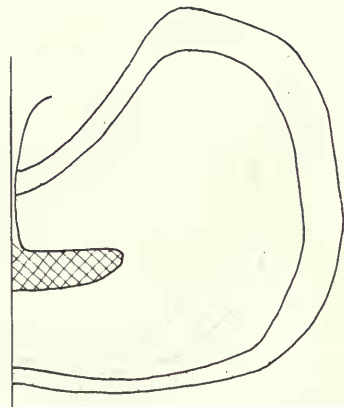
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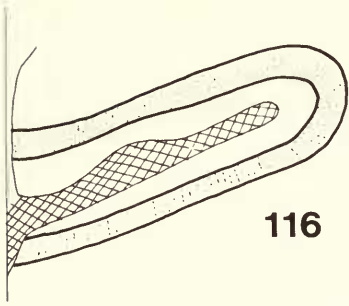


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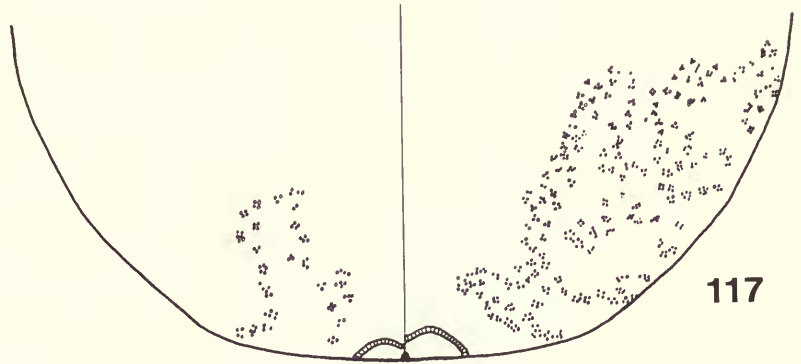


115

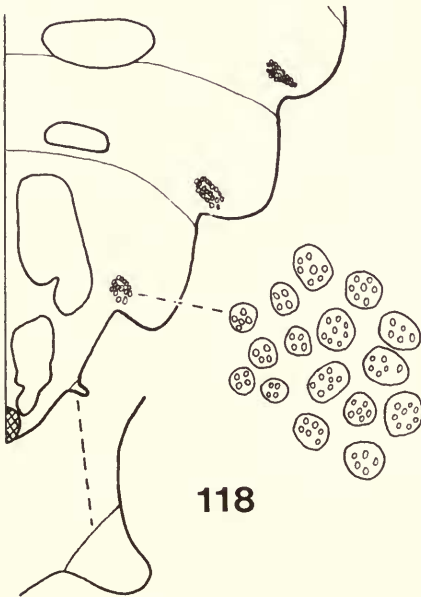
Figs 112–115 Anal pore-fields of Aphalaridae. 112, *Neophyllura bicolor*; 113, *Paraphalaroida fremontiae*; 114, *Paurocephala gossypii*; 115, *Psyllopsis fraxinicola*.



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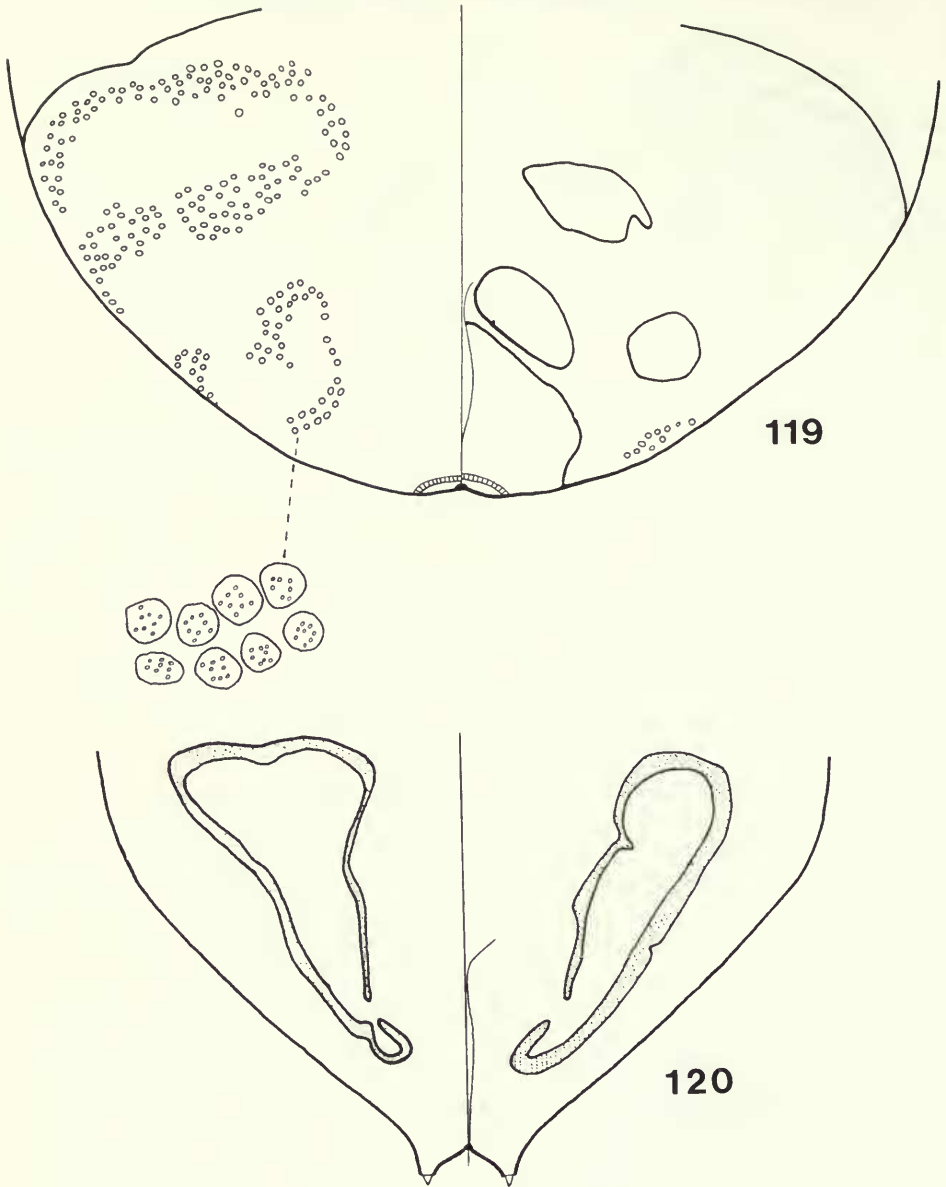


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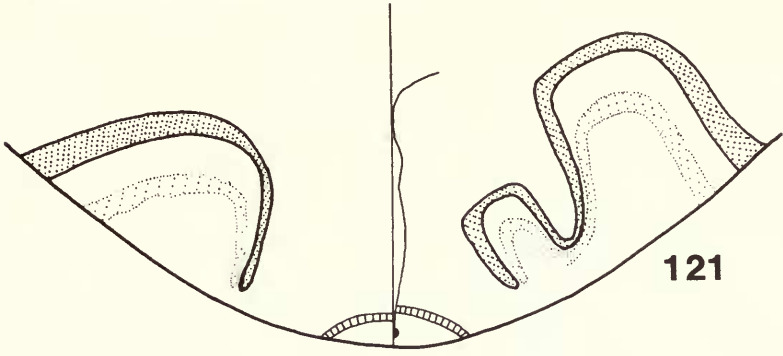


118

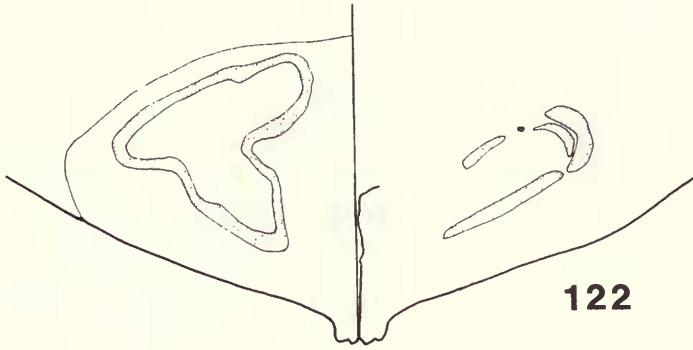
Figs 116–118 Anal pore-fields. Aphalaridae: 116, *Strophingia cinereae*. Spondylaspididae: 117, *Colophorina cassiae*; 118, *Creiis* sp. (insets show pore details and 'tooth' at apex of abdomen).



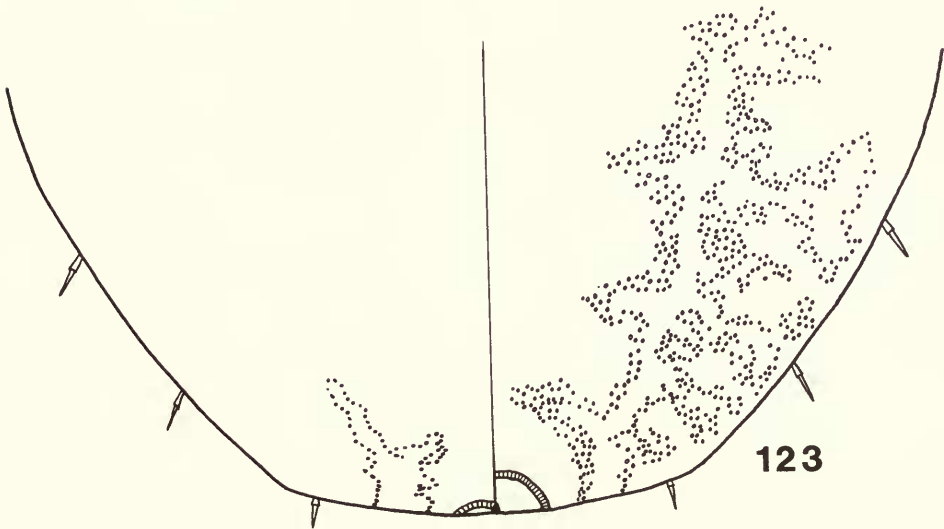
Figs 119, 120 Anal pore-fields. Aphalaridae: 119, *'Eucalyptolyma'* sp. (inset shows detail of pore field).
Spondyliaspidae: 120, *Euphalerus gallicolus*.



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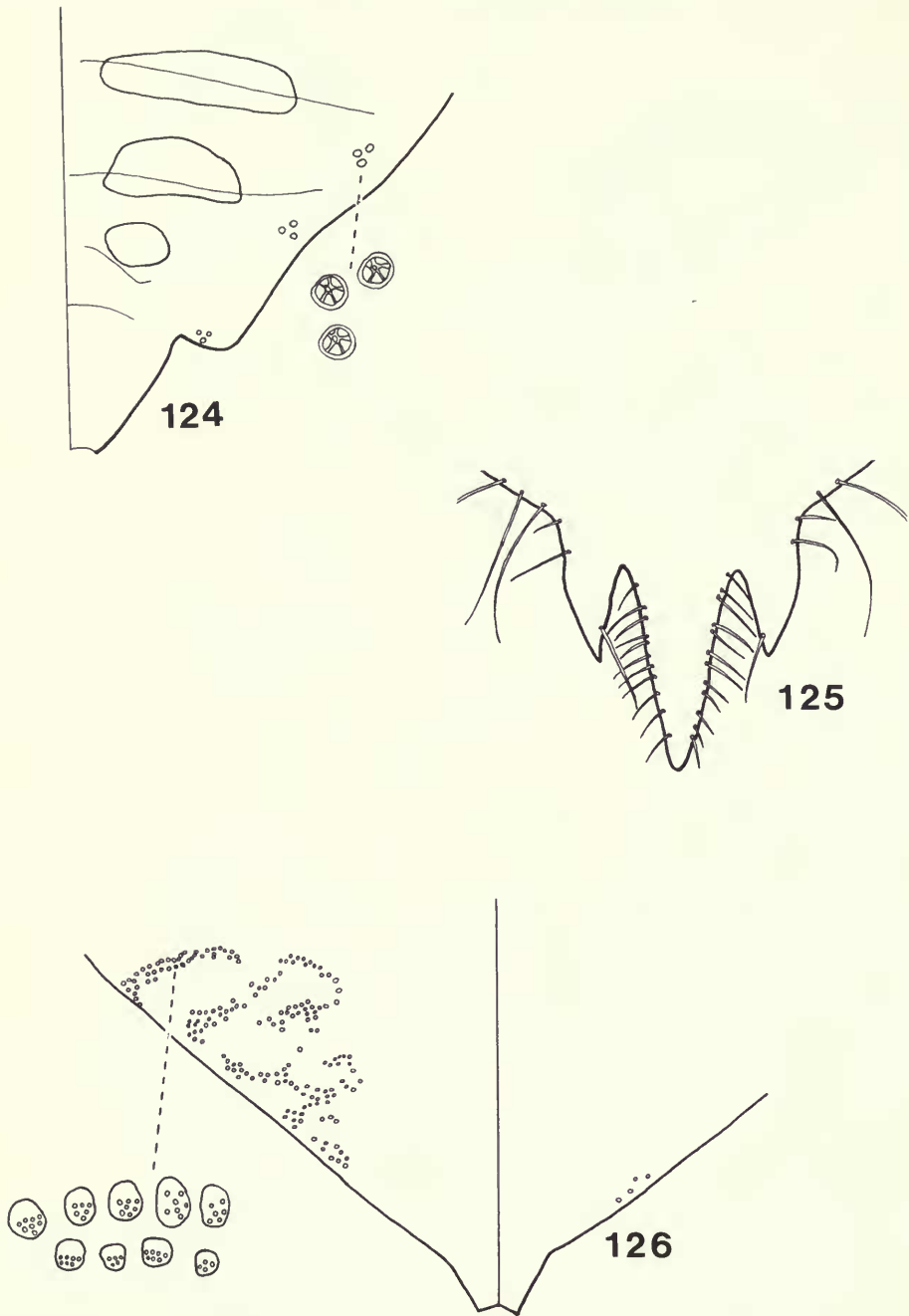


122

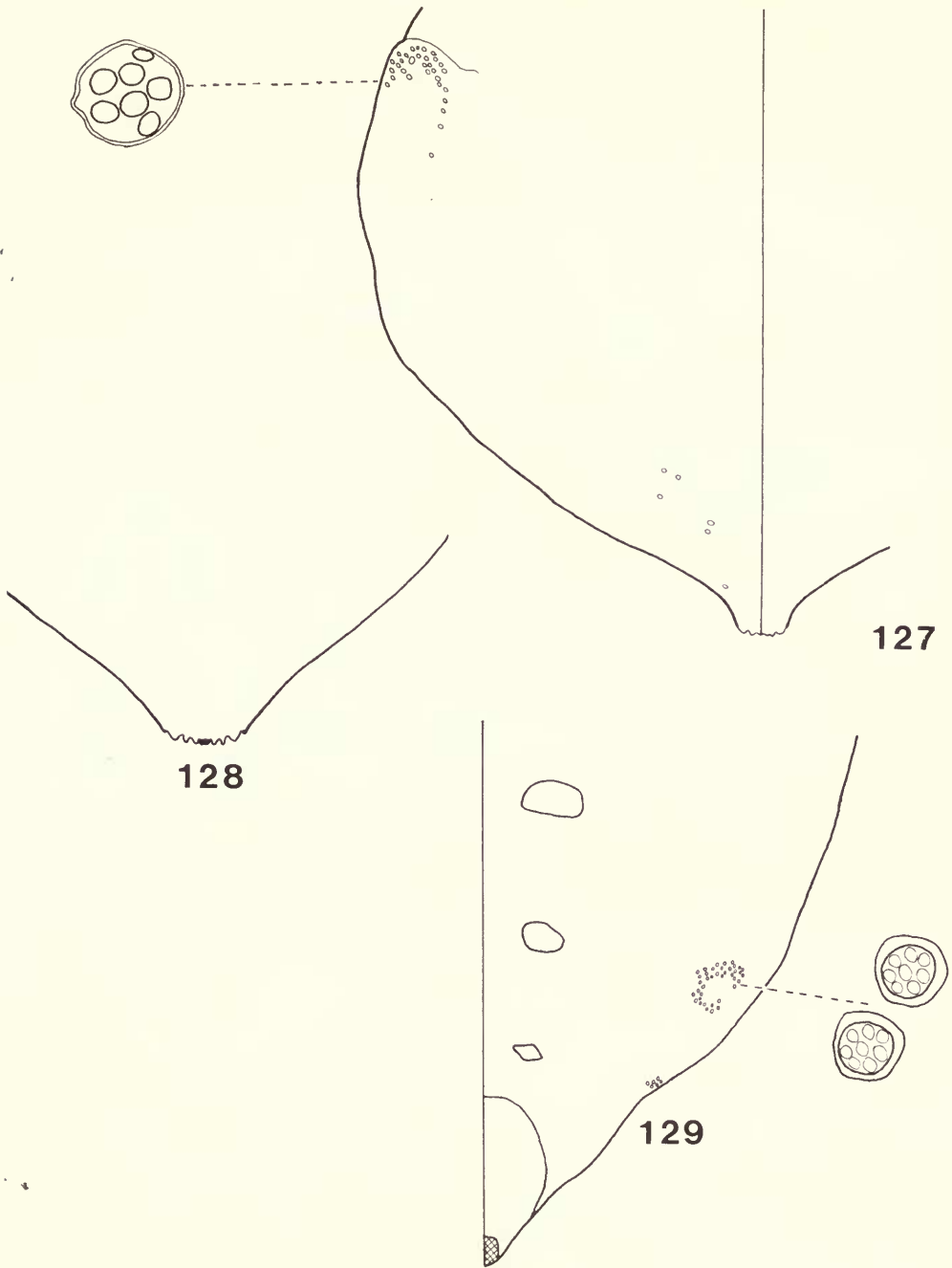


123

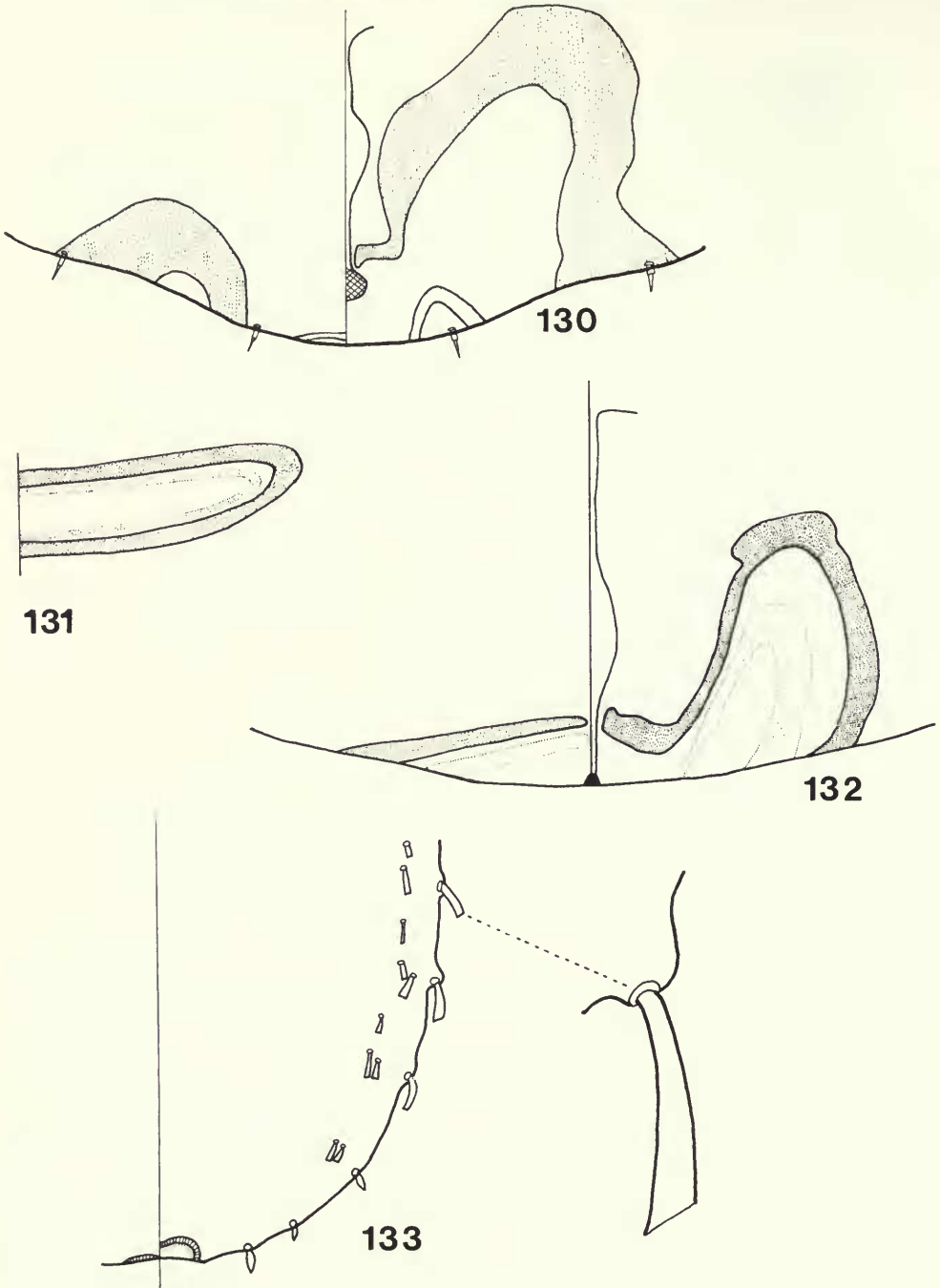
Figs 121–123 Anal pore-fields of Spondyliaspidae. 121, *Euphalerus jugovenosus*; 122, *E. nidifex*; 123, *Euphalerus* sp. (A).



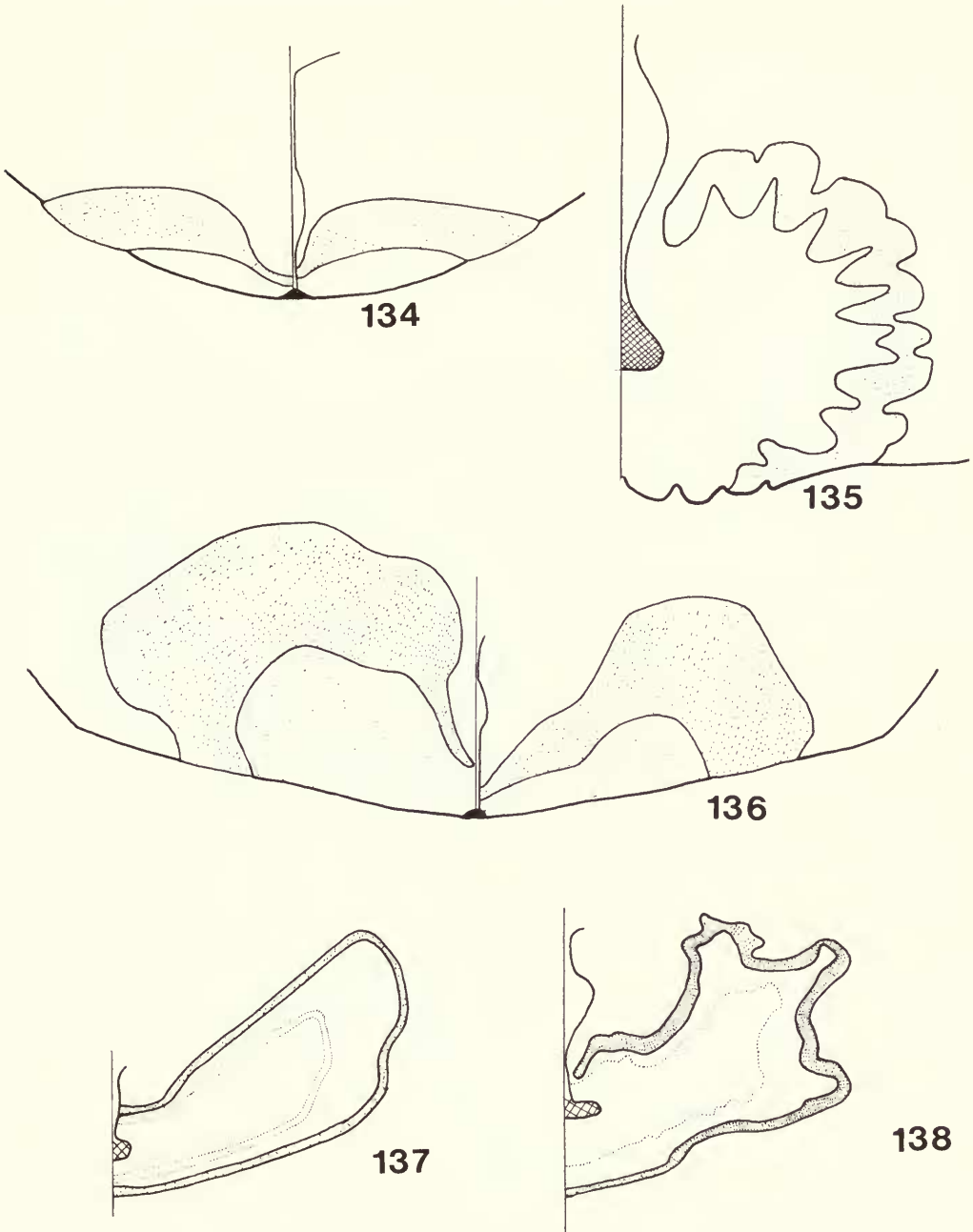
Figs 124–126 Anal pore-fields and abdomen apex shapes of Spondyliaspidae. 124, *Glycaspis baileyi* (inset shows detail of pore-field); 125, *Pachypsylla celtidismamma*, which lacks a pore-field; 126, *P. japonica* (inset shows detail of pore-field).



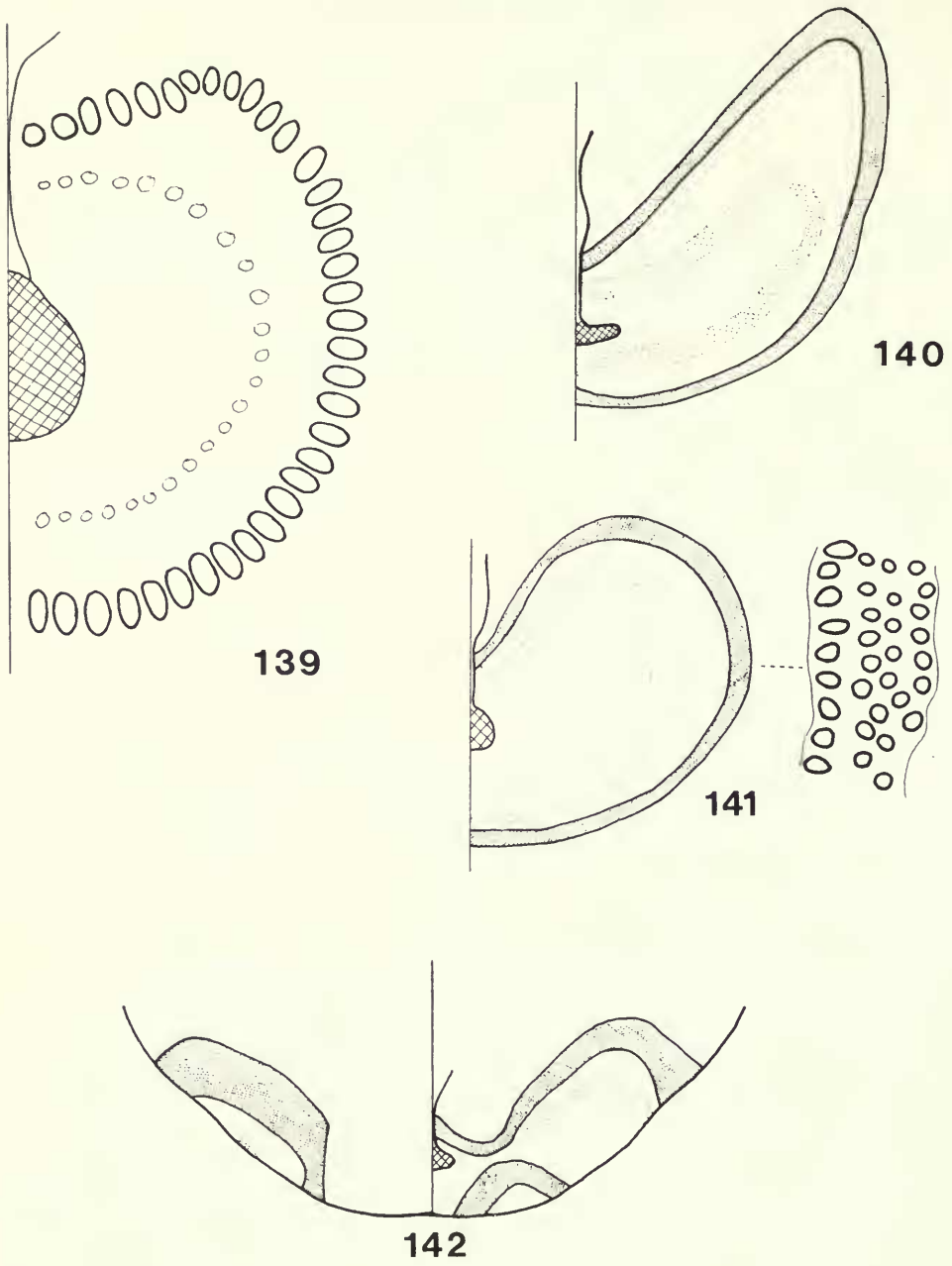
Figs 127–129 Anal pore-fields and abdomen apex shapes of Spondyliaspidae. 127, *Phellopsylla* sp. (inset shows detail of a pore group); 128, *Retroacizzia antennata*, which lacks a pore-field; 129, *Spondyliaspis* sp. (inset shows detail of two of the pore groups).



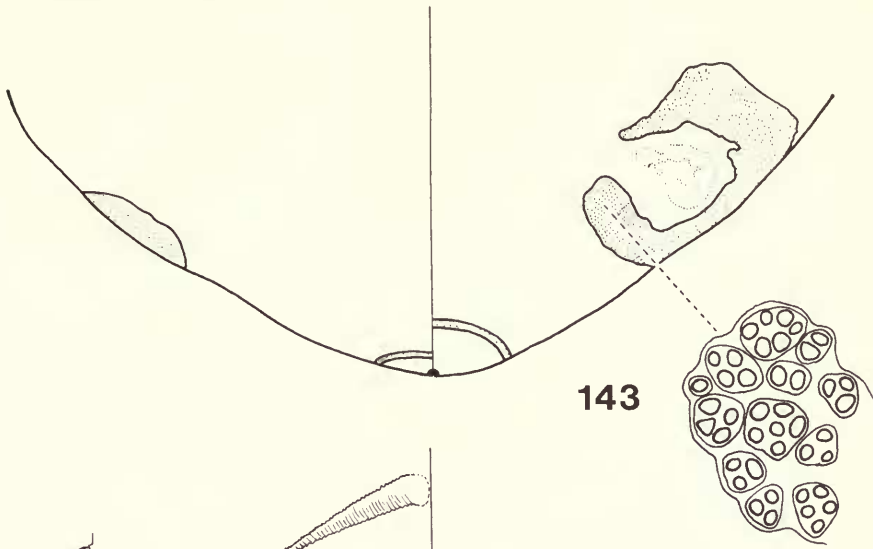
Figs 130–133 Anal pore-fields and abdomen chaetotaxy of Psyllidae. 130, *Anomoneura mori*; 131, '*Euphalerus*' sp. (C); 132, *Euglyptoneura fuscipennis*; 133, *Mitrapsylla deserata* (inset shows detail of funnel setae).



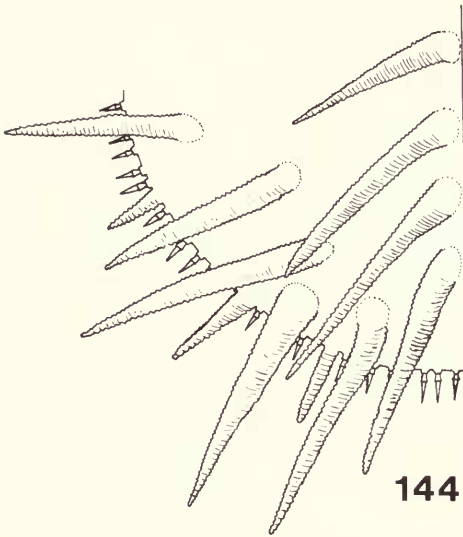
Figs 134–138 Anal pore-fields of Psyllidae. 134, *Psylla buxi*; 135, *P. foersteri*; 136, *P. galeaformis*; 137, *P. phoradendrae*; 138, *P. pulchella*.



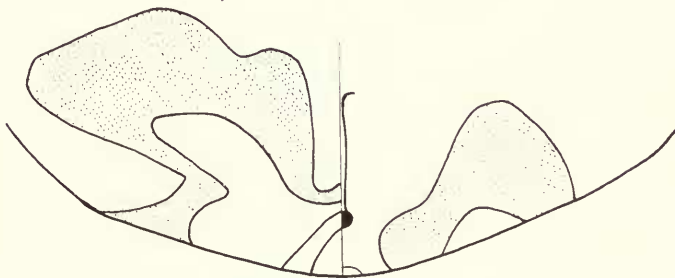
Figs 139–142 Anal pore-fields of Psyllidae. 139, *Psylla saliceti*; 140, *P. simlae*; 141, *P. sorbi* (inset shows pore structure of part of outer circum-anal ring); 142. *Spanioneura fonscolombii*.



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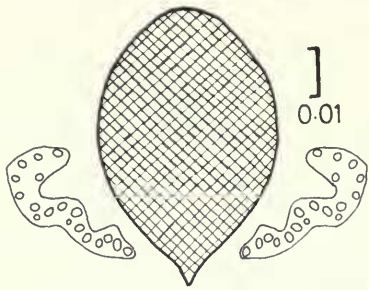


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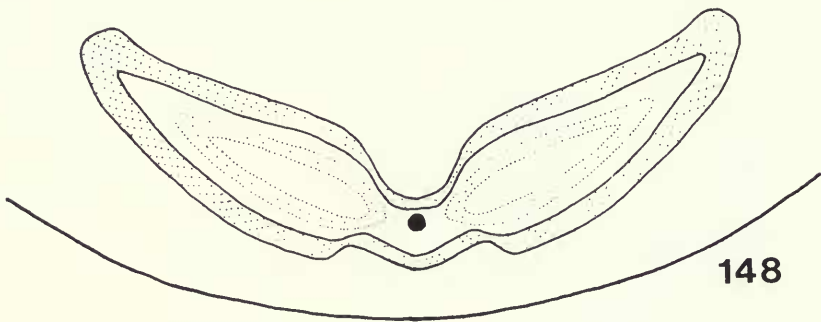
Figs 143–145 Anal pore-fields and abdominal structures of Calophyidae and Phacopteronidae. Calophyidae: 143, *Apsylla cistellata* (inset shows pore structure of parts of the pore-field which is outside the circum-anal rings); 144, *Calophya californica*, showing the long processes which cover the dorsal surfaces of the abdomen and thorax. Phacopteronidae: 145, *Bharatiana octospinosa*.



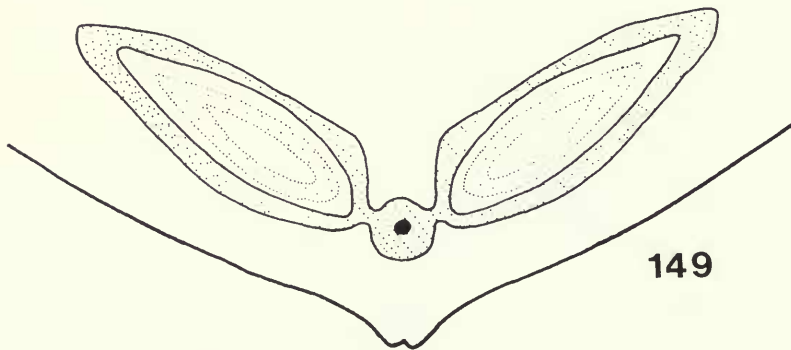
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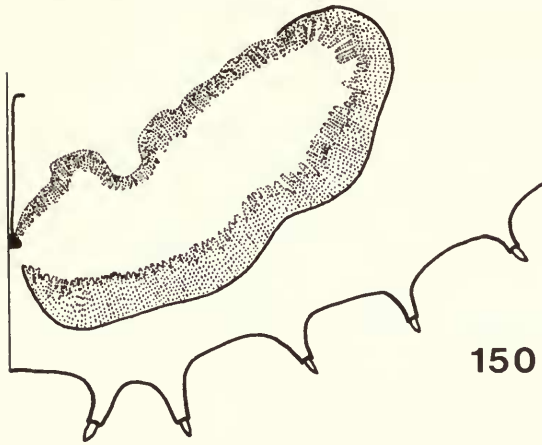


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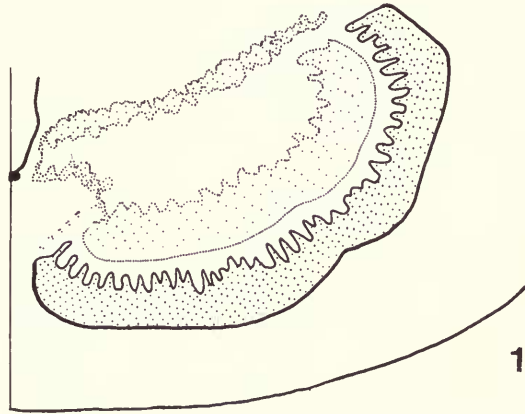


149

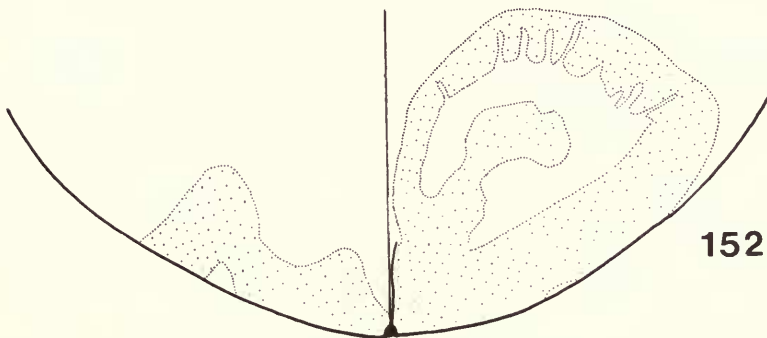
Figs 146–149 Anal pore-fields. Phacopteronidae: 146, *Phacopteron lentiginosum* (anus crosshatched); 147, *Pseudophacopteron* sp. (B). Homotomidae: 148, *Macrohomotoma gladiatum*; 149, *M. striatum*.



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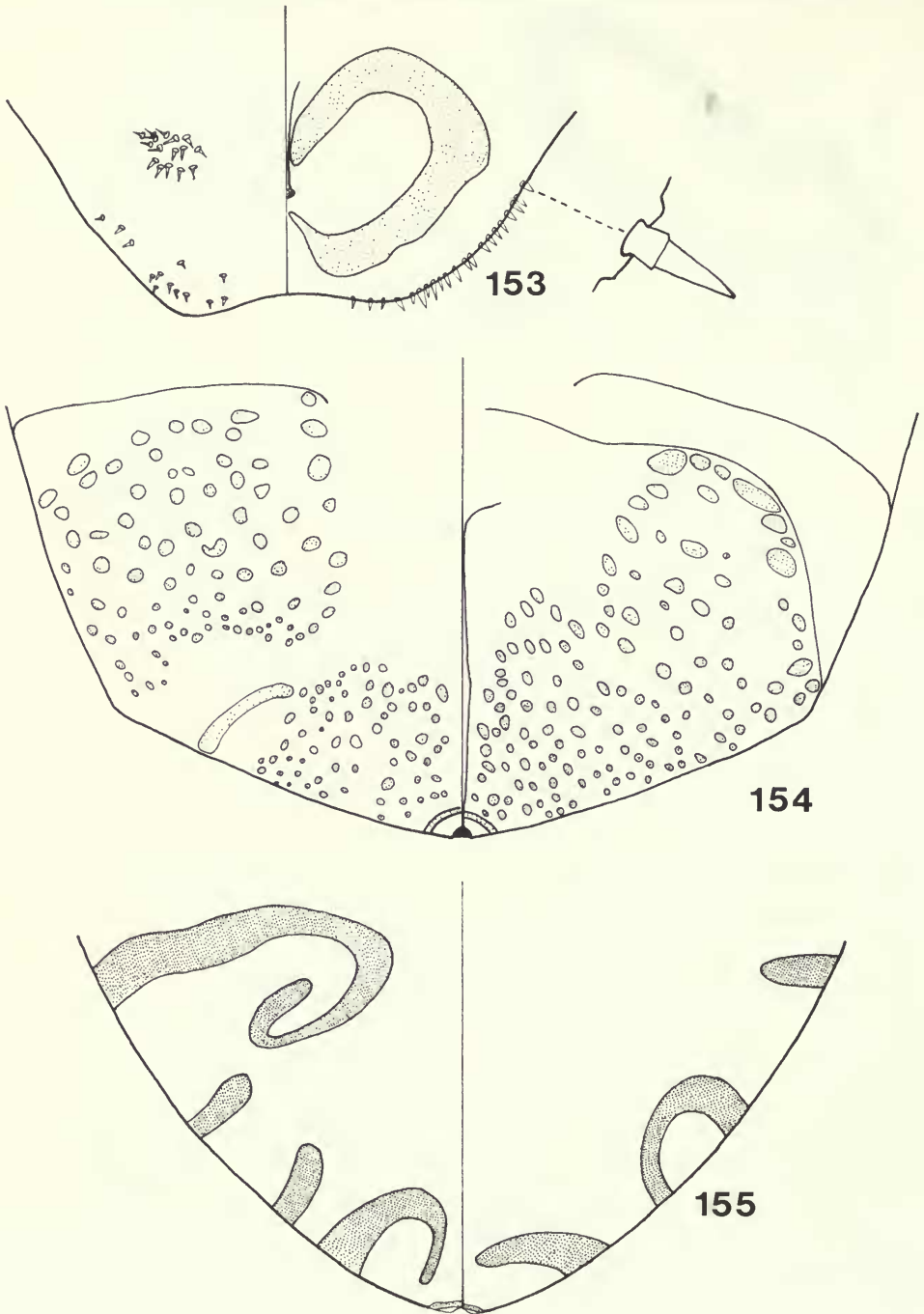


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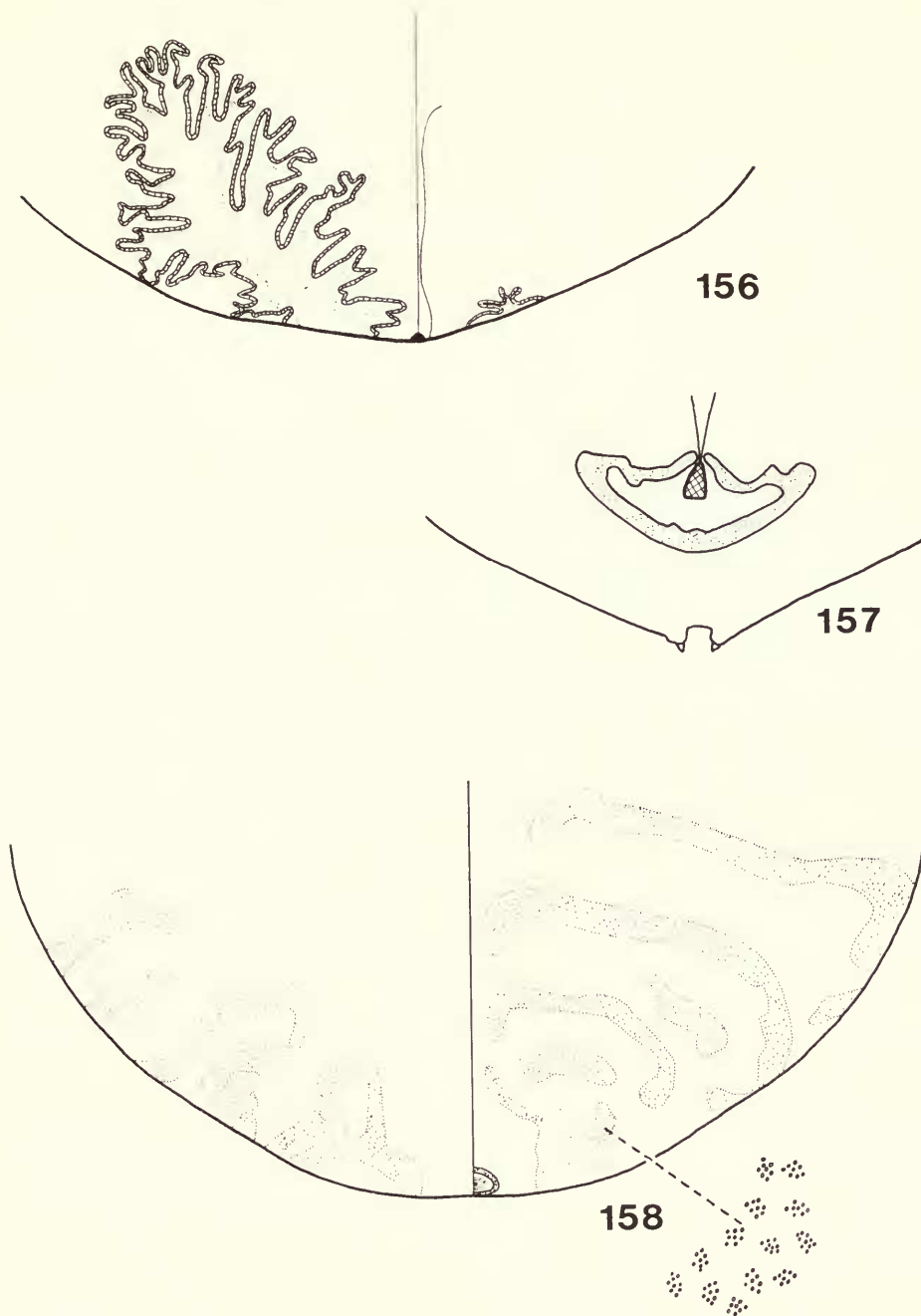


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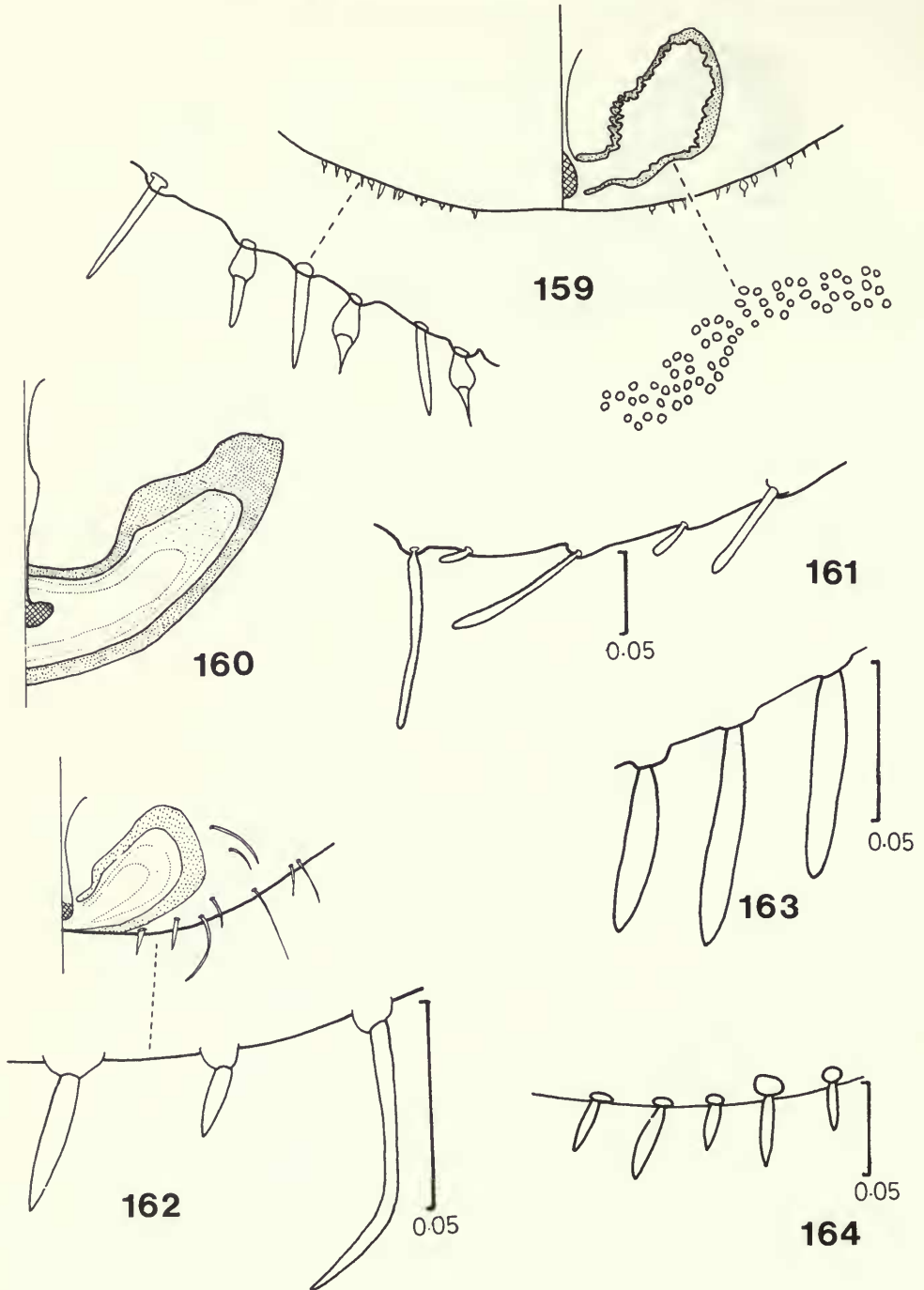
Figs 150–152 Anal pore-fields of Homotomidae. 150, *Mycopsylla ? fici*; 151, *M. gardenensis*; 152, *Pseudoeriopsylla nyasae*.



Figs 153–155 Anal pore-fields and abdomen chaetotaxy. Homotomidae: 153, *Synozia floccosa* (inset shows abdomen margin sectaseta). Carsidaridae: 154, *Mastigimas cedrelae*; 155, *Mesohomotoma hibisci*.



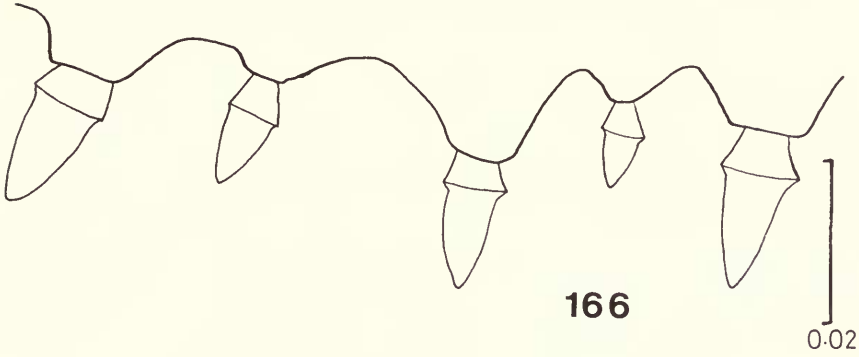
Figs 156–158 Anal pore-fields and abdomen margin shapes of Triozidae. 156, *Leuronota michoacana*; 157, *Neolithus* sp., showing shape of abdomen apex; 158, *Tiozamia lamborni* (inset shows detail of a pore area).



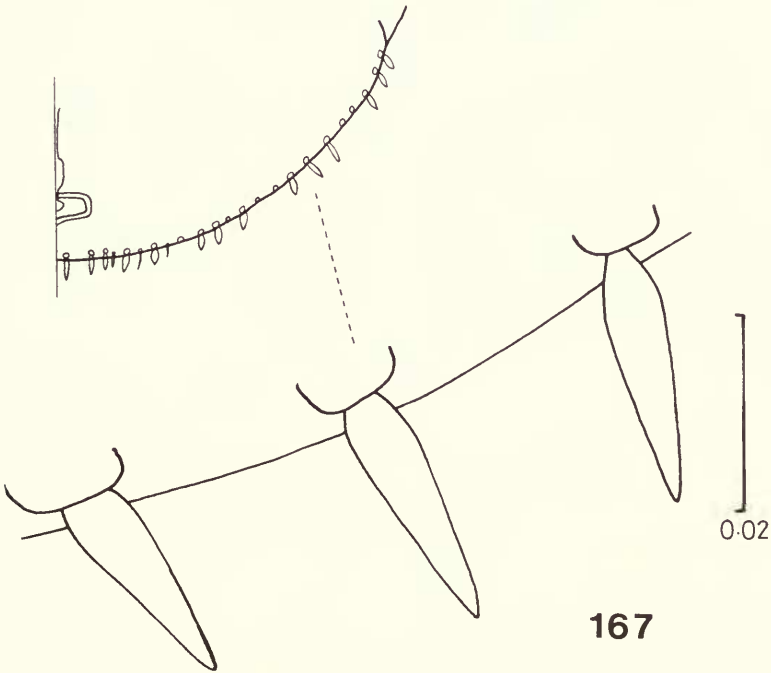
Figs 159–164 Anal pore-fields and chaetotaxy. Triozidae: 159, *Trioza alacris*, with details of circum-anal pore ring and abdomen margin setae; 160, *Triozoida silvestris*, circum-anal pore rings. Aphalaridae: 161, *Aphalaroida pithecolobia*, abdomen margin rod setae; 162, *Phytolyma minuta*, circum-anal pore rings and abdomen margin lanceolate setae; 163, *Crastina linavuorii*, abdomen margin lanceolate setae; 164, *Aphalara persicaria*, abdomen margin lanceolate setae.



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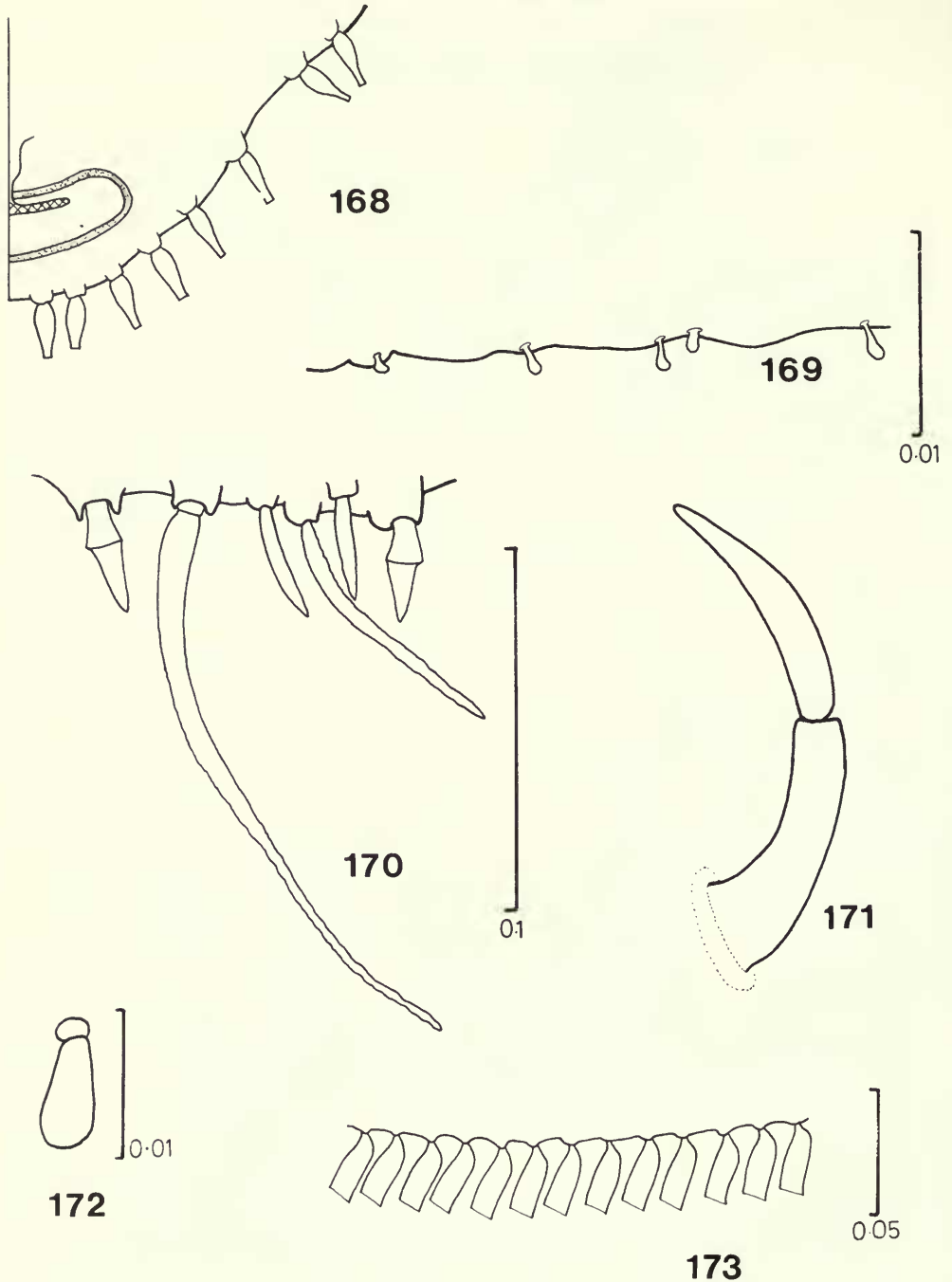


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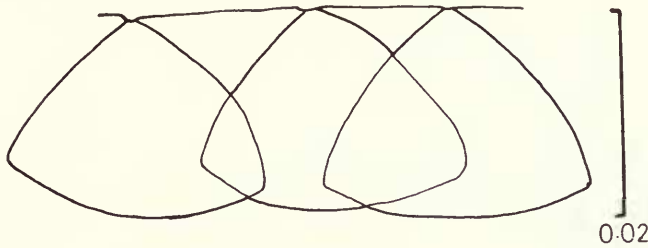
Figs 165–167 Chaetotaxy of Aphalaridae. 165, *Diaphorina putonii*, abdomen margin lanceolate setae; 166, *Moraniella calodendri*, forewing-pad margin sectasetae; 167, *Tainarys schini*, abdomen margin lanceolate setae.



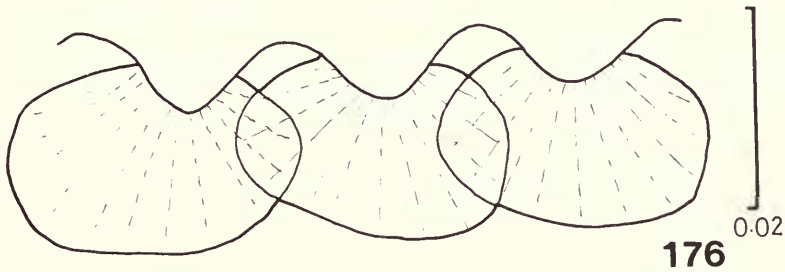
Figs 168–173 Chaetotaxy. Aphalaridae: 168, *Rhinocola aceris*, abdomen margin with truncate lanceolate setae. Spondyliaspidae: 169, *Arepuna* sp., abdomen margin clavate setae. Psyllidae: 170, *Pexopsylla cercocarpi*, abdomen margin rod and sectasetae. Homotomidae: 171, *Homotoma ficus*, lanceolate seta mounted on a tubercle. Triozidae: 172, *Crawforda triopsyllina*, forewing-pad dorsal surface clavate seta; 173, *Hevaheva swezeyi*, abdomen margin scales.



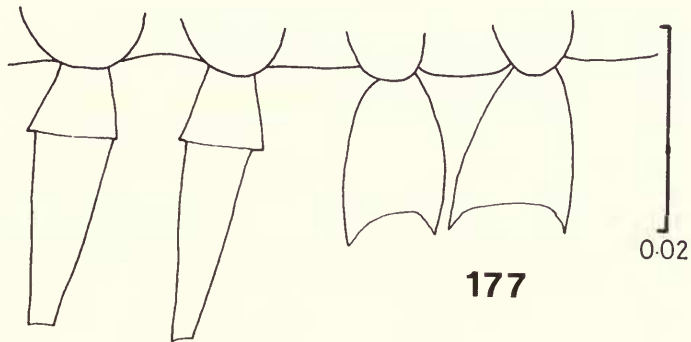
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Figs 174–177 Abdomen margin scales of Triozidae. 174, *Ceropsylla sideroxyli*; 175, *Kuwayama pisonia*; 176, *Swezeyana elongagena*; 177, *Trioza palmicola*, showing both scales and sectasetae.

Table 4 Selected nymphal characters.

Selected characters are numbered N1–N34. All the character states in the original list of 88 characters are tabulated. However, some character states became combined by the selection procedure and, hence, in some characters two consecutive states are marked with the same value.

Characters describing shape and position

- N1. Humeral lobe (in the case of variability the code chosen was the highest observed).
 No humeral lobe (Fig. 15). = 0
 Humeral lobe present, anterior margin of forewing-pad not extending anterior to procoxa (Fig. 16). = 1
 Humeral lobe present, anterior margin of forewing-pad anterior to procoxa and posterior to eye (Fig. 17). = 2
 Humeral lobe present, anterior margin of forewing-pad anterior to posterior of eye and posterior to anterior of eye (Fig. 18). = 3
 Humeral lobe present, anterior margin of forewing-pad anterior to eye (Fig. 19). = 4
- N2. Forewing-pad; position of apex.
 Apex exterior to margin of hindwing-pad (Fig. 20). = 0
 Apex adjacent or interior to margin of hindwing-pad, margin of forewing-pad not confluent with margin of hindwing-pad (Fig. 21). = 0
 Apex adjacent or interior to margin of hindwing-pad, margin of forewing-pad confluent with margin of hindwing-pad (Fig. 22). = 1
- N3. Hindwing-pad; position of apex.
 Apex exterior to margin of abdomen (Fig. 21). = 0
 Apex adjacent or interior to margin of abdomen, margin of hindwing-pad not confluent with margin of abdomen (Fig. 22). = 0
 Apex adjacent or interior to margin of abdomen, margin of hindwing-pad confluent with margin of abdomen (Fig. 23). = 1
- N4–N5. Form of tarsal arolium (clarifying characters of N41).
- N4. Triangular and petiolate (Fig. 25).
 No = 0 Yes = 1
- N5. Disc-like or more than semicircular (Fig. 26).
 No = 0 Yes = 1
- N6. Anal opening ventral.
 No = 0 Yes = 1

Characters of sclerite fusion

- N7. Prothorax dorsal sclerites. Extent of fusion with head.
 Prothorax dorsal sclerites completely separate from head. = 0
 Prothorax dorsal sclerites partly fused with head. At least 2 + 2 sclerites of prothorax separate to cephaloprothorax (Fig. 9). = 0
 Prothorax dorsal sclerites fused with head. 1 + 1 sclerite of prothorax separate to cephaloprothorax (Fig. 10). = 1
 Prothorax dorsal sclerites fused with head. = 2
- N8. Mesothorax and metathorax dorsal surface sclerite arrangement (species which are membranous or completely sclerotized, i.e., the separate sclerites are undifferentiated, are coded zero).
 Medial sclerites (more than 1 + 1) small. Lateral sclerites small (Fig. 11). = 0
 Medial sclerites (more than 1 + 1) large. Lateral sclerites small (Fig. 12). = 1
 Medial sclerites (more than 1 + 1) large. Lateral sclerites absent (Fig. 13). = 1
 Medial sclerite (1 + 1) large. Lateral sclerites absent (Fig. 14). = 1
- N9. Abdomen dorsal surface with many free sclerites. Caudal plate, if present, covering less than whole abdomen (small transverse sclerites at base of abdomen are discounted) (Fig. 2).
 No = 0 Yes = 1
- N10. Abdomen dorsal surface heavily sclerotized (caudal plate). At most with a few small transverse sclerites at the base of the abdomen (Fig. 4).
 No = 0 Yes = 1

Chaetotaxy characters

Twelve following characters (N11–N22). Capitulate setae present.

No = 0 Yes = 1

- N11. Head margin capitulate setae.
- N12. Antenna with capitulate setae close to rhinaria IV and VI.
- N13. Capitulate seta placed laterally or sublaterally behind eye (Fig. 39).
- N14. Thorax dorsal capitulate setae.
- N15. Forewing-pad dorsal capitulate setae.
- N16. Forewing-pad margin capitulate setae.
- N17. Hindwing-pad margin capitulate setae.
- N18. Abdomen dorsal capitulate setae.
- N19. Abdomen margin capitulate setae.
- N20–N22. Tarsal apex with 2 capitulate setae (Fig. 38).
- N20. Foretarsi.
- N21. Midtarsi.
- N22. Hindtarsi.

Three following characters (N23–N25). Lanceolate setae present.

No = 0 Yes = 1

- N23. Forewing-pad margin lanceolate setae.
- N24. Hindwing-pad margin lanceolate setae.
- N25. Abdomen margin lanceolate setae present, numbering more than 4 + 4, or if fewer than 5 + 5 they are separated by less than their own length.

Eight following characters (N26–N33).

Sectasetae. Up to three ‘present’ states were recognised in the initial coding.

Absent.

= 0

Present and pointed (Figs 32, 33).

= 1

Present and truncate (Fig. 34).

= 2

Present, truncate and each seta adjacent to the next or separated by less than one-quarter its maximum breadth from the next seta (Fig. 35).

= 3

- N26. Head margin sectasetae.
Absent = 0; Pointed = 1; Truncate = 2; Adjacent = 2
- N27. Head dorsal sectasetae.
Absent = 0; Pointed = 1.
- N28. Mesothoracic and metathoracic dorsal sectasetae.
Absent = 0; Pointed = 1; Truncate = 2.
- N29. Forewing-pad dorsal sectasetae.
Absent = 0; Pointed = 1; Truncate = 2.
- N30. Forewing-pad margin sectasetae.
Absent = 0; Pointed = 1; Truncate = 2; Adjacent = 2.
- N31. Hindwing-pad margin sectasetae.
Absent = 0; Pointed = 1; Truncate = 2; Adjacent = 2.
- N32. Abdomen dorsal surface sectasetae.
Absent = 0; Pointed = 1; Truncate = 2.
- N33. Abdomen margin sectasetae numbering more than 4 + 4, or if less than 5 + 5 they are each separated from the next by less than their own length.
Absent = 0; Pointed = 1; Truncate = 2; Adjacent = 2.
- N34. Abdomen margin sectasetae or lanceolate setae present and numbering 1 + 1, 2 + 2, 3 + 3, or 4 + 4 and each separated by more than their own length (Fig. 37).
No = 0 Yes = 1

Table 5 Rejected nymphal characters.

Rejected characters are numbered N35–N88. Values are not given against the states, which are separated by a '/'.

Characters describing shape and position

- N35. Antenna base position.
On head margin, or if ventral antenna apex extends beyond head margin (Fig. 4)/Ventral, antenna apex not extending beyond margin of head (Fig. 8).
- N36. Antenna with one rhinarium (Fig. 42). No/Yes.
- N37. Antenna with five rhinaria. No/Yes.
- N38. Antenna with six rhinaria. No/Yes.
- N39. Thorax with pairs of large depressed areas on each segment. No/Yes.
- N40. Hindwing-pad very small (Fig. 48). No/Yes.
- N41. Tarsal arolia. Very reduced or apparently absent/triangular (Figs 24, 25) or disc-like (Fig. 26).
- N42. Thoracic and abdominal dorsal sclerites with large 'perforations'. No/Yes.
- N43. Thoracic and abdominal dorsal surfaces with cuticular processes (Fig. 144). No/Yes.
- N44. Abdominal segments laterally bulging or serrate. No. Margin evenly shaped/Lateral bulges (Fig. 27)/Serrate (Fig. 28).
- N45. Apical margin of abdomen with 'tooth-like' processes. No/Yes (plus the two following clarifying characters).
- N46. No medial 'tooth' (Figs 120, 122). No/Yes.
- N47. Medial 'tooth' present (Fig. 125). No/Yes.
- N48. Anal pore-field present (in any form). No/Yes (plus 6 following clarifying characters).
- N49. Circum-anal ring with two additional rings placed laterally to it (Fig. 121). No/Yes.
- N50. Two rings each lateral to the anus, no circum-anal ring (Fig. 150). No/Yes.
- N51. Four rings, no circum-anal ring (Fig. 120). No/Yes.
- N52. Outer circum-anal ring broken at two or more places. No/Yes, but remaining in form of a circum-anal ring (Fig. 97)/Bands dispersed. Not forming a circum-anal ring. A small circum-anal ring may remain which is assumed to derive from an inner ring (Fig. 155)/Bands dispersed and broken. Not forming a circum-anal ring. A small circum-anal ring may remain which is assumed to derive from an inner ring (Fig. 154).
- N53. As N52 but describing absence of small circum-anal ring. Present/Absent.
- N54. Outer circum-anal ring broken into single pores or small groups of pores. No/Yes, pores or groups of pores in the form of rings (Fig. 117)/Yes, pores or groups of pores dispersed (Fig. 129).

Characters of sclerite fusion

- N55. Mesothorax and metathorax dorsal surface. Numerous very small sclerites. No/Yes.

Three following characters (N56–N58):

Tibio-tarsal fusion of each leg. Two tarsal segments free, articulate (Fig. 55)/Two tarsal segments free, not articulate (Fig. 52)/One tarsal segment free, (segment II) not articulate (Fig. 51)/No tarsal segment free.

- N56. Foreleg (as above).
- N57. Midleg (as above).
- N58. Hindleg (as above).
- N59. Abdomen dorsal surface membraneous. No/Yes.

Chaetotaxy characters

- N60. Head dorsal capitate setae present. No/Yes.
- N61. Antenna segment I inner apical angle capitate seta present. No/Yes.
- N62. Abdomen ventral capitate setae present. No/Yes.
- N63. Rod setae on body surface present. No/Yes.

Nine following characters (N64–N72). Clavate setae present. No/Yes.

- N64. Head margin clavate setae.
- N65. Head dorsal clavate setae.
- N66. Antenna segment I inner apical angle clavate seta.
- N67. Thorax dorsal clavate setae.
- N68. Forewing-pad dorsal clavate setae.
- N69. Forewing-pad margin clavate setae.
- N70. Hindwing-pad margin clavate setae.
- N71. Abdomen dorsal clavate setae.
- N72. Abdomen margin clavate setae.

Six following characters (N73–N78). Lanceolate setae present. No/Yes.

- N73. Head margin lanceolate setae.
- N74. Head dorsal lanceolate setae.
- N75. Antenna segment II with lanceolate setae.
- N76. Thorax dorsal lanceolate setae.
- N77. Forewing-pad dorsal lanceolate setae.
- N78. Abdomen dorsal lanceolate setae.
- N79. Lanceolate setae present and placed on tall tubercles (Fig. 171). No/Yes.
- N80. Antenna with one row of sectasetae located on the opposite margin of the antenna to the rhinaria (Fig. 40). No/Yes.
- N81. Antenna with more than one row of sectasetae (Fig. 45). No/Yes.
- N82. Antenna with one row of sectasetae located on the same margin as the rhinaria. No/Yes.
- N83. Tibia with stout setae (Fig. 51). No/Yes.
- N84. Abdomen margin sectasetae present and based on large clustered tubercles (Fig. 114). No/Yes.
- N85. Scales present on body margin (Fig. 36). No/Yes.

Three clarifying characters of N34.

- N86. Sectasetae (of N34 type) tubular. No/Yes.
- N87. Lanceolate setae (of N34 type) present. No/Yes.
- N88. Sectasetae (of N34 type) pointed. No/Yes.

Table 6 Groups of species identical with the selected nymphal characters. The species chosen to represent the group is named at the top of each list.

- | | |
|---|--|
| 1. <i>Acanthocnema casuarinae</i>
<i>Ceropsylla matorelli</i> | 6. <i>Calophya trioanomima</i>
<i>Calophya dubia</i> |
| 2. <i>Acizzia acaciae</i>
<i>Acizzia acaciaebaileyanae</i>
<i>Psylla phoradendrae</i> | 7. <i>Ceanothia ceanothi</i>
<i>Euphalerus tantillus</i>
<i>Psylla simlae</i> |
| 3. <i>Agonosцена</i> sp. (C).
<i>Agonosцена</i> sp. (B).
<i>Strophingia cinerea</i> | 8. <i>Colophorina cassiae</i>
<i>Epipsylla</i> sp. (B). |
| 4. <i>Apsylla cistellata</i>
<i>Mastigimas cedrelae</i>
<i>M.</i> sp. (B)
<i>Mesohomotoma tessmanni</i>
<i>Tenaphalara malayensis</i> | 9. <i>Colopscenia</i> sp.
<i>Craspedolepta minuta</i>
<i>C. minutissima</i>
<i>Diaphorina cardiae</i>
<i>D. chobauti</i> |
| 5. <i>Calophya nigripennis</i>
<i>Calophya flavida</i> | 10. <i>Creiis</i> sp.
<i>Livia coloradensis</i>
<i>L. maculipennis</i> |

11. *Ctenarytaina eucalypti*
Craspedolepta subpunctata
12. *Diaphorina citri*
Craspedolepta constricta
Diaphorina florea
13. *Diaphorina putonii*
Diaphorina clutiae
D. punctulata
14. *Euceropsylla russoi*
Ciriacremum capense
Euceropsylla minuticonica
E. sp.
15. *Euphalerus jugovenosus*
E. rugipennis
E. vermiculosus
Psylla betulaenanae
P. carpinicola
P. floccosa
P. galeaformis
P. striata
P. trimaculata
16. *Glycaspis baileyi*
Cardiaspina albitextura
C. sp.
C. squamula
Glycaspis spp.
17. *Gyropsylla ilicis*
Gyropsylla spgazziniana
18. *Insnesia glabruscuta*
Mitrapsylla deserata
19. *Mycopsylla fici*
Macrohomotoma gladiatum
Mycopsylla gardenensis
20. *Neophyllura arctostaphyli*
Neophyllura arbuti
21. *Neopsyllia erythrinae*
Euglyptoneura sp.
Neopsyllia sp.
Platycorypha princeps
22. *Pachyopsylla venusta*
Pachyopsylla spp.
Tetragonocephala sp.
23. *Paracarsidara gigantea*
Bharatiana octospinosa
Mastigimas sp. (A)
Mesohomotoma hibisci
Paracarsidara spp.
Tenaphalara acutipennis
24. *Paratrioza cockerelli*
Paratrioza arbolensis
P. maculipennis
Trioza curvatineris
T. minuta
T. salicivora
25. *Paurocephala gossypii*
Paurocephala urenae
26. *Pennavena fabulosa*
Craspedolepta furcata
C. nervosa
27. *Psylla alba*
Psylla sinuata
28. *Psylla alni*
Psylla buxi
Spanioneura fonscolombii
29. *Psylla brevistigmata*
Psylla minuta
P. parallela
30. *Psylla brunneipennis*
Psylla coryli
P. hirsuta
P. moscovita
Purshivora chelifera
31. *Psylla mali*
Euglyptoneura robusta
Pexopsylla cercocarpi
Psylla ribesiae
32. *Psylla media*
Arytainilla hakani
33. *Psylla minor*
Psylla magnicauda
34. *Psylla nigrita*
Psylla saliceti
35. *Psylla pulchra*
Psylla hamata
36. *Psylla pyricola*
Psylla myrtilli
P. visci
37. *Psylla pyrisuga*
Arytainilla cytisi
Psylla melanoneura
38. *Psylloopsis fraxinicola*
Aphalaroida pithecolobia
Psylloopsis fraxini
39. *Spondylia sp.*
Cardiaspina densitexta
40. *Strophingia ericae*
Aphalara curta
A. nubifera
A. polygona
A. simila
Craspedolepta augustipennis
C. artemisiae
C. sonchi
C. suaedae
C. vancouverensis
C. veaziei
Tainarys schini
41. *Swezeyana elongata*
Trioza palmicola
42. *Trichohermes walkeri*
Trioza phoradendrae
43. *Trioza albifrons*
Paratrioza lavaterae
Trioza beameri
T. quadripunctata
44. *Trioza albiventris*
Trioza atkasookensis
T. crithmi

45. *Trioza chenopodii*
Trioza litseae
 46. *Trioza diospyri*
Trioza bakeri
T. frontalis

47. *Trioza incidata*
Trioza tripunctata
 48. *Trioza marginepunctata*
Trioza vitiensis
T. sp.

The following species have unique descriptions:

Acizzia hakeae
A. russellae
A. uncatoides
Agonosцена sp. (A)
Amorphicola amorphae
Anomoneura mori
Aphalara exilis
A. monticola
A. persicaria
A. rumicis
Aphalaroidea inermis
Arepuna sp.
Arytaina genistae
Arytainilla spartiicola
A. spartiophila
Calophya californica
C. rhois
C. schini
C. rotundipennis
C. sp.
Camarotoscena spp.
Ceanothia aculeata
Ceropsylla sideroxyli
C. sp.
Ciriacremum capeneri
C. harteni
C. julbernardioides
Craspedolepta nebulosa
Crastina linavuorii
Crawforda triopsyllina
Diaphorina albomaculata
D. solani
Diclidophlebia eastopi
Egeirotrioza spp.
Epicarsa sp.
Epipsylla sp. (A)
Eucalyptolyma sp.
Euceropsylla cayeyensis
Euglyptoneura fuscipennis
Euphalerus gallicolus
E. nidifex
E. sp. (A).
E. sp. (B).
E. sp. (C).
E. sp. (D).
Euphyllura spp.
Floria variegata
Freysuila sp.
Heteropsylla spp.
Hevaheva swezeyi
Homotoma spp.

Isogonoceraia divergipennis
Kuwayama pisonia
Leptynoptera sulfurea
Leurolophus vittatus
Leuronota michoacana
Livia crefeldensis
L. juncorum
L. vernalis
Macrohomotoma striata
Microceropsylla sp.
Moraniella calodendri
Neolithus sp.
Neophyllura bicolor
Paraphalaroidea fremontiae
Pauropsylla spp.
Pelmatobrachia sp.
Phacopteron lentiginosum
Phellopsylla sp.
Phytolyma spp.
Protyora sterculiae
Pseudoeriopsylla nyasae
Pseudophacopteron spp.
Psylla albagena
P. ambigua
P. americana
P. annulata
P. foersteri
P. magna
P. negundinis
P. palmeni
P. peregrina
P. pruni
P. pulchella
P. pyri
P. rhamnicola
P. rhododendri
P. stricklandi
P. sorbi
P. subspiculata
P. ulmi
Purshivora pubescens
Retroacizzia antennata
Rhinocola aceris
Synozia spp.
Tenaphalara sp.
Togepsylla matsumurana
Trigonon longicornis
Trioza alacris
T. aylmeriae
T. anceps
T. cinnamomi

T. erytreae
T. falcata
T. hirsuta
T. lobata
T. magnoliae
T. nigricornis
T. obsoleta
T. obtusa
T. panacis

T. remota
T. urticae
T. vitreoradiata
Triozamia lamborni
Triozoida silvestris
 indet. (A).
 indet. (B).
 indet. (C).

Phenetic analysis of nymphs

The selected characters are used for these analyses of 182 selected species and resemblance was measured using the mean character difference (Cain & Harrison, 1958).

Minimum spanning network (MSN)

The MSN (Fig. 178) was constructed using an algorithm given by Farris (1970). In a MSN a set of taxa are joined by the shortest possible set of linkages (numbering $t - 1$) and it indicates which species are phenetically most similar to each other. The main features of the MSN relative to the Becker-Migdisova (1973) families are as follows.

1. The following genera of Psyllidae form one group (Fig. 178a): *Acizzia*, *Amorphicola*, *Anomoneura*, *Arepuna*, *Arytaina*, *Arytainilla*, *Ceanothia*, *Ciriactremum*, *Colophorina*, *Eucero-psylla*, *Euglyptoneura*, *Floria*, *Freysulla*, *Heteropsylla*, *Insnesia*, *Isogonoceraia*, *Mitrapsylla*, *Neopsyllia*, *Pexopsylla*, *Platycorypha*, *Psylla*, *Purshivora*, *Retroacizzia*, *Spanioneura* and *Trigonon* plus *Epipsylla* sp. (B) and many *Euphalerus* spp. Genera of Psyllidae not included in this group are: *Diaphorina*, *Pennavena* and *Psyllopsis* plus *Epipsylla* sp. (A)., *Euphalerus gallicolus*, *E. nidifex* and *E. sp.* (A).
2. The following genera of Triozidae form one group (Fig. 178c): *Aacanthocnema*, *Ceropsylla*, *Crawforda*, *Hevaheva*, *Kuwayama*, *Paratrioza*, *Swezeyana*, *Trichochemes*, *Trioza* (minus 2 spp.) and *Triozoida*. Genera of Triozidae not included in this group are: *Egeirotrioza*, *Leuronota*, *Neolithus* and *Triozamia* plus *Trioza alacris* and *T. hirsuta*.
3. All members of the Liviidae form one group; however, two are included with *Creiis* sp. (Fig. 178b).
4. The following genera of Aphalaridae form one group (Fig. 178b): *Agonoscena*, *Aphalara*, *Colposcena*, *Craspedolepta*, *Crastina*, *Euphyllura* (minus *E. phillyreae*), *Leurolophus*, *Neophyllura*, *Rhinocola*, *Strophingia* and *Tainarys* plus *Aphalaroida pithecolobia* and *Camarotoscena speciosa*. Genera of Aphalaridae not included in this group are: *Apsylla*, *Gyropsylla*, *Moraniella*, *Paraphalaroida*, *Paurocephala* and *Phytolyma* plus *Aphalaroida inermis*, *Camarotoscena unicolor* and *Euphyllura phillyreae*.
5. The following genera of Spondyliaspidae form one group (Fig. 178c): *Cardiaspina*, *Eucalyptolyma*, *Glycaspis* and *Spondyliaspis*.
6. A second group of Spondyliaspidae consists of the genera (Fig. 178b) *Creiis*, *Pachypsylla*, *Phellopsylla* and *Tetragonocephala*.
7. The Carsidaridae failed to form as one major group.

In the MSN many genera and species are not placed with the majority of their family. The main discordant features are as follows.

1. *Aphalaroida inermis* and *Paraphalaroida* (Aphalaridae), and *Diclidophlebia* (Carsidaridae) are placed with the Psyllidae (Fig. 178a) because they share the feature of a petiolate tarsal arolium.
2. *Calophya schini*, *Calophya rotundipennis* and *Microceropsylla* (Carsidaridae) are placed with the Triozidae (Fig. 178c). These species have a well-developed humeral lobe of the

fore-wing pad like most Triozidae. *Calophya schini* is surrounded by pointed sectasetae like *Crawforda* to which it is linked, whereas *Calophya rotundipennis* and *Microceropsylla* lack sectasetae like *Kuwayama pisonia* to which they link.

3. *Creiis* (Spondyliaspidae) is identical to some species of *Livia* (Liviidae), as defined by the selected characters. This is because these species have almost entirely zero character states. *Euphalerus* sp. (A) (Psyllidae) also links to *Livia*.

4. *Diaphorina*, *Pennavena* and *Psyllopsis* (Psyllidae), *Ctenarytaina* (Spondyliaspidae) plus *Epicara*, *Homotoma ficus*, *Phacopteron* and *Pseudophacopteron floccosa* (Carsidaridae) are placed with most Aphalaridae (Fig. 178b). Group 4 is a collection of species with lanceolate setae.

5. *Euphalerus nidifex* (Psyllidae) is linked with *Glycaspis* (Spondyliaspidae).

6. *Euphalerus gallicolus* (Psyllidae) is linked with *Creiis* (Spondyliaspidae).

7. Most taxa with pointed sectasetae form one group (Fig. 178b): most *Calophya* spp., *Camarotoscena unicolor*, most *Egeirotrioza* spp., *Homotoma indica*, *Leuronota*, *Moraniella*, *Paurocephala*, *Synozia floccosa* and *Trioza alacris*.

The remaining genera and species lack specialised chaetotaxy. They are placed near to the centre of the minimum spanning network and the distinct groups branch from them.

Average linkage phenogram (AL)

Further insight into the resemblances between nymphs is provided by a hierarchical representation of data as provided by an average linkage phenogram.

An average linkage phenogram was constructed using the 'weighted pair group method with arithmetic averages' (Fig. 179) which was computed by the 'JOIN' algorithm of Hartigan (1975).

Most of the groups formed in the minimum spanning network were also recognised by average linkage. Three major clusters were formed (Figs 179b–d).

Cluster 1 (Fig. 179b). This includes members of the family Psyllidae which have capitate setae: *Acizzia hakeae*, *A. uncatoides*, *Amorphicola*, *Arytaina*, *Arytainilla*, *Ceanothia*, *Ciriactremum*, *Euceropsylla*, *Euphalerus tantillus*, *E. sp. (B).*, *E. sp. (C).*, *Floria*, *Freysuila*, *Heteropsylla*, *Insnesia*, *Isogonoceraia*, *Mitrapsylla*, *Psylla* (minus subgen. *Asphagidella*, subgen. *Psylla*, *P. annulata*, *P. mali*, *P. phoradendrae* & *P. ribesiae*), *Purshivora* and *Trigonon*. The remaining Psyllidae are in cluster 3 (except *Retroacizzia*).

Cluster 2 (Fig. 179c). This contains taxa with sectasetae. It also includes *Retroacizzia*: *Camarotoscena unicolor*, *Moraniella*, *Paraphalaroida* and *Paurocephala* (Aphalaridae), *Calophya*, *Diclidophlebia*, *Homotoma*, *Leptynoptera*, *Microceropsylla*, *Pauropsylla depressa*, *P. trichaeta*, *Synozia floccosa* and *Togepsylla* (Carsidaridae), *Retroacizzia* (Psyllidae), *Aacanthocnema*, *Ceropsylla*, *Crawforda*, *Egeirotrioza*, *Hevaheva*, *Kuwayama*, *Leuronota*, *Neolithus*, *Paratrioza*, *Swezeyana*, *Trichohermes*, *Trioza* (minus *T. hirsuta*), *Triozoidea* and indet. sp. (A). (Triozidae).

Cluster 3 (Fig. 179d,e). This includes taxa with lanceolate setae plus most taxa which lack capitate setae and sectasetae: *Agonoscena*, *Aphalara*, *Aphalaroida*, *Apsylla*, *Camarotoscena speciosa*, *Colposcena*, *Craspedolepta*, *Crastina*, *Euphyllura*, *Gyropsylla*, *Leurolophus*, *Neophyllura*, *Phytolyma*, *Rhinocola*, *Strophingia* and *Tainarys* (Aphalaridae), *Bharatiana*, *Epicara*, *Macrohomotoma*, *Mastigimas*, *Mesohomotoma*, *Mycopssylla*, *Paracarsidara*, *Pauropsylla beasoni*, *Pelmatobranchia*, *Phacopteron*, *Protorya*, *Pseudoeriopsylla*, *Pseudophacopteron*, *Synozia* sp. and *Tenaphalara* (Carsidaridae), *Livia* (Liviidae), *Acizzia acaciae*, *A. acaciaebaileyanae*, *A. russellae*, *Anomoneura*, *Arepuna*, *Diaphorina*, *Diaphorina*, *Epipsylla*, *Euglyptoneura*, *Euphalerus gallicolus*, *E. jugovenosus*, *E. nidifex*, *E. rugipennis*, *E. vermiculosus*, *E. sp. (A).*, *E. sp. (D).*, *Neopsyllia*, *Pennavena*, *Pexopsylla*, *Platycorpha*, some *Psylla* spp. (subgen. *Asphagidella*, subgen. *Psylla*, *P. annulata*, *P. mali*, *P. phoradendrae* and *P. ribesiae*) and *Psyllopsis* (Psyllidae), *Cardiaspina*, *Creiis*, *Ctenarytaina*, *Eucalyptolyma*, *Glycaspis*, *Pachyopsylla*, *Phellopsylla*, *Spondyliaspis* and *Tetranocephala* (Spondyliaspidae).

Cluster 3 (Fig. 179d) is clearly least congruent with the classification of Becker-Migdisova (1973). Capitate setae (N 11 – N 19) and sectasetae (N 26 – N 33) are described by nine and eight

selected characters respectively. However, lanceolate setae (N 23–N 25) are only described by three selected characters and therefore contribute less weight to the classification than either capitate setae or sectasetae. Hence most taxa which lack any of these three major setal types are phenetically closer to taxa with lanceolate setae than to taxa with capitate setae or sectasetae and cluster 3 is produced.

Detailed analysis of the characters which are responsible for groups is more easily performed using principal component analysis.

Principal component analysis (PC)

Principal component analysis, like other forms of ordination, aims to transform a data matrix, whose variance is in many dimensions, into a matrix with most of the variance explained by a

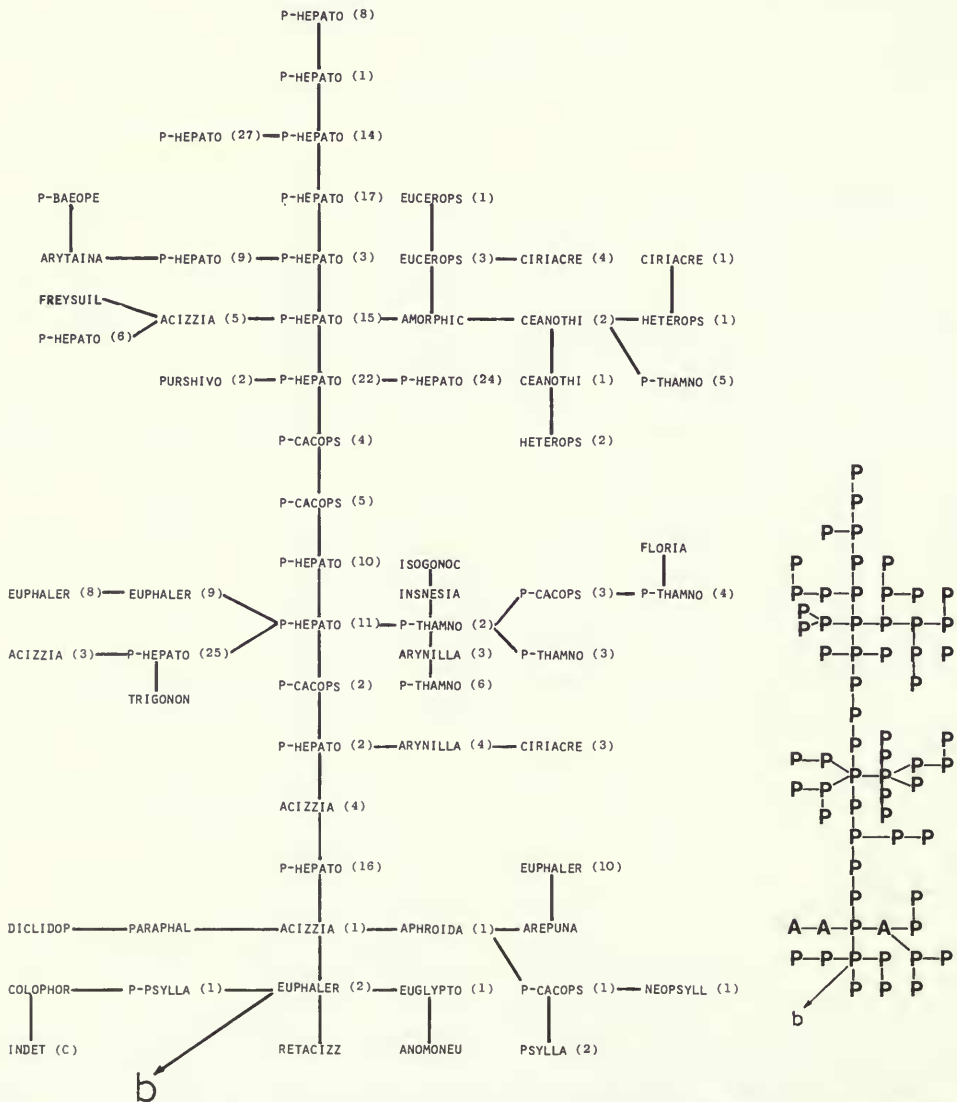


Fig 178a Part of a minimum spanning network of 182 selected species with 34 nymphal characters. Internode lengths are not drawn in proportion to taxonomic distance and for convenience the network is divided into 3 sections. Continued in Figs 178b–c.

very few dimensions. In this case 34 dimensions (because there are 34 characters) would be needed to illustrate the spatial relationships of 182 species. However, when principal component analysis was carried out almost 60% (58.2%) of the variance was accounted for by just three dimensions, i.e. a three dimensional figure of spatial relationships of the species could illustrate more than half of the variance in the data. Other forms of ordination, such as principal coordinate analysis, tend to yield very similar results (Boratynski & Davies, 1971) and are not practical when the number of taxa is large and in excess of the number of characters (Rohlf, 1972).

For this analysis data were scaled by ranging and eigenvectors were extracted from correlation and covariance matrices for the first 10 principal components, which accounted for most of the variance (82.8% when extracted from a correlation matrix and 83.7% from a covariance

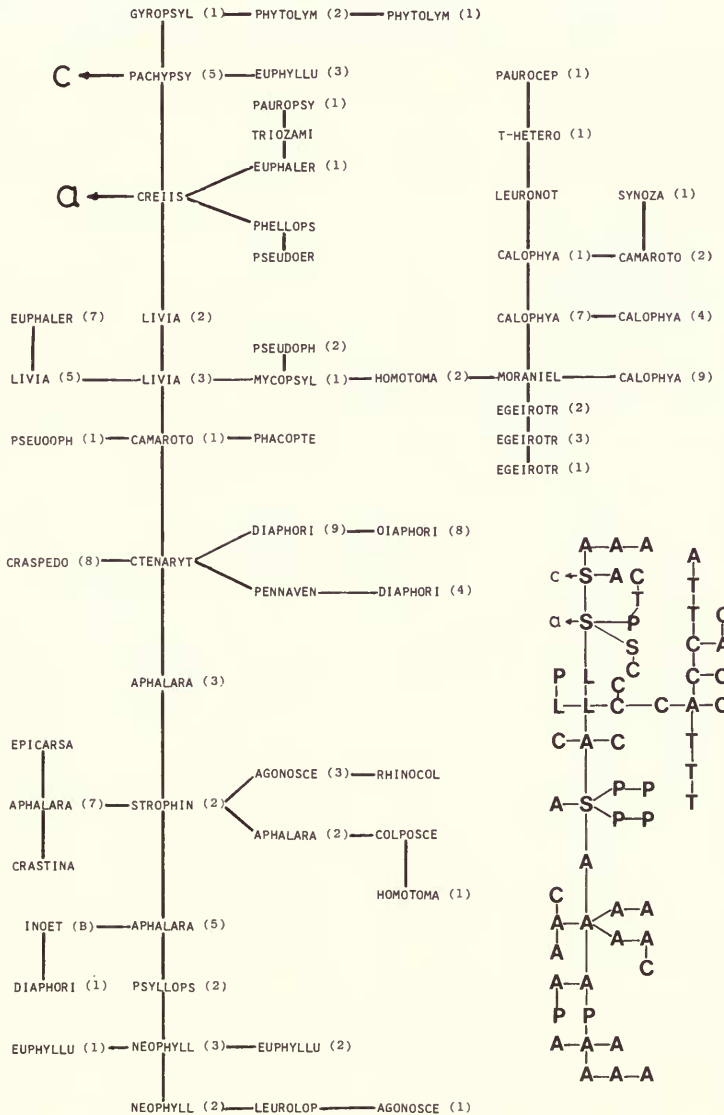


Fig. 178b Part of a minimum spanning network of 182 species; continued in Figs 178a and 178c.

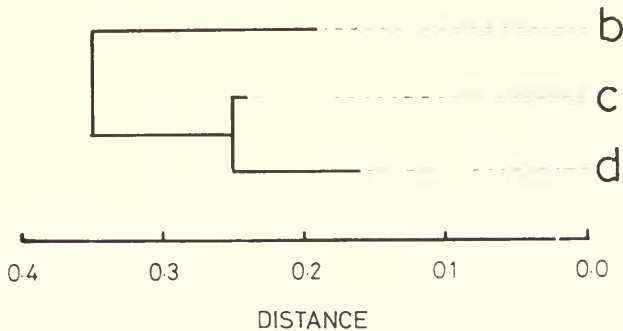


Fig. 179a Average linkage phenogram of 182 selected species with 34 nymphal characters; key diagram showing linkages to Figs 179b-d.

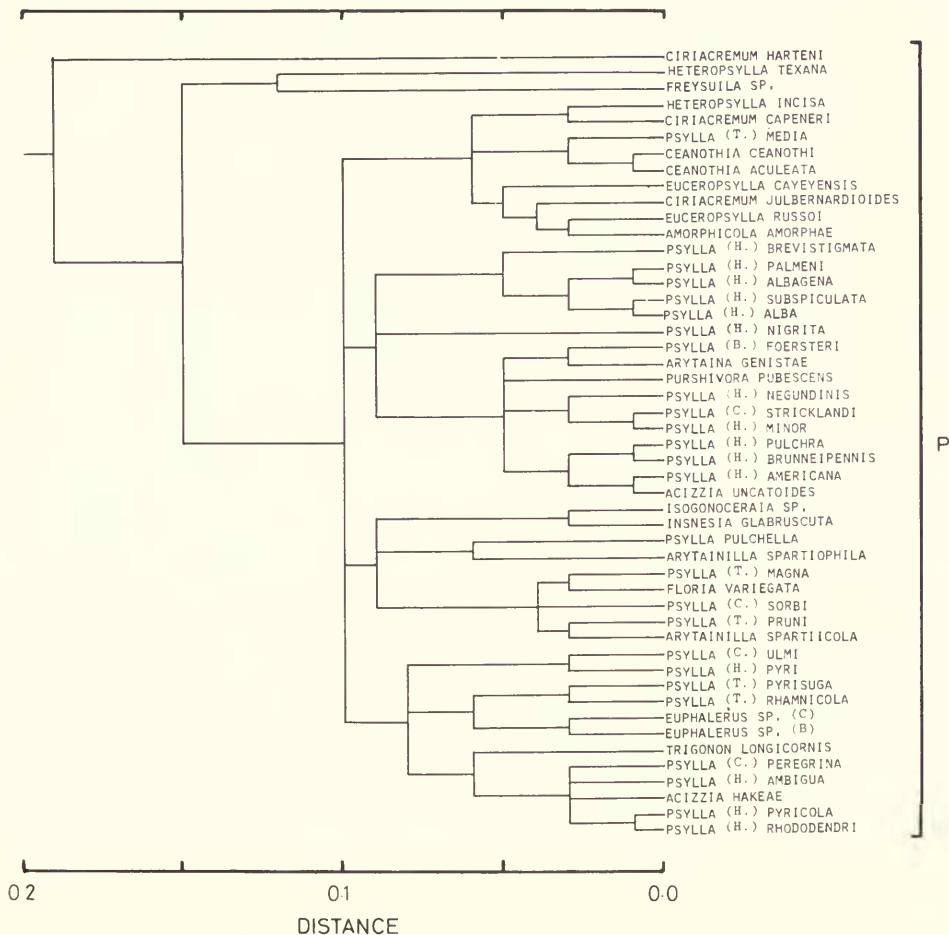


Fig. 179b Part of a phenogram of 182 species; continued from Fig. 179a.

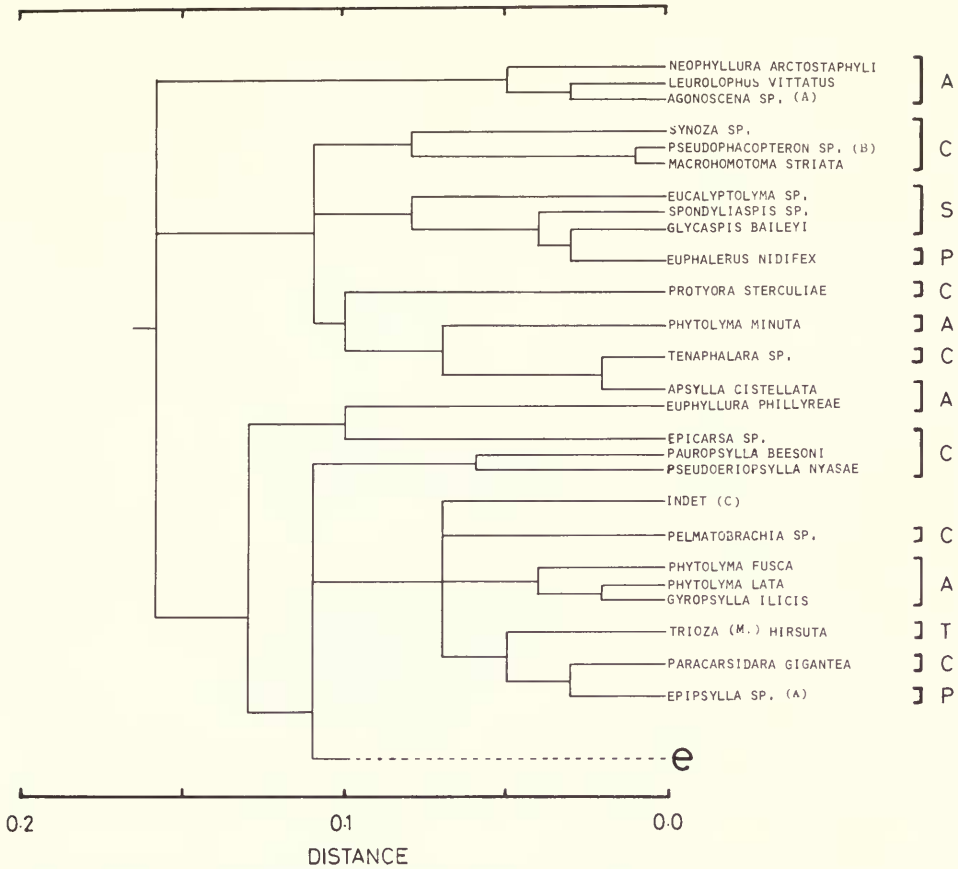


Fig. 179d Part of a phenogram of 182 species; continued in Fig. 179e and from Fig. 179a.

Epicarsa. The Carsidaridae and Aphalaridae placed with Triozidae have sectasetae, e.g. *Pauropsylla trichaeta* and *Paurocephala* spp. However, the major advantage of principal component analysis is that it permits the analysis of characters that are responsible for the formation of major groupings.

Characters with absolute eigenvector values on PCs I to III of at least the mean eigenvector value (0.17) are listed in Table 7. These are the characters which largely control the placing of species on PCs I to III.

On PC I (Table 7) the positive eigenvectors account for sectasetae (other than N 34) and shape (N 7) while the large negative values correspond to the petiolate tarsal arolium and capitate setae. The present states of those characters are mainly associated with Triozidae (positive values) and Psyllidae (negative values). On PC II the positive values are those applying to Triozidae and Psyllidae while the negative ones relate to the Aphalaridae (plus Diaphorini and *Psyllopsis*). PC III has a very high positive value for anus position, while other characters with positive values apply to Aphalaridae (plus Diaphorini and *Psyllopsis*). The remaining negative value is a shape character which relates to the Triozidae.

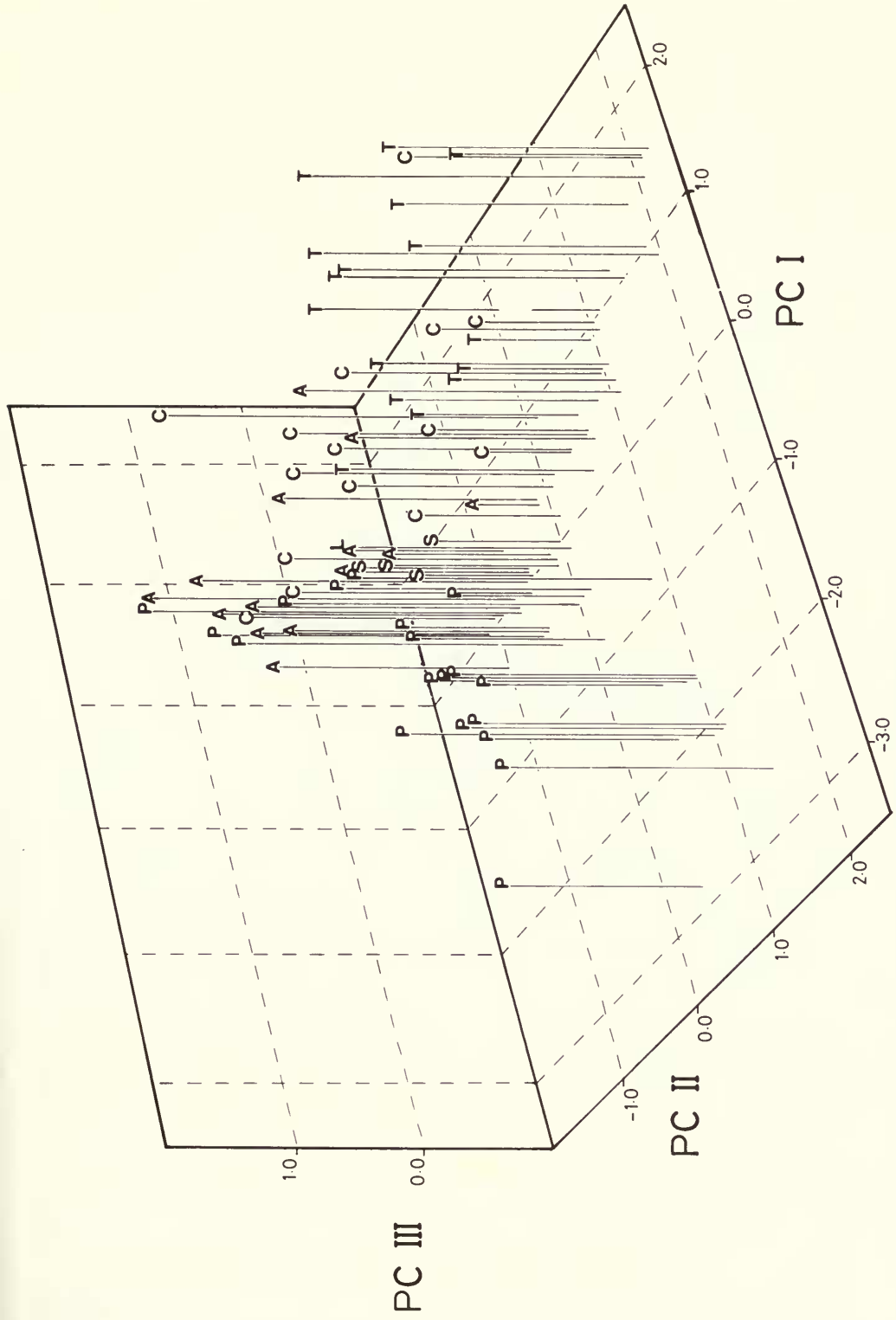


Fig. 180 Principal component analysis of 182 selected species with 34 nymphal characters. For practical illustration 68 species were chosen, each representing a cluster at the 0.2 phenon level of an average linkage cluster analysis performed on the first 10 principal components. The figure shows the 68 species, each marked by the initial letter of the Becker-Migdisova (1973) family to which it belongs, plotted on the first three principal components.

Table 7 Absolute eigenvector values in excess of the mean on principal component I, II and III.

Character	PC I	PC II	PC III
N3			-0.21
N4	-0.30		
N6		0.18	0.47
N7	0.27	0.24	
N8		-0.22	0.33
N9			0.44
N11	-0.22		
N13	-0.27	0.17	
N14	-0.18		
N16	-0.31	0.18	
N17	-0.31	0.18	
N18	-0.22		
N19	-0.32	0.18	
N23		-0.19	0.22
N24		-0.22	0.21
N25		-0.28	0.32
N26	0.19	0.28	
N30	0.19	0.28	
N31	0.20	0.27	
N33	0.20	0.27	

When the eigenvector values (EVs) of the 34 selected characters are plotted in three dimensions they form eight major groups (Fig. 181).

1. Characters N7, N26, N30, N31 and N33 describe the fusion of the head and prothorax and marginal positions of setasetae. These characters have positive states for most Triozidae.
2. Characters N1, N2, N3, N5, N10, N27, N28, N29, and N32 describe the humeral lobe position, position of wing-pad apices, disc-like tarsal arolium, sclerotization of dorsal surface of abdomen and dorsal positions of setasetae. The taxonomic distribution of positive states of these characters is similar to those in group 1.
3. Character N6 refers to the position of the anus. The extreme lack of compatibility of this character with most other characters causes it to be placed alone. All previously recognised major taxa have some species with each state of this character.
4. Characters N11, N12, N13, N14, N15, N16, N17, N18, N19 and N34 are positions of capitate setae and positioned abdominal margin lanceolate setae/setasetae. These are exclusively features of the Psyllidae. As with the setasetae the dorsal surface setal positions fall nearer the zero eigenvector values than the marginal setal positions.
5. Character N4 described the presence or absence of a petiole on the tarsal arolium. This feature is present in most Psyllidae as well as a few other groups.
6. Characters N20, N21 and N22 refer to the pair of tarsal capitate setae which are best developed in the Spondyliaspinae.
7. Characters N8, N23, N24 and N25 refer to the large thoracic sclerites and marginal lanceolate setae typical of the Aphalaridae.

Character groups 1, 2 and 3, groups 4 and 5, plus groups 6 and 7 each form one of three 'arms' of a trifurcate scatter (Fig. 181). Group 8 however, consisting only of characters N9 (free dorsal sclerites on abdomen), does not fit this trifurcate scatter because it is a feature of both Aphalaridae and Psyllidae.

Overall, the scatter of characters shown in Fig. 181 mirrors the trifurcate scatter of species (Fig. 180). This is because only the data matrix is required to transform the character eigenvector values to principal component values.

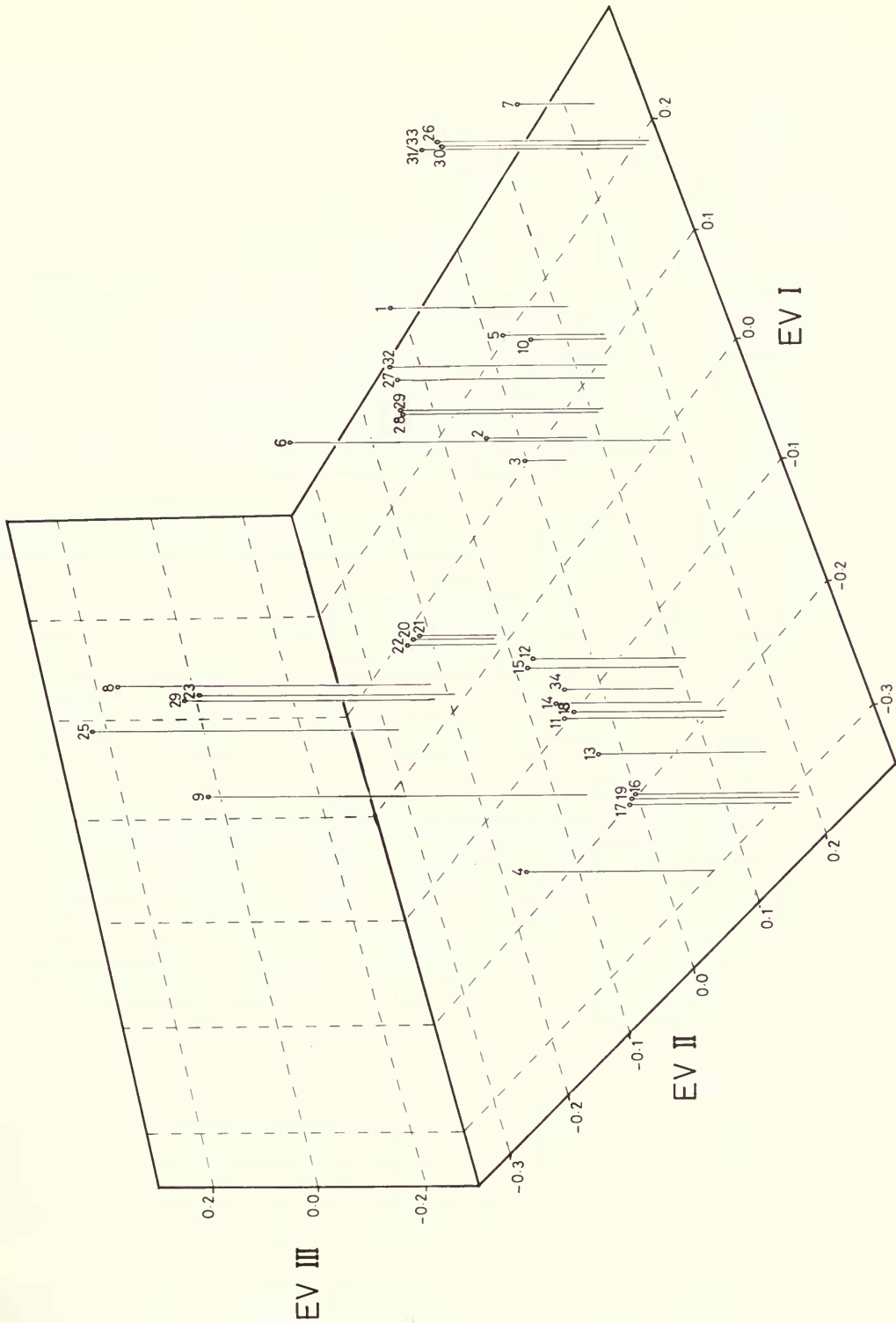


Fig. 181 Principal component analysis of 182 selected species with 34 nymphal characters. The figure shows the 34 characters plotted against their eigenvector values on the first three principal components.

Incorporation of adult characters

Selection of characters

Examination of the adults of the species studied was beyond the scope of this work. However, it was desirable to study adult characters as the interpretation of possible cladistic relationships requires the incorporation of characters controlled by different selection pressures. Characters selected from two rather than one life cycle stages are more likely to meet this criterion. Furthermore, such a study should provide insight into the underlying causes of the partial congruence between the nymphal phenetic relationships and the classification of Becker-Migdisova (1973), which was based almost exclusively upon adult data.

Twenty-seven adult characters were coded largely from the literature (Tables 8, 9). Major sources of information included those of Crawford (1914), Eastop (1958), Heslop-Harrison (1959), Hodkinson & White (1979*b*), Klimaszewski (1964), Loginova (1964*a*, 1972), Mathur (1975), Tuthill (1943, 1959, 1964*a*), Tuthill & Taylor (1955) and Zimmerman (1948). When descriptions are coded in this way several problems occur (Young & Watson, 1970). The greatest problem was the lack of consistency in the conventional approach to description which often made it impossible to distinguish between a genuine absence and mere failure to record the state of the character concerned. The least recorded characters are marked by an asterisk in the character listings (Tables 8, 9). In several cases the states of characters were deduced from family or tribal descriptions.

The 27 characters were coded identically for all species within each genus except for *Euphalerus* and *Pauropsylla*. These genera are variable intra-generically and the species were grouped as follows.

Euphalerus spp. received four different group descriptions:

- a. *E. nidifex*, *E. tantillus*, *E. sp.* (A), *E. sp.* (B) and *E. sp.* (D).
- b. *E. gallicolus*
- c. *E. jugovenosus*, *E. rugipennis* and *E. vermiculosus*
- d. *E. sp.* (C)

Pauropsylla spp. received two different group descriptions:

- a. *P. beelsoni*
- b. *P. depressa* and *P. trichaeta*

The 27 adult characters were combined with the original 88 nymphal characters (Tables 4, 5) and the ordered multistate characters were recoded into additive two-state code to give 33 adult and 120 nymphal characters. The SUMRAT information statistic was applied and 18 adult and 40 nymphal two-state characters were selected. These were then combined to form 14 adult (Table 8) and 30 nymphal (Table 10) multistate and two-state characters.

Several groups of species were identical with respect to the selected adult plus nymphal characters. Forty-seven species groups were formed and one representative species was chosen from each (Table 11). A further 161 species remained distinct (Table 11) making a total of 208 'taxa' available for further analysis.

Cluster analysis of combined adult and nymphal data

A MSN was generated across the data (Fig. 182). It was not possible to place an average linkage (AL) phenogram across the combined data because the required computing time was in excess of that available. Instead, as the first 10 principal components (PCs), extracted from a between character covariance matrix, explain most of the variance (79%), an AL phenogram calculated across them should approximate an AL phenogram using the untreated combined data. Such an AL phenogram using average distance is given in Fig. 183.

Five major clusters are formed by the AL.

- 1 (Fig. 183*b*). The members of the family Psyllidae whose nymphs have capitate setae.
- 2 (Fig. 183*c*). The members of the families Trioizidae and Carsidaridae which are typified by adult 'trioizine' wing venation (Character A6) and nymphal sectasetae.

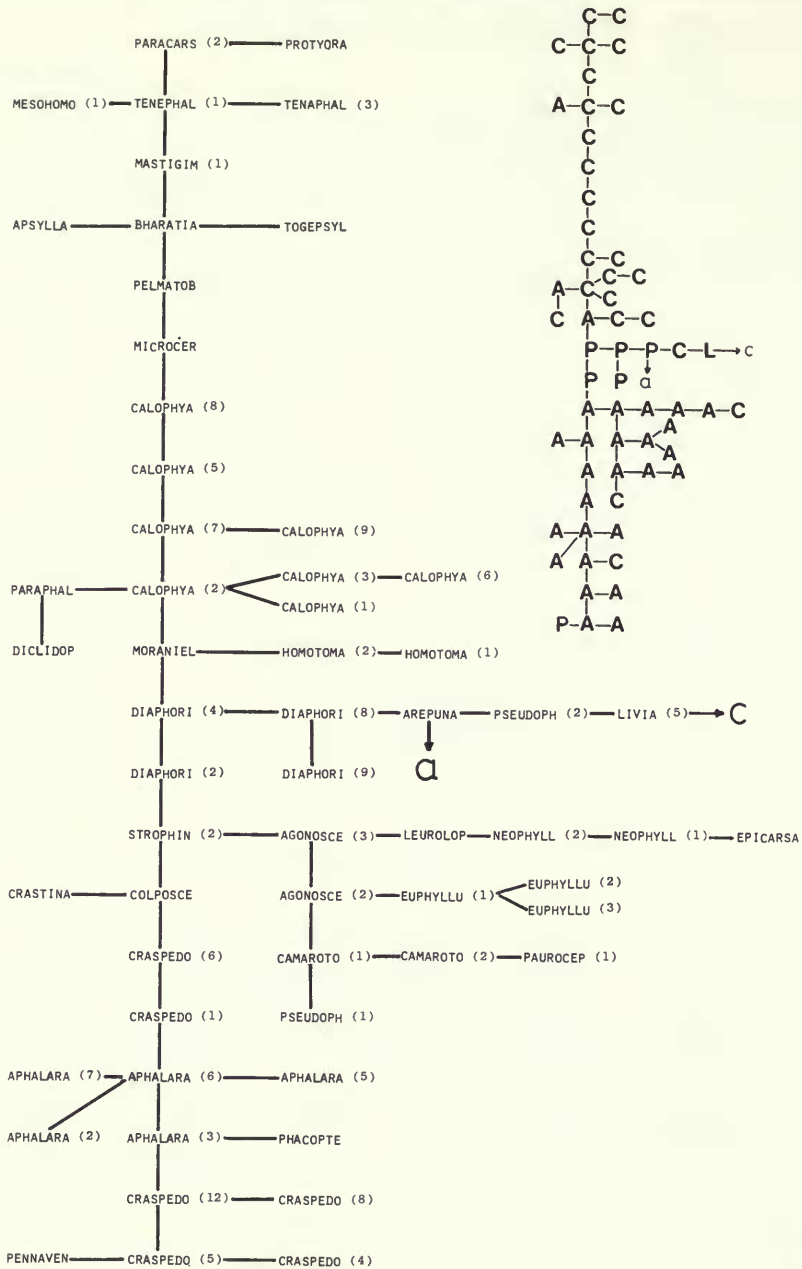


Fig. 182b Part of a minimum spanning network of 208 species; continued in Figs 182a and 182c.

3 (Fig. 183d). The members of this cluster are typified by numerous adult metatibial spines, usually with a lack of pronounced adult genal cones and the presence of nymphal lanceolate setae. It includes many Aphalaridae, all Liviidae, some Carsidaridae (many Homotominae and Phacopterinae) and a few Psyllidae (Diaphorini and *Psyllopsis*).

4 (Fig. 183e). This cluster contains species whose nymphs have pointed sectasetae together with those lacking capitate setae, lanceolate setae and truncate sectasetae. The incorporated taxa are Aphalaridae (e.g. *Paraphalaroida*) and Carsidaridae (e.g. *Calophya*) whose nymphs have

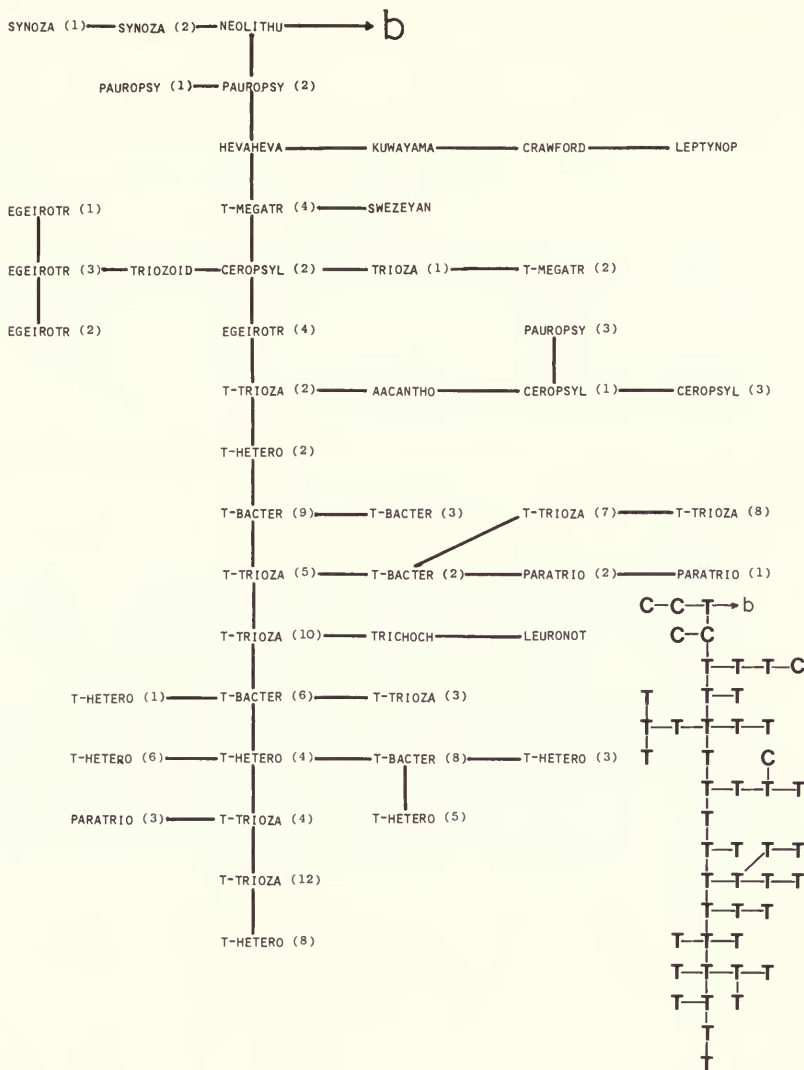


Fig. 182c Part of a minimum spanning network of 208 species; continued in Figs 182a–b.

pointed sectasetae, Psyllidae lacking capitate setae (e.g. *Acizzia acaciae*) and species with no specialised setae belonging to the families Carsidaridae (e.g. *Tenaphalara*) and Spondyliaspidiidae (e.g. *Glycaspis*). The genera *Ctenarytaina*, *Eucalyptolyma* and *Phellopsylla* (all Spondyliaspidiidae) are exceptional in that their nymphs do have lanceolate setae).

5 (Fig. 183a). This cluster is the genus *Euglyptoneura* which is a long distance from other species and hence are not included in any larger hierarchical cluster. However, in the MSN this genus is joined to *Psylla*.

In general, these clusters are very similar to those formed by analysis of nymphal data only.

The incorporation of adult data now enables observations to be made of the causes of congruence and incongruence between adult and nymphal resemblances.

A between character correlation matrix was generated across the selected adult plus nymphal data. The high correlations (r greater than 0.5) were as follows.

1. *Triozidae* attributes of adults and nymphs correlate (A3, A5, A6 and A12 with N1, N7, N10, N26, N30, N31 and N33), e.g. the adult wing venation and nymphal sectasetae.

2. *Aphalaridae* attributes of adults and nymphs correlate (A11 with N8, N23, N24 and N25), i.e. large numbers of adult metatibial spines with, for example, nymphal lanceolate setae.

3. *Psyllinae* attributes of adults and nymphs correlate (A4 with N4, N16, N17 and N19), i.e. a diagonal suture between the epimeron and episternum of the adult with, on the nymph, a petiolate tarsal arolium and capitate setae.

These correlated sets of characters, whose positive states roughly define currently recognised higher taxa, are the characters which weight the analyses towards complete congruence with the existing classification.

One observed form of incongruence is that groups of species that are regarded as genera on the basis of adult morphology often fail to cluster when nymphal data are analysed. In the minimum spanning network (MSN) (Fig. 182) 11 genera failed to cluster. These were *Acizzia*, *Aphalaroida*, *Ceropsylla*, *Ciriactremum*, *Craspedolepta*, *Egeirotrioza*, *Euphalerus*, *Paratrioza*, *Pauropsylla*, *Pseudophacopteron* and *Trioza*. A total of 21 other genera, of which more than one species was examined, are clustered. It is tentatively concluded that nymphal dissimilarity within a genus does not usually outweigh adult similarity.

Cladistic analysis

Ground plan construction

Prior to carrying out a cladistic analysis a ground plan was formed, i.e. a description of the hypothetical ancestor to present day Psylloidea. Various 'directional arguments' have been proposed for deducing which character states are primitive and therefore belong to the ground plan, and the methods are reviewed by de Jong (1980) and Arnold (1981). The favoured technique is known as OUT-GROUP COMPARISON, i.e. a character state that is not restricted to a single monophyletic group is likely to be ancestral. To apply the out-group criterion a previously suggested phylogeny is needed. Watrous & Wheeler (1981) noted that there could be circularity involved in forming monophyletic groups from directional arguments based upon monophyletic groups. Instead a previous classification can be used and in this study directional arguments were based on the results of the phenetic analyses presented earlier. For example, pointed sectasetae are present in many clusters in any given phenogram and so they appear to be an ancestral

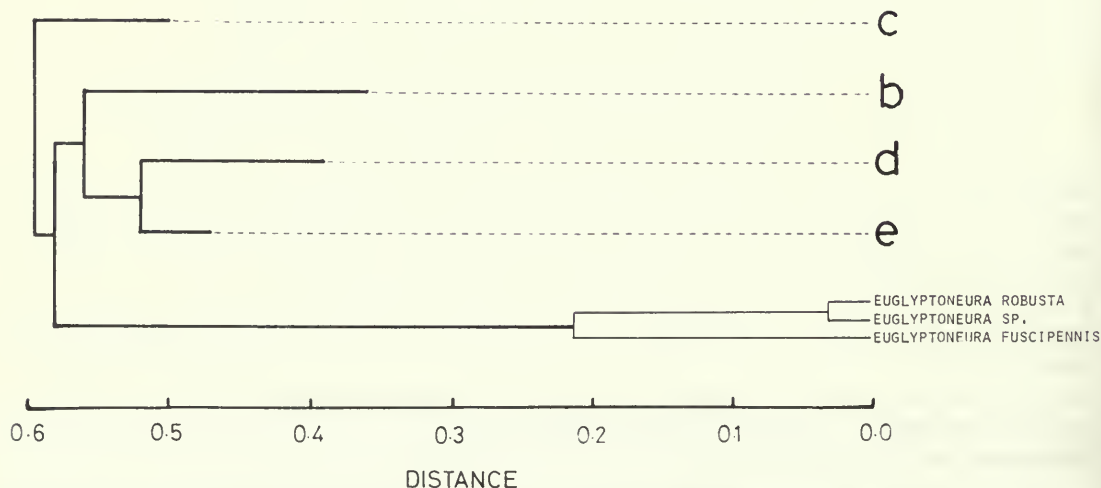


Fig. 183a Average linkage phenogram of 208 selected species. Distances were calculated from the first 10 principal components derived from 14 adult and 30 nymphal characters; key diagram showing linkages to Figs 183d–e.

feature. Conversely, truncate sectasetae, capitate setae and lanceolate setae each occur in a single large cluster and are therefore assumed to be derived features.

A summary of the ground plan is as follows.

ADULT

Head rounded. Genal cones absent. Anteoccipital lobes present. Antenna with narrow flagellar segments and rhinaria on segments III, IV, V, VI, VII, VIII, IX.

Suture between epimeron and episternum vertical. Forewing: coriaceous, rhomboidal in shape, costal break present, pterostigma present, nodal line present and veins *Cu+M* with a common stalk after the branching of *R* from the *R+M+Cu* stalk. Hind leg: meracanthus well developed, genual spine present, apex of tibia with a crown of many (c. 12) spines and apex of tarsal segment I with two spines.

Proctiger of male bipartite.

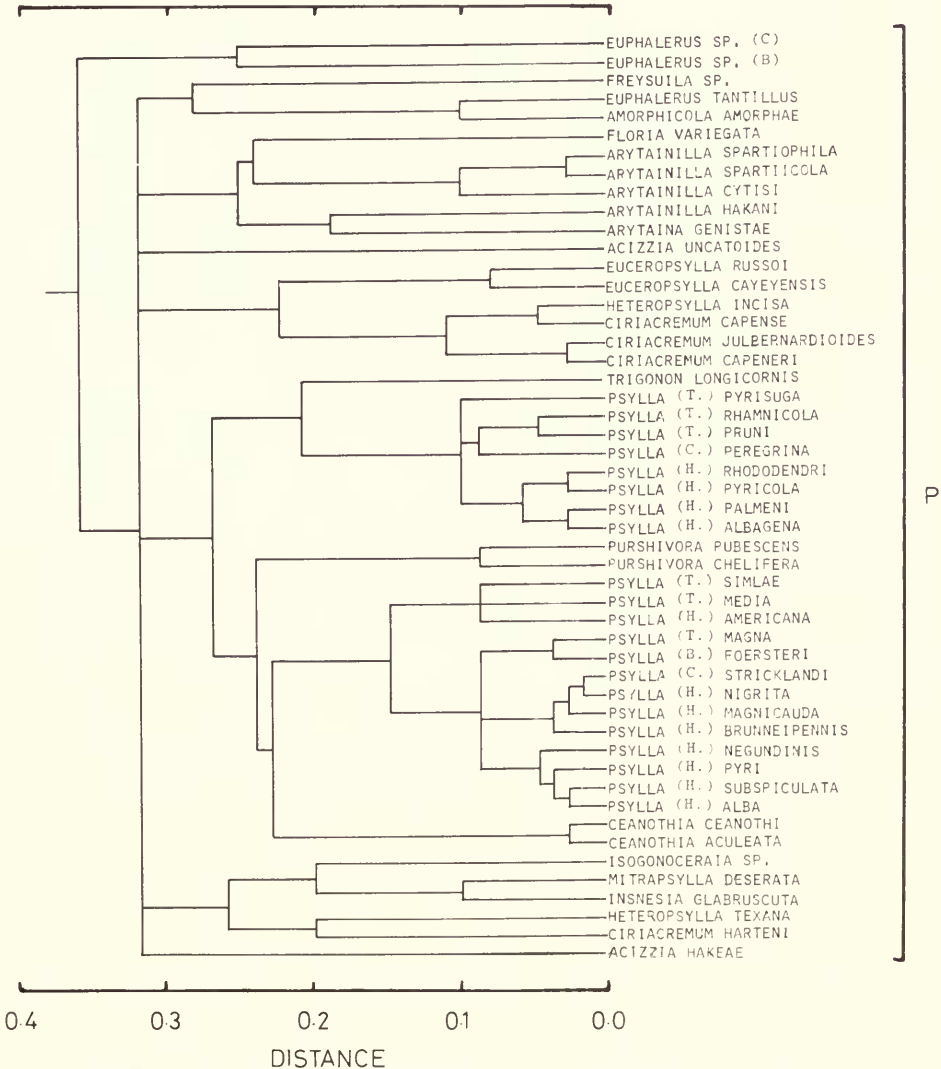


Fig. 183b Part of a phenogram of 208 species; continued from Fig. 183a.

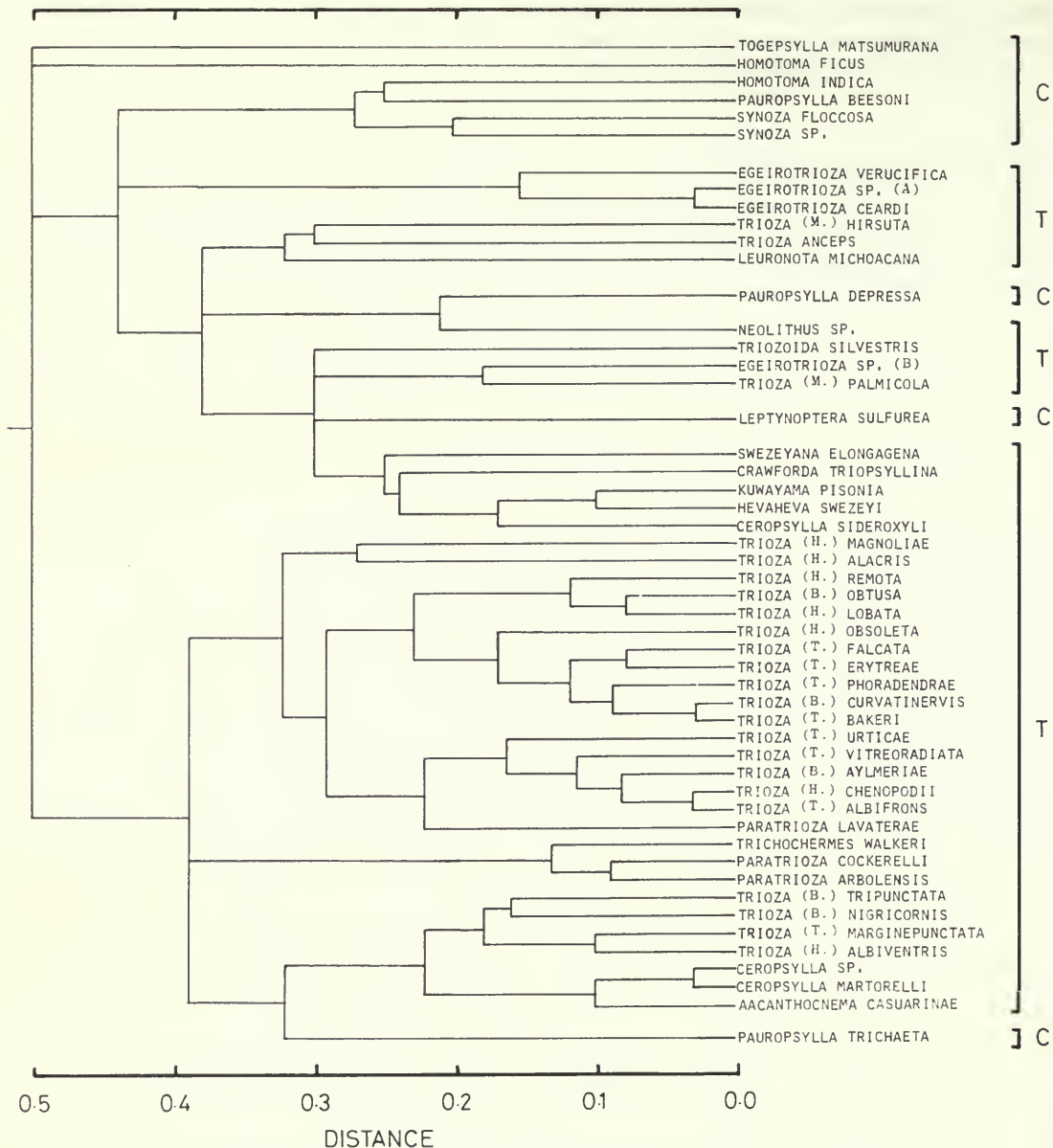


Fig. 183c Part of a phenogram of 208 species; continued from Fig. 183a.

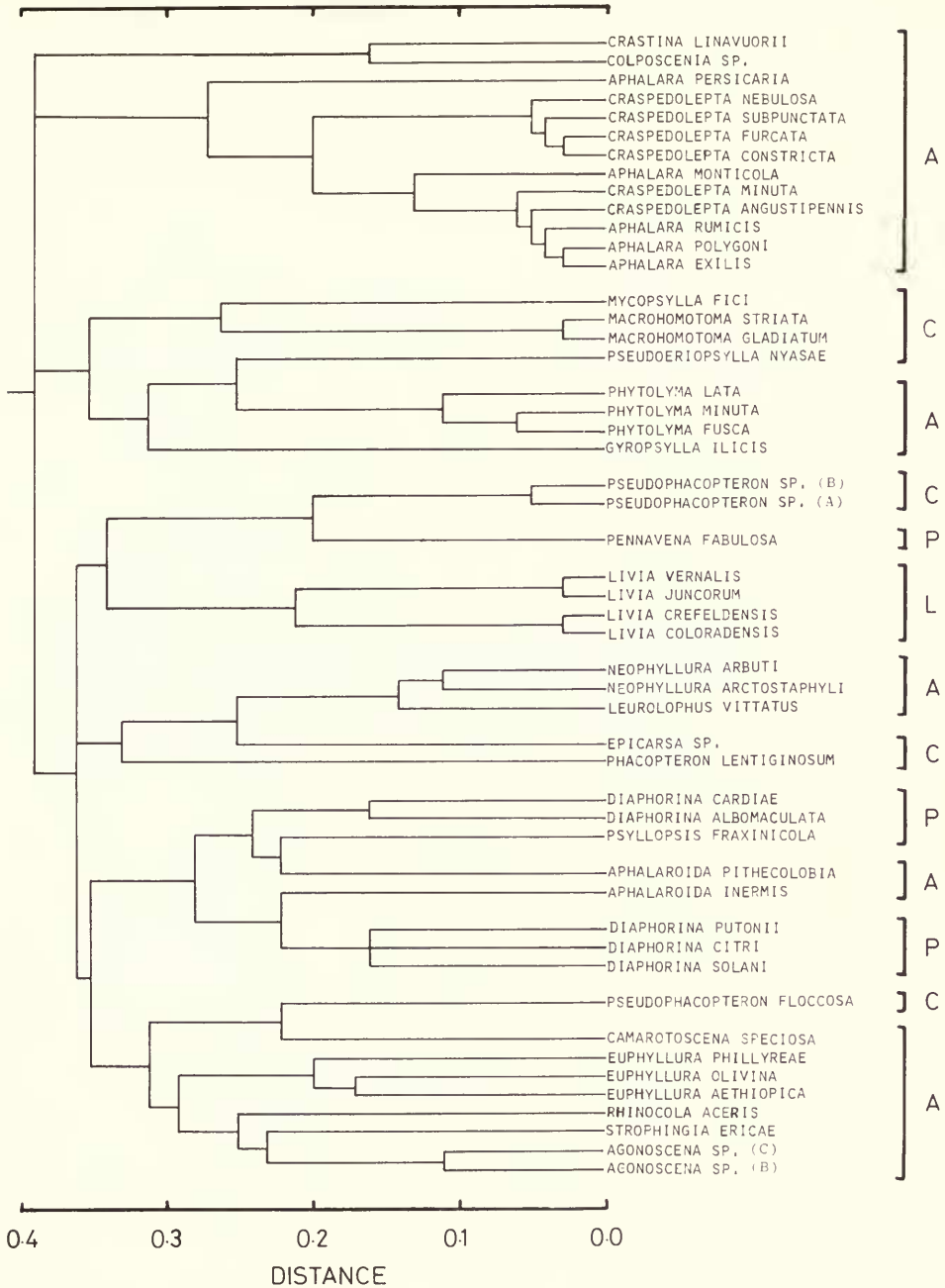


Fig. 183d Part of a phenogram of 208 species; continued from Fig. 183a.

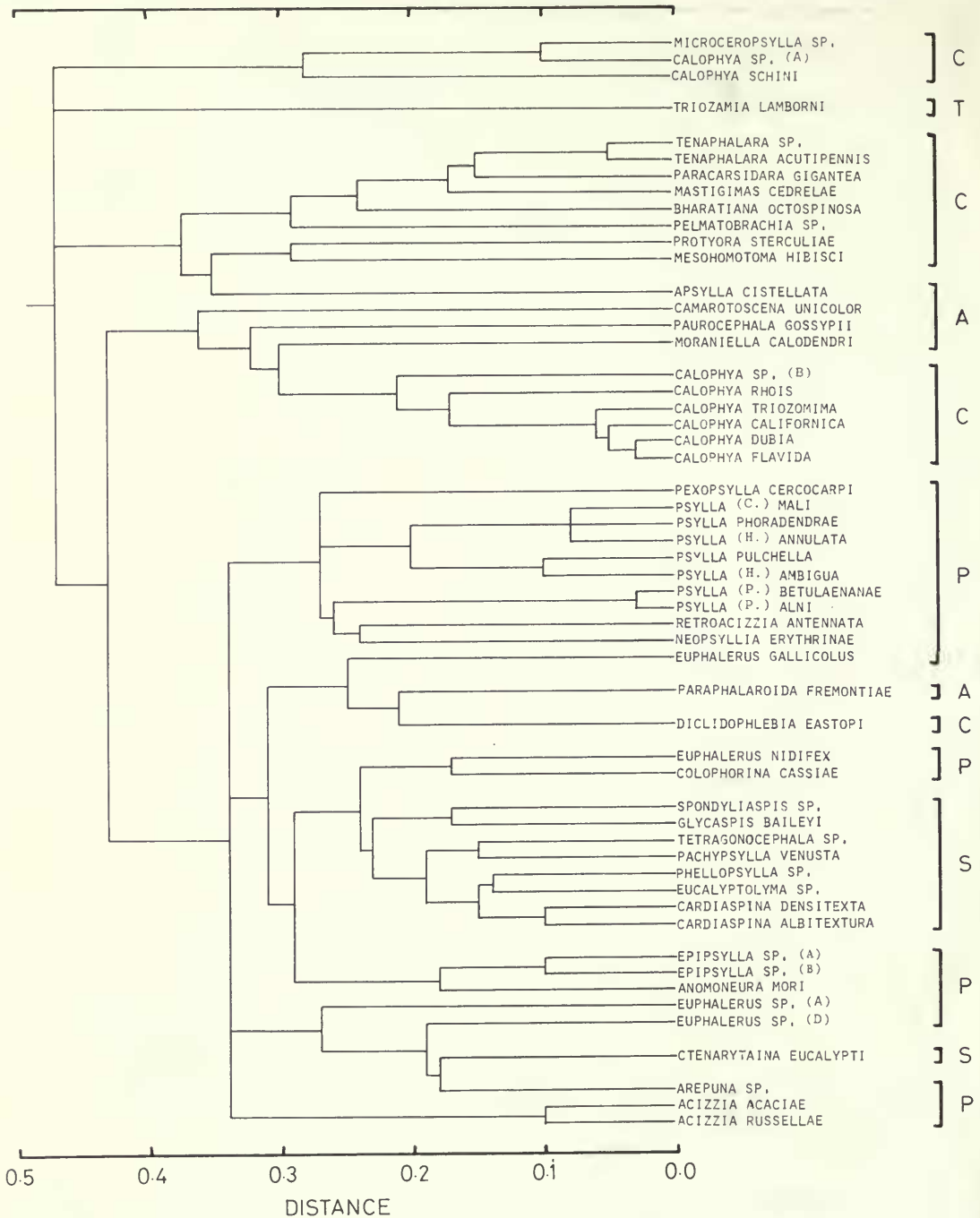


Fig. 183e Part of a phenogram of 208 species; continued from Fig. 183a.

Table 8 Selected adult characters.

Selected characters are numbered A1–A14. All the character states in the original list of 27 characters are tabulated. However, some character states become combined by the selection procedure and, hence, in some characters two consecutive states are marked with the same value. An asterisk indicates a character which was poorly recorded in the literature.

Head characters

A1.	Form of genae.	
	Genae not swollen	= 0
	Genae swollen but not conical	= 1
	Genae conical, frons not enveloped by genae	= 2
	Genae conical, frons enveloped by genae	= 3
*A2.	Antenna with rhinaria on following segments.	
	III, IV, V, VI, VII, VIII, IX	= 0
	IV, V, VI, VII, VIII, IX	= 0
	IV, V, VI, VIII, IX	= 1
	IV, VI, VIII, IX	= 2
	III, VI, VIII, IX	= 2

Thorax characters

*A3.	Pronotum vertically or subvertically inclined, and laterally constricted. Often completely or partly concealed by head.	
	No = 0 Yes = 1	
*A4.	Suture between epimeron and episternum.	
	Horizontal	= 0
	Vertical (dorsally terminating at mid point of pronotal lateral margin)	= 0
	Diagonal (dorsally terminating at posterior of pronotal lateral margin)	= 1

Forewing characters

A5.	Forewing with apex acute or acutely rounded. Costal margin curved. M_{1+2} terminating at or anterior to apex.	
	No = 0 Yes = 1	
A6.	$Cu+M+R$ or $M+R$ common stalk present.	
	No = 0 Yes = 1	
*A7.	Costal break absent.	
	No = 0 Yes = 1	
A8.	Pterostigma absent.	
	No = 0 Yes = 1	
A9.	Cu_2 not terminating adjacent to Cu_{1b}	
	No = 0 Yes = 1	

Hind-leg characters

*A10.	Metatibia with basal (genual) spine present.	
	No = 0 Yes = 1	
*A11.	Metatibial apical spines or platellae numbering more than five.	
	No = 0 Yes = 1	
*A12.	Metatarsal spines.	
	Absent	= 0
	One present	= 1
	Two present	= 2

Male genitalia characters

A13.	Male proctiger unipartite.	
	No = 0 Yes = 1	
A14.	Male proctiger with long caudal lobes present in at least some species of the genus.	
	No = 0 Yes = 1	

Table 9 Rejected adult characters.

Rejected characters are numbered A15–A27. Values are not given against the states, which are separated by a '/'. An asterisk indicates a character which was poorly recorded in the literature.

Head characters

- A15. Vertex with cleft and antennae based upon apices of blunt vertex lobes. No/Yes.
 A16. Vertex produced into lobes and enveloping genae. No/Yes.
 A17. Preoccipital lobes present. No/Yes.
 A18. Preocular tubercles present: No/Yes.
 A19. Antenna segment II greatly enlarged. No/Yes.
 A20. Apical antennal spines longer than antennal segment III. No/Yes.
 A21. Clypeus long and cylindrical, projecting to anterior margin of head. No/Yes.

Forewing characters

- A22. Forewing with apex acute or acutely rounded. Costal margin curved. M_{1+2} terminating posterior to apex. No/Yes.
 A23. Nodal line absent. No/Yes.
 A24. $R-M_{1+2}$ cross vein or anastomosis present. No/Yes.
 A25. $R-M$ (bifurcation of M_{1+2} and M_{3+4}) cross vein present. No/Yes.

Hind-leg characters

- *A26. Meracanthus reduced or absent. No/Yes.

Male genitalia characters

- A27. Male subgenital plate with hypovalves. No/Yes.

Table 10 Nymphal characters selected after incorporation of adult characters.

Characters previously selected and now reselected: N1, N3, N4, N5, N6, N7, N8, N9, N10, N11, N13, N14, N15, N16, N17, N18, N19, N23, N24, N25, N26, N27, N28, N30, N31, N32, N33 and N34. Two further characters were selected, as follows.

- Outer circum-anal pore ring broken at two or more places (modified N52).
 No = 0 Yes = 1
- Forewing-pad dorsal surface sectasetae (modified N29).
 Absent = 0 Pointed = 1 Truncate = 1

Table 11 Groups of species identical with the selected adult plus nymphal characters. The species chosen to represent the group is named at the top of each list.

- | | |
|--|--|
| 1. <i>Acizzia acaciae</i>
<i>Acizzia acaciaebaileyanae</i> | 8. <i>Craspedolepta furcata</i>
<i>Craspedolepta nervosa</i> |
| 2. <i>Agonosцена</i> sp. (B).
<i>Agonosцена</i> sp. (A). | 9. <i>Craspedolepta minuta</i>
<i>Craspedolepta minutissima</i> |
| 3. <i>Agonosцена</i> sp. (C).
<i>Strophingia cinerea</i> | 10. <i>Diaphorina cardiae</i>
<i>Diaphorina chobauti</i> |
| 4. <i>Aphalara polygona</i>
<i>Aphalara curta</i>
<i>A. nubifera</i>
<i>A. simila</i> | 11. <i>Diaphorina citri</i>
<i>Diaphorina florea</i> |
| 5. <i>Calophya flavida</i>
<i>Calophya nigripennis</i> | 12. <i>Diaphorina putonii</i>
<i>Diaphorina clutiae</i>
<i>D. punctulata</i> |
| 6. <i>Cardiaspina albitextura</i>
<i>Cardiaspina spinifera</i>
<i>C. squamula</i>
<i>Creiis</i> sp. | 13. <i>Euceropsylla russoi</i>
<i>Euceropsylla minuticonica</i>
<i>E. sp.</i> |
| 7. <i>Craspedolepta augustipennis</i>
<i>Craspedolepta artemisiae</i>
<i>C. sonchi</i>
<i>C. suaedae</i>
<i>C. vancouverensis</i>
<i>C. veaziei</i> | 14. <i>Euphalerus nidifex</i>
<i>Euphalerus jugovenosus</i>
<i>E. rugipennis</i>
<i>E. vermiculosus</i> |
| | 15. <i>Glycaspis baileyi</i>
<i>Glycaspis</i> spp. |
| | 16. <i>Gyropsylla ilicis</i>
<i>Gyropsylla</i> spp. |

- | | |
|--|--|
| 17. <i>Livia coloradensis</i>
<i>Livia maculipennis</i> | 31. <i>Psylla magnicauda</i>
<i>Psylla minor</i> |
| 18. <i>Mastigimas cedrelae</i>
<i>Mastigimas</i> spp. | 32. <i>Psylla mali</i>
<i>Psylla ribesiae</i> |
| 19. <i>Mesohomotoma hibisci</i>
<i>Mesohomotoma</i> spp. | 33. <i>Psylla nigrita</i>
<i>Psylla saliceti</i> |
| 20. <i>Mycopsylla fici</i>
<i>Mycopsylla</i> spp. | 34. <i>Psylla pyri</i>
<i>Psylla ulmi</i> |
| 21. <i>Neophyllura arctostaphyli</i>
<i>Neophyllura bicolor</i> | 35. <i>Psylla pyricola</i>
<i>Psylla myrtilli</i>
<i>P. visci</i> |
| 22. <i>Neopsyllia erythrinae</i>
<i>Neopsyllia</i> spp.
<i>Platycorypha princeps</i> | 36. <i>Psylla pyrisuga</i>
<i>Psylla melanoneura</i>
<i>P. sorbi</i> |
| 23. <i>Pachyopsylla venusta</i>
<i>Pachyopsylla</i> spp. | 37. <i>Psyllopsis fraxinicola</i>
<i>Psyllopsis</i> spp. |
| 24. <i>Paracarsidara gigantea</i>
<i>Paracarsidara</i> spp. | 38. <i>Strothingia ericae</i>
<i>Tainarys schini</i> |
| 25. <i>Paratrioza cockerelli</i>
<i>Paratrioza maculipennis</i> | 39. <i>Tenaphalara acutipennis</i>
<i>Tenaphalara malayensis</i> |
| 26. <i>Paurocephala gossypii</i>
<i>Paurocephala urenae</i> | 40. <i>Trioza albifrons</i>
<i>Trioza beameri</i>
<i>T. quadripunctata</i> |
| 27. <i>Psylla alba</i>
<i>Psylla sinuata</i> | 41. <i>Trioza albiventris</i>
<i>Trioza atkasookensis</i>
<i>T. crithmi</i> |
| 28. <i>Psylla alni</i>
<i>Psylla buxi</i>
<i>Spanioneura fonscolombii</i> | 42. <i>Trioza bakeri</i>
<i>Trioza cinnamomi</i>
<i>T. diospyri</i>
<i>T. frontalis</i> |
| 29. <i>Psylla betulaenanae</i>
<i>Psylla carpinicola</i>
<i>P. floccosa</i>
<i>P. galeaformis</i>
<i>P. striata</i>
<i>P. trimaculata</i> | 43. <i>Trioza chenopodii</i>
<i>Trioza litseae</i> |
| 30. <i>Psylla brunneipennis</i>
<i>Psylla brevistigmata</i>
<i>P. coryli</i>
<i>P. hamata</i>
<i>P. hirsuta</i>
<i>P. minuta</i>
<i>P. moscovita</i>
<i>P. parallela</i>
<i>P. pulchra</i> | 44. <i>Trioza curvatineris</i>
<i>Trioza minuta</i>
<i>T. salicivora</i> |
| | 45. <i>Trioza erytreae</i>
<i>Trioza panacis</i> |
| | 46. <i>Trioza marginepunctata</i>
<i>Trioza vitiensis</i>
<i>T. sp.</i> |
| | 47. <i>Trioza tripunctata</i>
<i>Trioza incidata</i> |

The following species have unique descriptions:

- | | |
|--------------------------------|-------------------------------|
| <i>Aacanthocnema casuarina</i> | <i>Bharatiana octospinosa</i> |
| <i>Acizzia hakeae</i> | <i>Calophya californica</i> |
| <i>A. russellae</i> | <i>C. dubia</i> |
| <i>A. uncatoides</i> | <i>C. rhois</i> |
| <i>Amorphicola amorphae</i> | <i>C. schini</i> |
| <i>Anomoneura mori</i> | <i>C. triozomima</i> |
| <i>Aphalara exilis</i> | <i>C. rotundipennis</i> |
| <i>A. monticola</i> | <i>C. sp.</i> |
| <i>A. persicaria</i> | <i>Camarotoscena</i> spp. |
| <i>A. rumicis</i> | <i>Cardiaspina densitexta</i> |
| <i>Aphalaroida</i> spp. | <i>Ceanothia</i> spp. |
| <i>Apsylla cistellata</i> | <i>Ceropsylla</i> spp. |
| <i>Arepuna</i> sp. | <i>Ciriacremum</i> spp. |
| <i>Arytaina genistae</i> | <i>Colophorina cassiae</i> |
| <i>Arytainilla</i> spp. | <i>Colposcena</i> sp. |

NYMPH

Prothorax completely separate to head. Mesothorax and metathorax with well-defined medial and lateral sclerites. Abdomen with well-defined sclerites and a small caudal plate. Anus ventral and surrounded by a pore field of uncertain form.

Whole body (dorsal, margin, including wing-pads, and antennae) covered in pointed sectasetae and simple setae.

It is interesting to note that pointed sectasetae appear to be an ancestral attribute. However, Becker-Migdisova (1973) believed the ancestral nymph lacked sectasetae and was similar to *Tenaphalara*. This would imply that sectasetae, which are a highly complex structure, must have evolved several times. Becker-Migdisova fails to explain this unparsimonious assumption.

Wagner tree

An attempt was made to analyse cladistic relationships by constructing a Wagner tree (Farris, 1970). Characters were selected by phyletic weighting (Cain & Harrison, 1960), so that only one character out of a set of characters that might be functionally or ecologically correlated was used in the analysis. This weighting left only 17 characters, which were inadequate for meaningful analysis (White, 1980). However, this analysis did indicate a need to re-examine the structure of the tarsal arolium.

Reanalysis of tarsal arolium structure

One large branch of the Wagner tree was initially defined by the presence of a petiolate tarsal arolium in the nymph and the branch included all the Psyllidae except Diaphorini and *Psyllopsis*. Furthermore, the presence or absence of a petiolate tarsal arolium in the nymph, received very high eigenvector and SUMRAT values in previous analyses, and the presence state appears to be largely confined to the Psyllidae. However, it was also recorded as present in a few Aphalaridae (*Aphalara persicaria* and *Paurocephala*) and Triozidae (*Trioza hirsuta*). Upon re-examination the finer structure of the arolium became apparent. Most species have a sclerotized 'rod' or 'rods' running longitudinally from the base of the arolium (shown black in Figs 59–94). The homology of this structure is uncertain, but it will be referred to as an unguitactor. Some species lack any visible arolium (most Spondyliaspidae), while others lack any visible unguitactor (Aphalarinae (Aphalaridae) and *Egeirotrioza* (Triozidae)) (Fig. 95). A short unguitactor is probably the ancestral state (Fig. 67). It is greatly elongated in almost all the Psyllidae, *Dictidophlebia* (Carsidaridae), *Aphalaroida*, *Camartoscena*, Euphyllurini, *Paraphalaroida* and *Paurocephala* (Aphalaridae) (Figs 59, 62–66, 69, 70, 79–93). Some species have retained a membrane adjacent to the long unguitactor: Diaphorini (Fig. 60) and Euphyllurini (Figs 62–64) while in others it is lost (Fig. 59). Careful analysis of arolium form was found to be of great value in cladistic analysis of species which otherwise differ little from the ground plan.

Cladistic method

The Wagner tree analysis indicated that a method of cladogram construction was needed which used all of the available characters. To overcome the problem of GAIN characters being of greater value than LOSS characters a two-phase method of cladogram construction was devised.

A GAIN character is here defined as one whose derived state is the presence of an attribute. A LOSS character is defined as one whose derived state is the absence of an attribute. Loss characters should be accorded low weight because a structure could be lost in many distantly related phyletic lines (Mayr, 1969). When a high proportion of characters are of the loss type certain modifications to the cladistic principles of Camin & Sokal (1965) and Hennig (1966) must be applied.

A total of 159 adult and nymphal characters was divided into two sets (Table 12): 1, gain characters and, 2, loss characters. Using gain characters only, the most parsimonious cladogram was formed. The loss characters were then added to the cladogram such that each group of taxa

which was divided by loss characters only had maximum parsimony. However, the loss characters were not most parsimonious over the entire tree.

When a section of the tree could only be structured by loss characters and many equally parsimonious solutions were possible, the characters were weighted and added to the tree in order of decreasing weight. The weights were the sum of the mutual information (Legendre & Rogers, 1972) values for each character with all other characters in the section of tree under study. This method is similar in principle to using the compatibility method of Le Quesne (1969).

In the illustration of the cladogram (Figs 184–196) the following convention was adopted.

1. Gain characters are marked by squares; black for derived and white for ancestral.
2. Loss characters are marked by circles; black for derived and white for ancestral. This enables clades which are only defined by loss characters to be instantly recognisable.
3. Each ancestor is numbered, e.g. the ancestral psyllid is number one. All descendants are said to belong to clade one. There are 94 ancestors giving rise to 106 taxa of generic, subgeneric and in some cases species level groupings.

Formation of initial branches in the cladogram (Fig. 185)

A few of the characters used by Schlee (1969) and Szelegiewicz (1971) are included at the base of the cladogram, to define both the Psylloidea and their supposed sister clade the Aleyrodoidea (Fig. 184).

Certain major clades (2, 6, 13, 15, 17, 32, 37 and 39) are defined by complex gain characters. *Apsylla*, *Bharatiana*, *Livia*, *Mastigimas* and *Strophingia* are separated from the ground plan almost entirely by loss characters and are not easily placed.

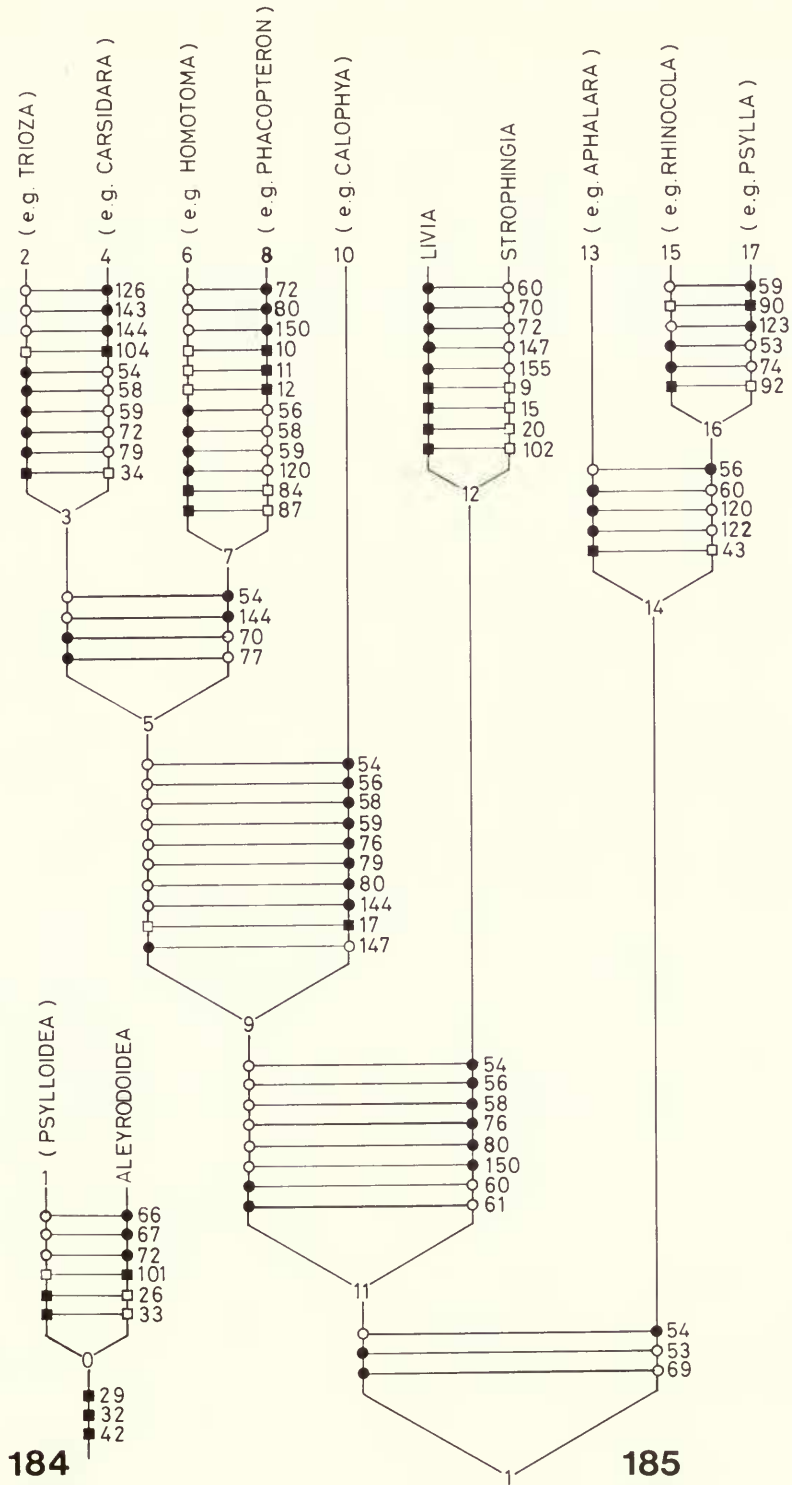
Apsylla adults have very long apical antennal spines, which is a gain character ancestral to clade 39 (Fig. 190), e.g. *Calophya*, although *Pseudophacopteron* (clade 37, Fig. 189) also has this attribute. *Apsylla* is therefore placed as a sister group to clade 39 (clade 10 is formed). *Bharatiana* adults have a fairly large clypeus and large lateral ocelli, though not as pronounced as in clade 37, e.g. *Phacopteron*. With hesitation, *Bharatiana* is placed as a sister group to clade 37 (clade 8 is formed). *Mastigimas* nymphs have broken bands of anal pores, a feature which could be derived from bands of anal pores, an attribute which is ancestral to clade 32, e.g. *Paracarsidara* (Fig. 187). Although anal pore bands also occur in *Epicarsa*, *Mastigimas* is placed as a sister group to clade 32 (clade 4 is formed). *Livia* and *Strophingia* are only separated from the ground plan by loss characters and cannot be placed with any clade so far formed.

The ten-way furcation from the ground plan (to clades 2, 4, 6, 8, 10, 13, 15 and 17 plus *Livia* and *Strophingia*) was resolved using weighting and the resulting branches are shown in Fig. 185.

Becker-Migdisova (1973) proposed that the ancestral psyllid gave rise to three separate lines (a *Carsidara/Trioza* line, an *Aphalara* line and a *Psylla* line). However, Klimaszewski (1964) proposed a bifurcation into a *Carsidara/Trioza* line and an *Aphalara/Psylla* line. Furthermore, Vondracek (1957) suggests a *Spondylaspis/Carsidara/Trioza* line and a *Calophya/Psylla/Aphalara* line. The present cladogram agrees with a line typified by *Trioza* and *Carsidara* (cf. *Paracarsidara*) and includes some of the groups which these authors have referred to *Carsidaridae*, such as *Calophya*, *Phacopteron* and *Homotoma*. However, the present cladogram provides no justification for the *Aphalaridae*, except as a collection of groups phenetically close to the ground plan from which other clades can be derived. The *Psyllidae* arise from one such group (clade 17).

Clade descriptions

Clade 2 (Fig. 186) corresponds with the *Triozidae* plus the *Leptynopterinae* and *Pauropsyllini* of Becker-Migdisova (1973). However, this is not the *Pauropsyllini* of Loginova (1972), many of which are placed in clade 17, e.g. *Paurocephala* (Figs. 193–196). The genera *Leptynoptera* and *Pauropsylla* have a typical *Trioza* type adult pronotum, wing venation and sometimes nymphal form. They are placed in clade 18 with other genera possessing these features. The pronotal structure of *Trioza* is also found, to a lesser extent of development, in *Homotoma* (clade 6,



Figs 184, 185 Clades 0 and 1. 184, clade 0, including the Psyllloidea (clade 1) and Aleyrodoidea; 185, clade 1, the Psyllloidea. Details of clades 2, 4, 6, 8, 10, 13, 15 and 17 are illustrated in Figs 186–196.

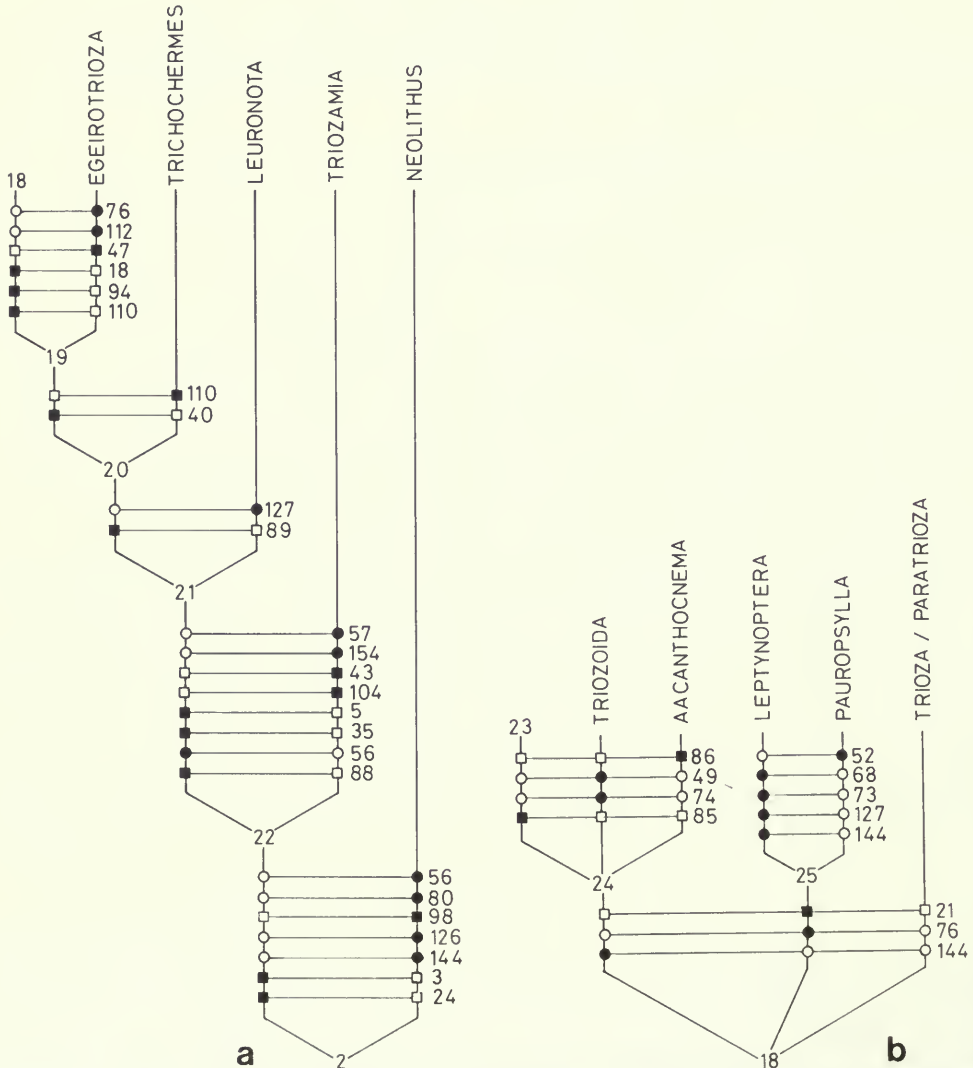
Fig. 188) and *Microceropsylla* (clade 10, Fig. 190). Clade 2 can be divided into three major sections.

(i) Clade 2 (minus clade 18) (Fig. 186a), e.g. *Trichohermes* includes those genera which lack the *Trioza* type adult pronotum and the fusion of the dorsal surface of the nymphal abdomen.

(ii) Clade 18 (minus clade 23) (Fig. 186b) contains genera in which the nymphs are fairly elongate, the hindwing-pad margin is not confluent with the abdomen margin and the marginal setae are normally well spaced apart.

(iii) Clade 23 (Fig. 186c) contains genera which have 'disc'-shaped nymphs, often with marginal scales, dorsal clavate setae or closely spaced marginal setae.

Clade 4 (Fig. 187) is equivalent to the Carsidarinae and Tenaphalarinae of Becker-Migdisova (1973) and Klimaszewski (1964). Clade 32 is defined by the presence of a cross-vein in the adult forewing. This is subdivided into *Tenaphalara* (with an extra cross vein) and clade 31 (with a deeply cleft adult head).



Figs 186a, b Clades 2 and 18. 186a, clade 2, continued in Figs 186b, c; 186b, clade 18, continued in Fig. 186c and from Fig. 186a.

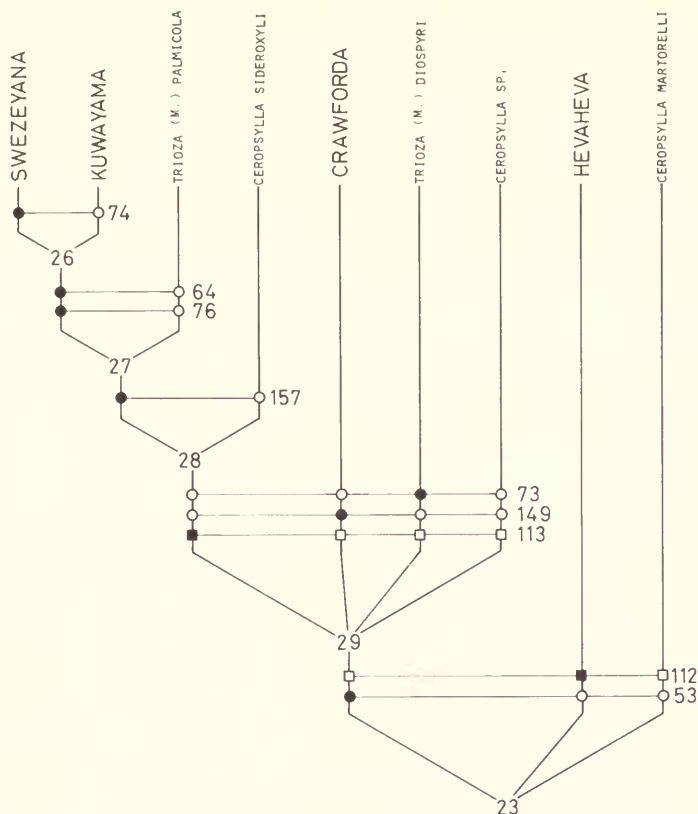
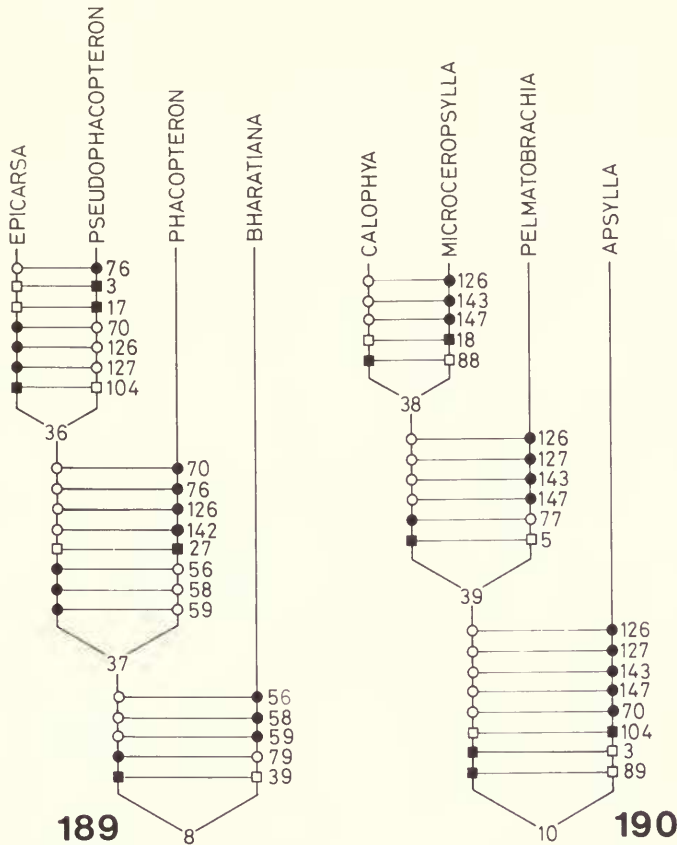


Fig. 186c Clade 23; continued from Fig. 186b.

Clade 6 (Fig. 188) is the Homotominae of Becker-Migdisova (1973). Clade 33 represents a group in need of some revision, for some *Homotoma* spp. not examined in this study may be placed with *Synoza* in the present cladogram, e.g. *H. gressitti* Miyatake has no *M+Cu* vein in the wing. Miyatake (1974) revised some *Homotoma* spp. but overlooked *Synoza* and was unaware of undescribed African species of the group (in coll. British Museum (Natural History)).

Clade 8 (Fig. 189) is the Phacopterinae of Becker-Migdisova (1973) plus ?*Epicarsa* and *Bharatiana*. The latter is only tentatively placed. The nymph examined of the former was labelled as being found with an adult close to *Epicarsa*, from Brazil. The adult characters in the present cladogram are largely those given by Crawford (1911); Ferris (1928b) described an *Epicarsa* from Mexico, but there is some doubt about its true identity. Lima & Guitton (1962) described another Brazilian member of clade 37 (*Phacosemoides sicki*). The Pacific genus *Chineura* Tuthill should also be placed here. In the cladogram *Pseudophacopteron* nymphs are described as having lanceolate setae. This only applies to material labelled as ?*P. floccosa* from Guam: these setae are lost in other *Pseudophacopteron* spp. examined. *P. floccosa* is a Sri Lanka species which is unlikely to occur on Guam. Since wing form in this group is distinct it is assumed that the material from Guam is a member of clade 37. Guam is the type locality of *Chineura paucivena* Tuthill which may have been confused with *Pseudophacopteron*.

Clade 10 (Fig. 190) includes *Calophya* plus some genera referred to Pauropsyllinae: Microceropsyllini and Anomalopsyllinae: Apsyllini by Becker-Migdisova (1973). Loginova (1972) places *Microceropsylla* and *Pelmatobrachia* in the Pauropsyllini. The genus *Calophya* itself is referred to the Carsidaridae by Becker-Migdisova (1973), the Pauropsyllinae by Crawford (1914), and the Psyllidae by many authors (Klimaszewski, 1964; Dobreanu & Manolache, 1962; Hodkinson & White, 1979b). Several species which probably belong within clade 34 are still



Figs 189, 190 Clades 8 and 10. 189, clade 8; 190, clade 10.

components of this group are poorly known; they probably derived from basic psyllid stock earlier than temperate forms, and are difficult to place in the existing classification.

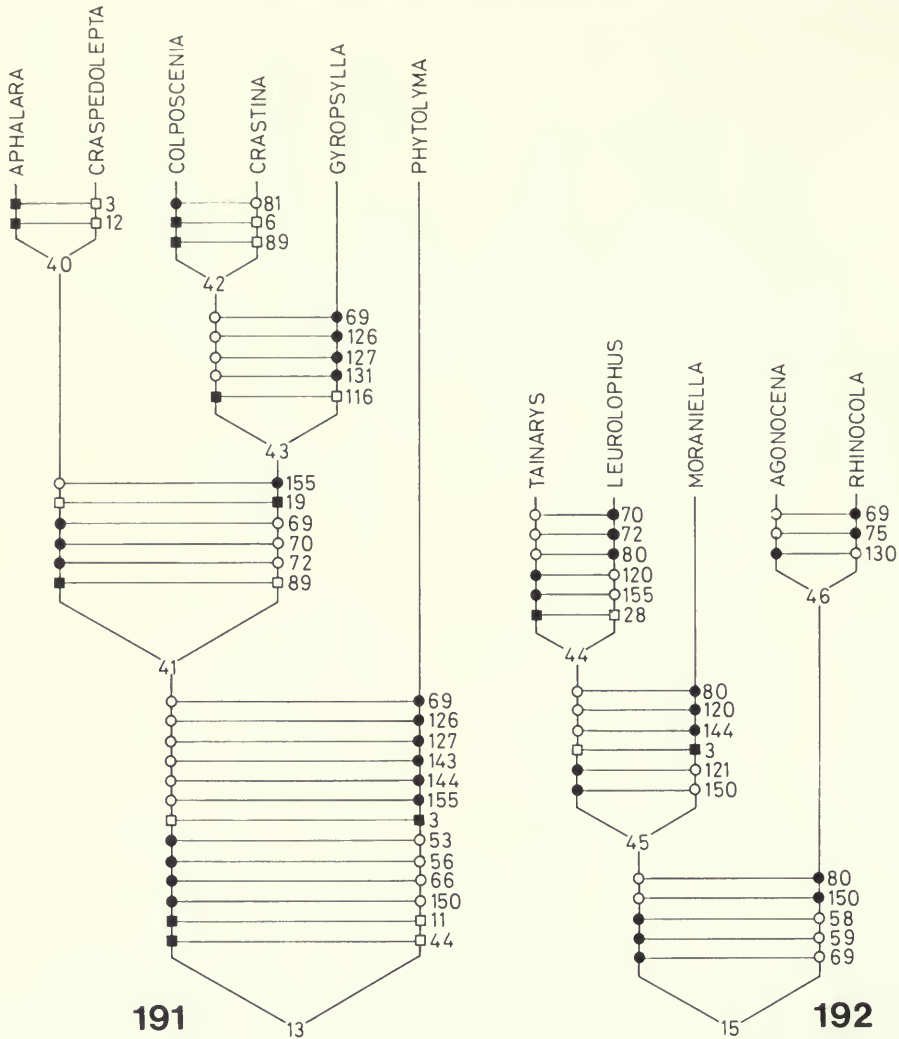
Clade 43 is defined by the diagonal suture between the adult epimeron and episternum. Clade 42 is the tribe Stigmaphalarini of Vondracek (1957) and Colposceniini of Becker-Migdisova (1973). Clade 40 is the Aphalarini of most authors.

Clade 15 (Fig. 192) contains species which have retained many ground plan features: *Moraniella* nymphs are surrounded by pointed sectasetae and adult males of *Tainarys* have a bipartite proctiger. However, the form of the tarsal arolium which defines clade 15 is unique. Nevertheless, the branching within the clade is based on loss characters only, and weights were applied.

Clade 17 (Figs 193–196) contains over half of the species studied and it is defined by the elongation of the unguitractor in the tarsal arolium of the nymph. The major division is into clades 48 and 53 (Fig. 193).

Clade 53 is defined by nymphal capitate setae, but excludes those species where the nymph has retained numerous sectasetae or where the sectasetae are reduced to lanceolate setae. Clade 48 is formed by adult loss characters, which are in common to all of these morphologically more primitive species. It is further divided into clades 47 and 50.

Clade 47 (Fig. 194), defined by the presence of 1 + 1 pore rings (or a derivable feature) on the nymphal abdomen, is divided into clades 60 and 62. Clade 62 contains the genera *Diclidophlebia* and *Paraphalaroida*. *Paraphalaroida* contains one species (*P. fremontiae*) which, prior to the revision of Loginova (1972), was regarded as a *Paurocephala* sp. *Diclidophlebia* was referred to the Carsidaridae: Tenaphalarinae, Diclidophlebiini by Becker-Migdisova (1973). The genus



Figs 191, 192 Clades 13 and 15. 191, clade 13; 192, clade 15.

Togepsylla (omitted from this cladogram due to lack of information on certain character states, e.g. the form of the tarsal arolium) may belong to clade 62 because its adult head structure is similar to *Diclidophlebia* (Becker-Migdisova, 1973). Certain species still referred to the genus *Paurocephala*, such as *P. tuxtlaensis* Conconi from Mexico and *P. menoni* Mathur from India, probably belong to clade 62.

Clade 60 is divided into clades 59 and 61 by the development of adult vertex lobes as opposed to genal cones and elongated wing cells. Clade 59 is the Euphyllurini of Loginova (1973) and part of the Euphyllurini of Becker-Migdisova (1973).

Clade 61 is referred to the Spondyliaspidae by most authors (Becker-Migdisova, 1973; Hodkinson & White, 1979b; the Spondyliaspidae by Heslop-Harrison, 1954). Unlike the nymphs of other Spondyliaspidae (clade 55, Fig. 195) examined, *Ctenarytaina* and *Eucalyptolyma* have marginal lanceolate setae and, therefore, fit the cladogram outside of clade 56. Both are characterised by the reduction or absence of tarsal arolia and if they do belong to clade 17 this must represent a secondary loss. The pore field on the nymphal abdomen of *Eucalyptolyma* sp. and *Ctenarytaina eucalypti* may be derived from 1 + 1 pore rings, the defining character of clade

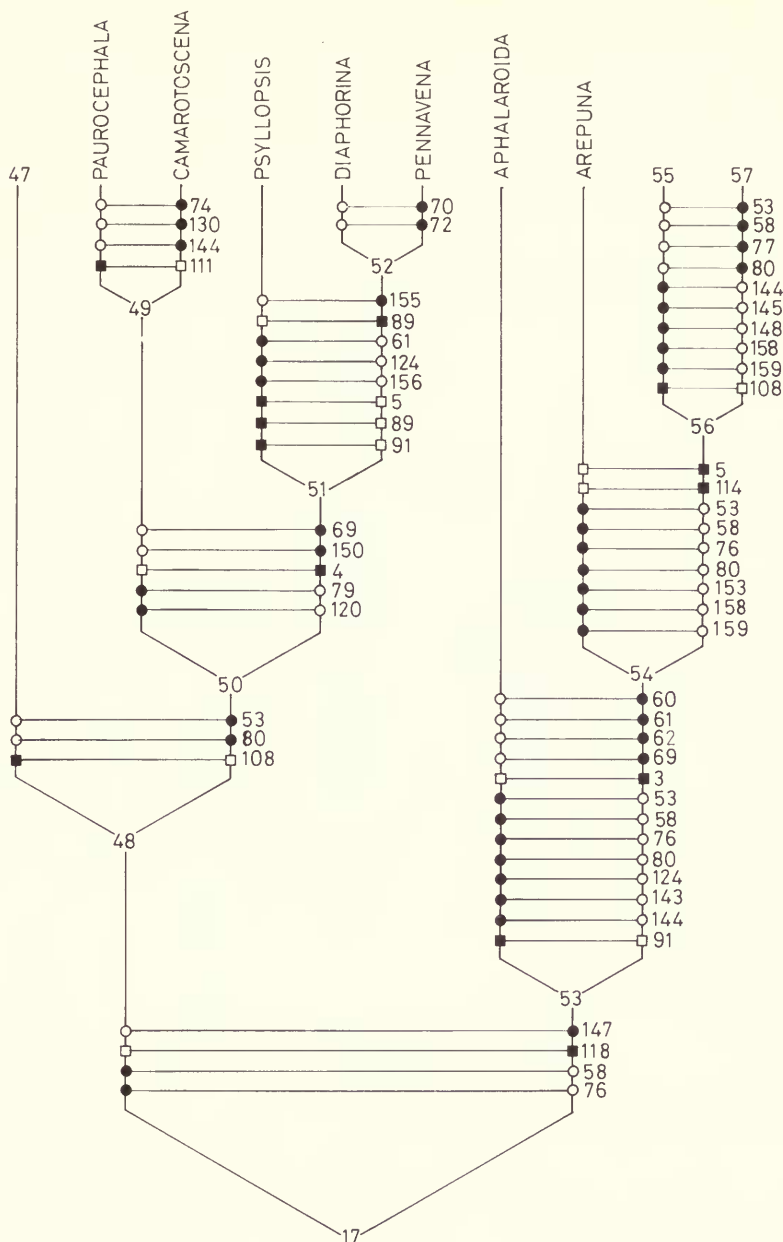


Fig. 193 Clade 17, giving rise to clades 47, 55 and 56 which are illustrated by Figs 194, 195 and 196 respectively.

47, and hence clade 61 is placed in a position of maximum parsimony. Nymphs of *Ctenarytaina thysanura* Ferris & Klyver, which we have subsequently seen, lack the abdominal pore field. The position of *Eucalyptolyma* requires further investigation since recently acquired material of *E. fuscipennis* Froggatt nymphs are of a structure concordant with clade 61 while those of *E. maideni* Froggatt are structurally close to clade 68. Two Indian species (*Euphyllura caudata* Mathur and *E. concolor* Mathur) may also belong to clade 61 on the basis of the pore field of the nymphal abdomen and the structure of the adult female proctiger.

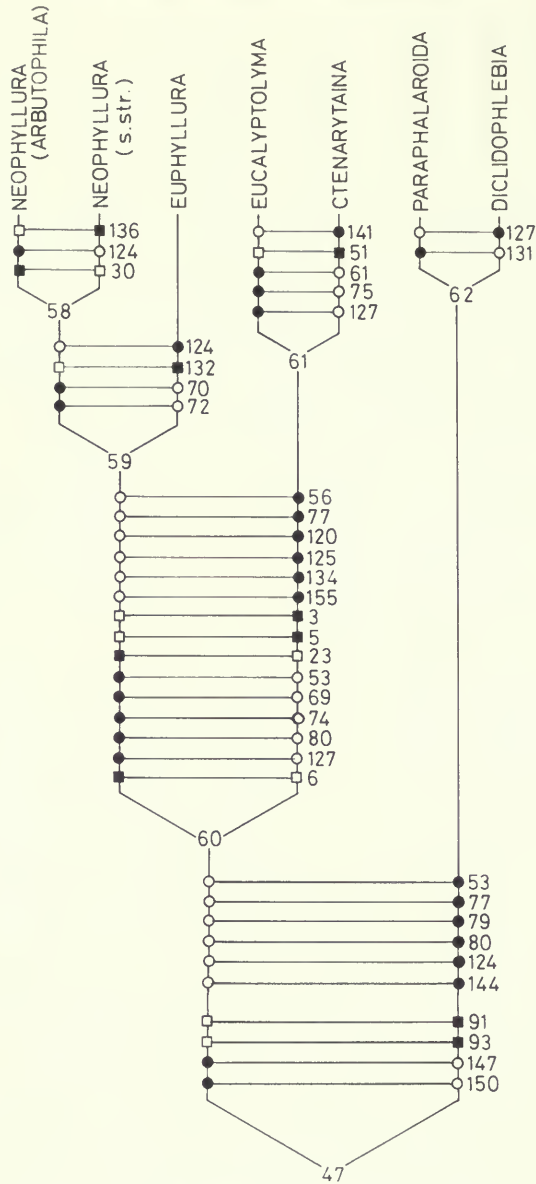


Fig. 194 Clade 47.

Clade 50 (Fig. 193) is a maximum parsimony collection, based on loss characters, of genera belonging to clade 17 but not clades 47 or 53. It is divided into clades 49 and 51. Clade 51 is defined by the presence of genal cones, a feature which occurs many times in the cladogram, and clade 49 is only formed by loss characters.

Clade 49 (Fig. 193) contains the genera *Camarotoscena* and *Paurocephala*, the former of which was regarded as a subgenus of *Paurocephala* by Vondracek (1957). Most authors have placed these genera in the tribe Paurocephalini of the Aphalaridae: Paurocephalinae (Becker-Migdisova, 1973; Klimaszewski, 1964). Because the general facies of the adult head is similar to *Pauropsylla* (clade 25, Fig. 186b) many authors placed *Paurocephala* in the Pauropsyllinae (Crawford, 1914; Loginova, 1972; Mathur, 1975).

Clade 51 (Fig. 193) is the Psyllidae: Arytaininae, Diaphorinini of Vondracek (1957), Dobreanu & Manolache (1962) and Klimaszewski (1975). Becker-Migdisova (1973) placed *Psyllopsis* in the Psyllidae: Arytaininae, Psyllopseini. Pflugfelder (1941) placed *Diaphorina* and *Psyllopsis* in the Aphalaridae, and Löw (1879) placed them in the Psyllidae and Aphalaridae respectively. The nymphs of *Psyllopsis*, *Diaphorina* and *Pennavena* have an 'Aphalara' facies and are surrounded by marginal lanceolate setae. The long unguitactor of the nymphal arolium suggests that these genera belong in clade 17. However, the presence of lanceolate setae excludes these genera from clade 56 where most former authors have placed them. Furthermore, the adults retain a crown of about 10 spines at the apex of the metatibia, a feature always reduced in clade 57 (Fig. 196).

Clade 53 (Figs 193–196) begins with a major transition between members of clade 17 with 'Aphalara' and 'Psylla' type facies. The nymph of *Aphalaroida* is in many respects similar to *Euphalerus* or *Acizzia* while the adult is phenetically similar to *Strophingia*. The nymph of *Aphalaroida pithecolobia* is covered by rod setae, similar to *Euglyptoneura robusta* and *Pexopsylla cercocarpi* (both Clade 56, Fig. 193). The position of *E. robusta* (clade 82, Fig. 196e) suggests that rod setae are modified capitate setae and therefore, in the cladogram, rod setae are not differentiated from capitate setae.

The adult of *Arepuna* has a wing of a *Euphalerus* type and the nymph is surrounded by clavate setae. These could be very reduced sectasetae, which would place *Arepuna* outside of clade 56, or reduced capitate setae, which would place it anywhere in clade 53. A larger number of losses must be proposed if *Arepuna* is to be placed within clade 56 rather than as a sister group to it.

Clade 55 (Fig. 195) is initially defined by the presence, in the nymph, of 1 + 1 pore rings additional to the circum-anal ring. It is assumed that these rings become split to form the 2 + 2 rings which initially define clade 66. Even without this assumption the contents of clades 64 and 66 would still arise from close to the start of clade 56 (Fig. 193). In clade 63 the preoccipital lobes are lost and the 1 + 1 pore rings become areas of separated pores. Although nymphal capitate setae are regarded as lost in clade 55, they may be retained in some species, such as *Psylla bengalensis* Mathur, which were not examined but appear to belong to clade 64.

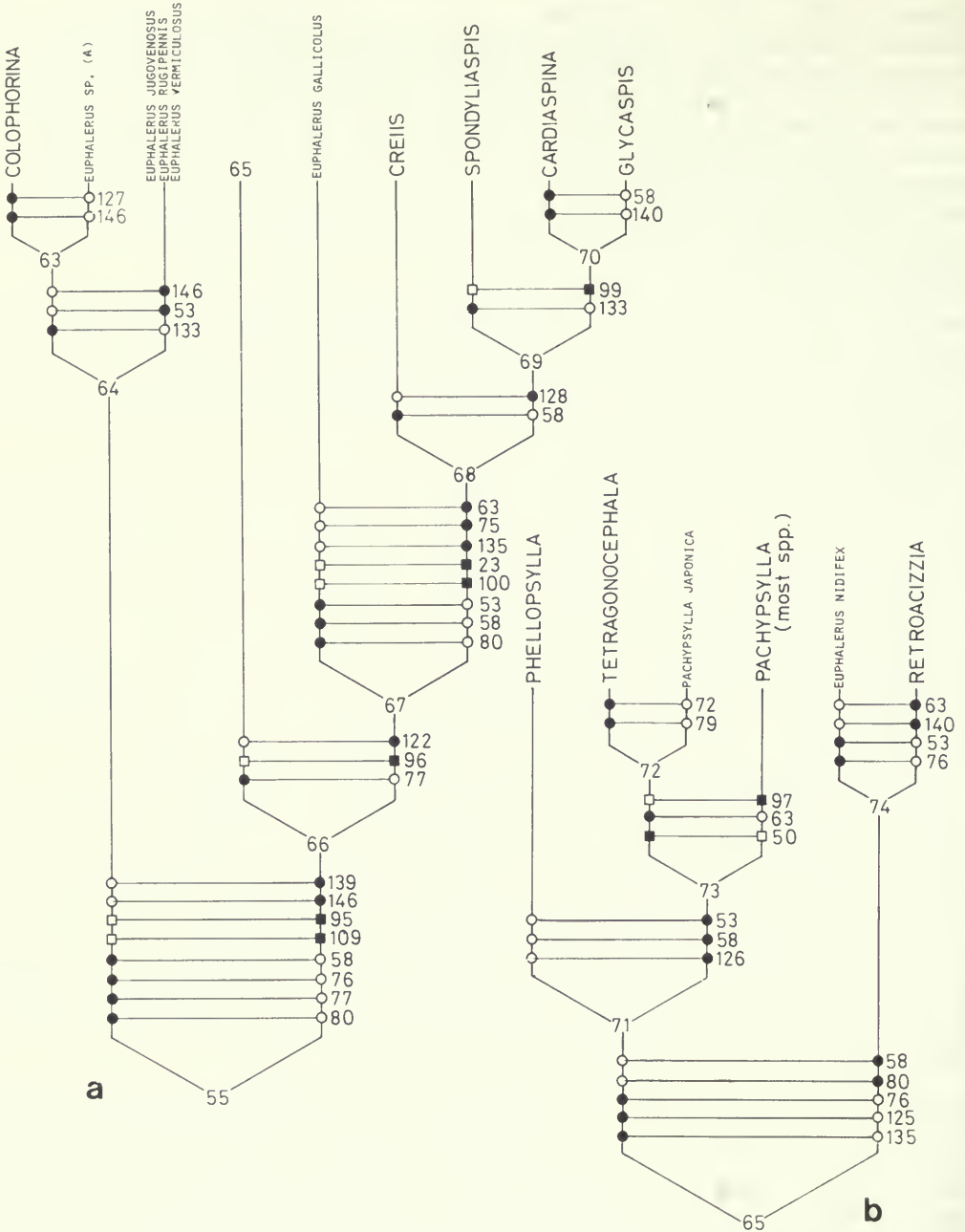
Clade 66 is initially defined both by the presence of 2 + 2 nymphal pore rings and a serrate apex to the nymphal abdomen. Clade 65 is a collection of species in which the serrate apex to the abdomen is retained but the pore rings are often lost or reduced to small groups of pores. This reduction could be derived from 1 + 1 or 2 + 2 pore rings and species which belong to clade 55, but are excluded from clades 64 and 67, are grouped for convenience into clade 65. Clade 65 consists of the following taxa: clade 72, *Euphalerus nidifex*, *Pachypsylla* spp. (other than *P. japonica*), *Phellopsylla* and *Retroacizzia* all of which are only separated from ancestor 65 by loss characters. The details of clade 65 were constructed by weighting. *Phellopsylla* belongs to the Spondyliaspidae of all authors, clade 73 to the Spondyliaspidae: Pachypsyllinae of Becker-Migdisova (1973) and clade 74 to the Psyllidae.

Ancestor 67 (Fig. 195a) marks a transition. Clade 67 is initially defined by having enlarged outer teeth on the serrate apex of the nymphal abdomen, as in *Euphalerus gallicolus*. Clade 68 is a collection of species with a pointed cauda in the nymph: *Creiis* has both a pointed cauda and 1 + 1 tooth-like structures near the apex of the abdomen. These are treated as being homologous with the enlarged outer teeth in *E. gallicolus*. Further evidence for the inclusion of clade 68 in 66 is provided by the fact that lerp-forming species are confined to clades 65 and 68.

Nymphs of species in clade 68 have weakly sclerotized abdomens and the caudal plate is rudimentary. This implies either that a large caudal plate has been derived separately in several branches, or that a reversal to separate segments has occurred. This appears to contradict Dollo's Law. However, the genotype must contain coding for all abdominal segments since they occur in the adult, i.e. Dollo's Law is not broken at the level of the genotype.

Clade 57 (Fig. 196) is defined by loss characters only and contains genera which belong within clade 56 but not 55. With the exception of clade 51 (Fig. 193), and some *Euphalerus* spp. (including the type-species of the genus, *E. nidifex*) and *Retroacizzia* which have been assigned to clade 55 (Fig. 195), it is the Psyllidae of most authors.

Certain clades (78, 82 and 85) are defined by gain characters leaving the genera *Acizzia*,

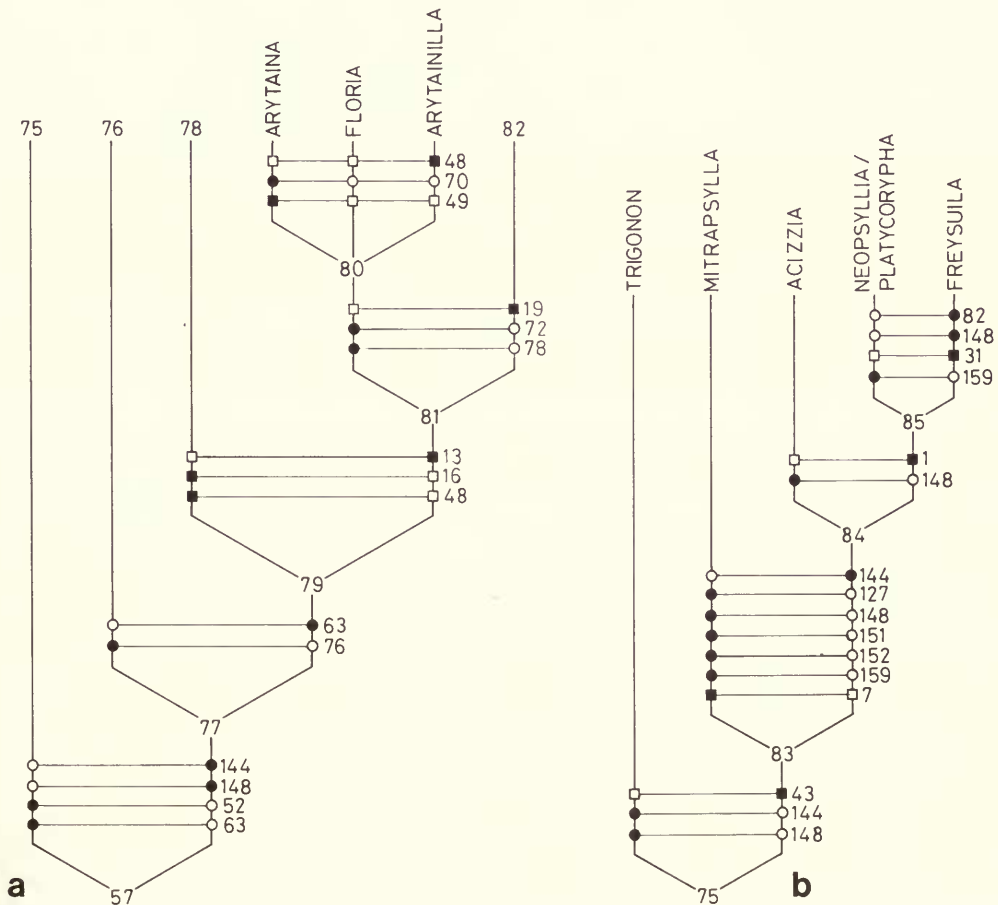


Figs 195a, b Clades 55 and 65. 195a, clade 55, continued in Fig. 195b; 195b, clade 65, continued from Fig. 195a.

Amorphicola, *Anomoneura*, *Arytaina*, *Arytainilla*, *Epipsylla*, *Floria*, *Mitrapsylla*, *Trigonon* and a few species referred to the genus *Euphalerus* unplaced. Character 43 (caudal lobe on adult male proctiger) was incompatible with character 1 (very broad head) and was initially ignored because it occurs in other apparently unrelated groups such as *Aphalara* and may also have evolved many times within clade 57. Character 13 (position of antennal insertions) was also omitted initially since a tendency for the antennal bases to move back not only occurs in all of

clade 82 (Fig. 196e), *Arytaina*, *Arytainilla* and *Floria* but also in a few species of other clades, such as *Ciriactremum nigripes* Hollis. Character 106 (broad anal ring) is also ignored since this occurs in *Psylla* s.str. (clade 82) as well as in *Anomoneura* and *Epipsylla*, and its derivation is uncertain. The details of clade 57 were then constructed by weighting to form five major clades (75, 76, 78, 80 and 82); characters 43, 13 and 106 were then replaced.

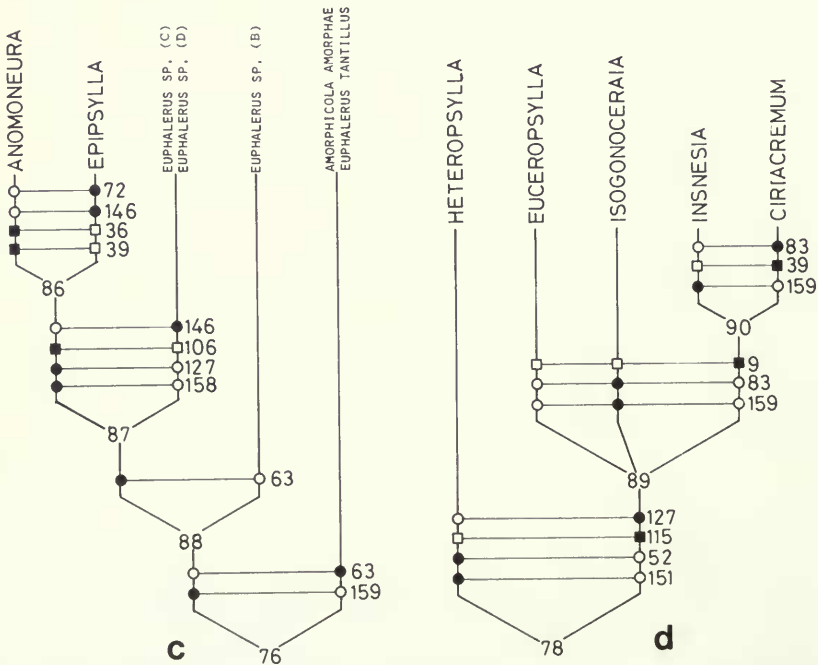
Clade 75 (Fig. 196b): the first branch, from the general line in clade 57, forms clade 75. The largest genus in this clade is *Acizzia*, some species of which, such as the type-species (*A. acaciae*), differ from the description used in the cladogram in that they have lost one spine from the apex of adult basal metatarsus. Furthermore, there is a very high diversity of nymphal form in the genus. *Neopsyllia* and *Platycorypha*, two genera which apparently differ only in the relative length of the caudal lobes of the adult male proctiger, are the only taxa in clade 57 to retain nymphal sectasetae on the hindwing-pad margins. *Freysuila* is placed as a sister group to *Neopsyllia* and *Platycorypha* on the basis of the very broad adult head and, therefore, a secondary loss of the caudal lobes is assumed to occur in *Freysuila*. *Mitrapssylla deserata* nymphs have lanceolate setae on the dorsal surface indicating the retention of dorsal sectasetae, or the derivative lanceolate setae, well into clade 57. The abdomen margin sectasetae (character 114) are reduced to lanceolate setae in *M. deserata*, a feature known elsewhere only in *Heteropsylla* (clade 78). In the remainder of clade 57 (clade 77) the only remaining sectasetae are (up to 4 + 4 in number) on the abdomen margin (character 114).



Figs 196a, b Clades 57 and 75. 196a, clade 57, continued in Figs 196b–e; 196b, clade 75, continued from Fig. 196a.

Clade 76 (Fig. 196c). In the character weighting procedure character 76 (loss of genual spine) received the greatest weight and defined clade 76, which includes *Amorphicola*, *Anomoneura*, *Epipsylla* and some species referred to the genus *Euphalerus*. *Euphalerus* spp. are placed in both major branches of clade 56 (Fig. 193) and these separate groups may only be recognisable in the nymphal stages. Some species at present referred to the genus *Psylla*, such as *P. hyalina* Mathur and *P. oblonga* Mathur, probably belong to clade 76. Adults of *Anomoneura* and *Epipsylla* are radically different in facies due to such characters as the presence of forewing cross veins in the former and very long genal cones in the latter. The nymphs, however, differ only in the presence of abdominal sectasetae in *A. mori*.

Clade 78 (Fig. 196d) is defined initially by the shape of the adult male paramere (character 46) and by the fact that antenna segment III is not the longest. Both these characters are subsequently lost by many species. There is also a tendency for the base of the pterostigma to be broader than the length of the vein *R* between the *R/Rs* fork and the *R*/pterostigma base positions. This feature reaches its maximum development in certain *Kleiniella* spp. (Hollis, 1976). The African genus *Kleiniella* Aulmann is one of several genera which probably belong to clade 90 but whose nymphs are unknown; others being *Delina* Blanchard (South America), *Palmapenna* Hollis (Africa) and *Panispelma* Enderlein (South America). Clade 89 is defined by tubular abdominal sectasetae (character 115) on the nymphs. The adults of *Eucero-psylla* and *Heteropsylla* differ only in the development of the genae, despite radically different nymphs. An absence of genal cones in *Heteropsylla* has previously caused it to be referred to the Pauropsyllinae by many authors, who also include *Paurocephala* in that group. There is also a tendency for the genal cones to be reduced in *Ciriacreum*, though only in some species. Contrary to the opinion of Becker-Migdisova (1973) *Ciriacreum* spp. have neither rudimentary genal cones nor a bipartite male proctiger. Further details of the cladistic relations of clade 90 are given by Hollis (1976). Many Neotropical species at present referred to the genus *Psylla*, such as *P. forcipata* Tuthill, *P. fusciodulus* Enderlein and *P. ingae* Tuthill, probably belong close to



Figs 196c, d Clades 76 and 78. 196c, clade 76, continued from Fig. 196a; 196d, clade 78, continued from Fig. 196a.

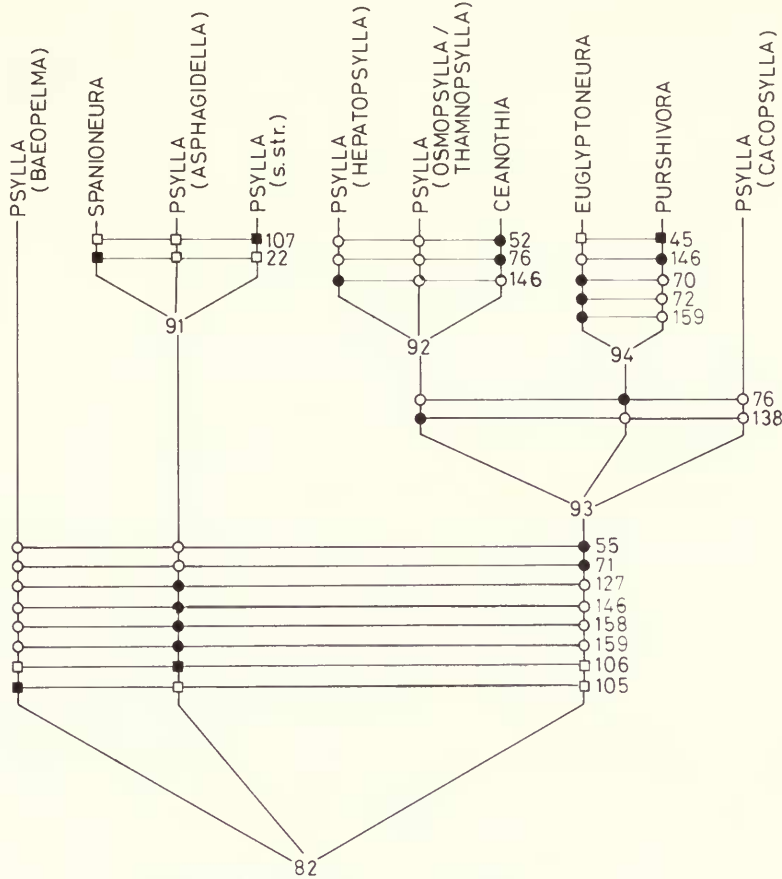


Fig. 196e Clade 82; continued from Fig. 196a.

Euceropsylla in clade 78. Many of the described species of *Euceropsylla* are very similar and a full revision is required. The genus *Arytaina* may contain some Pacific species belonging close to *Insnesia* or *Isogonoceraia*.

Clade 81 (Fig. 196a) is formed by replacing character 13 (antennal base position) which was omitted in the initial weighted analysis of clade 57 and is divided into clades 80 and 82.

Clade 80 (Fig. 196a) is the Arytainini of Becker-Migdisova (1973). Loginova (1976a, 1977) divided the Arytaininae into the tribes Arytainini (containing *Arytaina* and *Floria*) and the Cyamophilini (containing *Arytainilla*, plus *Acizzia* of clade 75 and *Amorphicola* of clade 76). The character used to separate the tribes was the absence and presence of the costal break in the forewing, respectively. However, this character is variable in the type-species of *Floria* (Hodkinson & White, 1979a) and is therefore a poor character on which to base tribal groups. Heslop-Harrison (1961) included within the Arytainini, *Amorphicola* (clade 76), *Ceanothia*, *Euglyptoneura* and *Purshivora* (all clade 82) together with *Acizzia* (clade 75) and clade 80.

Nymphs of *Amblyrhina torifrons* Löw which we recently collected are, within the bounds of the characters used in the cladogram, identical to *Arytaina*. Other genera which probably fit clade 80 are *Allooneura* Löw and *Livilla* Curtis.

Clade 82 (Fig. 196e) is the genus *Psylla* s.l. (minus species which have already been referred to other clades) plus *Spanioneura* and three North American genera, *Ceanothia*, *Euglyptoneura* and *Purshivora*, placed in the Arytainini by Heslop-Harrison (1961). Additional information, on the number of gonads, is available for a few of the subgenera of *Psylla* shown in clade 82 and

Table 12 Characters used in the cladogram.

There are four categories of characters used in the cladogram: 50 adult gain, 32 adult loss, 35 nymphal gain and 41 nymphal loss. In some cases shape changes could not easily be categorized as gain or loss. In general, such characters were described as gains, especially if of a complex nature. However, when a shape change was lacking in compatibility with complex type gain characters, i.e. liable to be multiply derived, it was listed with the loss type characters. Only the derived state of each character is given in the following tabulation.

Adult 'gain' characters

1. Head, with eyes, more than six times as broad as vertex is long.
2. Vertex deeply cleft and antennae based upon apices of blunt vertex lobes.
3. Genae swollen.
4. Genae formed into cones which are in the same plane as the vertex.
5. Genae formed into cones which are deflected ventrally from plane of vertex.
6. Vertex produced into lobes and enveloping genae.
7. Vertex mid-line paralleled by closely proximal ridges.
9. Preocular tubercles present.
10. Lateral ocelli at extreme posterior margin of head and very prominent.
11. Clypeus large.
12. Clypeus produced anteriorly.
13. Antennal insertions high on vertex, not on front vertex/genal area.
14. Antennal flageller segments (III-X) as broad as basal two segments.
15. Antennal segment II greatly enlarged.
16. Antennal segment VIII longer than segment III.
17. Antennal apical spines very long (at least as long as segments IX and X together or segment III and often almost as long as whole antenna).
18. Pronotum vertically or subvertically inclined, and laterally constricted. Often completely or partly concealed by head.
19. Suture between episternum and epimeron diagonal (dorsally terminating at posterior of pronotal lateral margin).
20. Suture between episternum and epimeron horizontal.
21. Wing very broad subapically (*Pauropsylla* shape).
22. Wing of *Spanioneura* shape.
23. Wing very elongate with veins straight and almost parallel.
24. Forewing with apex acute or acutely rounded. Costal margin curved. M_{1+2} terminating at or anterior to apex.
25. Forewing with apex acute or acutely rounded. Costal margin curved. M_{1+2} terminating posterior to apex.
26. Wing thick or coriaceous, not membranous. Shape rhomboidal.
27. Wing veins broad.
28. Costa broad.
29. Lenticula costal field.
30. Veins *Rs* and *M* sinuate (*Neophyllura* subgenus *Arbutophila*).
31. Cells cu_1 and m_2 very elongate. Wing fairly broad (*Auchmerina*, *Caradocia*, *Freysuila*, *Geijerolyma* and *Macrocorsa* wing forms).
32. Subcosta and costa coalesced.
33. Veins *R*, *M* and Cu_1 with a common stem.
34. Veins *R*, *M* and Cu_1 separated from common stem at one point or veins *R* and *M* with a common stalk after the branching of Cu_1 .
35. Cu_2 terminating at a point well separated from Cu_{1b} , and often closer to the wing base (this separation occurs in many clades but is only well expressed in clade 22, e.g. *Trioza*).
36. Cross veins: pterostigma-*Rs*.
37. Cross vein: *R-Rs*.
38. Cross vein: *R-M* (bifurcation of M_{1+2} and M_{3+4}) cross vein.
39. Cross vein: *R-M*₁₊₂ (or anastomosis of *R* and M_{1+2}).
40. Well-developed radular spinules.
41. Mid tibia with a dark heavily sclerotized band around apex.
42. Sperm pump of form common to Psylloidea and Aleyrodoidea.
43. Male proctiger expanded posteriorly to form caudal lobes.

44. 'Tooth'-like armature placed ventrally in basal half of caudal lobe.
45. Paramere with inner spiniform process (*Purshivora*).
46. Paramere bifid when viewed posteriorly (e.g. *Heteropsylla*).
47. Paramere bifid when viewed laterally (*Egeirotioza*).
48. Long thin paramere (*Arytainilla*).
49. Stout paramere with a heavily sclerotized and thickened blunt apex (*Arytaina*).
50. Female dorsal valve short, rounded down and densely covered by long thin setae (*Pachypsylla japonica* and *Tetragonocephala* sp.).
51. Female dorsal valve (proctiger) with lanceolate setae arranged along margin (*Ctenarytaina*, *Euphyllura caudata* and *E. concolor*).

Adult 'loss' characters

52. Genal cones greatly reduced or lost (derived from character 5).
53. Anteoccipital lobes absent.
54. Antenna without very narrow (*Mastigimas* type) flagellum (segments III to X).
55. Antenna less than twice as long as head breadth (a character of secondary loss which is only applied to clade 82, e.g. *Psylla*).
56. Rhinarium absent from segment III.
57. Rhinarium absent from segment IV.
58. Rhinarium absent from segment V.
59. Rhinarium absent from segment VII.
60. Wing apex rounded, remaining coriaceous (unless combined with character 61) (derived from character 26).
61. Wing membranous (derived from characters 26 or 60).
62. Euphalerine wing (derived from character 26). Generally maculate.
63. Wing apex rounded (derived from character 62).
64. Wing apex rounded (derived from character 24).
65. Wing apex rounded (derived from character 25).
66. Branches of *M* and *Cu* reduced.
67. Cell *cu*₂ (claval field) and anal vein absent.
68. Cell *cu*₁ absent.
69. Nodal (fold) line absent.
70. Costal break absent.
71. Pterostigma reduced (only applied to clade 82, e.g. *Psylla*).
72. Pterostigma absent or very reduced.
73. Hind wing very reduced or absent.
74. Meracanthus very small.
75. Meracanthus absent.
76. Metatibia basal (genual) spine absent.
77. Fewer than six spines at apex of metatibia.
78. Metatarsus segment I with one apical spine.
79. Metatarsus segment I with no apical spines.
80. Male proctiger not bipartite (segment X and XI of abdomen fused to produced a unipartite proctiger).
81. 'Tooth'-like armature in basal half of caudal lobe absent. (Applies only to clade 41. Secondary loss of character 44.)
82. Caudal lobe absent (secondary loss of character 43).
83. Paramere of bifid form (character 46) secondarily lost.

Nymphal 'gain' characters

84. General body form broader than long (*Homotoma*, *Macrohomotoma*, *Mycopsylla* and *Pseudoeriopsylla*).
85. General body form rounded (facies of e.g. *Ceropsylla*).
86. General body form very elongate (facies of *Aacanthocnema*).
87. Antenna short and narrowed evenly to apex (Fig. 44).
88. Head and prothorax completely fused dorsally.
89. Humeral lobe of forewing-pad anteriorly produced to an extreme which is anterior to the procoxa (Figs 17-19).
90. Unguitractor long (Figs 77-94).
91. Arolium with a long petiole (Figs 65, 66).

92. Arolium broader than long, without petiole and with a pair of darkened areas (Figs 72–76).
93. Arolium base/petiole apex with a semicircular membranous area (Fig. 65).
94. Abdomen with all dorsal sclerites fused with caudal plate.
95. Abdominal apex serrate (Fig. 122).
96. Abdominal apex with large 'teeth' at lateral extremities of serrate area (follows from character 95) (Figs 118, 120).
97. Abdominal apex with large medial 'teeth' (Fig. 125) (from character 95).
98. Abdominal apex with a pair of apical 'teeth'.
99. Abdominal segments produced laterally as rounded or 'tooth' like projections (Fig. 118).
100. Cauda pointed (Fig. 118).
101. Lingula present.
102. Circum-anal ring constricted either side of anus (Fig. 111) or broken into three rings (*Livia*) (Fig. 110).
103. Circum-anal ring constricted either side of anus (Fig. 148) or broken into three rings (Fig. 149).
104. Anal pore-field arranged as bands (Fig. 155).
105. Specialised circum-anal ring (subgenus *Baeopelma* of *Psylla*) present (Fig. 135).
106. Broad circum-anal ring present (Figs 134, 136, 142).
107. Specialised shape of broad circum-anal ring (Fig. 136).
108. Anal pore-field (other than circum-anal ring) arranged as 1 + 1 rings or of derivable form (discount characters 102 and 103). Rings placed ventrally or dorso-ventrally, i.e. each ring is partly dorsal and partly ventral) (Figs 106, 107, 112, 113, 117, 119, 121).
109. Anal pore field (other than circum-anal ring) arranged as 2 + 2 rings or of derivable form. The rings are arranged ventrally 1 + 1 and dorsally 1 + 1 (Fig. 120).
110. Sectasetae (marginal and dorsal) truncate (Fig. 34).
111. Abdominal sectasetae arranged on large tubercles (Fig. 114).
112. Body margin surrounded by long scales (probably derived from sectasetae) (Fig. 173).
113. Body margin surrounded by broad scales (probably derived from sectasetae) (Figs 174–176).
114. Most abdominal margin sectasetae lost, leaving a distinct arrangement (treated as a gain character because of complexity) of up to 4 + 4 sectasetae. Secondary loss may reduce this number to 3 + 3, 2 + 2 or 1 + 1 (Fig. 37).
115. Sectasetae of character 114 type truncated to form tubes which are normally based on slight tubercles (Fig. 37 [ts]).
116. Lanceolate setae (marginal) greatly elongated.
117. Very thin lanceolate setae (assumed to derive from thickened simple setae) present.
118. Capitate setae present on body plus wing-pad margins and dorsal surfaces (Fig. 29).

Nymphal 'loss' characters

119. General body form not broader than long (secondary loss of character 84).
120. Thorax dorsal surface with distinct sclerites (at least medials); lateral sclerites small or absent (Figs 12–14).
121. Tarsal claws absent.
122. Unguitractor not visible with optical microscope. Arolium present (Figs 56–58).
123. Basal area of arolium reduced to a thin membrane (Figs 60, 64).
124. Basal membrane of arolium absent (derived from character 123) (Fig. 59) (or reduced; Fig. 62).
125. Unguitractor and arolium not visible with optical microscope.
126. Dorsal surface of abdomen lacking distinct sclerites (membrane only anterior to caudal plate area).
127. Anus at posterior of abdomen, not on ventral surface.
128. Abdominal apical teeth absent (secondary loss of 95 and 96).
129. Anal pore-field bands broken into round areas of pores (derived from 104) (Fig. 154).
130. Broad outer area of circum-anal ring broken into round or ovoid areas of pores (Figs 97, 99, 100).
131. Anal pore-field of type described by character 108 broken into round areas of pores (Fig. 113).
132. Anal pore-field of type described by character 108 reduced to narrow bands (Fig. 107).
133. Anal pore-field of type described by character 108 with pores reduced as in Fig. 117.
134. Small groups of pores in abdominal areas such that a reduction of rings as described by character 108 may have occurred (used in clades containing character 108 but not 109) (Fig. 119).
135. Small groups of pores in abdominal areas such that a reduction of rings as described by character 108 may have occurred (used in clades containing characters 108 and 109) (Fig. 129).
136. Anal pore-field in broken rings, probably derived from character 108, as in Fig. 112.
137. Circum-anal pore ring of type described by character 103 with pores widely separated.
138. Outer circum-anal pore ring reduced to a single row of pores (only applied to clade 82) (Fig. 139).

139. Circum-anal pore ring absent.
 140. Anal pore-field absent.
 141. Anal pore-field of 1 + 1 rings very reduced (derived from character 134), or absent.
 142. Circum-anal pore ring reduced to a few large pores (Fig. 146).
 143. Body margin without sectasetae or derivable structures.
 144. Body dorsal surface without sectasetae or derivable structures.
 145. Body margin (other than abdomen) without sectasetae except for a small number around the hindwing-pad.
 146. Abdomen margin without sectasetae (derived from 114).
 147. Antennae without sectasetae or derivable structures.
 148. Hindwing-pad without marginal sectasetae (derived from character 145).
 149. Pointed sectasetae (derived from character 110).
 150. Body and wing-pad surfaces (antennae, dorsal body surface and body margin) with lanceolate setae (assumed to derive from reduced sectasetae).
 151. Abdominal 4 + 4 (or fewer) sectasetae positions with lanceolate setae (assumed to derive from character 114) (Fig. 37).
 152. Dorsal surface of body and wing-pads with lanceolate setae (assumed to derive from reduced sectasetae). Character only applied when other sectasetae characters are in a derived state.
 153. Clavate setae present on body (probably very small sectasetae or lanceolate setae and therefore regarded as a loss character).
 154. Body margin lanceolate setae absent (derived from character 150).
 155. Dorsal surface of body without lanceolate setae (derived from character 150).
 156. Antennae without lanceolate setae (derived from character 150).
 157. Clavate setae absent (derived from character 153).
 158. Body margin without capitate setae (except in some species which retain one seta behind each eye) (derived from character 118).
 159. Body dorsal surface without capitate setae (derived from character 118).
-

this has been incorporated in a cladogram of these subgenera by Burckhardt (1979). The details of clade 82 are largely governed by loss characters and it is very unlikely that any cladogram of the subgenera of *Psylla*, based upon present knowledge, will approximate its true cladistic history.

Host-plant considerations

Psyllids are monophagous or narrowly polyphagous and breed almost exclusively upon angiosperms. Eastop (1972) considered the plant family level relations of 847 species of Psylloidea, of which only 8 were associated with the Monocotyledoneae and the remainder (99%) with the Dicotyledoneae. In this study the probable hosts of 298 of the 303 species examined were known. Of these, only five species of *Livia*, on *Juncus* and *Carex* in the Holarctic region, and *Trioza palmicola*, on an endemic Hawaiian palm, were associated with monocotyledons, and very few species are associated with annual or biennial herbs.

Closely related psyllid species usually occur on closely related host-plants, i.e. psyllid clades are usually restricted to definite angiosperm taxa (Table 13) (Hodkinson, 1974). Individual species of Psylloidea usually occur on host-plants of only one genus and almost exclusively of one family. Examples of psyllids breeding on host-plants in separate families are rare.

Empirical observation suggests that certain psyllid taxa have a narrow taxonomic distribution of host-plants while others have a broad distribution. It is instructive to examine the taxonomic distribution of host-plants, for certain psyllid clades, across the 28 plant orders of relevance to this study. Such an analysis was performed for clades in which at least one terminal taxon descends directly from the ancestor of the clade. The null hypothesis is as follows:

$$\frac{a}{b} = \frac{c}{d}$$

where

- a = no. psyllid species in clade x associated with plant order y;
- b = no. psyllids in all clades associated with plant order y;
- c = no. psyllids in clade x;
- d = no. psyllids in all clades.

The deviation from the regular distribution was measured by the Kolmogorov-Smirnov two-sample test (with two tails of significance). This was converted to a χ^2 value, by an approximation, with two degrees of freedom (Siegel, 1956). It is expected that χ^2 is underestimated for any clade with less than 40 species, that is all except 2 and 53, which makes the test conservative (Siegel, 1956), i.e. the significance level may be underestimated. This test (Table 14) indicates that most clades have a taxonomic distribution of host-plants which is significantly non-regular. The variance (s^2) and the mean (\bar{x}) number of psyllid species in each of the 28 host-plant orders were calculated for each clade shown to depart significantly from a regular distribution. These values were expressed as a ratio (Table 14) which is a measure of dispersion, such that the greater the value the more *clumped* the host-plant distribution. Clades with very small variance-mean ratios, and with large sample sizes (more than 10 psyllid species) are clade 51, e.g. *Diaphorina*, and clade 2, e.g. *Trioza*. The clade with the most clumped, that is most restricted host distribution, is clade 53, e.g. *Psylla*.

This does not imply that genera such as *Trioza* lack distinct groups feeding upon related groups of plants; for example one subgroup of *Trioza* is exclusively associated with the plant genus *Salix* (Salicaceae). Taxa such as clade 53, e.g. *Psylla*, of which 49% feed on Rosales, and most of those on Fabaceae, differ from taxa such as clade 2 (e.g. *Trioza*) in that distinct host associations exist at a suprageneric rather than subgeneric level. If the cladogram roughly represents the true cladistic history of the Psylloidea, then in clade 53 (e.g. *Psylla*) morphological divergence exceeds host-plant choice divergence. However, in clade 2 (e.g. *Trioza*) host-plant choice has undergone more evolutionary changes than morphological form.

The cladogram was assumed to be a true record of the cladistic history of the Psylloidea and an attempt was made to find the most parsimonious fit of the host relationships to the cladogram.

Clade 2 (Fig. 186) (e.g. *Trioza*) is a large highly polyphagous taxon. Widely separate branch tips feed on plant taxa such as Annonales, Moraceae and Salicaceae. At this stage no hypothesis can be made about the ancestral host of clade 2.

Clade 4 (Fig. 187) is associated with Malvales (e.g. *Paracarsidara*) and Rutales: Meliaceae (*Mastigimas*). Either of these plant groups could represent the ancestral host of clade 4.

Clade 6 (Fig. 188) is associated exclusively with *Ficus* (Moraceae), the most likely ancestral host of clade 6.

Clade 8 (Fig. 189) is associated with two families of Rutales, i.e. Burseraceae and Meliaceae. The host of *Epicarsa*, however, is unknown.

Clade 10 (Fig. 190) is associated with the Rutales (mainly Anacardiaceae, plus Burseraceae and Rutaceae), e.g. *Calophya*.

It is now reasonable to suggest that Rutales-feeding is an ancestral feature retained by disjunct groups of the above clades and, by the parsimony criterion, is the most likely ancestral host of clade 9. The association with *Ficus* evolved with clade 6, with Malvales in clade 32 and the ancestral host of clade 2 remains unknown. In the remaining branches of the cladogram *Livia* and *Strophingia* are associated with Commelinales (Cyperaceae and Juncaceae) and Ericaceae respectively; none feeds on Rutales.

Clade 13 (Fig. 191) contains several groups with distinct host relations: *Phytolyma* on Moraceae, *Gyropsylla* on *Ilex* (Aquifoliaceae) and *Nectandra* (Lauraceae), clade 42 on *Tamarix* and *Myricaria* (Tamaricaceae) and clade 40 on herbs. Clade 40 (*Aphalara* and *Craspedolepta*) has several distinct groups of species restricted to certain families or genera of plants. *Aphalara* live on Brassicaceae, Polygonaceae and Ranunculaceae, while *Craspedolepta* are associated

Table 13 Psyllid taxa which, in the present study, are restricted to specified taxa of angiosperms. An asterisk marks entries which are known to occur on other angiosperm taxa, when psyllid species not covered in the present survey are considered.

i. Psyllid taxa restricted to plant orders.

TAXON	HOST ORDER
Clades 8, 15	Rutales
Clade 32	Malvales
<i>Livia</i>	Commelinales

ii. Psyllid taxa restricted to plant families.

TAXON	HOST FAMILY	HOST ORDER
Clade 58	Ericaceae	Ericales
Clade 62*	Sterculiaceae	Malvales
Clades 63, 74, 78*, 80	Fabaceae	Rosales
<i>Epipsylla</i> , <i>Neopsyllia</i>	Fabaceae	Rosales
<i>Euphyllura</i>	Oleaceae	Santalales
<i>Paurocephala</i> *	Malvaceae	Malvales
<i>Phytolyma</i>	Moraceae	Urticales
<i>Pseudophacopteron</i>	Meliaceae	Rutales
<i>Strophingia</i> , <i>Neophyllura</i>	Ericaceae	Ericales
<i>Tenaphalara</i>	Bombacaceae	Malvales

iii. Psyllid taxa restricted to plant genera

TAXON	HOST GENUS	HOST FAMILY	HOST ORDER
Clade 6	<i>Ficus</i>	Moraceae	Urticales
Clade 42*	<i>Tamarix</i>	Tamaricaceae	Tamaricales
Clades 61*, 68	<i>Eucalyptus</i>	Myrtaceae	Myrtales
Clade 73	<i>Celtis</i>	Ulmaceae	Urticales
<i>Agonoscena</i> *	<i>Pistacia</i>	Anacardiaceae	Rutales
<i>Aphalaroida</i> *	<i>Prosopis</i>	Fabaceae	Rosales
<i>Camarotoscena</i> , <i>Egeirotrioza</i>	<i>Populus</i>	Salicaceae	Salicales
<i>Euglyptoneura</i>	<i>Ceanothus</i>	Rhamnaceae	Rhamnales
<i>Gyropsylla</i> *	<i>Ilex</i>	Aquifoliaceae	Theales
<i>Psyllopsis</i>	<i>Fraxinus</i>	Oleaceae	Santalales
<i>Purshivora</i>	<i>Purshia</i>	Rosaceae	Rosales

with Asteraceae, Chenopodiaceae and Onagraceae. The ancestral host of clade 13 is uncertain and none feeds on Rutales.

Species in clade 15 (Fig. 192) feed exclusively on Rutales and the ancestral host is assumed to be a species of Rutales.

Clade 17 (Fig. 192) is divided into two major taxa; clades 48 and 53.

Clade 8 (Fig. 193) has a high diversity of host relationships; clade 58 on Ericaceae, *Euphyllura* on Oleaceae, clade 61 on Myrtaceae, Onagraceae and Rutaceae, clade 62 on Sterculiaceae and Melastomataceae, *Paurocephala* on Malvaceae and Moraceae, *Camarotoscena* on Salicaceae, *Psyllopsis* on Oleaceae, *Diaphorina* on several families (e.g. Rutaceae and Solanaceae), and *Pennavena* on Loganiaceae. The ancestral host is most likely to be a plant taxon associated with more than one branch tip, i.e. Malvales (Malvaceae and Sterculiaceae), Oleaceae or Rutales (Rutaceae).

Clade 53 (Fig. 193) is associated with Rosales except for: *Arepuna* (Solanaceae), *Euphalerus jugovenosus* group (p. 224) (Rhamnaceae), *Phellopsylla* (Myrtaceae), clade 73 (Ulmaceae), *E. gallicolus* (Rhamnaceae), clade 68 (Myrtaceae), *Trigonon* (host unknown), *Freysuila* sp. (Solanaceae), one *Acizzia* sp. (*A. hakeae*, Proteaceae), *Anomoneura* (Moraceae), some *Insnesia* spp. (Euphorbiaceae), and many species in clade 82 (e.g. Betulaceae, Rhamnaceae and Salicaceae). Of those species on Rosales, most (63%) are associated with Fabaceae.

Table 14 Values of χ^2 approximation to Kolmogorov-Smirnov test, variance/mean ratio, and most favoured host-plant order, of selected clades. Significance levels: *** $P < 0.001$, ** $P < 0.01$ & * $P < 0.05$.

Clade	χ^2	s^2/\bar{x}	Favoured host order
2	10.71**	4.11	Salicales
4	7.38*	7.48	Malvales
8	10.25**	6.00	Rutales
10	20.10***	13.00	Rutales
12	18.85***	5.04	Commelinales
13	28.59***	6.81	Asterales
33	5.13	—	Urticales
34	6.39*	5.00	Urticales
45	5.18	—	Rutales
46	6.88*	4.00	Rutales
49	4.27	—	Malvales/Salicales
51	12.84**	2.56	Santalales
53	27.77***	34.26	Rosales
59	13.95***	3.89	Ericales/Santalales
61	1.91	—	Myrtales
62	0.72	—	Malvales

Only *Euphalerus tantillus* (Rosaceae) and most members of clade 82 (Buxaceae, Rosaceae and Saxifragaceae) are not. It is assumed that Fabaceae-feeding is ancestral to clade 53. No species occur on Rutales. From Fabaceae host changes to Myrtaceae, Rhamnaceae, Rosaceae and Solanaceae must have occurred more than once. The evidence suggests that this has occurred repeatedly in different zoogeographic regions.

Among the remaining clades, Rutales-feeding occurs exclusively in clade 15 and may also be the ancestral host of clade 48. Rutales-feeding therefore occurs commonly in disjunct clades throughout the cladogram, and application of the parsimony criterion suggests that the ancestral Psylloidea are associated with plants of the order Rutales or a direct ancestral group to the Rutales.

There is evidence, based on a belief that the Rutaceae and Anacardiaceae appeared early enough for direct migration to Australia, that the Rutales evolved at least 95 million years ago (Raven & Axelrod, 1974). If angiosperm-feeding in psyllids evolved only once then initially this was most likely to have been in conjunction with primitive Rutales, possibly prior to differentiation of the host-plant families Aceraceae, Anacardiaceae, Burseraceae, Meliaceae and Rutaceae. Much of the primary differentiation of the Rutales seems to have taken place in Africa-South America, with long standing connections to Eurasia (Raven & Axelrod, 1974).

The clades which are restricted to a single plant taxon other than Rutales are as follows: clade 3 (e.g. *Carsidara*) on Malvales and clade 6 (e.g. *Homotoma*) on *Ficus*. Examples of large clades on a diverse range of plants are: clade 2 (e.g. *Trioza*), clade 13 (e.g. *Aphalara*) and clade 17 (e.g. *Paurocephala*, *Spondyliaspis* and *Psylla*).

Zoogeographic evidence

A vicariance approach (Platnick & Nelson, 1978) was applied to fit zoogeographic evidence to the cladogram. The model was restricted to the time period since the earliest appearance of the angiosperms (125 million years before present or 125 m.y.B.P.; Raven & Axelrod, 1974), and it was assumed that the modern psyllids have evolved since the splitting of Pangea into Laurasia and Gondwanaland (180 m.y.B.P.). Therefore any track or distribution which includes areas of both Laurasia and Gondwanaland is assumed to have been caused by a dispersal event. Furthermore, dispersal is also assumed to account for the presence of psyllids on oceanic islands as this is a more tenable explanation of such tracks than the assumption of an as yet unknown vicariance event (Cracraft, 1975). Additionally some Nearctic-Palaeartic tracks may be better

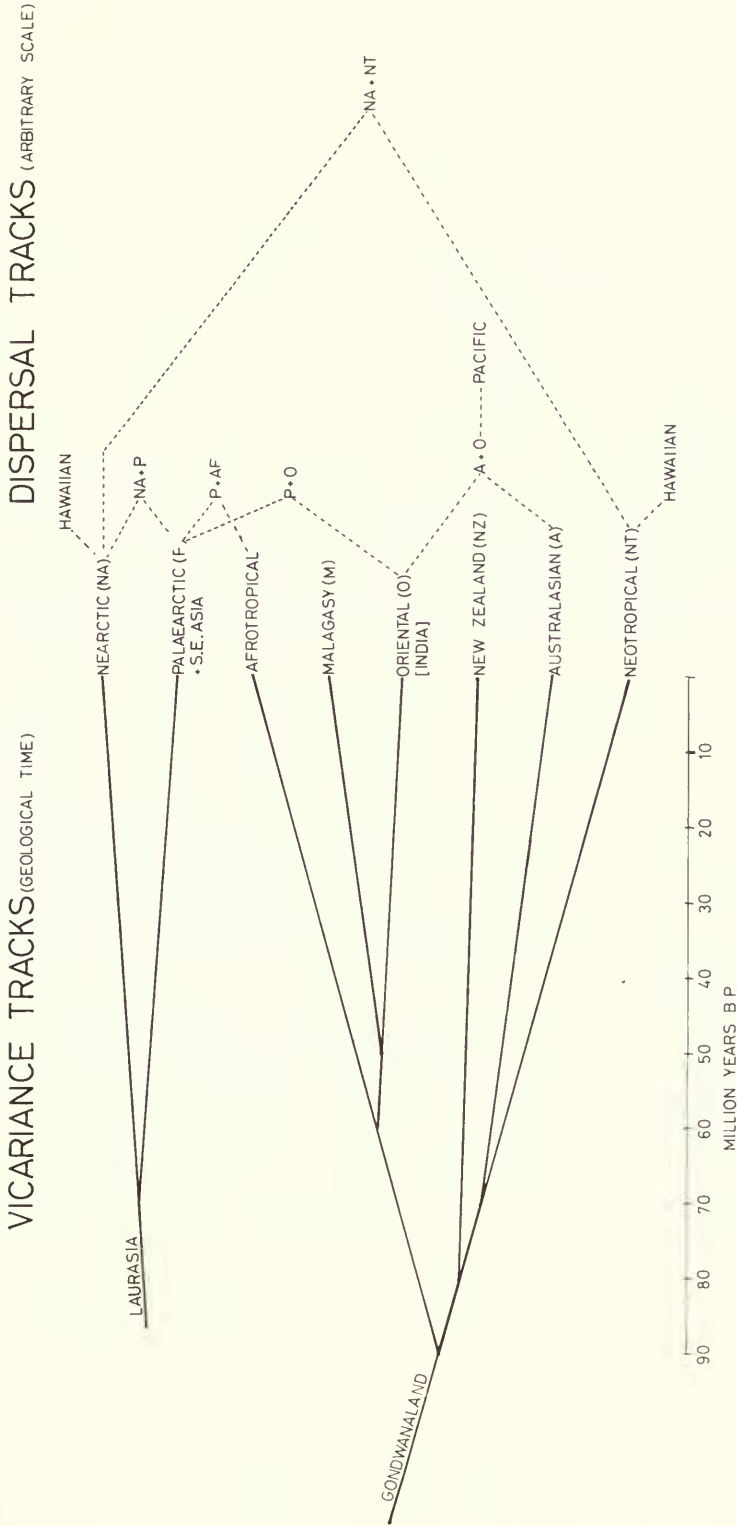


Fig. 197 Reduced geological area cladogram of the splitting of Laurasia and Gondwanaland. Probable dispersal tracks are also shown (broken lines).

explained by dispersal across Beringia than by vicariance of Laurasia (Hodkinson, 1980). The vicariance/dispersal tracks are shown as a reduced geological area cladogram, based on Rosen (1978) (Fig. 197).

Each section of the psyllid cladogram (Figs 185–196) was compared to the geological area cladogram (Fig. 197). As an example of the reasoning applied, consider a hypothetical clade occurring in the Afrotropical, Malagasy, Oriental, Austro-Oriental and Palaeartic regions. The Palaeartic is not joined by a vicariance track in Fig. 197 to any of these other regions. Dispersal to the Palaeartic is proposed. The Austro-Oriental region must also be reached by dispersal. The Afrotropical, Malagasy and Oriental regions can be seen to have originated from one biota (Fig. 197). The ancestral species of this hypothetical clade is, therefore, assumed to have been distributed in the Afrotropical-Malagasy-Oriental biota, i.e. this is the ancestral track and distribution. Other solutions are less parsimonious.

Extinctions must occasionally be proposed to explain disjunct patterns of distribution. However, 'not yet discovered' may be the correct interpretation in many cases. The full analysis for each major clade is given by White (1980).

The general conclusions to be drawn from this analysis are as follows:

1. Most major clades probably had a Gondwanaland origin, i.e. clade 2 (Fig. 186) (e.g. *Trioza*), clade 4 (Fig. 187) (e.g. *Paracarsidara*), clade 6 (Fig. 188) (e.g. *Homotoma*), clade 8 (Fig. 189) (e.g. *Phacopteron*), clade 10 (Fig. 190) (e.g. *Calophya*), clade 13 (Fig. 191) (e.g. *Gyropsylla*), clade 15 (Fig. 192) (e.g. *Tainarys*) and clade 17 (Fig. 193) (e.g. *Paurocephala* and *Euphalerus*).
2. The ancestor of the Psylloidea probably had a Gondwanaland track. This is consistent with the host-plant evidence, i.e. that the ancestral host was a species of Rutales and that this group of plants must have been distributed throughout Gondwanaland prior to its breakup.

In the geological area cladogram no allowance was made for the possibility of dispersal across the South Atlantic between the Afrotropical and Neotropical regions. Raven & Axelrod (1974) review the evidence for such a dispersal between the two continents, as they are thought to have remained in near contact until at least 90 m.y.B.P. This dispersal route existed before the breakup of the Australian-Antarctic-South American continent (45 m.y.B.P.). Any taxon present in both the Afro-Oriental biota and the Neotropical region could be explained by dispersal across the Atlantic or by vicariance of a Gondwanaland track followed by extinction in New Zealand and Australia. Because of this choice of explanations the vicariance model was adhered to purely as a convention. Australia was probably quite humid at a time when it was still joined to South America (Frakes & Kemp, 1974), and the subsequent lowering of humidity may account for many extinctions.

As the distribution patterns of most clades can be explained largely by vicariance events occurring during the breakup of Gondwanaland, the minimum, and sometimes maximum, age of many of the major clades can be determined from the estimated dates of vicariance events.

Clade 4 (Fig. 187) (e.g. *Paracarsidara*) had a Gondwanaland ancestor (90–180 m.y.B.P.). The initial host was a species of Rutales. Ancestors 30, 31 and 32 also appeared to have evolved during this time in association with Malvales. The origin of the Malvales seems uncertain. Raven & Axelrod (1974) state that the primary radiation of Malvales probably took place in Africa and South America in Maastrichtian time (65–70 m.y.B.P.) or earlier. There are, however, some doubtful Upper Cretaceous (65–110 m.y.B.P.) macrofossils of Malvaceae (Raven & Axelrod, 1974). The origin of clade 32 remains uncertain.

Clade 6 (Fig. 188) (e.g. *Homotoma*) also appears to have originated in Gondwanaland and these taxa are all associated with *Ficus* (Moraceae). Raven & Axelrod (1974) say that Moraceae were probably in existence early enough to have been dispersed more or less directly between Africa and South America. Ancestor 6 may have had an Afro-Indian range and been dispersed to South America (*Synozia*) and later from India to Australia (*Mycopsylla*) by island hopping. Whichever route was taken ancestor 6 must have existed at least 90 m.y.B.P.

Clades 8, 10 and 15 (Figs 189, 190, 192) are all associated with the Rutales and all appear to have a Gondwanaland distributed ancestor. These groups must each have been distinct by 90 m.y.B.P.

Ancestors 13 and 17 (Figs 191, 193) are of unknown host relations and each probably had a Gondwanaland distribution. These groups must also have been distinct by 90 m.y.B.P. In clade 17 the major host preference is for Rosales, especially Fabaceae (clade 53). However, Raven & Axelrod (1974) imply that the Fabaceae were of later origin (c. 65 m.y.B.P.) although the Rosales probably existed much earlier.

Despite several problems a number of major conclusions can be drawn. Firstly that most major clades have a distribution which is consistent with a southern ancestry, probably prior to the breakup of Gondwanaland (90 m.y.B.P.). Furthermore, the flowering plants, typified by Annonales, probably evolved about 125 m.y.B.P. (as indicated by data reviewed by Raven & Axelrod, 1974). The modern psyllids probably evolved with the Rurales (p. 258) and, therefore, later than 125 m.y.B.P. but earlier than 90 m.y.B.P. (although *Togepssylla*, a morphologically very primitive psyllid associated with Annonales, may be a relic member of a group antedating ancestor 1).

Conversely, the following major groups probably evolved from ancestors in the northern land mass of Laurasia: *Livia*, *Strophingia* in the Palaearctic, clade 40 (e.g. *Aphalara*), clade 81 (e.g. *Psylla*) and clade 73 (e.g. *Pachypsylla*). This is assuming that their ancestors dispersed to Laurasia from Gondwanaland. An alternative hypothesis is available if a pure vicariance model is adopted, i.e. that the ancestral psyllid was distributed throughout Pangea. If this were the case then we must accept that modern psyllids diversified before angiosperms evolved and psyllids therefore moved onto angiosperm hosts on several separate occasions, remarkably, often onto the same group of plants, namely the Rurales. On balance, our initial hypothesis that modern psyllids only evolved since the appearance of the angiosperms, and therefore since the splitting of Pangea into the southern Gondwanaland and northern Laurasia, seems more tenable.

Classification and phylogeny

Nymphal phenetic classification

Several phenetic classifications have been presented which provide different summaries of the resemblances between taxa. It now becomes necessary to identify the common factors and produce a SUMMARY classification.

Analyses based upon character resemblance, such as principal component and SUMRAT information statistic, indicated the characters of greatest importance in forming a phenetic classification of nymphs. The species groups defined by the presence of each of these 'important' characters coincide with the major groups formed in the minimum spanning networks, phenograms and principal component analyses. Therefore the listing of these species groups forms a summary phenetic classification.

The relationships of the phenetic groups, as defined by the 'important' characters, are shown in Fig. 198 and the approximate positions of the groups and subgroups, of the summary classification, are shown relative to principal components I and II (Fig. 199). This provides a visual representation of the between group relationships. A list of the species in each group, together with the initial letter of the family to which the taxon belongs in the classification of Becker-Migdisova (1973): Aphalaridae (A), Carsidaridae (C), Liviidae (L), Psyllidae (P), Spondyliaspidae (S) and Triozidae (T), is given in Table 15.

Previous phenetic classifications of psyllid nymphs (Ferris, 1925; Rahman, 1932) were based on wing-pad shape. The only similarity between these and the above classification is that the 'truncate sectasetae' subgroup roughly corresponds to the 'triozine' group of Ferris and Rahman.

The percentage of species examined from each of the Becker-Migdisova (1973) families, relative to the new summary classification, is shown in Table 16. The most highly congruent group is 3 (capitate setae) plus subgroups 1.ii (truncate sectasetae) and 4.i (petiolate arolium). These groups are defined by gain characters and correspond to some Psyllidae, Triozidae and the remaining Psyllidae respectively. By contrast, group 2 (lanceolate setae) and subgroup 4.ii (remainder) are characterised by loss characters. Such characters would be expected to form

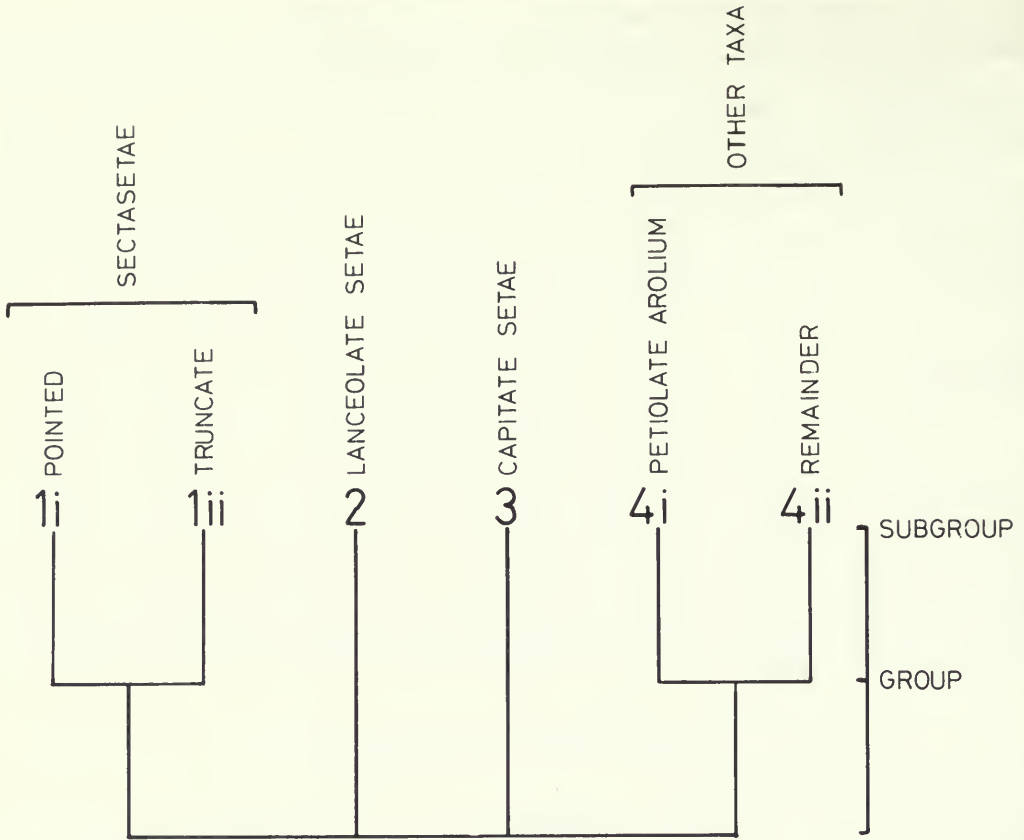


Fig. 198 Phenogram of groups and subgroups of species defined by the summary phenetic classification, based on nymphal characters.

evolutionary convergent clusters. Group 2 and subgroups 4.ii and 1.i (pointed sectasetae) are least congruent with the families of Becker-Migdisova. Pointed sectasetae are probably the ancestral character state and, therefore, subgroup 1.i contains those species which have retained an ancestral feature.

Empirical taxonomic studies of psyllid classification have failed to find stable positions for certain genera; for instance, the suggested relationships between *Paurocephala* and *Pauropsylla* are radically different in the classifications of Crawford (1914), Becker-Migdisova (1973) and Loginova (1972). In this study, these problematical groups again tended to cluster in different positions in different analyses. The most stable groups in each analysis, group 3 (species with capitulate setae) and subgroup 1.ii (species with truncate sectasetae), are highly congruent with the most stable families recognised by empirical taxonomy, that is the Psyllidae and Triozidae respectively. Numerical phenetic methods were, therefore, of little direct value in the placement of problem groups in a new general classification. However, such methods did indicate nymphal groupings which might not be predicted from the existing empirical adult classifications. Furthermore, numerical phenetics were particularly relevant to ground plan construction for cladistic analysis and for the recognition of characters with the greatest classificatory power such as the form of the nymphal tarsal arolium. This was found to have far greater power than had been empirically expected and upon re-examination was found to be one of the most useful characters for later cladistic analysis.

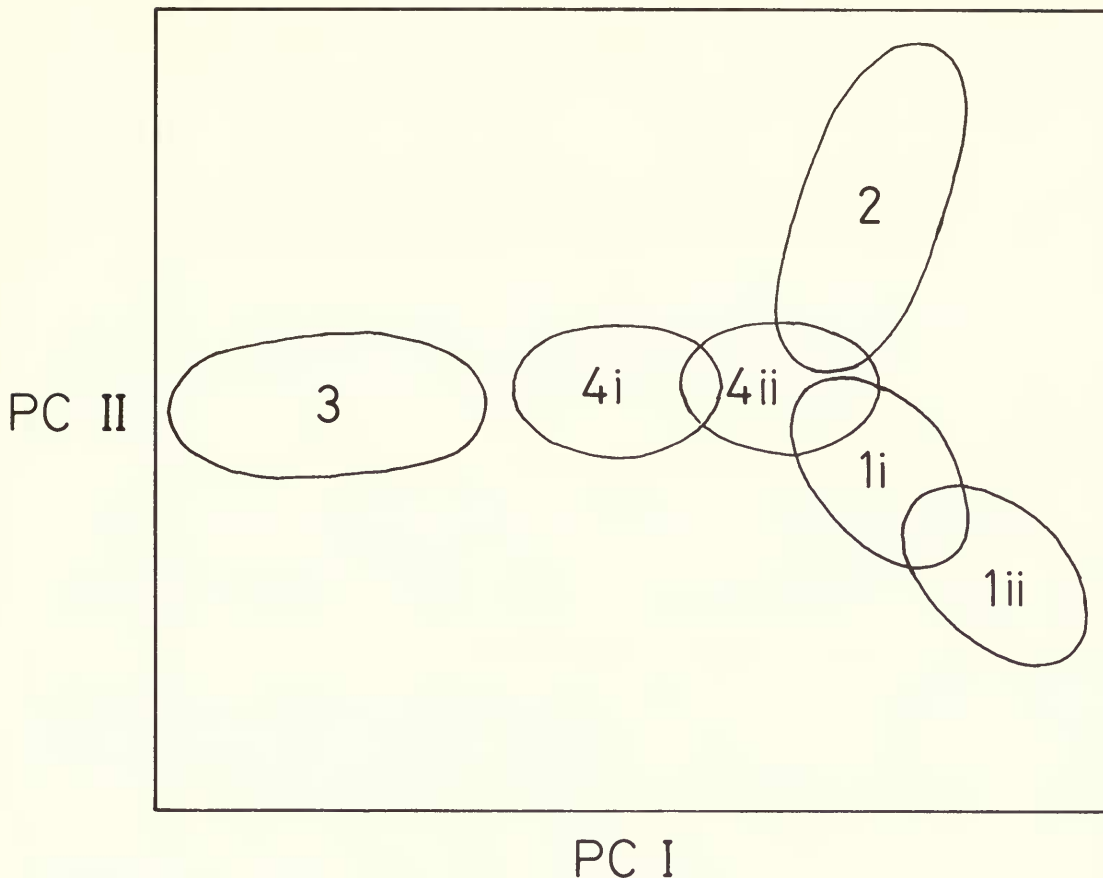


Fig. 199 Groups and subgroups in the summary classification, placed relative to principal components I and II.

General classification

The most convincing argument in favour of cladistic analysis as a basis for a general reference classification is provided by Mickevich (1978), who compared congruence of phenetic versus cladistic classifications. The latter were found to have greater stability, probably because they were less sensitive to the adverse effects of heterogeneity in the evolutionary rates of characters and, furthermore, they were the most predictive (Platnick, 1978). However, a truly predictive classification, based upon a cladogram, may be impractical if the taxon (clade) to which a species belongs can only be determined from a life-cycle stage which may be unavailable. Therefore, as the nymphs of most species are unknown and many clades are defined by attributes of one life-cycle stage only, it is necessary to produce a compromise 'practical-predictive' classification. For example, clade 13 (Fig. 191, p. 224) (e.g. *Aphalara*) and clade 15 (Fig. 192) (e.g. *Rhinocola*) are defined by an adult and a nymphal attribute and are impracticable in a nymphal and an adult classification respectively. If predictability is to be retained some impractical groups have to be tolerated. However, for practical reasons more emphasis has occasionally been placed on adult rather than nymphal characters in finally deciding the position of a taxon.

In deriving the general classification monophyletic groups were preferred. No polyphyletic groups, in the sense of Hennig (1966) or Farris (1974), were formed and paraphyletic groups, of Hennig (1966) and Farris (1974), were allowed if they increased practicality in identifying adults.

This combination of both cladistic and phenetic information is, in general principle, the 'evolutionary' method of Mayr (1969).

The suggested classification (Table 17) includes eight families of which three are new. The probable positions of some taxa not examined are included and these are marked by an asterisk. A major source of information for the inclusion of these additional taxa was Loginova (1964*b*). The probable family or subfamily to which the residual genera belong are listed in Table 18.

Aphalaridae

This is probably a paraphyletic group, in the sense of Hennig (1966) and Farris (1974), but polyphyletic according to Nelson (1971). It comprises species which are phenetically close to the ground plan of the Psylloidea: clade 1 (Fig. 185) minus clades 9 (Fig. 185) and 54 (Fig. 193). It would be impractical to make each whole clade a separate monophyletic family because most are defined only by derived nymphal attributes and adults could only be assigned to such families when accompanied by nymphs of the same species. This is still a problem at the subfamily level and only polyphyletic subfamily groupings within Aphalaridae would form a practical classification.

The content of the family is similar to the Aphalaridae of Becker-Migdisova (1973) but with the addition of the Diaphorininae (from Psyllidae of Becker-Migdisova), Ctenarytainini (from Spondyliaspidae) and Liviinae (formerly Liviidae). The Diaphorininae and Ctenarytainini are included in the Aphalaridae largely on the basis of nymphal features. Phenetically the Liviinae are distant from other Aphalaridae but the relationship of the single genus *Livia* is best illustrated by placing it within the family.

Spondyliaspidae

This family is probably a paraphyletic group (in all senses) (clade 54 (Fig. 193) minus clade 57). However, it is only the genus *Arepuna* which falls outside of a probable monophyletic grouping (clade 55, Fig. 195). *Arepuna* spp. have a '*Euphalerus*' adult facies and it would, therefore, be impractical to place this genus in a separate family to the genus *Euphalerus*.

Psyllidae

This is a probable monophyletic group (clade 57, Fig. 196). Five subfamilies are tentatively proposed, based upon clades which could only be defined by loss characters. This family is the Psyllidae of Becker-Migdisova (1973) minus the Diaphorinini and Psyllopseini which are now placed in the Aphalaridae: Diaphorininae, and the Euphalerini which are now in the Spondyliaspidae.

Loginova (1976*a*, 1977) proposed a tribe Cyamophilini, which includes *Amorphicola*. Nymphs of *Cyamophila*, the type-genus, were not examined and it is possible that *Cyamophila* belongs close to *Amorphicola* in the cladogram. Therefore, no name is proposed for a tribe containing *Amorphicola*.

Calophyidae

This family is a possible monophyletic group (clade 10, Fig. 190), although *Apsylla* is only tentatively included. All other genera belong to the subfamily Calophyinae (clade 39). Many species at present referred to the genus *Pauropsylla* probably belong to the Calophyinae (p. 241).

Phacopteronidae

A family which is a possible monophyletic group (clade 8, Fig. 189). *Bharatiana* is only provisionally included and all other genera belong to the subfamily Phacopteroninae (clade 37).

Homotomidae

This is the subfamily Homotominae of Becker-Migdisova (1973) and a probable monophyletic group (clade 6, Fig. 188).

Carsidaridae

This family is not the Carsidaridae of Becker-Migdisova (1973) as the following genera have been placed elsewhere in the present classification: *Diclidophlebia* and *Togepsylla* (Aphalaridae), *Calophya*, *Microceropsylla* and *Pelmatobrachia* (Calophyidae), *Homotoma*, *Macro-*

homotoma, *Mycopsylla*, *Pseudoeriopsylla* and *Synoza* (Homotomidae), *Bharatiana*, *Epicarsa*, *Phacopteron* and *Pseudophacopteron* (Phacopteronidae) plus *Leptynoptera* and *Pauropsylla* (Triozidae). As now defined, the Carsidaridae is a probable monophyletic group (clade 4, Fig. 187). The genus *Mastigimas*, however, is only tentatively included and all other genera form the Carsidarinae (clade 32). Unfortunately, nymphs of the type-genus, *Carsidara*, were not included in the study but the predictive properties of the cladogram suggest that the nymph of *Carsidara* should be of the type found in clade 4 which is thus referred to the existing family Carsidaridae.

Triozidae

This is a probable monophyletic group (clade 2, Fig. 186) which is the Triozidae of Becker-Migdisova (1973) plus *Leptynoptera* and *Pauropsylla* from her Carsidaridae. The tribe Triozini is probably a paraphyletic group (clade 21 minus clade 25) which requires much further study of generic limits before the classification can be improved.

Possible phylogeny

It is conventional to illustrate a phylogeny as a lateral view of a tree diagram (Fig. 200). The ancestral group is extinct and in the absence of fossil evidence the information required to make more than a tentative estimate of the branching sequence is unavailable.

It is more informative to illustrate a terminal cross section of the phyletic tree as an unresolved BUSH PHYLOGENY (Thorne, 1976) (Fig. 201). Such a phylogeny is said to be unresolved, as no attempt is made to show the exact sequence of branching.

The Ancestral Group comprises extinct species which probably had a Gondwanaland distribution, fed on Rutales and evolved 90–125 million years before present. A southern ancestry for the psyllids has also been suggested by Eastop (1978) and Hodkinson (1980). Klimaszewski (1964), however, believed that psyllids evolved in South East Asia which, according to Takhtajan (1969), is the ‘cradle of the angiosperms’. South East Asia (the Australian plate in the vicinity of Asia, and angiosperms could not have originated there (Raven & Axelrod, 1974) and, by the same logic, neither could the psyllids. Unfortunately most of the fossils of insects resembling psyllids, as reviewed by Szelegiewicz (1971), antedate the angiosperms. Furthermore, their morphology suggests that they were not on the direct line of descent to the modern Psylloidea. However, there are a few genera which may be as closely related to the ancestral group as they are to any other extant taxa. They include *Apsylla* (Calophyidae), *Bharatiana* (Phacopteronidae), *Mastigimas* (Carsidaridae) and *Strophingia* (Aphalaridae) and, with the exception of *Strophingia* (on Ericales), they are all Rutales-feeders. The most primitive (Cronquist, 1968; Takhtajan, 1969; Thorne, 1976) and thereby the probable ancestral group of angiosperms (Takhtajan, 1969) are thought to be the Annonales. *Togepsylla* (Aphalaridae), which feeds on Lauraceae (Annonales), may possibly be a relic genus of a psyllid group which antedates the Rutales-feeders.

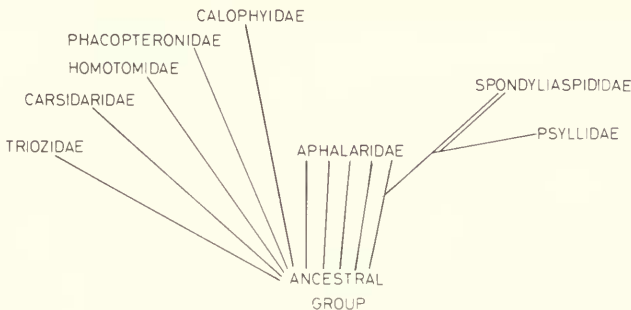


Fig. 200 Suggested phylogenetic relationships of the families of Psylloidea; as a tree with more than one line leading to the paraphyletic families Aphalaridae and Spondylaspididae.

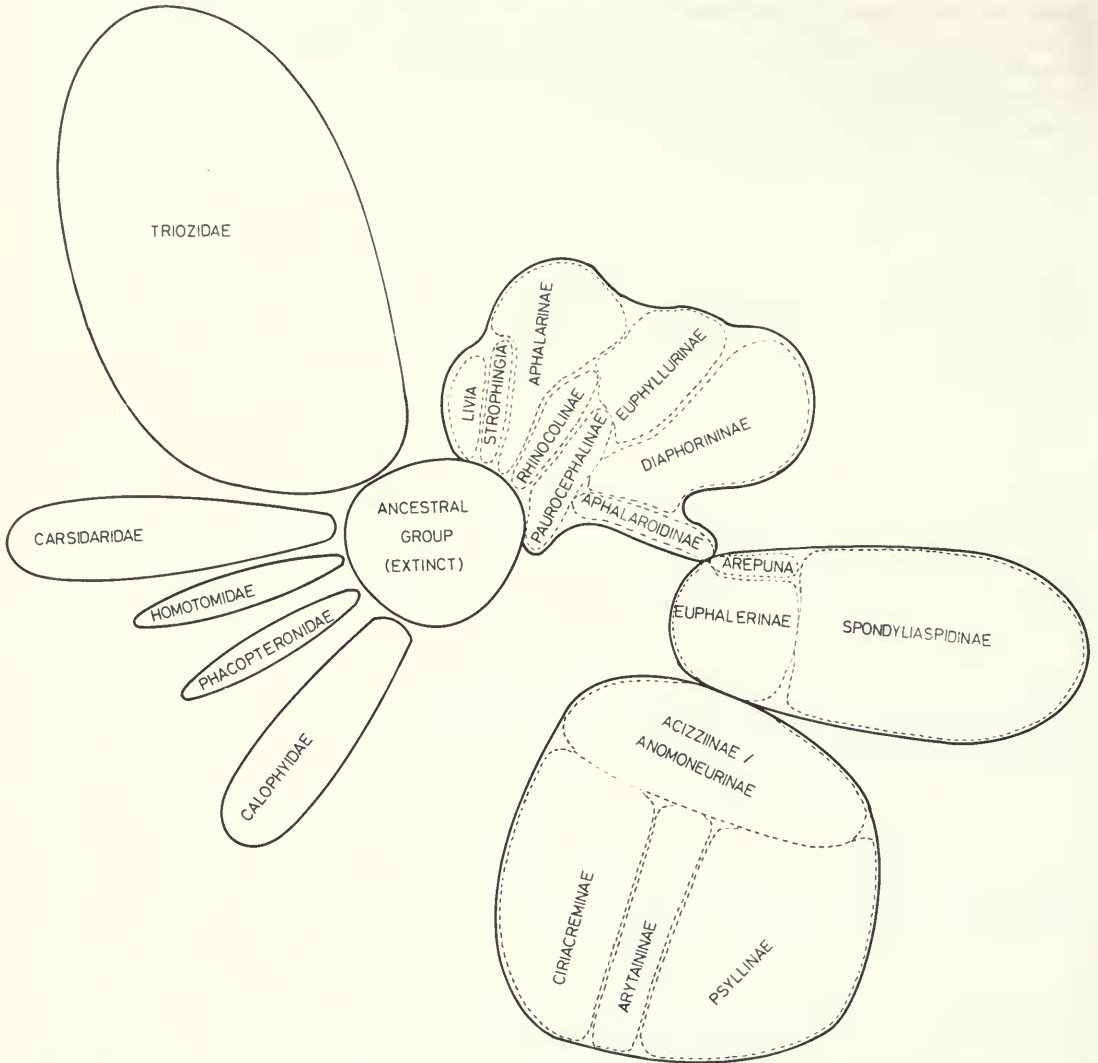


Fig. 201 Suggested phylogenetic relationships of the families of Psylloidea; a cross section of the unresolved bush phylogeny, in which each family (solid border) and subfamily (broken border) is shown covering an area roughly in proportion to the number of species it contains.

The Aphalaridae is a collection of five phyletic lines, Strophingiinae, Liviinae, Aphalarinae, Rhinocolinae and Paurocephalinae which originate from close to the probable ancestor. The Strophingiinae are only separated from the ground plan by loss characters. The Liviinae probably had a Laurasian ancestor associated with the Commelinales but further evidence suggesting the origin of the group is unavailable. The Aphalarinae, by contrast, were most likely to have had a Gondwanaland ancestor, although the greatest diversification of species and genera has occurred in northern regions. However, their host-plants are diverse and do not include Rutales. It is conceivable that if Annonales-feeding antedates Rutales-feeding, the ancestor of Aphalarinae was an Annonales-feeder. At least one extant member of the family, *Gyropsylla cannella* (Crawford) on Lauraceae, is associated with Annonales.

The Rhinocolinae probably had an ancestor with a Gondwanaland distribution. All members of the subfamily examined feed on Rutales.

Table 15 Nymphal summary classification

1. Sectasetae group.

Taxa with pointed or truncate sectasetae (characters N26 to N33, Table 4, p. 207). The forewing-pad generally has a well-formed humeral lobe (N1) and the tarsal arolia are very rarely petiolate (N4). There are two subgroups.

i. Pointed sectasetae subgroup.

Taxa with pointed sectasetae (characters N26 to N33)

<i>Calophya</i> (most spp.)	C
<i>Camartoscena unicolor</i>	A
<i>Crawforda triopsyllina</i>	T
<i>Diclidophlebia eastopi</i>	C
<i>Egeirotrioza</i> spp.	T
<i>Homotoma</i> spp.	C
<i>Leptynoptera sulfurea</i>	C
<i>Leuronota michoacana</i>	T
<i>Moraniella calodendri</i>	A
<i>Paraphalaroida fremontiae</i>	A
<i>Paurocephala</i> spp.	A
<i>Synozia pulchra</i>	C
<i>Trioza alacris</i>	T
<i>Triozoidea silvestris</i>	T

ii. Truncate sectasetae subgroup.

Taxa with truncate sectasetae (characters N26 to N33).

<i>Acanthocnema casuarinae</i>	T
<i>Ceropsylla martorelli</i>	T
<i>Paratrioza</i> spp.	T
<i>Pauropsylla trichaeta</i>	C
<i>Togepsylla matsumurana</i>	C
<i>Trichohermes walkeri</i>	T
<i>Trioza</i> (most spp.)	T

2. Lanceolate setae group.

Taxa with lanceolate setae (characters N23 to N25). There is often a humeral lobe (N1) and the tarsal arolia are rarely petiolate (N4).

<i>Agonosцена</i> spp.	A
<i>Aphalara</i> spp.	A
<i>Bharatiana octopsinosa</i>	C
<i>Camartoscena speciosa</i>	A
<i>Colposcena</i> sp.	A
<i>Craspedolepta</i> spp.	A
<i>Crastina linavuorii</i>	A
<i>Ctenarytaina eucalypti</i>	S
<i>Diaphorina</i> spp.	P
<i>Epicarsa</i> sp.	C
<i>Eucalyptolyma</i> sp.	S
<i>Euphyllura</i> spp.	A
<i>Leurolophus vittatus</i>	A
<i>Livia crefeldensis</i>	L
<i>L. vernalis</i>	L
<i>Neophyllura</i> spp.	A
<i>Pennavena fabulosa</i>	P
<i>Phacopteron lentiginosum</i>	C
<i>Phellopsylla</i> sp.	S
<i>Phytolyma</i> (most spp.)	A
<i>Pseudoeriopsylla nyasae</i>	C
<i>Pseudophacopteron floccosa</i>	C
<i>Psyllopsis</i> spp.	P

<i>Rhinocola aceris</i>	A
<i>Strophiingia</i> spp.	A
<i>Tainarys schini</i>	A

3. Capitulate setae group.

Taxa with capitulate setae (N11 to N19). All of these species also have a petiolate tarsal arolium (N4).

<i>Acizzia hakeae</i>	P
<i>A. russellae</i>	P
<i>A. uncatoides</i>	P
<i>Amorphicola amorphae</i>	P
<i>Arytaina genistae</i>	P
<i>Arytainilla</i> spp.	P
<i>Ceanothia</i> spp.	P
<i>Ciriacremum</i> spp.	P
<i>Euceropsylla</i> spp.	P
<i>Euphalerus tantillus</i>	P
<i>E. sp. (B)</i> .	P
<i>Floria variegata</i>	P
<i>Freysuila</i> sp.	P
<i>Heteropsylla</i> spp.	P
<i>Insnesia glabruscuta</i>	P
<i>Isogonoceraia divergipennis</i>	P
<i>Mitropsylla deserata</i>	P
<i>Psylla</i> (most spp.)	P
<i>Purshivora</i> spp.	P
<i>Trigonon longicornis</i>	P

4. Other taxa.

Taxa which lack sectasetae (characters N26 to N33), lanceolate setae (N23 to N25) and capitulate setae (N11 to N19). Two subgroups may, however, be recognised by the presence or absence of the petiolate tarsal arolium, a character which received high eigenvector and SUMRAT values.

i. Petiolate arolium subgroup.

The following taxa have a petiolate tarsal arolium.

<i>Acizzia acaciae</i>	P
<i>A. acaciaebaileyanae</i>	P
<i>Anomoneura mori</i>	P
<i>Aphalaroida</i> spp.	A
<i>Arepuna</i> sp.	P
<i>Colophorina cassiae</i>	P
<i>Epipsylla</i> spp.	P
<i>Euglyptoneura</i> spp.	P
<i>Euphalerus</i> (most spp.)	P
<i>Neopsyllia</i> spp.	P
<i>Pexopsylla cercocarpi</i>	P
<i>Platycorpha princeps</i>	P
<i>Psylla betulaenanae</i>	P
<i>P. carpinicola</i>	P
<i>P. floccosa</i>	P
<i>P. galeaformis</i>	P
<i>P. mali</i>	P
<i>P. phoradendrae</i>	P
<i>P. ribesiae</i>	P
<i>P. striata</i>	P
<i>P. trimaculata</i>	P
<i>Retroacizzia antennata</i>	P
<i>Spanioneura fonscolombii</i>	P

ii. Remainder.

<i>Apsylla cistellata</i>	A
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<i>Calophya rhois</i>	C
<i>C. rotundipennis</i>	C
<i>Cardiaspina</i> spp.	S
<i>Ceropsylla sideroxyli</i>	T
<i>Creiis</i> sp.	S
<i>Euphalerus gallicolus</i>	P
<i>Glycaspis</i> spp.	S
<i>Gyropsylla</i> spp.	A
<i>Hevaheva swezeyi</i>	T
<i>Kuwayama pisonia</i>	T
<i>Livia</i> (most spp.)	L
<i>Macrohomotoma</i> spp.	C
<i>Mastigimas</i> spp.	C
<i>Mesohomotoma</i> spp.	C
<i>Microceropsylla</i> sp.	C
<i>Mycopsylla</i> sp.	C
<i>Neolithus</i> sp.	T
<i>Pachypsylla</i> spp.	S
<i>Paracarsidara</i> spp.	C
<i>Pauropsylla</i> (most spp.)	C
<i>Pelmatobrachia</i> sp.	C
<i>Phytolyma lata</i>	A
<i>Protyora sterculiae</i>	C
<i>Pseudophacopteron</i> (most spp.)	C
<i>Spondylaspis</i> sp.	S
<i>Swezeyana elongagena</i>	T
<i>Synoza</i> sp.	C
<i>Tenaphalara</i> spp.	C
<i>Tetragonocephala</i> sp.	S
<i>Trioza anceps</i>	T
<i>T. hirsuta</i>	T
<i>T. palmicola</i>	T
<i>Triozamia lamborni</i>	T

There are four remaining subfamilies of Aphalaridae; Paurocephalinae, Euphyllurinae, Diaphorininae and Aphalaroidinae. The Paurocephalinae are morphologically most primitive and, hence, this subfamily is illustrated (Fig. 201) as deriving from the ancestral group and giving rise to the other three subfamilies. The Paurocephalinae, Euphyllurinae and Diaphorininae probably had Gondwanaland origins associated with unknown hosts.

The ancestor of the extant Aphalaroidinae was most likely to have had a Gondwanaland distribution, associated with Fabaceae. From such an ancestor the present day Nearctic genus *Aphalaroida* evolved together with the ancestor of the Spondyliaspididae.

Table 16 Percentage of species in each family of Becker-Migdisova (1973) in each group or subgroup of the nymphal summary classification (rows total 100%).

	Group or subgroup					
	1.i.	1.ii.	2.	3.	4.i.	4.ii.
APHALARIDAE	10	0	80	0	4	6
CARSIDARIDAE	28	5	9	0	0	58
LIVIIDAE	0	0	40	0	0	60
PSYLLIDAE	0	0	10	64	25	1
SPONDYLIASPIDIDAE	0	0	13	0	0	87
TRIOZIDAE	13	72	0	0	0	15

Table 17 A general classification of the Psylloidea.

The following classification includes eight families. An asterisk indicates the probable position in the classification of some taxa not examined.

Psylloidea Löw

- Aphalaridae Löw
 - Togepssyllinae Becker-Migdisova
 - Togepssylla* Kuwayama*
 - Strophinginae **subfam. n.** (type-genus: *Strophingia* Enderlein)
 - Strophingia* Enderlein
 - Liviinae Löw
 - Livia* Latreille
 - Aphalarinae Löw
 - Phytolymini Becker-Migdisova
 - Phytolyma* Scott
 - Gyropsyllini **trib. n.** (type-genus: *Gyropsylla* Bréthes)
 - Gyropsylla* Bréthes
 - Colposceniini Becker-Migdisova
 - Colposcencia* Enderlein
 - Crastina* Loginova
 - Aphalarini Löw
 - Aphalara* Förster
 - Craspedolepta* Enderlein
 - Brachystetha* Loginova*
 - Epheloscyta* Loginova*
 - Xanioptera* Enderlein*
 - Caillardiini Loginova*
 - Caillardia* Bergevin*
 - Eumetoecus* Loginova*
 - Rhodochlanis* Loginova*
 - Rhombaphalara* Loginova*
 - Xenaphalarini Loginova*
 - Eurotica* Loginova*
 - Xenaphalara* Loginova*
 - Rhinocolinae Becker-Migdisova
 - Rhinocolini Becker-Migdisova
 - Tainarys* Bréthes
 - Leurolophus* Tuthill
 - Moraniella* Loginova
 - Rhinocola* Förster
 - Agonosцена* Enderlein
 - Aphorma* Hodkinson*
 - Lisronia* Loginova*
 - Rhachistoneura* Hodkinson & Hollis*
 - Pachypsylloidini Loginova*
 - Acaerus* Loginova*
 - Eremopsylloides* Loginova*
 - Pachypsylloides* Bergevin*
 - Paurocephalinae Becker-Migdisova
 - Camarotoscena* Haupt
 - Paurocephala* Crawford
 - Euphyllurinae Becker-Migdisova
 - Diclidophlebiini Becker-Migdisova
 - Diclidophlebia* Crawford
 - Paraphalaroida* Loginova
 - Haplaphalara* Uichanco*
 - Euphyllurini Becker-Migdisova
 - Euphyllura* Förster

- Neophyllura* Loginova
- Katecephala* Crawford*
- Ligustrinia* Loginova*
- Syntomoza* Enderlein*
- Syringilla* Loginova*
- Ctenarytainini **trib. n.** (type-genus: *Ctenarytaina* Ferris & Klyver)
 - Ctenarytaina* Ferris & Klyver
 - (some spp. referred to *Eucalyptolyma*)
 - Eurhinocola* Crawford*
 - Syncarpiolyma* Froggatt*
- Diaphorininae Vondracek
 - Diaphorinini Vondracek
 - Diaphorina* Löw
 - Pennavena* Capener
 - Eudiaphorina* Loginova*
 - Psyllopseini Vondracek
 - Psyllopsis* Löw
- Aphalaroidinae Loginova
 - Aphalaroida* Crawford
- Spondyliaepididae Schwarz
 - Arepuniinae **subfam. n.** (type-genus: *Arepuna* Tuthill)
 - Arepuna* Tuthill
 - Euphalerinae Becker-Migdisova
 - Euphalerus* Schwarz
 - Retroacizzia* Heslop-Harrison
 - ?*Pachyparia* Loginova*
 - Phellopsylla* Taylor
 - Colophorina* Capener
 - Cometopsylla* Froggatt*
 - Pachypsyllinae Becker-Migdisova
 - Pachypsylla* Riley
 - Tetragonocephala* Crawford
- Spondyliaepidinae
 - Spondyliaepis* Signoret
 - Creiis* Scott
 - Cardiaspina* Crawford
 - Glycaspis* Taylor
 - Australopsylla* Tuthill & Taylor*
 - Eucalyptolyma* Froggatt* (not including species examined in this study)
 - Hyalinaspis* Taylor*
 - Lasiopsylla* Froggatt*
- Psyllidae Löw
 - Acizziinae **subfam. n.** (type-genus: *Acizzia* Heslop-Harrison)
 - Acizziini **trib. n.** (type-genus: *Acizzia* Heslop-Harrison)
 - Trigonon* Crawford
 - Mitrapssylla* Crawford
 - Acizzia* Heslop-Harrison
 - Platycorypha* Tuthill
 - Neopsyllia* Caldwell
 - Freysuila* Aleman
 - Macrocorsini Becker-Migdisova*
 - Auchmerina* Enderlein*
 - Caradocia* Laing*
 - Geijerolyma* Froggatt*
 - Macrocorsa* Vondracek*
 - Anomoneurinae Becker-Migdisova
 - Anomoneurini Becker-Migdisova
 - Anomoneura* Schwarz
 - Epipsylla* Kuwayama

- Tribe – unnamed (may be Cyamophilini Loginova)
Amorphicola Heslop-Harrison
 (many species referred to *Euphalerus*)
 ?*Cyamophila* Loginova*
- Ciriacreminae Enderlein
 Ciriacremini Enderlein
Euceropsylla Boselli
Heteropsylla Crawford
Insnesia Tuthill
Isogonoceraia Tuthill
Ciriacremum Enderlein
Aremica Tuthill*
Delina Blanchard*
Kleiniella Aulmann*
Palmapenna Hollis*
Panisopelma Enderlein*
Russelliana Tuthill*
- Arytaininae Crawford
Arytaina Förster
Floria Löw
Arytainilla Loginova
Alloeoneura Löw*
Amblyrhina Löw*
Livilla Curtis*
- Psyllinae Löw
Psylla Geoffroy sensu lato (including all subgenera)
Spanioneura Förster
Ceanothia Heslop-Harrison
Euglyptoneura Heslop-Harrison
Purshivora Heslop-Harrison
- Calophyidae Vondracek **stat. n.**
 Apsyllinae Becker-Migdisova
Apsylla Crawford
- Calophyinae Vondracek
Pelmatobrachia Enderlein
Microceropsylla Boselli
Calophya Löw
Holotrioza Bréthes*
Paracalophya Tuthill*
- Phacopteronidae Becker-Migdisova **stat. n.**
 Bharatianinae **subfam. n.** (type-genus: *Bharatiana* Mathur)
Bharatiana Mathur
- Phacopteroninae Becker-Migdisova
Phacopteron Buckton
Pseudophacopteron Enderlein
Epicarsa Crawford
Chineura Tuthill*
Phacosemoides Lima & Guitton*
- Homotomidae Heslop-Harrison **stat. n.**
 Homotominae Heslop-Harrison
Homotoma Guérin-Méneville
Synozia Enderlein
- Macrohomotominae **subfam. n.** (type-genus: *Macrohomotoma* Kuwayama)
 Mycopsyllini **trib. n.** (type-genus: *Mycopsylla* Froggatt)
Mycopsylla Froggatt
- Macrohomotomini **trib. n.** (type-genus: *Macrohomotoma* Kuwayama)
Macrohomotoma Kuwayama
Pseudoeriopsylla Newstead

- Carsidaridae Crawford
Mastigmatinae Becker-Migdisova
Mastigimas Enderlein
Carsidarinae Crawford
Tenaphalarini Heslop-Harrison
Tenaphalara Kuwayama
Carsidarini Crawford
Protyora Kieffer
Mesohomotoma Kuwayama
Paracarsidara Heslop-Harrison
Carsidara Walker*
- Triozidae Löw
Neolithinae **subfam. n.** (type-genus: *Neolithus* Scott)
Neolithus Scott
Schedoneolithus Tuthill*
- Triozamiinae Becker-Migdisova
Triozamia Vondracek
- Triozinae Löw
Triozini Löw
Leuronota Crawford
Trichohermes Kirkaldy
Egeirotrioza Boselli
Aacanthocnema Tuthill & Taylor
Triozoida Crawford
Triozia Förster
Paratriozia Crawford
Kuwayama Crawford
Ceropsylla Riley
Swezeyana Caldwell
Crawforda Caldwell
Hevaheva Kirkaldy
Anomocephala Tuthill*
Bactericera Puton*
Calinda Blanchard*
Epitrioza Kuwayama*
Eutrioza Loginova*
Hemischizocranium Tuthill*
Hemitrioza Crawford*
Izpania Klimaszewski*
Metatriozia Tuthill*
Myrmecephala Tuthill*
Neotrioza Kieffer*
Neotriozella Crawford*
Ozotrioza Kieffer*
Paracomeca Laing*
Pseudotrioza Miyatake*
Rhegmoza Enderlein*
Schedotrioza Tuthill & Taylor*
Stenopsylla Kuwayama*
- Pauropsyllini Crawford
Pauropsylla Rübsaamen
Leptynoptera Crawford
Sympauropsylla Enderlein*
-

Table 18 Genera not examined in this study, and the family or subfamily to which they probably belong.

<i>Aconopsylla</i> Tuthill & Taylor	Carsidarinae
<i>Anomalopsylla</i> Tuthill	Aphalaridae
<i>Astragilita</i> Loginova	Psyllidae
<i>Atmetocranium</i> Tuthill	Aphalaridae
<i>Brachyopsylla</i> Froggatt	Psyllidae
<i>Carsidaroida</i> Crawford	Carsidarinae
<i>Cecidopsylla</i> Kieffer	Phacopteronidae
<i>Cecidotrioza</i> Kieffer	Triozidae
<i>Cerotrioza</i> Crawford	Triozidae
<i>Diceraopsylla</i> Crawford	Aphalaridae
<i>Dynopsylla</i> Crawford	Homotomidae
<i>Engyatoneura</i> Loginova	Triozidae
<i>Eriopsylla</i> Froggatt	Psyllidae
<i>Jensiella</i> Tuthill	Aphalaridae
<i>Labicria</i> Enderlein	Psyllidae
<i>Lanthanaphalara</i> Tuthill	Aphalaridae
<i>Leptotrioza</i> Miyatake	Triozidae
<i>Levidea</i> Tuthill	Triozidae
<i>Lindbergiella</i> Heslop-Harrison	Psyllidae
<i>Megadicrania</i> Loginova	Aphalaridae
<i>Metapsylla</i> Kuwayama	Spondyliaspidae
<i>Nesiopie</i> Kirkaldy	Carsidarinae
<i>Optomopsylla</i> Caldwell	Triozidae
<i>Paurotriozana</i> Caldwell	Triozidae
<i>Pexopsylla</i> Jensen	Psyllidae
<i>Pseudacanthopsylla</i> Samy	Psyllidae
<i>Rhinopsylla</i> Riley	Triozidae
<i>Sphingocladia</i> Enderlein	Homotomidae
<i>Sphinia</i> Blanchard	Aphalaridae
<i>Tyora</i> Walker	Carsidarinae

The Spondyliaspidae probably derived from a Gondwanaland ancestor associated with Fabaceae. However, the largest group, the Spondyliaspinae, is associated with the genus *Eucalyptus* (Myrtaceae).

It is most likely that the Psyllidae shared a common ancestor with the Spondyliaspidae (minus *Arepuniinae*) in Gondwanaland in association with the Fabaceae. Present day psyllids are largely associated with Fabaceae and Rosaceae (Rosales). The morphologically most primitive, and probably oldest, subfamilies of Psyllidae are the *Acizziinae* and *Anomoneurinae*, most species of which retain the habit of Fabaceae-feeding. The *Ciriacreminae* have a Gondwanaland distribution suggesting that they are also an old group. The *Arytaininae* (as here defined) are probably a more recent group, restricted to the Palaearctic, but like most *Ciriacreminae*, retaining the habit of Fabaceae-feeding. The *Psyllinae* live on a variety of host-plants, particularly the Rosaceae, a north temperate family (Good, 1974). They are largely Holarctic and may have had a Laurasian ancestor.

The Calophyidae and Phacopteronidae have retained the habit of Rutales-feeding and probably had Gondwanaland origins. However, the families of Rutales with which most species of these families are associated differ; Calophyidae feed on Anacardiaceae and Phacopteronidae feed on Meliaceae.

The family Homotomidae probably had a Gondwanaland origin in association with *Ficus* (Moraceae). With the exception of a few Indian species on Santalaceae (Mathur, 1975) they feed on *Ficus*.

Once again, the most probable origin of the Carsidaridae was in Gondwanaland. The genus *Mastigimas*, which is only tentatively assigned to this family, has retained the habit of

Rutales-feeding, the remaining genera are placed in the subfamily Carsidarinae, which feed on Malvales.

The Triozidae is a cosmopolitan group for which a Gondwanaland origin appears most likely. There is no indication of the ancestral host relationship and, unlike other families, host-plant diversity appears to exceed morphological diversity (p. 256).

Keys

Key construction

These keys are intended to place most psyllid nymphs in the correct subfamily, tribe or in some cases genus. The keys are an application of the predictive properties of the new classification and, hence, they should work for the majority of species not examined by this study as well as the 15% of species which were. To maintain practicality it was sometimes necessary to artificially split some polythetic taxa. For example, the family Triozidae is keyed out in 11 sections in the key to families. In many polythetic taxa no morphological features of the nymphs could be used to separate subordinate taxa. In such cases host-plant differences were often of more practical value than morphological attributes and, hence, some key couplets contain host-plant characters.

Confirmatory data are given after most couplets. Nomomeristic and metric (Figs 5–7) characters are also given as confirmatory data; with the following abbreviations.

Nomomeristic characters

- A = Number of antenna divisions (i.e. apparent segments).
- R = Antennal divisions upon which rhinaria occur.

Metric characters (lengths)

- AL = Antenna length (Figs. 5, 6).
- ARB = Circum-anal pore ring breadth (Fig. 7).
- BL = Body length (Figs 5, 6).
- WL = Forewing-pad length (Figs 5, 6).

Metric characters (ratios)

- AWL = Antenna length to forewing-pad length ratio.
- BBBL = Body breadth (Figs 5, 6) to body length ratio.

Scale lines are given on drawings of structures whose dimensions are not indicated in the text.

Artificial key to families

The phenetic groups which are usually monothetic, that are most congruent with the classification, are separated first. In this way, the key should have maximum reliability for species which 'key-out' prior to couplet 39. Many of the characters used in the key were shown to have high classificatory power, as indicated by high values of the SUMRAT information statistic and principal component eigenvectors. The key to families of White & Hodkinson (1982) should be used as an additional check on identity when Holarctic material is being examined.

Artificial key to families of Psylloidea

- 1 Truncate sectasetae present on margin of forewing-pad (Fig. 50). [Sectasetae not present on antenna. Forewing-pad usually anteriorly produced as a humeral lobe]
 - **TRIOZIDAE** (most species)(p. 289)
 - Sectasetae usually absent from margin of forewing-pad; if present they are pointed (except *Togepssylla matsumurana* Kuwayama which has two rows of truncate sectasetae on the antenna) 2
- 2 Scales present on body margin (Figs 173–176)
 - **TRIOZIDAE** (many Hawaiian and tropical New World species)(p. 289)
 - Scales not present on body margin 3
- 3 Sectasetae (pointed or truncate) present on abdomen margin and numbering more than 4 + 4.. 4
 - Sectasetae usually absent from abdomen margin; if present then numbering at most 4 + 4..... 12

- 4 Tarsal arolium without a visible unguitactor (Fig. 95). [Palaeartic and Oriental. On *Populus* spp.] **TRIOZIDAE** (*Egeirotrioza*) (p. 289) 5
- Tarsal arolium with a distinctly visible unguitactor (Figs 65, 66, 69–71, 74) 5
- 5 Clavate setae present on dorsal surface of abdomen (Fig. 172). [Forewing-pad anteriorly produced as a humeral lobe which extends anterior to eye. Hawaii. On *Tetraplasandra*] **TRIOZIDAE** (*Crawforda*) (p. 289)
- Clavate setae absent from dorsal surface of abdomen 6
- 6 Setae present on antenna (Figs 40, 43, 45) 7
- Setae absent from antenna 8
- 7 Antenna length to forewing-pad length ratio 0.18–0.47. On Rutales, especially Anacardiaceae. Antennal setae arranged in one row, opposite rhinaria (Fig. 40). **CALOPHYIDAE** (most New World spp.) (p. 288)
- Antenna length to forewing-pad length ratio 0.52–1.62. Usually not on Rutales, not known on Anacardiaceae. Antennal setae usually in more than one row (Fig. 45). [On Malvales, Melastomataceae, Moraceae and Rutaceae.] **APHALARIDAE** (*Paurocephala* and other genera often confused with *Paurocephala*) (p. 278)
- 8 Apex of abdomen inwardly emarginate (Fig. 153). [Neotropical. On *Ficus*.] **HOMOTOMIDAE** (*Synozia*) (p. 288)
- Apex of abdomen not inwardly emarginate 9
- 9 Tarsal arolium with an unguitactor which forms a petiole (Fig. 69). [Palaeartic. On *Populus*.] **APHALARIDAE** (*Camarotoscena*) (p. 278)
- Tarsal arolium with a short unguitactor and no petiole 10
- 10 Hindwing-pad very reduced, its apex interior to margin of abdomen (Fig. 48). [Austro-Oriental and Pacific. On *Calophyllum*.] **TRIOZIDAE** (*Leptynoptera*) (p. 289)
- Hindwing-pad of normal proportions, its apex exterior to margin of abdomen 11
- 11 General body form very broad; body breadth more than 0.75 times body length. [Old World. On *Ficus*.] **HOMOTOMIDAE** (p. 288)
- General body form elongate; body breadth less than 0.70 times body length **TRIOZIDAE** (some spp.) (p. 289)
- 12 Lanceolate setae present on abdomen margin and numbering 3 + 3 or 4 + 4. Capitate setae (sometimes modified into tubular structures, Fig. 133; *Mitrapsylla deserata* Caldwell) present on abdomen margin and/or dorsal surface. [Tropical and warm temperate New World. On Fabaceae.] **PSYLLIDAE** (*Heteropsylla* and *Mitrapsylla*) (p. 285)
- Lanceolate setae usually absent from abdomen margin; if present, then capitate setae absent from body and wing-pads 13
- 13 Lanceolate setae present on abdomen margin and/or forewing-pad margin (Figs 162, 165, 167, 168) 14
- Lanceolate setae absent from abdomen and forewing-pad margins 22
- 14 Circum-anal pore ring reduced to a few large pores (Fig. 146). [Oriental. On Burseraceae.] **PHACOPTERONIDAE** (*Phacopteron*) (p. 288)
- Circum-anal pore ring not reduced to a few large pores 15
- 15 Tibia each with a row of stout setae on outer edge (Figs 51, 54) 16
- Tibia without a row of stout setae on outer edge 17
- 16 Tarsal arolium with a long unguitactor which forms a petiole (Fig. 69). [Palaeartic. On *Populus*.] **APHALARIDAE** (*Camarotoscena*) (p. 278)
- Tarsal arolium very reduced (not or hardly visible). [Tropical Old World. On Meliaceae.] **PHACOPTERONIDAE** (*Chineura*) (p. 288)
- 17 Anal pore-field arranged as bands (similar to Fig. 155). Antenna with 10 divisions. [Neotropical.] **PHACOPTERONIDAE** (*Epicarsa*) (p. 288)
- Anal pore-field usually not arranged as bands; or if arranged as bands then antenna with at most 8 divisions 18
- 18 Anal pore-field arranged as 2 rings which are each placed to one side of the anus (Figs 150–152). [Tropical Old World. On *Ficus*.] **HOMOTOMIDAE** (some Macrohomotominae) (p. 288)
- Anal pore-field not arranged as 2 rings which are each placed to one side of the anus 19
- 19 On Anacardiaceae. Antenna with 3 divisions. Small (BL = 0.93–1.20 mm). **CALOPHYIDAE** (*Calophya rhois*) (p. 288)
- Usually not on Anacardiaceae; or if on Anacardiaceae, antenna with 7 or 8 divisions (some Rhinocolinae) or larger (some *Diaphorina*, BL = 1.34–2.13 mm) 20
- 20 Apical margin of abdomen truncate-acuminate (Fig. 127). Anal pore-field not arranged as a

circum-anal ring, pores concentrated at antero-lateral angle of caudal plate (Fig. 127); pores not visible on anal plate. [Australia. On *Eucalyptus*.]

- SPONDYLIASPIDIDAE** (*Phellopsylla*) (p. 284)
- Apical margin of abdomen not truncate-acuminate. Anal pore-field usually comprised of a circum-anal ring only; if pores present on caudal plate then they also occur on the anal plate. 21
- 21 Circum-anal pore ring partly on caudal plate, broad and convoluted (Fig. 145). [Oriental. On *Toona*.] **PHACOPTERONIDAE** (*Bharatiana*) (p. 288)
- Circum-anal pore ring usually confined to anal plate; if partly on caudal plate then usually not convoluted (Fig. 108), or if convoluted then pores in a narrow row (Fig. 112)
- APHALARIDAE** (most species) (p. 278)
- 22 Anal pore-field (excluding circum-anal ring) arranged as 1 + 1 (Fig. 121) or 2 + 2 (Figs 120, 122) rings, which are slightly convoluted. [Tarsal arolium usually with a long unguitactor which forms a petiole (Fig. 77); except *Euphalerus gallicolus*. On Fabaceae and Rhamnaceae.] **SPONDYLIASPIDIDAE** (*Euphalerus*) (p. 284)
- Anal pore-field (excluding circum-anal ring) usually not arranged as 1 + 1 or 2 + 2 rings; if arranged as 1 + 1 rings then rings not convoluted (Figs 110, 149) 23
- 23 Apical margin of abdomen serrate-acuminate (Figs 125, 126, 128). Circum-anal pore ring absent. Anus posterior. [Anal pore-field, if present, comprised of small groups of pores, most of which occur on the caudal plate. On *Celtis* and *Colophospermum*.]
- SPONDYLIASPIDIDAE** (*Pachypsyllinae* and *Retroacizzia*) (p. 284)
- Apical margin of abdomen usually not serrate-acuminate; or if serrate-acuminate (Figs 149, 157) circum-anal pore ring present and anus ventral 24
- 24 Caudal plate pointed (Figs 118, 124). [Abdomen segments usually laterally bulging (Fig. 27). Anal pore-field, if present, comprised of small groups of pores placed ventrally (Figs 118, 124, 129). Anus posterior. Tarsal apical setae usually strongly capitate (Fig. 38). Australia. On *Eucalyptus*.] **SPONDYLIASPIDIDAE** (Spondyliaspidae) (p. 284)
- Caudal plate (if developed) not pointed 25
- 25 Abdomen margin with 1 + 1, 2 + 2, 3 + 3 or 4 + 4 sectasetae **PSYLLIDAE** (many spp.) (p. 285)
- Abdomen margin without sectasetae 26
- 26 Abdomen margin with capitate setae **PSYLLIDAE** (many spp.) (p. 285)
- Abdomen margin without capitate setae 27
- 27 Tarsal arolium with a petiole. Arolium pad usually large relative to tarsal claws (Figs 59, 80–93); if pad small (Fig. 179) then host-plant is a species of Fabaceae (some *Acizzia* spp.) 28
- Tarsal arolium usually without a petiole; if with a petiole then arolium pad small and host-plant is a species of Meliaceae (some *Pseudophacopteron* spp., Fig. 94) or *Terminalia* (*Trioza hirsuta*, Fig. 96) 31
- 28 Abdomen margin with rod setae (Fig. 161) 29
- Abdomen margin without rod setae 30
- 29 Tarsal arolium with a very long petiole (Fig. 59). Antenna with 7 divisions. New World. On Fabaceae **APHALARIDAE** (*Aphalaroida pithocolobia*) (p. 278)
- Tarsal arolium with a short petiole (similar to Fig. 92). Antenna with 7 or 8 divisions. Palaearctic. On *Ulmus* **PSYLLIDAE** (*Psylla ulmi*) (p. 285)
- 30 Tarsal arolium with a very long petiole (Fig. 59). [New World. On Fabaceae.]
- APHALARIDAE** (*Aphalaroida inermis*) (p. 278)
- Tarsal arolium with a short petiole (Figs 79–93) **PSYLLIDAE** (many spp.) (p. 285)
- 31 Abdomen margin with clavate setae (Fig. 169). [Neotropical. On Solanaceae.]
- SPONDYLIASPIDIDAE** (*Arepuna*) (p. 284)
- Abdomen margin without clavate setae 32
- 32 Anal pore-field with 1 + 1 incomplete rings in addition to circum-anal pore rings (Fig. 143). Host-plant is *Mangifera indica*. [Oriental.] **CALOPHYIDAE** (*Apsylla*) (p. 288)
- Anal pore-field usually comprised of circum-anal rings only; if 1 + 1 additional rings present they are complete and the host-plant is *Juncus* (some *Livia* spp., Fig. 110) or *Ficus* (*Macrohomotoma striata*, Fig. 149) 33
- 33 Anal pore-field comprised of circum-anal rings plus bands of pores which cover a more extensive area of the anal plate than of the caudal plate (Fig. 158). [Aftrotropical. On *Antiaria*.] **TRIOZIDAE** (*Trioza*) (p. 289)
- Anal pore-field usually comprised of circum-anal pore rings only; if pore bands present then they are more extensive on the caudal plate than on the anal plate (Fig. 155) 34
- 34 Anal pore-field (excluding circum-anal ring which may be present or absent) comprised of pore

- bands (Fig. 155) or a single band plus numerous ovoid pore areas (Fig. 154). [On Meliaceae and Malvales.] **CARSIDARIDAE** (p. 289)
- Anal pore-field (excluding circum-anal pore ring which is present) usually absent; if present then comprised of 1 + 1 rings (Figs 110, 149) 35
- 35 Apical margin of abdomen notched and with 1 + 1 stout setae (Fig. 157). [Neotropical. On Euphorbiaceae, Myrtaceae and Solanaceae.] **TRIOZIDAE** (*Neolithus*) (p. 289)
- Apical margin of abdomen not notched and without 1 + 1 stout setae 36
- 36 Anal pore-field comprised of a circum-anal ring plus 1 + 1 additional rings each of which is separated from the circum-anal ring (Fig. 110). [Holarctic and northern Oriental. On *Juncus*.] **APHALARIDAE** (some *Livia* spp.) (p. 278)
- Anal pore-field usually comprised of circum-anal pore rings only; if 1 + 1 additional rings present then they are adjacent to the circum-anal pore ring (Fig. 149) 37
- 37 Anal pore-field comprised of circum-anal pore rings plus 1 + 1 additional rings (Fig. 149). [Austro-Oriental and Oriental. On *Ficus*.] **HOMOTOMIDAE** (*Macrohomotoma*) (p. 288)
- Anal pore-field comprised of circum-anal pore rings only (which may occasionally be incomplete, Figs 150, 151; *Mycopsylla*) 38
- 38 Circum-anal pore rings broken and with a convoluted inner margin to the outer ring (Figs 150, 151). [BBBL more than 0.83. Australasian, Austro-Oriental and Oriental. On *Ficus*.] **HOMOTOMIDAE** (*Mycopsylla*) (p. 288)
- Circum-anal pore rings usually not broken; if broken (Fig. 147) then inner margin of outer ring not convoluted 39
- 39 Antenna with 1 division. [On Rutales.] **CALOPHYIDAE** (*Calophya rotundipennis* and *Microceropsylla*) (p. 288)
- Antenna with more than 1 division 40
- 40 Antenna with 2 divisions. [Oriental. On *Ficus*.] **TRIOZIDAE** (*Pauropsylla depressa*) (p. 289)
- Antenna with more than 2 divisions 41
- 41 Antenna with 3 divisions 42
- Antenna with more than 3 divisions 43
- 42 Tarsus with 2 segments (Fig. 52). [Oriental. On Anacardiaceae.] **CALOPHYIDAE** (*Pelmatobrachia*) (p. 288)
- Tarsus with 1 segment separate from the tibiotarsus (Fig. 53). [Afrotropical and Palaearctic. On Moraceae and *Tamarix*.] **APHALARIDAE** (*Phytolyma* and some *Colposceniini*) (p. 278)
- 43 General form broad (BBBL more than 0.90). [Austro-Oriental and Oriental. On *Ficus*.] **HOMOTOMIDAE** (*Macrohomotoma*) (p. 288)
- General form elongate (BBBL less than 0.85) 44
- 44 Antenna with 5 or 6 divisions. [On Lauraceae.] **TRIOZIDAE** (*Pauropsylla beelsoni* and *Trioza anceps*) (p. 289)
- Antenna with 8, 9 or 10 divisions 45
- 45 General form broad (BBBL more than 0.77). Antenna with 6 rhinaria (Fig. 41; often difficult to see). [Tarsal arolium without a visible unguitactor (Fig. 58). New Zealand and New World. On *Ilex* and *Nectandra*.] **APHALARIDAE** (*Gyropsylla*) (p. 278)
- General form elongate (BBBL less than 0.76). Antenna with 4 rhinaria 46
- 46 Tarsal arolium usually not visible; if visible then very small relative to claws, with a short petiole and a well-developed pad (Fig. 94). [Old World tropics. On Meliaceae.] **PHACOPTERONIDAE** (*Pseudophacopteron*) (p. 288)
- Tarsal arolium large relative to claws, with a stout petiole and a very reduced pad (Fig. 96). [Oriental. On *Terminalia*.] **TRIOZIDAE** (*Trioza hirsuta*) (p. 289)

Keys to subfamilies and genera of Aphalaridae

Many subfamilies are largely characterised by the form of the tarsal arolium, which is often difficult to observe. Because of this two keys to subfamilies are provided: (1) a key which follows the classification as closely as possible and (2) a much simplified artificial key. Material of *Togepsylla* sp. was not available for the analyses described earlier in this paper. However, material has since become available and the genus is tentatively included in the following keys (material in British Museum (Natural History); from New Guinea).

Key to subfamilies of Aphalaridae

- 1 Tarsus without an arolium, but with a pair of pulvilli (each situated beneath a claw). [Austro-Oriental, Oriental and Palearctic. On Lauraceae.] **TOGEPHYLLINAE** (p. 281)
- Tarsus usually with a well-developed arolium; or if without a visible arolium, pulvilli also absent 2
- 2 Tarsal arolium not visible 3
- Tarsal arolium well developed and visible 4
- 3 Abdomen margin with short lanceolate setae (similar in proportion to those in Fig. 164). [Anal pore-field usually comprised of groups of pores on the caudal plate in addition to the circum-anal ring (Fig. 105). Australasian, Oriental, Pacific, New Zealand and introduced to other areas on cultivated *Eucalyptus*. On Myrtaceae, Onagraceae and Rutaceae.] **EUPHYLLURINAE** (Ctenarytainini) (p. 282)
- Abdomen margin usually with long simple setae; exceptionally slightly lanceolate (Fig. 162; *Phytolyma minuta*). [Anal pore-field comprised of circum-anal pore rings only (Fig. 162). Afrotropical. On Moraceae.] **APHALARINAE** (*Phytolyma*) (p. 281)
- 4 Tarsal arolium without a visible unguitactor (Figs 56–58). **APHALARINAE** (minus *Phytolyma*) (p. 281)
- Tarsal arolium with a well-developed unguitactor (Figs 59–76) 5
- 5 Anal pore-field comprised of circum-anal pore rings plus 1 + 1 incomplete rings (Figs 106, 107, 112, 113) **EUPHYLLURINAE** (minus Ctenarytainini) (p. 282)
- Anal pore-field usually comprised of circum-anal rings only; or if additional pore areas present they form ovoid areas (Figs 97, 99, 100) or complete rings (Fig. 110) 6
- 6 Unguitactor less than half as long as whole arolium and not forming a petiole (Figs 67, 68, 71–76) 7
- Unguitactor usually more than half as long as whole arolium (Figs 59–61, 69, 70); if less than half as long as whole arolium then arolium petiolate (Fig. 69) 9
- 7 Tarsal arolium pad longer than broad (Fig. 71). [Palearctic. On Ericaceae.] **STROPHINGIINAE** (p. 281)
- Tarsal arolium pad broader than long (Figs 67, 68, 72–76) 8
- 8 Tarsal arolium pad more than 2.0 times as broad as long and with a pair of sclerotized areas (Figs 72–76). [On Rurales.] **RHINOCOLINAE** (Rhinocolini) (p. 282)
- Tarsal arolium pad less than 1.5 times as broad as long and without sclerotized areas (Figs 67, 68). [Holarctic and Oriental. On *Carex* and *Juncus*.] **LIVIINAE** (p. 281)
- 9 Abdomen margin with lanceolate setae. Anal pore-field comprised of circum-anal rings only. Tarsal arolium as in Figs 60, 61 **DIAPHORININAE** (p. 283)
- Abdomen margin usually without lanceolate setae; or if with lanceolate setae anal pore-field comprised of circum-anal rings plus ovoid pore areas (Figs 97, 99, 100). Tarsal arolium petiolate (Figs 59, 69, 70) 10
- 10 Abdomen margin with sectasetae or lanceolate setae. Petiole of tarsal arolium short relative to extension of claws (Figs 69, 70). [On *Populus*, Malvales and Urticales.] **PAUROCEPHALINAE** (p. 283)
- Abdomen margin without sectasetae or lanceolate setae. Petiole of tarsal arolium long relative to extension of claws (Fig. 59). [New World. On Fabaceae.] **APHALAROIDINAE** (p. 283)

Simplified key to subfamilies of Aphalaridae

- 1 Abdomen margin with rod setae. [Tarsal arolium with a very long petiole (Fig. 59). New World. On Fabaceae.] **APHALAROIDINAE** (*Aphalaroida pithecolobia*) (p. 283)
- Abdomen margin without rod setae 2
- 2 On Moraceae (*Clorophora* and *Ficus*). [Abdomen margin with long setae, which may be slightly lanceolate (Fig. 162). Anus posterior. Tarsal arolium not visible. Afrotropical.] **APHALARINAE** (*Phytolyma*) (p. 281)
- Not on Moraceae 3
- 3 Abdomen margin with sectasetae 4
- Abdomen margin without sectasetae 9
- 4 Antenna without sectasetae 5
- Antenna with sectasetae 6

- Abdomen margin not sinuate before apex and anal pore-field comprised of circum-anal rings only 20
- 20 Abdomen margin lanceolate setae at least 4 times as long as broad (Fig. 164). Tarsal arolium without a visible unguitactor (Fig. 56). Antenna usually with 5 or 6 rhinaria, sometimes 4. Humeral lobe of forewing-pad not usually extended anterior to the posterior margin of the eye. [Cool temperate Holarctic and Oriental. On Asteraceae, Brassicaceae, Chenopodiaceae, Onagraceae, Polygonaceae and Ranunculaceae.] **APHALARINAE** (Aphalarini) (p. 281)
- Abdomen margin lanceolate setae less than 4 times as long as broad (Fig. 165). Tarsal arolium with a long unguitactor (Fig. 60). Antenna with 4 rhinaria. Humeral lobe of forewing-pad usually extended anterior to the posterior margin of the eye. [Warm temperate and tropical Afrotropical, Oriental and Palaearctic. On numerous hosts.]
- DIAPHORININAE** (Diaphorinini) (p. 283)
- 21 Anal pore-field comprised of a circum-anal ring plus 1 + 1 additional rings (Fig. 110). Tarsal arolium with a distinct unguitactor but not petiolate (Fig. 67). [Holarctic. On *Juncus*.]
- LIVIINAE** (some spp.) (p. 281)
- Anal pore-field comprised of circum-anal rings only. Tarsal arolium without a distinct unguitactor (Figs 57, 58) or, if with an unguitactor then petiolate (Fig. 59)..... 22
- 22 Tarsal arolium with a long petiole (Fig. 59). On Fabaceae. [New World.]
- APHALAROIDINAE** (*Aphalaroida inermis*) (p. 283)
- Tarsal arolium without a long petiole (Figs 57, 58). On *Ilex*, *Nectandra* or *Tamarix*
- APHALARINAE** (*Colposceniini* and *Gyropsylla*) (p. 281)

Confirmatory characters of Togepsyllinae

Body, antenna and wing-pads with truncate sectasetae. Tarsus with paired pulvilli, one under each claw. BL = 0.93–1.27 mm, WL = 0.35–0.46 mm, ARB = 0.08 mm, AWL = 0.89–1.12, BBBL = 0.40–0.51, A = 7, R = 3456. Austro-oriental, Oriental and eastern Palaearctic. On Lauraceae **TOGEPSYLLA**

Key to species groups of Liviinae

One genus only: *Livia*. Species formerly referred to *Diraphia* Waga can be separated from other species of *Livia*, as follows.

- 1 Anal pore-field comprised of circum-anal pore rings plus 1 + 1 additional rings (Fig. 110). Tarsal arolium pad with angles acutely rounded (Fig. 67). On *Juncus*. [BL = 1.44–2.45 mm, WL = 0.65–0.83 mm, ARB = 0.06–0.08 mm, AWL = 0.49–0.75, BBBL = 0.48–0.71, A = 3 or 7, R = 3333 or 3577.]..... **LIVIA** (minus species formerly referred to *Diraphia*)
- Anal pore-field comprised of circum-anal rings only (Fig. 111). Tarsal arolium pad with angles broadly rounded (Fig. 68). On *Carex*. [BL = 1.75–2.63 mm, WL = 0.80–0.92 mm, ARB = 0.47–0.60 mm, AWL = 0.55–0.76, BBBL = 0.51–0.75, A = 7 or 10, R = 4677 or 4689.]
- LIVIA** (formerly *Diraphia* spp.)

Confirmatory characters of Strophingiinae

Abdomen and wing-pad margins with lanceolate setae or pointed sectasetae. Tarsal arolium as in Fig. 71. BL = 1.11–1.58 mm, WL = 0.46–0.60 mm, ARB = 0.09–0.13 mm, AWL = 0.41–0.56, BBBL = 0.72–0.86, A = 3, R = 3333. Palaearctic. On *Calluna* and *Erica*

STROPHINGIA

Key to genera of Aphalarinae

- 1 Each tarsus without a visible arolium. On Moraceae. [Longest seta on abdomen margin simple, others at most only slightly lanceolate (Fig. 162). Anus posterior, Fig. 162. BL = 1.72–2.47 mm, WL = 0.72–1.11 mm, ARB = 0.31–0.69 mm, AWL = 0.60–0.78, BBBL = 0.82–1.11, A = 3, R = 3333. Afrotropical. On *Clorophora* and *Ficus*.] **PHYTOLYMA**
- Each tarsus with a visible and well-developed arolium (Figs 56–58). Not on Moraceae..... 2
- 2 Anus posterior. Circum-anal pore ring more than 0.35 mm broad and without sharp angles (Fig. 108). [Body and wing-pads without lanceolate setae. Antenna with 6 rhinaria (may be very difficult to see) (Fig. 41). BL = 1.52–1.87 mm, WL = 0.74–0.79 mm, ARB = 0.36–0.39 mm, AWL = 0.65–0.87, BBBL = 0.78–0.81, A = 8 or 10, R = 456788 or 456789. New World and New Zealand. On *Ilex* and *Nectandra*.]..... **GYROPSYLLA**

- Anus ventral. Circum-anal pore ring usually less than 0.35 mm broad; if more than 0.35 mm broad (some *Craspedolepta* spp.) then ring with some sharp angles (Figs 102, 103) 3
- 3 On Tamaricaceae. Lanceolate setae often absent; or if present they are more than 6 times as long as broad (Fig. 163). Forewing-pad margin sometimes with a deep oblique notch 4
- Not on Tamaricaceae. Lanceolate setae present and less than 6 times as long as broad (Fig. 164). Forewing-pad margin without a deep oblique notch 5
- 4 General form broad (BBBL more than 0.83). [Forewing-pad usually with a humeral lobe. BL = 0.95–1.07 mm, WL = 0.37–0.43 mm, ARB = 0.09–0.11 mm, AWL = 0.38–0.43, BBBL = 0.91–0.95, A = 3, R = 3333. Afrotropical, Oriental and Palearctic. On *Tamarix*.]
 - COLPOSCENIA**
 - General form elongate (BBBL less than 0.83). [Forewing-pad without a humeral lobe. BL = 1.84 mm, WL = 0.64 mm, ARB = 0.14 mm, AWL = 0.47, BBBL = 0.75, A = 3, R = 333333. Afrotropical and Palearctic. On *Tamarix* and *Myricaria*.] **CRASTINA**
 - 5 On *Caltha*, *Polygonum*, *Rumex* or *Sisymbrium*. [Antenna usually with 7 divisions, rarely 3 or 8. BL = 1.65–2.46 mm, WL = 0.70–0.93 mm, ARB = 0.16–0.31 mm, AWL = 0.40–0.62, BBBL = 0.55–0.80, R = 333333, 3577, 34577, 345677 or 456788. Holarctic and Mexico.]
 - APHALARA**
 - On Asteraceae or Onagraceae. [Antenna usually with 3 divisions, rarely 7. BL = 1.58–2.80 mm, WL = 0.60–1.15 mm, ARB = 0.10–0.38 mm, AWL = 0.34–0.66, BBBL = 0.52–0.91, R = 3333, 33333, 333333, 3577, 35677 or 345677. Holarctic and Mexico.]
 - CRASPEDOLEPTA**

Key to genera of Rhinocolinae: Rhinocolini

- 1 Forewing-pad and abdomen margins with sectasetae (Fig. 166). [Tarsal arolium as in Fig. 74. BL = 1.41–1.59 mm, WL = 0.60–0.68 mm, ARB = 0.14–0.16 mm, AWL = 0.52–0.58, BBBL = 0.74–0.79, A = 3, R = 3333. Afrotropical. On *Calodendrum*.] .. **MORANIELLA** 2
- Forewing-pad and abdomen margins without sectasetae 2
- 2 Anal pore-field comprised of circum-anal rings plus adjacent ovoid groups of pores (Fig. 97). [Tarsal arolium as in Fig. 72. BL = 0.91–1.30 mm, WL = 0.34–0.42 mm, ARB = 0.12–0.18 mm, AWL = 0.76–1.17, BBBL = 0.71–0.78, A = 7, R = 3577. Afrotropical, Oriental and Palearctic. On *Pistacia* and *Ruta*.]..... **AGONOSCENA** 3
- Anal pore-field comprised of circum-anal rings only 3
- 3 Anus posterior or nearly so. Outer circum-anal pore ring comprised of multiple rows of pores (Fig. 109). Antenna with 8 divisions. [Tarsal arolium as in Fig. 73. BL = 1.05–1.16 mm, WL = 0.42–0.50 mm, ARB = 0.19 mm, AWL = 0.70–0.76, BBBL = 0.68–0.76, R = 3577. Nearctic. On *Rhus*.]..... **LEUROLOPHUS** 4
- Anus ventral. Outer circum-anal pore ring comprised of a single row of pores (Fig. 168). Antenna with 7 divisions 4
- 4 Lanceolate setae on the head, wing-pads and abdomen truncate (Fig. 168). Antenna with lanceolate setae. [Tarsal arolium as in Fig. 75. BL = 1.56–2.20 mm, WL = 0.53–0.68 mm, ARB = 0.13–0.19 mm, AWL = 0.61–0.91, BBBL = 0.55–0.70, R = 3577. Palearctic. On *Acer*.]..... **RHINOCOLA**
- Lanceolate setae on the head, wing-pads and abdomen pointed (Fig. 167). Antenna without lanceolate setae. [Tarsal arolium as in Fig. 76. BL = 1.61 mm, WL = 0.58 mm, ARB = 0.09 mm, AWL = 0.57, BBBL = 0.78, R = 3577. Neotropical. On *Schinus*.] **TAINARYS**

Key to genera and subgenera of Euphyllurinae

- 1 Abdomen margin with sectasetae 2
- Abdomen margin with lanceolate or stout simple setae 3
- 2 Anal pore-field (other than circum-anal rings) comprised of unbroken bands (Fig. 106). [Tarsal arolium as in Fig. 65. BL = 2.25–2.75 mm, WL = 0.68–0.72 mm, ARB = 0.08–0.09 mm, AWL = 1.24–1.37, BBBL = 0.58–0.60, A = 9, R = 3578. Old World tropics. On Sterculiaceae.] **DICLIDOPHLEBIA**
- Anal pore-field (other than circum-anal rings) comprised of broken bands (Fig. 113). [Tarsal arolium as in Fig. 66. BL = 1.34–1.53 mm, WL = 0.59–0.68 mm, ARB = 0.07–0.10 mm, AWL = 1.44–1.62, BBBL = 0.79–0.85, A = 9, R = 3577. Tropical. On Melastomataceae, Sterculiaceae and Tiliaceae.]..... **PARAPHALAROIDA**
- 3 Tarsal arolium visible and well developed (Figs 62–64) 4

- Tarsal arolium not visible 6
- 4 Anal pore-field comprised of circum-anal pore rings, pore bands and ovoid pore groups (Fig. 107). [Tarsal arolium as in Fig. 62. BL = 1.22–2.00 mm, WL = 0.51–0.75 mm, ARB = 0.08–0.12 mm, AWL = 0.72–0.89, BBBL = 0.71–0.92, A = 8–9, R = 3578. Afrotropical, Oriental and Palaearctic. On *Olea* and *Phillyrea*.] **EUPHYLLURA**
- Anal pore-field comprised of convoluted rings (Fig. 112)..... 5
- 5 Tarsal arolium not petiolate (Fig. 64). On *Arctostaphylos*. [BL = 1.90–2.37 mm, WL = 0.74–1.10 mm, AWL = 0.75–1.10 mm, BBBL = 0.71–0.76, A = 7, R = 3577. Nearctic.]..... **NEOPHYLLURA (NEOPHYLLURA)**
- Tarsal arolium petiolate (Fig. 63). On *Arbutus*. [BL = 2.15–2.65 mm, WL = 0.53–0.80 mm, AWL = 0.80–1.02, BBBL = 0.66–0.68, A = 7, R = 3577. Nearctic.] **NEOPHYLLURA (ARBUTOPHILA)**
- 6 Anal pore-field comprised of circum-anal rings only, or circum-anal rings plus ovoid groups of pores which are confined to the lateral areas of the abdomen (Fig. 105). [BL = 1.18–1.38 mm, WL = 0.48–0.60 mm, ARB = 0.07–0.09 mm, AWL = 0.68–0.78, BBBL = 0.58–0.70, A = 8, R = 3577. Australia, New Zealand and Pacific. On *Eucalyptus*, *Fuchsia* and *Boronia*. Introduced to Afrotropical and Palaearctic on cultivated *Eucalyptus*.] **CTENARYTAINA**
- Anal pore-field comprised of circum-anal rings plus broken bands of pore groups which are predominantly dorsal in position (Fig. 119). [BL = 1.51–2.00 mm, WL = 0.55–0.64 mm, AWL = 0.67–0.73, BBBL = 0.50–0.56, A = 9, R = 3578. Australia and Oriental. On *Eucalyptus* and other Myrtaceae.] **'EUCALYPTOLYMA', 'EUPHYLLURA'**
(some species currently referred, but excluding the type-species)

Key to genera of Paurocephalinae

- 1 Abdomen margin with sectasetae based upon large clustered tubercles (Fig. 114). Antenna with sectasetae (Fig. 45). Anal pore-field comprised of circum-anal rings only. On Malvales and Moraceae. [Tarsal arolium as in Fig. 70. BL = 0.97–1.41 mm, WL = 0.40–0.53 mm, ARB = 0.13–0.16 mm, AWL = 0.81–1.00, BBBL = 0.74–0.92, A = 3, R = 3333. Old World.]..... **PAUROCEPHALA**
- Abdomen margin usually with lanceolate setae; if with sectasetae, then they are not based upon large clustered tubercles. Antenna without sectasetae. Anal pore-field comprised of circum-anal rings plus adjacent crescent-shaped (Fig. 99) or ovoid (Fig. 100) pore areas. On *Populus*. [Tarsal arolium as in Fig. 69. BL = 1.04–1.98 mm, WL = 0.44–0.71 mm, ARB = 0.05–0.23 mm, AWL = 0.70–0.84, BBBL = 0.76–0.85, A = 7, R = 3577. Palaearctic.] **CAMAROTOSCENA**

Key to genera of Diaphorininae

- 1 Tarsal arolium with a long petiole (Fig. 61). Antenna with 8 divisions and very long (AL = 0.79–0.87 mm, AWL = 0.91–1.23). On *Fraxinus*. Forewing-pad at most slightly extended anteriorly as a humeral lobe, which does not extend anterior to procoxa. [BL = 1.52–2.57 mm, WL = 0.64–0.89 mm, ARB = 0.16–0.27 mm, BBBL = 0.64–0.81, R = 3578. Palaearctic and Oriental. Introduced to Nearctic.] **PSYLLOPSIS**
- Tarsal arolium without a long petiole (Fig. 60). Antenna with 3 divisions and short (AL = 0.29–0.45 mm, AWL = 0.26–0.54). Not on *Fraxinus*. Forewing-pad usually extended anteriorly as a humeral lobe, which extends anterior to procoxa 2
- 2 Body and wing-pads broad (BBBL = 0.78–0.93). [BL = 1.34–2.13 mm, WL = 0.75–1.24 mm, ARB = 0.11–0.24 mm, AWL = 0.26–0.54, R = 3333. Afrotropical, Oriental and Palaearctic. Introduced to Neotropical. On a wide variety of host-plants.] **DIAPHORINA**
- Body and wing-pads narrow (BBBL = 0.73–0.75). [BL = 1.91–2.06 mm, WL = 0.87–0.88 mm, ARB = 0.28 mm, AWL = 0.38–0.43, R = 3333. Afrotropical. On *Strychnos*.] **PENNAVENA**

Confirmatory characters of Aphalaroidinae

Tarsal arolium with a very long petiole (Fig. 59). BL = 1.51–1.75 mm, WL = 0.59–0.66 mm, ARB = 0.07–0.09 mm, AWL = 0.63–0.77, BBBL = 0.71–0.76, A = 7, R = 3577. New World. On Fabaceae **APHALAROIDA**

Key to genera and species groups of Spondylaspididae

- 1 Caudal plate pointed (Figs 118, 124), without apical 'teeth' 2
- Caudal plate not pointed (Fig. 121), with apical 'teeth' (Figs 122, 125, 127, 128) 5
- 2 Margin of abdomen with 'teeth' placed 1 + 1 either side of caudal plate area (Fig. 118). [BL = 3.35-3.91 mm, WL = 1.03-1.18 mm, AWL = 0.83-0.90, BBBL = 0.53-0.30, A = 10, R = 4689. Australia. On *Eucalyptus*.] **CREIIS**
- Margin of abdomen without 'teeth' placed 1 + 1 either side of caudal plate area (Figs 124, 129) 3
- 3 Anal pore-field absent. Antenna short relative to forewing-pad (AWL = 0.57-0.79). [BL = 1.61-2.89 mm, WL = 0.68-0.92 mm, BBBL = 0.54-0.78, A = 9 or 10, R = 3578 or 4689. Australia. On *Eucalyptus*.] **CARDIASPINA**
- Anal pore-field comprised of scattered pore groups (Figs 124-129) 4
- 4 Antenna with 10 divisions and about twice as long as forewing-pad (AWL = 2.02). [BL = 2.44 mm, WL = 0.61 mm, BBBL = 0.55, R = 4689. Australia. On *Eucalyptus*.] **SPONDYLIASPIS**
- Antenna with 9 divisions and about as long as forewing-pad (AWL = 0.87-1.14). [BL = 1.41-2.15 mm, WL = 0.66-0.89 mm, BBBL = 0.67-0.84, R = 3578 or 34578. Australia. On *Eucalyptus*.] **GLYCASPIS**
- 5 Apical margin of abdomen with 'tooth-like' processes (Figs 120, 122, 125) 6
- Apical margin of abdomen without 'tooth-like' processes 13
- 6 Anal pore-field comprised of 1 + 1 ventral and 1 + 1 dorsal rings (Figs 120, 122) 7
- Anal pore-field usually comprised of scattered pore groups (Fig. 126), or absent 8
- 7 Abdomen with large apical 'teeth' arranged 1 + 1 (Fig. 120). Forming galls on Rhamnaceae. [BL = 2.78-2.88 mm, WL = 0.73-0.80 mm, AWL = 1.56-1.68, BBBL = 0.55-0.68, A = 7, R = 3567. New World tropics.] **EUPHALERUS** (*E. gallicolus*)
- Abdomen with about 4 small apical 'teeth' (Fig. 122). Forming lerps on Fabaceae. [BL = 1.15-1.17 mm, WL = 0.44-0.58 mm, AWL = 1.00-1.36, BBBL = 0.85-0.94, A = 9, R = 3578. New World tropics.] **EUPHALERUS** (*E. nidifex*)
- 8 Antenna with 10 divisions. On *Celtis* 9
- Antenna with 8 or 9 divisions. Usually not on *Celtis*, or if on *Celtis* antenna with 8 divisions 11
- 9 Abdomen apical 'teeth' without medial 'tooth' or 'teeth' enlarged (Fig. 126). Lerp forming. [BL = 3.08 mm, WL = 0.84 mm, AWL = 0.99, BBBL = 0.51, R = 4689. Eastern Palaearctic.] **PACHYPSYLLA** (*P. japonica*)
- Abdomen apical 'teeth' with median 'tooth' or 'teeth' enlarged (Fig. 125). Gall forming 10
- 10 Large, body length more than 4.5 mm. Forming galls on stems and leaf petioles. [BL = 4.91 mm, WL = 1.22-1.53 mm, AWL = 0.65-0.75, BBBL = 0.61-0.63, R = 4689. Nearctic.] **PACHYPSYLLA** (*P. venusta*)
- Small, body length less than 4.5 mm. Forming galls on leaves. [BL = 2.03-4.25 mm, WL = 0.69-1.03 mm, AWL = 0.73-1.00, BBBL = 0.48-0.75, R = 4689. Nearctic and Mexico.] **PACHYPSYLLA** (minus *P. japonica* and *P. venusta*)
- 11 Anal pore-field absent. Tarsal arolium petiolate (Fig. 78). [Apical 'teeth' of abdomen as in Fig. 128. BL = 2.20-2.61 mm, WL = 0.76-0.87 mm, AWL = 1.25-1.43, BBBL = 0.67-0.69, A = 8, R = 4688. Afrotropical. Forming lerps on *Colophospermum*.] **RETROACIZZIA**
- Anal pore-field comprised of scattered pore groups (Fig. 127). Tarsal arolium not visible 12
- 12 Abdomen margin with lanceolate setae. Antenna with 9 divisions. [BL = 2.18-2.66 mm, WL = 0.70-0.71 mm, AWL = 1.08-1.21, BBBL = 0.59-0.66, R = 3578. Australia. In discarded lerps of Spondylaspidinae on *Eucalyptus*.] **PHELLOPSYLLA**
- Abdomen margin without lanceolate setae. Antenna with 8 divisions. [BL = 3 mm, WL = 1.1 mm, AWL = 0.9, BBBL = 0.7, R = 4688, all estimated from Ferris (1926). Nearctic and Mexico. Forming lerps on *Celtis*.] **TETRAGONOCEPHALA**
- 13 Anal pore-field comprised of circum-anal rings only. Abdomen and wing-pad margins with clavate setae (Fig. 169). [BL = 1.44 mm, WL = 0.57 mm, ARB = 0.08 mm, AWL = 0.81, BBBL = 0.72, A = 7, R = 3577. Neotropical. On Solanaceae.] **AREPUNA**
- Anal pore-field comprised of circum-anal rings plus pore bands (Fig. 121) or pore groups (Figs 117, 123) arranged as rings. Abdomen and wing-pad margins without clavate setae 14
- 14 Anal pore-field comprised of circum-anal rings plus pore bands (Fig. 121). [BL = 1.56-1.77 mm, WL = 0.53-0.66 mm, AWL = 1.06-1.45, BBBL = 0.60-0.80, A = 7, R = 3577 or 4677. Nearctic. On Rhamnaceae.] **EUPHALERUS** (*E. jugovenosus*, *E. rugipennis* and *E. vermiculosus*, but not the type-species of *Euphalerus*)

- Anal pore-field comprised of circum-anal rings plus pore groups (Figs 117, 123)..... 15
- 15 Abdomen margin with 3 + 3 sectasetae (Fig. 123). [Anal pore-field as in Fig. 123. BL = 1.44–1.72 mm, WL = 0.48–0.53 mm, AWL = 1.13–1.15, BBBL = 0.65–0.66, A = 8, R = 3578. Afrotropical. On Fabaceae.]
 - EUPHALERUS** (some species assigned to the genus, but not the type species)
 - Abdomen margin without sectasetae. [Anal pore-field as in Fig. 117. BL = 1.69 mm, WL = 0.64 mm, ARB = 0.12 mm, AWL = 1.11, BBBL = 0.65, A = 8, R = 3578. Afrotropical. On Fabaceae.]..... **COLOPHORINA**

Keys to subfamilies and genera of Psyllidae

Key to subfamilies of Psyllidae

- 1 Hindwing-pad margin with a pointed sectaseta. [Neotropical. On Fabaceae.]
 - ACIZZIINAE** (*Neopsyllia* and *Platycorypha*) (p. 285)
 - Hindwing-pad margin without sectasetae 2
- 2 Dorsal surface of abdomen and thorax with lanceolate setae. [Neotropical. On Fabaceae.]
 - ACIZZIINAE** (*Mitrapsylla*) (p. 285)
 - Dorsal surface of abdomen and thorax without lanceolate setae 3
- 3 Abdomen margin with 3 + 3 or 4 + 4 tubular sectasetae (Fig. 37 [ts]) or lanceolate setae (Fig. 37 [l]). [Tropical. On Fabaceae and Euphorbiaceae.]..... **CIRIACREMINAE** (p. 286)
 - Abdomen margin without tubular sectasetae or lanceolate setae 4
- 4 Tarsal arolium pad with two separate spinule-covered areas (Figs 81, 83, 84). Circum-anal pore rings partly on the dorsal surface of the abdomen (Fig. 130). [Tropical Old World and eastern Palaearctic. On Fabaceae and Moraceae.]..... **ANOMONEURINAE** (*Anomoneurini*) (p. 286)
 - Tarsal arolium pad with one spinule-covered area (Figs 79, 80, 86, 92, 93). Circum-anal pore rings usually confined to the ventral surface of the abdomen (the exceptions being some Psyllinae, Figs 132, 134, 136, 142) 5
- 5 Antenna with 9 divisions 6
 - Antenna with less than 9 divisions 7
- 6 On *Cercocarpus*. [Nearctic.] **PSYLLINAE** (*Psylla magna*) (p. 287)
 - On Fabaceae or Proteaceae **ACIZZIINAE** (*Acizzia*) (p. 285)
- 7 Tarsal arolium pad only slightly broader at apex than at base (Fig. 93)
 - ACIZZIINAE** (*Trigonon*) (p. 285)
 - Tarsal arolium pad very much broader at apex than at base (Figs 86, 92) 8
- 8 Antenna with 5 divisions **ANOMONEURINAE** (some species assigned to *Euphalerus* but excluding the type-species) (p. 286)
 - Antenna with 7 or 8 divisions 9
- 9 On *Cercocarpus*. Circum-anal pore ring breadth to antenna length ratio more than 0.3 (0.36–0.40)
 - ANOMONEURINAE** (*Euphalerus tantillus* but not the type-species of *Euphalerus*) (p. 286)
 - Usually not on *Cercocarpus*; or if on *Cercocarpus* then circum-anal pore ring breadth to antenna length ratio less than 0.3 (0.11–0.25) 10
- 10 Not on Fabaceae or Solanaceae **PSYLLINAE** (most species) (p. 287)
 - On Fabaceae or Solanaceae 11
- 11 Circum-anal pore rings convoluted (Fig. 138)..... **PSYLLINAE** (*Psylla pulchella*) (p. 287)
 - Circum-anal pore rings not convoluted 12
- 12 On *Bauhinia* **PSYLLINAE** (*Psylla simlæ*) (p. 287)
 - Not on *Bauhinia* 13
- 13 On Genisteae **ARYTAININAE** (p. 287)
 - Not on Genisteae 14
- 14 Ventral surface of abdomen with capitate setae **ACIZZIINAE** (*Freysuila*) (p. 285)
 - Ventral surface of abdomen without capitate setae **ANOMONEURINAE** (some species assigned to *Euphalerus* but excluding the type-species) (p. 286)

Key to genera of Acizziinae

- 1 Dorsal surface of thorax and abdomen with lanceolate setae. Abdomen margin with 3 + 3 lanceolate setae and 'funnel' shaped setae (Fig. 133). [Tarsal arolium as in Fig. 89. BL = 1.25

- mm, WL = 0.45 mm, ARB = 0.09 mm, AWL = 1.67, BBBL = 0.67, A = 7, R = 3577. Neotropical. On Mimosoideae.] **MITRAPSYLLA**
- Dorsal surface of thorax and abdomen without lanceolate setae. Abdomen margin without lanceolate setae and 'funnel'-shaped setae 2
- 2 Hindwing-pad margin with a pointed sectaseta. Abdomen margin with 3 + 3 pointed sectasetae 3
- Hindwing-pad margin and abdomen margin without sectasetae 4
- 3 Antenna with 9 divisions. [Tarsal arolium as in Fig. 91. BL = 2.41 mm, WL = 0.82 mm, ARB = 0.14 mm, AWL = 2.68, BBBL = 0.58, R = 3578. Cuba. On *Myroxylon*.] **PLATYCORYPHA**
- Antenna with 10 divisions. [Tarsal arolium as in Fig. 90. BL = 2.11-2.31 mm, WL = 0.84-0.90 mm, ARB = 0.22-0.24 mm, AWL = 1.22-2.11, BBBL = 0.66-0.69, R = 4689. South America. On *Erythrina* and *Tipuana*.] **NEOPSYLLIA**
- 4 Antenna with 7 divisions. Ventral surface of abdomen with capitate setae. [Tarsal arolium as in Fig. 86. BL = 1.54 mm, WL = 0.61 mm, ARB = 0.11 mm, AWL = 1.75, BBBL = 0.71, R = 3577. South America. On Caesalpinoideae and Solanaceae.] **FREYSUILLA**
- Antenna with 8 or 9 divisions. Ventral surface of abdomen without capitate setae 5
- 5 Antenna with 8 divisions. Tarsal arolium pad only slightly broader at apex than at base (Fig. 93). [BL = 2.23 mm, WL = 0.64 mm, ARB = 0.25 mm, AWL = 2.77, BBBL = 0.64, R = 3578. Austro-Oriental and Pacific. Introduced to Hawaii.] **TRIGONON**
- Antenna with 9 divisions. Tarsal arolium pad much broader at apex than at base (Fig. 80) or very reduced (Fig. 79). [BL = 0.95-1.66 mm, WL = 0.41-0.61 mm, ARB = 0.07-0.11 mm, AWL = 0.91-1.57, BBBL = 0.63-0.85, R = 3578. An almost cosmopolitan tropical and warm temperate genus. On Mimosoideae and Proteaceae.] **ACIZZIA**

Key to genera of Anomoneurinae

The 'unnamed tribe' includes the genus *Amorphicola* and several species which are currently referred to the genus *Euphalerus* (the type-species of which, *E. nidifex*, is here placed in the Spondyliaspidae). It is possible that this tribe should include *Cyamophila* Loginova. However, this is not *Cyamophilini* in the sense in which Loginova (1976a; 1977) defined it. Because of the uncertain status of this tribe it is not further divided in the following key.

- 1 Circum-anal pore rings confined to ventral surface of abdomen. [BL = 1.13-1.98 mm, WL = 0.45-0.68 mm, ARB = 0.11-0.13 mm, AWL = 0.72-0.89, BBBL = 0.60-0.81, A = 5 or 7, R = 3455 or 3577. On Fabaceae and Rhamnaceae.] 'unnamed tribe'
- Circum-anal pore rings partly on the dorsal surface of the abdomen (Fig. 130) 2
- 2 Abdomen margin with 3 + 3 sectasetae. Antenna with 9 divisions. [Tarsal arolium as in Fig. 81. BL = 2.49-3.11 mm, WL = 1.02-1.03 mm, ARB = 0.55-0.65 mm, AWL = 1.63-1.71, BBBL = 0.69-0.75, R = 4689. Oriental and Palaearctic. On *Morus*.] **ANOMONEURA**
- Abdomen margin without sectasetae. Antenna with 7 divisions. [Tarsal arolium as in Figs 83, 84. BL = 2.09-3.38 mm, WL = 1.02-1.03 mm, ARB = 0.33-0.91 mm, AWL = 2.33-2.45, BBBL = 0.56-0.65, R = 3577. Tropical Old World. On Fabaceae.] **EPIPSYLLA**

Key to genera of Ciriacreminae

- 1 Abdomen margin with 3 + 3 or 4 + 4 lanceolate setae, without tubular sectasetae (Fig. 37 [l]). [BL = 1.12-1.53 mm, WL = 0.41-0.55 mm, ARB = 0.10-0.18 mm, AWL = 1.59-2.17, BBBL = 0.58-0.74, A = 7-8, R = 3577 or 3578. Tropical and warm temperature New World. On Mimosoideae.] **HETEROPSYLLA**
- Abdomen margin without lanceolate setae but with 3 + 3 or 4 + 4 tubular sectasetae which are usually placed on slightly raised tubercles (Fig. 37 [ts]). [Tropical. Anus posterior.] 2
- 2 Antenna with 9 divisions and abdomen margin with 3 + 3 sectasetae. [Tarsal arolium as in Fig. 88. BL = 1.46 mm, WL = 0.49 mm, ARB = 0.11 mm, AWL = 1.71, BBBL = 0.55, R = 3578. Neotropical and Pacific. On Mimosoideae.] **ISOGONOCERAIA**
- Antenna usually with 7 divisions. If antenna with 9 divisions (*Ciriacrellum harteni* and *C. julbernardioides*) then abdomen margin with 4 + 4 sectasetae 3
- 3 Abdomen margin with 4 + 4 tubular sectasetae. Antenna with 7 divisions. [Tarsal arolium as in Fig. 85. BL = 1.57-2.58 mm, WL = 0.62-0.79 mm, ARB = 0.24-0.26 mm, AWL = 1.97-2.53, BBBL = 0.57-0.72, R = 3577. Neotropical. On Mimosoideae.] **EUCEROPSYLLA**

- Abdomen margin usually with 3 + 3 tubular sectasetae. If abdomen margin with 4 + 4 tubular sectasetae antenna with 9 divisions 4
- 4 Forewing-pad dorsal surface without capitate setae. Antenna with 7 divisions. [Tarsal arolium as in Fig. 87. Abdomen margin with 3 + 3 tubular sectasetae. BL = 1.80–2.43 mm, WL = 0.70–0.75 mm, ARB = 0.36–0.40 mm, AWL = 1.90–1.91, BBBL = 0.59–0.69, R = 3577. Pacific. On Caesalpinoideae and Euphorbiaceae.] **INSNESIA**
- Forewing-pad dorsal surface usually with capitate setae. If forewing-pad dorsal surface without capitate setae then antenna with 9 divisions. [Tarsal arolium as in Fig. 82. Abdomen margin with 3 + 3 or 4 + 4 tubular sectasetae. BL = 1.33–2.25 mm, WL = 0.51–0.74 mm, ARB = 0.12–0.34 mm, AWL = 1.54–2.46, BBBL = 0.60–0.71, R = 3577 or 3578.] **CIRIACREMUM**

Key to genera of Arytaininae

- 1 Antenna without capitate setae. [Forewing-pad dorsal surface without capitate setae. Abdomen margin with 3 + 3 or 4 + 4 pointed sectasetae. BL = 1.37–2.09 mm, WL = 0.57–0.72 mm, ARB = 0.14–0.28 mm, AWL = 0.93–1.89, BBBL = 0.59–0.98, A = 7, R = 3577. Palaearctic. On Genisteae.] **ARYTAINILLA**
- Antenna with a capitate seta positioned close to rhinarium IV 2
- 2 Dorsal surface of forewing-pad with capitate setae. Abdomen margin with up to 3 + 3 (sometimes none) pointed sectasetae. [BL = 1.81–2.62 mm, WL = 0.62–0.73 mm, ARB = 0.19–0.23 mm, AWL = 1.53–1.61, BBBL = 0.53–0.71, A = 7, R = 3577. Palaearctic and Oriental. On Genisteae.] **ARYTAINA**
- Dorsal surface of forewing-pad without capitate setae. Abdomen margin with 4 + 4 pointed sectasetae. [BL = 1.91–2.25 mm, WL = 0.62–0.79 mm, ARB = 0.17–0.22 mm, AWL = 1.14–1.37, BBBL = 0.66–0.72, A = 7, R = 3577. Palaearctic and Afrotropical. On Genisteae.] **FLORIA**

Key to genera of Psyllinae

Keys for the separation of *Psylla* into subgenera have been provided by Ossiannilsson (1970), Loginova (1978) and White & Hodkinson (1982). In the following key to genera no tenable method could be found to distinguish *Purshivora pubescens* (Crawford) from some members of *Psylla* subgenus *Hepatopsylla* Ossiannilsson.

- 1 Circum-anal pore rings extending onto dorsal surface of abdomen and of a convoluted shape (Fig. 142). Antenna with 7 divisions. [BL = 1.34–1.98 mm, WL = 0.68–0.75 mm, ARB = 0.51–0.57 mm, AWL = 0.87–1.18, BBBL = 0.66–0.77, R = 3577. Palaearctic. On *Buxus*.] **SPANIONEURA**
- Circum-anal pore rings usually not extending onto dorsal surface of abdomen (Figs 135–141); or if rings convoluted and extending onto dorsal surface of abdomen (Fig. 134), antenna with 9 divisions 2
- 2 Dorsal surface of forewing-pad with capitate or clavate setae. Abdomen margin with 3 + 3 pointed sectasetae. [BL = 1.25–1.62 mm, WL = 0.45–0.52 mm, ARB = 0.11–0.13 mm, AWL = 0.45–1.09, BBBL = 0.60–0.72, A = 7, R = 3577. Nearctic. On *Ceanothus* and *Cercocarpus*.] **CEANOTHIA**
- Dorsal surface of forewing-pad usually without capitate and clavate setae; if dorsal surface of forewing-pad with capitate setae, abdomen with 4 + 4 pointed sectasetae (*Psylla simlae*) 3
- 3 On *Ceanothus*. [Outer circum-anal pore ring multiple (Fig. 132). BL = 1.25–2.16 mm, WL = 0.56–0.75 mm, ARB = 0.11–0.37 mm, AWL = 0.75–1.27, BBBL = 0.69–0.85, A = 7, R = 3577. Nearctic.] **EUGLYPTONEURA**
- Not on *Ceanothus* 4
- 4 On *Purshia*. Outer circum-anal pore ring comprised of a multiple row of pores. [Abdomen margin without sectasetae. BL = 1.27–1.56 mm, WL = 0.43–0.53 mm, ARB = 0.13–0.20 mm, AWL = 1.08–1.27, BBBL = 0.69–0.79, A = 7, R = 3577. Nearctic.] **PURSHIVORA** (*P. chelifera*)
- Usually not on *Purshia*; or if on *Purshia* outer circum-anal pore ring comprised of a single row of pores (similar to Figs 137–139) 5
- 5 On *Purshia*. [Confirmatory characters included with *Purshivora chelifera* and *Psylla* confirmatory descriptions.] **Purshivora pubescens**, **Psylla coryli**, **P. hirsuta**, **P. minuta**

- Not on *Purshia*. [Circum-anal pore rings of various forms (Figs 134–141). BL = 1.31–3.08 mm, WL = 0.46–1.15 mm, ARB = 0.06–0.85 mm, AWL = 0.61–2.20, BBBL = 0.50–1.08, A = 7 or 8, R = 3577 or 3578. Holarctic and northern Oriental. On a wide variety of hosts, especially Betulaceae, Rhamnaceae, Rosaceae and Salicaceae.] **PSYLLA** (most species)

Key to genera of Calophyidae

- 1 Anal pore-field comprised of circum-anal pore rings plus 1 + 1 pairs of partial rings (Fig. 143). Antenna with 10 divisions. [BL = 2.22 mm, WL = 0.81 mm, ARB = 0.13 mm, AWL = 1.05, BBBL = 0.80, R = 4689. Oriental. On *Mangifera*.] **APSYLLA**
- Anal pore-field comprised of circum-anal pore rings only, or not discernible. Antenna with 1 to 3 divisions..... 2
- 2 Antenna length to forewing-pad length ratio 0.65–0.73. Humeral lobe of forewing-pad not extended as far forward as eye. [BL = 1.47–1.75 mm, WL = 0.60–0.68 mm, ARB = 0.08 mm, BBBL = 0.83–0.96, R = 3333. Oriental. On *Buchanania*.]..... **PELMATOBRACHIA**
- Antenna length to forewing-pad length ratio 0.18–0.55. Humeral lobe of forewing-pad extended forward beyond the posterior margin of the eye..... 3
- 3 Antenna with one rhinarium. Body breadth with wing-pads to body length ratio 1.23–1.25. Margin of head, wing-pads and abdomen without sectasetae. [BL = 1.15–1.34 mm, WL = 0.64–0.75 mm, ARB = 0.03–0.04 mm, AWL = 0.49–0.53, A = 1. Oriental. On *Mangifera*.] **MICROCEROPSYLLA**
- Antenna with 3 or 4 rhinaria. Body breadth with wing-pads to body length ratio 0.83–1.16. Margin of head, wing-pads and abdomen usually with sectasetae. [BL = 0.93–1.52 mm, WL = 0.49–0.84 mm, ARB = 0.07–0.15 mm, AWL = 0.18–0.56, A = 1, 2 or 3, R = 111, 1111, 2222 or 3333. Tropical and warm temperate areas. On Anacardiaceae, Burseraceae and Rutaceae.]..... **CALOPHYA**

Key to genera of Phacopterionidae

- 1 Anal pore-field arranged as bands (similar to Fig. 155). Antenna with 10 divisions. [Abdomen margin with lanceolate setae. BL = 2.20 mm, WL = 0.70 mm, AWL = 2.14, BBBL = 0.68, R = 4689. Neotropical.]..... **?EPICARSA**
- Anal pore-field arranged as circum-anal rings only (Figs 145–147), often very reduced (Fig. 146). Antenna with 3–9 divisions..... 2
- 2 Outer circum-anal pore ring convoluted and extending onto the dorsal surface of the abdomen (Fig. 145). Antenna longer than forewing-pad length (AWL = 1.20). [Abdomen margin with small lanceolate setae. BL = 3.06 mm, WL = 1.25 mm, ARB = 0.91 mm, BBBL = 0.71, A = 8, R = 3578. Oriental. On *Toona*.]..... **BHARATIANA**
- Outer circum-anal pore ring not convoluted and confined to ventral surface of abdomen. Antenna shorter than forewing-pad length (AWL = 0.50–0.64)..... 3
- 3 Antenna with 3 divisions, the last of which is covered in prominent hairs (Fig. 47). On Burseraceae. [Abdomen margin with short lanceolate setae. Circum-anal pore ring very reduced (Fig. 146). BL = 2.90–4.10 mm, WL = 1.15 mm, AWL = 0.50, BBBL = 0.64, R = 3333. Oriental.]..... **PHACOPTERON**
- Antenna with more than 3 divisions. On Meliaceae..... 4
- 4 Antenna with 5 divisions. Tibia each with a row of stout setae on outer edge (Fig. 54). Abdomen margin with lanceolate setae. [BL = 1.03 mm, WL = 0.37 mm, ARB = 0.29 mm, AWL = 0.62, BBBL = 0.66, R = 3355. Pacific. On *Aglaiia*.]..... **?CHINEURA**
- Antenna with 8 or 9 divisions. Tibia without stout setae. Abdomen margin without lanceolate setae. [Tarsal arolium often with a short petiole (Fig. 94). Circum-anal pore rings often with separated pores (Fig. 147). BL = 1.78–2.31 mm, WL = 0.61–0.71 mm, ARB = 0.17–0.21 mm, AWL = 0.50–0.64, BBBL = 0.60–0.75, R = 3578 or 4689. Afrotropical. On *Khaya*.] **PSEUDOPHACOPTERON**

Key to genera of Homotomidae

- 1 Abdomen margin with sectasetae..... 2
- Abdomen margin without sectasetae..... 3
- 2 Dorsal surface of abdomen with pointed sectasetae. Apical margin of abdomen inwardly

- marginate (Fig. 153). General form elongate (BBBL = 0.65–0.81). [BL = 1.97–3.17 mm, WL = 0.75–1.13 mm, ARB = 0.61–0.76 mm, AWL = 1.05–1.48, A = 3, R = 3333. Neotropical. On *Ficus*.] **SYNOZA**
- Dorsal surface of abdomen without pointed setae. Apical margin of abdomen evenly rounded. General form broad (BBBL = 0.83–1.04). [BL = 1.59–2.68 mm, WL = 0.81–1.45 mm, ARB = 0.34–0.46 mm, AWL = 0.48–0.69, A = 2–3, R = 2222 or 3333. Tropical and warm temperate Old World. On *Ficus*.] **HOMOTOMA**
- 3 Inner margin of outer circum-anal pore ring convoluted and pore rings confined to the ventral surface of the abdomen (Figs 150, 151). Antenna with 2 divisions. [BL = 2.33–3.09 mm, WL = 1.13–1.40 mm, AWL = 0.43–0.53, BBBL = 0.87–1.10, R = 2222. Australasian, Austro-Oriental and Oriental. On *Ficus*.] **MYCOPSYLLA**
- Inner margin of outer circum-anal pore ring usually not convoluted (Figs 148, 149); if convoluted then pore rings extending onto the dorsal surface of the abdomen (Fig. 152). Antenna with more than 2 divisions 4
- 4 Circum-anal pore rings extending onto dorsal surface of abdomen (Fig. 152). Antenna with 3 divisions. [BL = 2.31–2.50 mm, WL = 1.20–1.40 mm, AWL = 0.46–0.53, BBBL = 1.61–1.25, R = 3333. Afrotropical. On *Ficus*.] **PSEUDOERIOPSYLLA**
- Circum-anal pore rings confined to ventral surface of abdomen (Figs 148, 149). Antenna with 9 or 10 divisions. [BL = 1.84–2.84 mm, WL = 0.87–1.09 mm, ARB = 0.72–0.93 mm, AWL = 0.70–0.82, BBBL = 0.84–0.98, R = 4578 or 4689. Austro-Oriental and Oriental. On *Ficus*.] **MACROHOMOTOMA**

Key to subfamilies of Carsidaridae

- 1 Anal pore-field comprised of numerous pore groups (Fig. 154). On *Cedrele* (Meliaceae). [BL = 1.87–2.71 mm, WL = 0.72–0.82 mm, AWL = 1.80–2.43, BBBL = 0.60–0.77, A = 9–10, R = 3578 or 4689. Neotropical.] **MASTIGIMATINAE** (*Mastigimas*)
- Anal pore-field comprised of pore bands (Fig. 155). On Malvales. [BL = 1.46–3.06 mm, WL = 0.59–0.87 mm, AWL = 1.53–2.73, BBBL = 0.50–0.78, A = 10, R = 4689. Tropical.] **CARSIDARINAE**

Key to genera of Triozidae

- 1 Apical margin of abdomen with ‘tooth-like’ processes (Fig. 157). [Head, thorax, abdomen and wing-pads without setae. BL = 2.80–3.02 mm, WL = 1.03–1.13 mm, ARB = 0.24–0.26 mm, AWL = 0.70–0.77, BBBL = 0.58–0.66, A = 6, R = 3355. Neotropical. On Euphorbiaceae, Myrtaceae and Solanaceae.] **NEOLITHUS**
- Apical margin of abdomen without ‘tooth-like’ processes 2
- 2 Anal pore-field comprised of circum-anal pore rings plus small groups of pores arranged as bands (Fig. 158). [Head, thorax, abdomen and wing-pads without setae. BL = 2.50–3.02 mm, WL = 1.15–1.16 mm, ARB = 0.08–0.09 mm, AWL = 1.40–1.46, BBBL = 0.91, A = 10, R = 4689. Afrotropical. On *Antiaria*.] **TRIOZAMIA**
- Anal pore-field comprised of circum-anal pore rings only 3
- 3 Head, abdomen and wing-pad margins with scales (Figs 173–177) 4
- Head, abdomen and wing-pad margins without scales, usually with setae 8
- 4 Marginal scales more than 3 times as long as broad (Fig. 173). [Forewing-pad with a well-developed humeral lobe. Marginal setae absent. BL = 1.46 mm, WL = 0.62 mm, AWL = 0.65, BBBL = 0.76, A = 7, R = 3467. Hawaiian. On *Pelea*.] **HEVAHEVA**
- Marginal scales less than 2 times as long as broad 5
- 5 Dorsal surface of body and wing-pads with clavate setae (similar to Fig. 172). [Forewing-pad with a well-developed humeral lobe. Marginal setae absent. BL = 2.06–2.31 mm, WL = 1.19–1.35 mm, ARB = 0.27–0.36 mm, AWL = 0.18–0.19, BBBL = 0.84–0.88, A = 2, R = 2222. Tropical New World. On *Sideroxylon*.] **CEROPSYLLA** (*C. sideroxyl*)
- Dorsal surface of body and wing-pads without clavate setae 6
- 6 Abdomen margin with setae near abdominal apex, scales only present on basal three-quarters of abdomen margin (Fig. 177). [Forewing-pad with a well-developed humeral lobe. BL = 3.78 mm, WL = 2.18 mm, ARB = 0.43 mm, AWL = 0.16, BBBL = 0.74, A = 2, R = 1222. Hawaiian. On *Pritchardia*.] **TRIOZA** (*T. palmicola*)
- Abdomen margin without setae 7

- 7 Marginal scales ridged (Fig. 176). [Forewing-pad with a well-developed humeral lobe. BL = 3.11 mm, WL = 1.30 mm, ARB = 0.26 mm, AWL = 0.15, BBBL = 0.65, A = 2, R = 2222. Hawaiian. On *Sideroxylon*.] **SWEZEYANA**
- Marginal scales not ridged (Fig. 175). [Forewing-pad with a well-developed humeral lobe. BL = 1.70 mm, WL = 0.95 mm, ARB = 0.21 mm, AWL = 0.20, A = 3, R = 1133. Hawaiian. On *Pisonia*.] **KUWAYAMA** (*K. pisonia*)
- 8 Forewing-pad margin with truncate sectasetae 9
- Forewing-pad margin without truncate sectasetae 12
- 9 General form elongate (BBBL = 0.37–0.46). [BL = 2.59–2.69 mm, WL = 1.00–1.11 mm, ARB = 0.15–0.16 mm, AWL = 0.18–0.24, A = 1, R = 1111. Australasian. On *Casuarina*.] **AACANTHOCNEMA**
- General form broader (BBBL = 0.48–0.87) 10
- 10 Antenna with 8 or 9 divisions. Outer circum-anal pore ring comprised of a multiple row of pores. [BL = 2.59–3.12 mm, WL = 1.26–1.48 mm, ARB = 0.33–0.36 mm, AWL = 0.37–0.40, BBBL = 0.52–0.56, R = 4688 or 4689. Afrotropical, Oriental and Palaearctic. On *Rhamnus*.] **TRICHOCHERMES**
- Antenna with 3–7 divisions. Outer circum-anal pore ring comprised of a single row of pores 11
- 11 On *Ficus*. Forewing-pad hind margin broadly rounded (Fig. 49). [BL = 1.41 mm, WL = 0.64–0.65 mm, ARB = 0.18–0.20 mm, AWL = 0.39–0.40, BBBL = 0.78, A = 4, R = 1244. Tropical Old World.] **PAUROPSYLLA** (*P. trichaeta*)
- Not on *Ficus*. Forewing-pad hind margin usually rounded (Fig. 50). [BL = 1.15–2.95 mm, WL = 0.59–1.67 mm, ARB = 0.16–0.67 mm, AWL = 0.17–1.01, BBBL = 0.58–0.85, A = 3–7.] **TRIOZA** (most species of *Trioza* plus *Paratrioza* and some *Ceropsylla* species)
- 12 Abdomen margin without sectasetae [Several species which form enclosed galls and which cannot be separated by any tenable characters.]
- Abdomen margin with pointed sectasetae 13
- 13 Tarsal arolium without a visible unguitactor (Fig. 95). [Abdomen margin usually with more than a single row of sectasetae. Usually forming enclosed galls. BL = 1.98–3.05 mm, WL = 1.10–1.54 mm, ARB = 0.21–0.43 mm, AWL = 0.21–0.60, BBBL = 0.51–0.79, A = 8 or 10, R = 3578 or 4689. Oriental and Palaearctic. On *Populus*, especially *P. euphratica*.] **EGEIROTIOZA**
- Tarsal arolium with a clearly visible unguitactor 14
- 14 Dorsal surface of abdomen with clavate setae (Fig. 172). [Humeral lobe of forewing-pad extending anterior to eye. BL = 2.77 mm, WL = 1.54 mm, AWL = 0.18, BBBL = 0.87, A = 3, R = 3333. Hawaiian. On *Tetraplasandra*.] **CRAWFORDA**
- Dorsal surface of abdomen without clavate setae 15
- 15 Hindwing-pad very reduced (Fig. 48). [BL = 1.44–1.66 mm, WL = 0.76–0.85 mm, ARB = 0.32–0.35 mm, AWL = 0.46–0.53, BBBL = 0.59–0.67, A = 6, R = 3466. Austro-Oriental and Pacific. On *Calophyllum*.] **LEPTYNOPTERA**
- Hindwing-pad of normal proportions 16
- 16 Dorsal surface of abdomen with pointed sectasetae (Fig. 159). [BL = 1.74–1.98 mm, WL = 0.89–0.97 mm, ARB = 0.34–0.37 mm, AWL = 0.40–0.44, BBBL = 0.62–0.65, A = 6, R = 3466. Palaearctic, introduced to New World. On *Laurus* and *Persea*.] **TRIOZA** (*T. alacris*)
- Dorsal surface of abdomen without sectasetae 17
- 17 Circum-anal pore rings convoluted (Fig. 156). [BL = 1.88 mm, WL = 0.73 mm, AWL = 0.51, BBBL = 0.48, A = 7, R = 3577. Tropical New World and Oriental. On *Celtis* and possibly Fabaceae and *Shorea*.] **LEURONOTA**
- Circum-anal pore rings not convoluted (Fig. 160). [BL = 1.59 mm, WL = 0.77 mm, ARB = 0.29 mm, AWL = 0.44, BBBL = 0.56, A = 1, R = 1111. Neotropical. On *Psidium*.] **TRIOZOIDA**

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