

The phylogenetic relationships of Chalcosiinae (Lepidoptera, Zygaenoidea, Zygaenidae)

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The chalcosiine zygaenid moths constitute one of the most striking groups within the lower-ditrysian Lepidoptera, with highly diverse mimetic patterns, chemical defence systems, scent organs, copulatory mechanisms, hostplant utilization and diapause biology, plus a very disjunctive biogeographical pattern. In this paper we focus on the genus-level phylogenetics of this subfamily. A cladistic study was performed using 414 morphological and biochemical characters obtained from 411 species belonging to 186 species-groups of 73 genera plus 21 outgroups. Phylogenetic analysis using maximum parsimony leads to the following conclusions: (1) neither the current concept of Zygaenidae nor that of Chalcosiinae is monophyletic; (2) the previously proposed sister-group relationship of Zygaeninae + Chalcosiinae is rejected in favour of the relationship (Zygaeninae + ((Callizygaeninae + *Cleoda*) + (*Heteropan* + Chalcosiinae))); (3) except for the monobasic Aglaopini, none of the tribes *sensu* Alberti (1954) is monophyletic; (4) chalcosiine synapomorphies include structures of the chemical defence system, scent organs of adults and of the apodemal system of the male genitalia. A paired metathoracic androconial organ and a series of abdominal tergal coremata organs have been discovered, both being new to Lepidoptera. Due to highly homoplastic patterns in copulatory structures and wings that demonstrate significant sexual dimorphism, polymorphism and mimicry, 17 of the 69 'true' chalcosiine genera (c. 25%) are shown to be either paraphyletic or polyphyletic. The present classification is therefore very misleading. Reductions of various parts of the male genitalia in some groups are accompanied by morphological and functional replacement involving the 8th abdominal segment. A prominent but convergent lock and key mechanism is revealed. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 143, 161–341.

ADDITIONAL KEYWORDS: chaetosoma – chemical defence – constraint analysis – cyanogenesis – genitalic reduction – mimicry.

INTRODUCTION

HISTORICAL REVIEW OF HIGHER CLASSIFICATION OF ZYGAENOIDEA

Like many other superfamilies within the ditrysian Lepidoptera, the Zygaenoidea are not characterized by clearly defined autapomorphies (Epstein *et al.*, 1999). The taxon appears at first glance to have become a wastebasket, including a number of family groups that may individually be well defined, but do little more than share a number, albeit numerous, of plesiomorphic characters. Its composition has been very far

from stable, including from seven (Scoble, 1992) to 13 families (Epstein *et al.*, 1999), and its monophyly is still highly debatable (Fig. 1).

Dyar (1894) brought Limacodidae (as Eucleidae), Megalopygidae, Zygaenidae and Procrarinae (as Pyromorphidae) into an assemblage called the 'Anthrocerina' based on larval chaetotaxy, which was subsequently combined with 'Cossina' within the superfamily 'Tineides' (Dyar, 1896). Chapman (1893, 1894) lumped the Zygaenidae with Limacodidae (as Cochliopodidae) and Micropterigidae into the pupal group 'Incompletae', although these views were not accepted by most authors at that time (Dyar & Morton, 1895; Packard, 1895, Hinton, 1955).

In 1895, Packard suggested a close relationship between Limacodidae and Megalopygidae, but he placed them under Tineina, and thus apart from the

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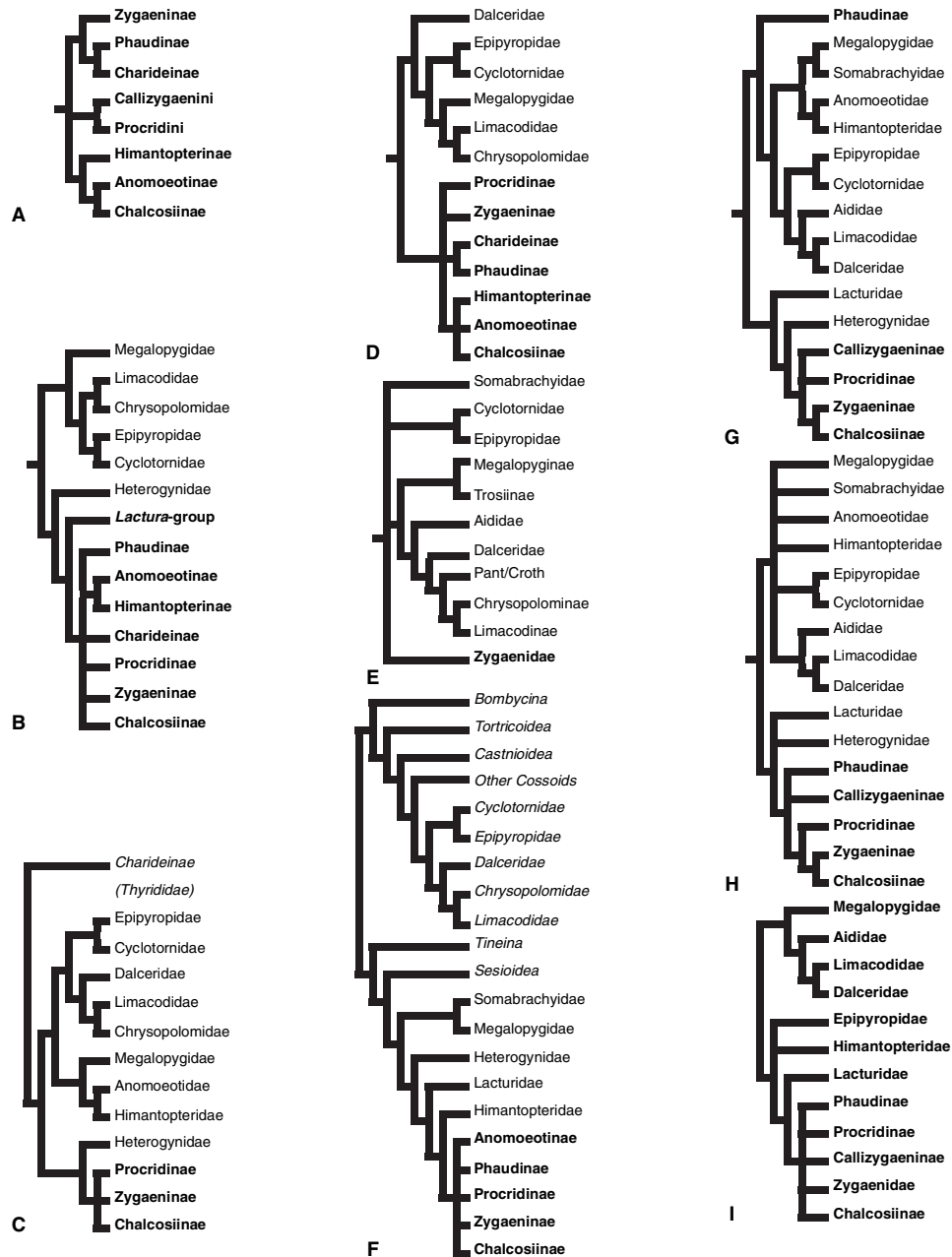


Figure 1. Schematic classifications and phylogenetic concepts of Zygaenoidea and Zygaenidae proposed by different authors. In each of the hypotheses, members of Zygaenidae are in bold and non-zygaenoid groups are in italic. A, Alberti (1954). B, Minet (1986, 1991, 1994). C, Common (1970) and Nielsen & Common (1991). D, Scoble (1992). E, Epstein (1996). F, Heppner (1998). G, Fänger *et al.* (1999). H, Epstein *et al.* (1999). I, Holloway *et al.* (2001).

Zygaenidae. The term 'Zygaenoidea' was first introduced by Fracker (1915), who included within it Chalcosiinae (as Chalcodidae [sic]), Procridinae (as Pyromorphidae), Epipyropidae, Dalceridae, Megalopygidae, and Limacodidae. This classification has been expanded by modern workers to include all of the current family groups of Zygaenoidea (Common, 1975,

1990; Kuznetzov & Stekolnikov, 1981; Minet, 1986; Scoble, 1992).

Except for Zygaenidae, Brock (1971) placed most families previously assigned to Zygaenoidea in the Cossioidea, based primarily on characters of the adult thorax and forewings. He also transferred Epipyropidae and Heterogynidae to the Tineoidea. Heppner

(1984, 1992, 1998) retained Megalopygidae, Somabrachyidae, and Heterogynidae in Zygaenoidea, but placed Epipyropidae, Cyclotornidae, and the remainder of the limacodid group (see below) in the Cossioidea. Brock's Cossioidea, except for the position of Epipyropidae and Heterogynidae, has been followed by Fletcher & Nye (1982). Brock did not provide justification for this arrangement. This classification has been criticized, however, both for the weakness of the adult characters involved and because of the strength of the immature stage characters as evidence for the monophyly of Zygaenoidea in its earlier sense (Common, 1975; Kuznetsov & Stekolnikov, 1981).

Minet (1986, following Common, 1975), proposed two potential autapomorphies of Zygaenoidea: the retractile head of the larva (at least in the later instars); and the position of the second abdominal spiracle of the pupa, which is covered by the wings. The latter character has been verified for Epipyropidae, Megalopygidae (including Somabrachyidae), Limacodidae, Heterogynidae, Zygaenidae (Epstein *et al.*, 1999), Cyclotornidae, Himantopteridae and Zygaenidae (Fänger, Yen & Naumann, 1999). Although it has been argued that both characters may easily have developed independently (Heppner, 1998), Epstein *et al.* (1999) argued that they can be used as characters to define the superfamily.

The first cladistic study of the superfamily was carried out by Epstein (1996) who defined the monophyly of the limacodid group, viz. Limacodidae, Megalopygidae, Somabrachyidae, Aididae and Dalceridae, based on a number of apparently synapomorphic characters of both adult and immature stages, including the presence of additional prolegs or crochets on A2 and A7, a sculptured eye flange in pupae, dense sensilla trichodea on all legs of adult females and the absence of ocelli. As a result of this study, two major lineages, the limacodid families, and Zygaenidae *sensu lato*, are tentatively recognized within the Zygaenoidea. Fänger *et al.* (1999) attempted a morphological survey of several family groups which had been given very little attention in previous studies, and provided a preliminary phylogenetic structure of the superfamily. However, the inter-relationships of the basal zygaenoids, ant-associated Cyclotornidae and Homoptera-parasitic Epipyropidae are still unclear, due to insufficient information on immature stages and uninformative adult characters.

THE FAMILY ZYGAENIDAE IN FLUX

The Zygaenidae, colloquially Burnet moths (Zygaeninae) and Forester moths (European Procridae), is one of the largest families within the Zygaenoidea, estimated to include c. 1200 species worldwide (Bryk, 1936, Epstein *et al.*, 1999). According to Naumann

Tarmann & Tremewan (1999) and Epstein *et al.* (1999), the current concept of zygaenids is not supported by general morphological features but rather by their ability to synthesize two cyanogenic compounds from the amino acids valine and isoleucine (Witthohn & Naumann, 1984a, b, 1987a, b; Epstein *et al.*, 1999; Naumann *et al.*, 1999).

The chemical defence ecology of Zygaenidae was first reported by Jones *et al.* (1962) who demonstrated that HCN is released from crushed tissues of all instars of *Zygaena filipendulae*, and that the highest concentrations of HCN precursors are found in the eggs. Subsequently, various studies on the biochemical mechanisms, interactions amongst hostplants, moths and their parasitoids, and the relevant morphological structures of several representative genera of Zygaenidae were conducted by a number of research teams. The chemical source of HCN in Burnet moths remained unknown until Davis & Nahrstedt (1979) demonstrated that it is derived from two cyanoglucosides, linamarin and lotaustralin. Linamarin and lotaustralin have long been known to occur in a number of plant families, e.g. Fabaceae, widely utilized as a host plant by the species of *Zygaena* (see Figs 5, 6). However, the fact that some Zygaeninae live on acyanogenic host plants, but remain cyanogenic, suggests that these insects are capable of synthesizing these compounds *de novo*.

Although cyanogenesis in the surveyed zygaenid species has been considered to be autapomorphic for this family (e.g. Naumann *et al.*, 1999), a similar chemical defence mechanism is known to exist in its potential sister group, the Heterogynidae (Zilli, 1987; Zilli & Racheli, 1989; Epstein *et al.*, 1999; Fänger & Naumann, 2001), and the current taxonomic composition of the Zygaenidae remains problematic (Yen, 2003c). The consistency of apomorphies recognized in previous studies has yet to be tested in a comprehensive study.

The chaotic taxonomic history of Zygaenidae has involved most family groups within the superfamily, as well as various non-zygaenoid groups. When established by Latreille (1809) as Zygaenides, only the well-known western Palaearctic genus *Zygaena* Fabricius, 1775 was included in Zygaenidae. Subsequently, the following groups were included in the family, and its concept varied between different authors: *Heterogynis* (in Zygaenides by Walker, 1854), Syntomini and Ctenuchini of Arctiidae (by Walker, 1854), Procridae Boisduval, 1828 (as Procridae = Pyromorphina Herich-Shaffer, 1855), Chalcosiinae Walker, 1864 [1865] (as Chalcosiidae), Charideinae Butler, 1876 (as Charideinae in Arctiidae = Glaucopidae Harris, 1839, Pompostolinae Jordan, 1907), Himantopteridae Rogenhofer, 1884, Phaudinae Kirby, 1892 and Anomoetidae Hering, 1937. There were, in addition, two little-known groups, *Lactura*-group (*sensu* Kyrki,

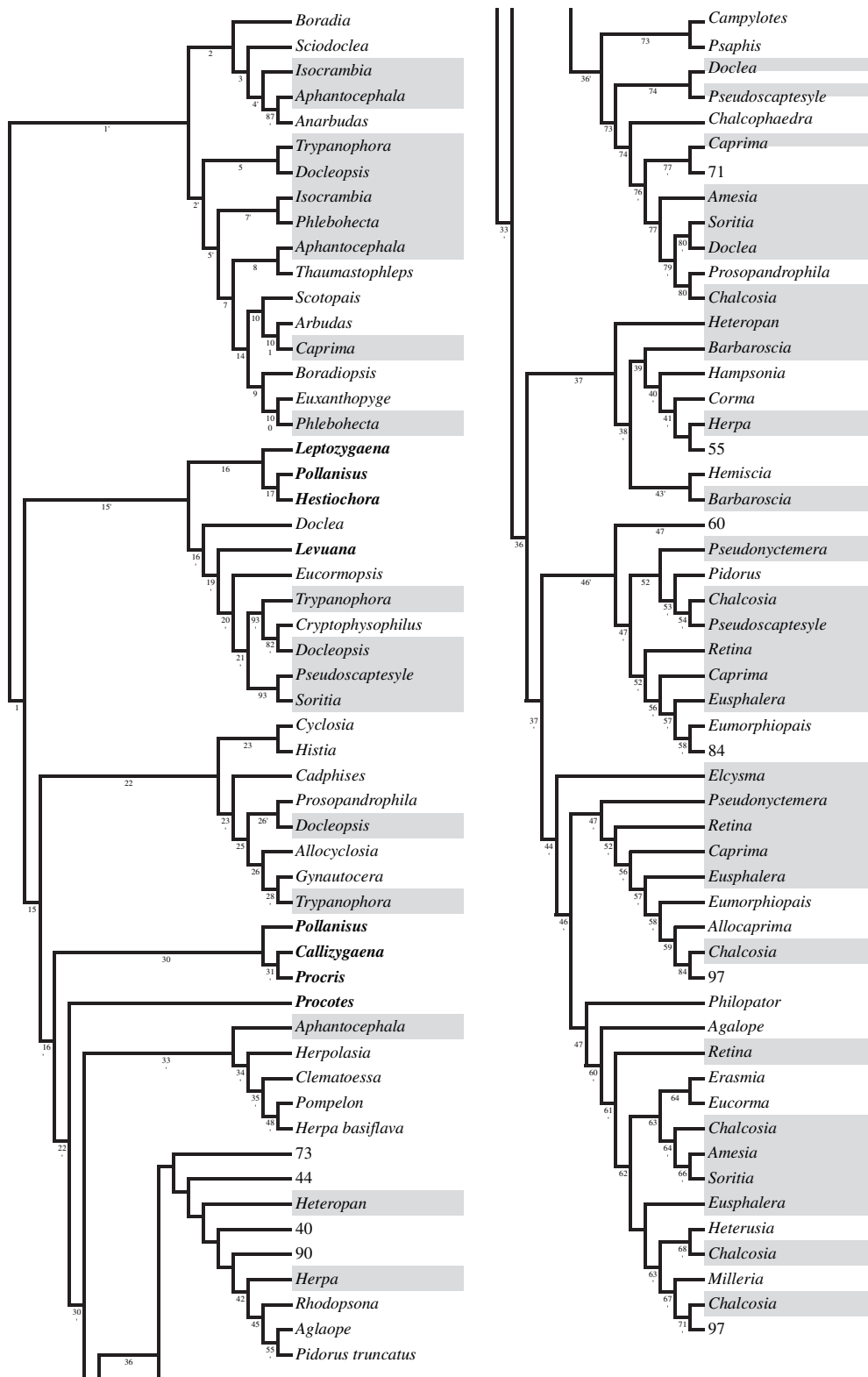


Figure 2. Dendrogram that interprets Hering's (1922) classification of Chalcosiinae based on the characters used in the key to the included genera. The numbers below the node refer to the number of the characters in the key. Genera not belonging to the current concept of Chalcosiinae are in bold. Genera that appear more than once on the dendrogram have a grey background.

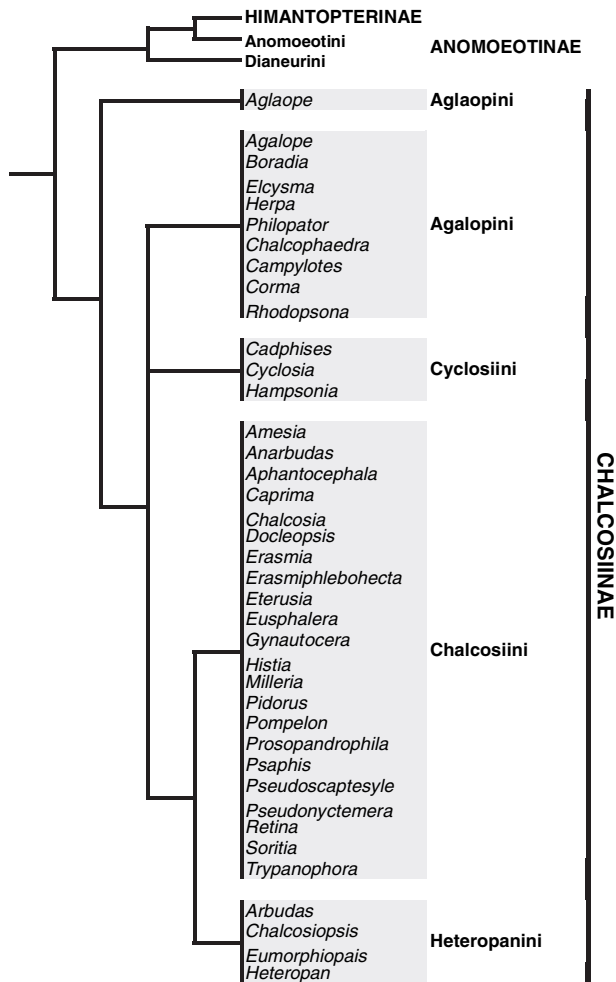


Figure 3. Diagram that interprets Alberti's (1954) concept of the relationships of 'Hauptstamm II of Zygaenidae' and the tribal classification of Chalcosiinae. Characters used to define each tribe: Chalcosiini: valvae and uncus keeled, A8 specialized, aedeagus stout and curved. Cyclosiini: uncus pointed, valvae elongated, aedeagus slender, median vein forked. Agalopini: uncus slender, valvae elongated, median vein straight or forked. Heteropanini: Lycaenidae-like, ovipositor not so developed, ductus seminalis arising from ductus bursae Aglaopini: R3–5 not anastomosed, genitalia similar to *Elcysma*. The following genera were not included because material was not available: *Allocaprima*, *Allocyclosia*, *Atelesia*, *Barbaroscia*, *Boradiopsis*, *Clematoessa*, *Cryptophysophilus*, *Cyanidia*, *Doclea*, *Docleomorpha*, *Eucormopsis*, *Euxanthopyge*, *Hadriionella*, *Hemiscia*, *Herpidia*, *Herpolasia*, *Heterusinula*, *Isocrambia*, *Mimascaptesytle*, *Opisoplatia*, *Panherpina*, *Phlebohecta*, *Sciodoclea*, *Scotopais* and *Thaumastophleps*.

1984; Common, 1990) and *Burlacena*-group (Heppner, 1981), which were transferred from Yponomeutidae and Glyphipterigidae *sensu lato*, respectively. Consequently, the boundary of Zygaenidae had been extended to include seven subfamilies (see Bryk, 1936;

Alberti, 1954; Common, 1970; Scoble, 1992) plus some genera without subfamilial attribution.

When Minet (1986, 1991) started to challenge the traditional classification of the Lepidoptera, he transferred Charideinae to Thyrididae (Thyridoidea) (Fig. 1C). He supported Fletcher & Nye's (1982) viewpoint that Himantopteridae and Anomoeotidae, which are assumed to be related to Megalopygidae + Somabrachyidae (Fänger *et al.*, 1999), should be treated as families distinct from Zygaenidae. Eventually, four subfamilies – Zygaeninae, Procridinae, Chalcosiinae and Phaudinae – were retained in Zygaenidae after Minet's re-arrangement. His proposal that Heterogyndidae may be most closely allied to Zygaenidae (Fig. 1C) was later followed by Scoble (1992), Naumann *et al.* (1999), Fänger *et al.* (1999) and Epstein *et al.* (1999).

However, the classification proposed by Heppner (1984, 1992, 1998) still lumped Anomoeotidae with Zygaenidae and suggested that the Himantopteridae was the sister group of all the other zygaenid subfamilies (Fig. 1F). The Callizygaeninae, as a newly elevated subfamily based on several features of genitalic structures, were separated from Procridinae by Tarmann (1994). Furthermore, Fänger *et al.* (1999) pointed out that the Phaudinae would probably have to be excluded from Zygaenidae, since this group obviously shared a number of apomorphic characters with the limacodid families; as a result, the inter-subfamilial relationships of the Zygaenidae have become even more contentious. The *Lactura*-group, which was suggested as belonging to Zygaenidae by Kyrki (1984) and Common (1990), was later established as a new family, Lacturidae, by Heppner (1995) and regarded as the sister group of Zygaenidae by Holloway *et al.* (2001). As for the *Burlacena*-group, its taxonomic association has wandered amongst various families (Glyphipterigidae, Yponomeutidae, Tineidae, Choreutidae); the Zygaenidae seems to be its current destination, but even this placement is dubious.

In summary, the monophyly of the current concept of Zygaenidae has never been tested cladistically. Scoble's (1992) placing of the genera *Heterogyndis* Rambur, 1837 and *Janseola* Hopp, 1923 in Heterogyndidae may well be correct. Of the subfamilies Zygaeninae, Procridinae, Callizygaeninae and Chalcosiinae, only the monophyly of Zygaeninae has been established (Naumann, 1987a, Naumann *et al.*, 1999), although no cladistic analysis is available for any of them. The historical changes of the relationships of zygaenid groups are shown in Figure 1.

THE CHALCOSIINAE

Amongst the zygaenid subfamilies, the Chalcosiinae *s.l.* are a diverse group. Second only in size to the Pro-



Figure 4. Distribution of some zygaenid subfamilies: Chalcosiinae *s.l.* (dark green), Callizygaeninae (light green) and Zygaeninae (yellow).

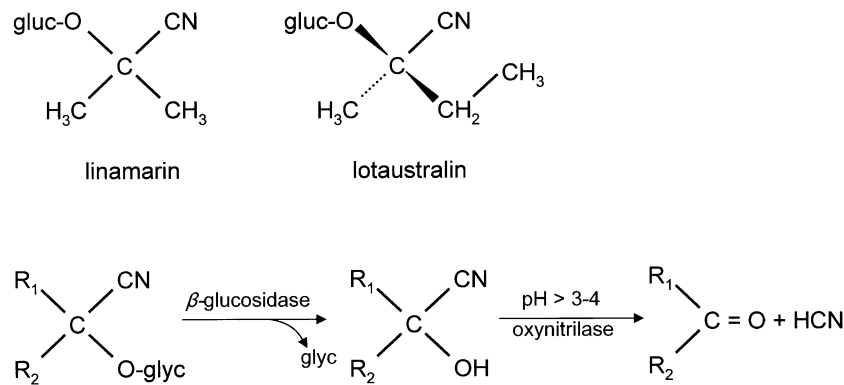


Figure 5. The two chemically related cyanoglucosides linamarin and lotaustralin are found in comparatively high concentrations in zygaenid moths and form the chemical basis for the evolution of the aposematic and mimicry patterns of this family. The release of hydrocyanic acid (hcn) by chemical decomposition of linamarin or lotaustralin depends on the presence of highly specialized glucosidases and is also pH-dependent (after Naumann *et al.*, 1999).

cridinae, they probably exhibit the highest diversity in morphology and ecology both within the Zygaenoidea and within the non-obtectomeran apoditrypsian Lepidoptera. Owing to their often brilliant coloration, high level of sexual dimorphism, complicated mimetic patterns, little-known biology and rarity in museum collections, they have received the attention of many researchers and insect collectors. The group's taxonomy has remained confusing since its initial documentation in the 18th century. Before Walker established the 'Chalcosiidae' in 1864, he (Walker, 1854) placed several chalcosiine genera in unrelated families, e.g. *Trypanophora* Kollar, 1844 in Sesiidae & *Pintia* Walker, 1854 (= *Cyclosia* Hübner, 1860) in Lithosiidae

(now Lithosiinae of Arctiidae). In his original concept, only 19 genera were included (Table 1); the subfamily subsequently increased in size and been associated with various unrelated lepidopteran families (e.g. Epicopeiidae, Geometridae, Arctiidae and Cossidae; see Table 1).

The subfamily currently comprises *c.* 70 genera and 370–400 species (Bryk, 1936; Endo & Kishida, 1999; Fletcher & Nye, 1982; Tremewan, 1973; Yen, 2002c) and is distributed in an area ranging from Palearctic eastern Asia, through subtropical south-east Asia, to the Melanesian and Micronesian archipelagos. It is unknown in Australia, New Zealand and the South Pacific islands. An isolated genus, *Aglaope* Latreille,

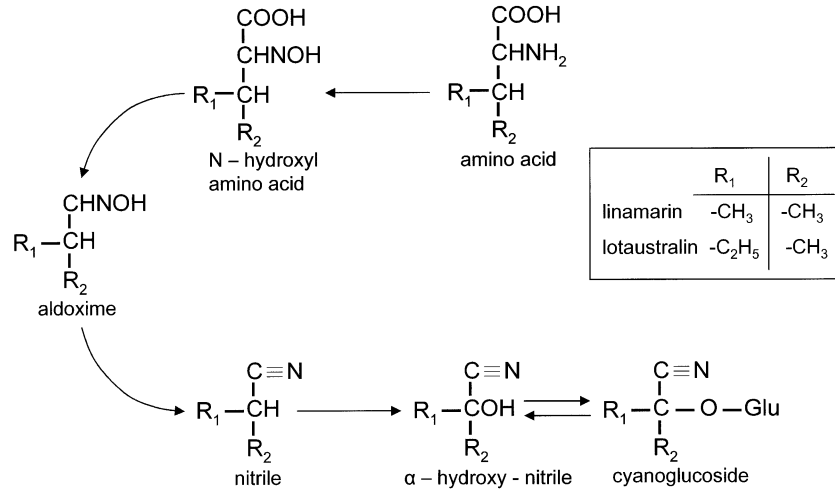


Figure 6. In the Zygaenidae biosynthesis of the cyanoglucosides linamarin and lotaustralin begins with the universally available amino acids valine and isoleucine, respectively. The cyanoglucosides found in the tissues of most developmental stages of the Zygaenidae are derived from a de novo biosynthesis. Only a relatively small proportion of cyanoglucosides may be plant-derived in species living on cyanogenic hostplants, usually species of Fabaceae (after Wittthohn & Naumann, 1987a).

Table 1. Major changes in the composition of Chalcosiinae during the last 150 years. Listing a genus under an author does not imply that the genus was proposed by that author. Each author’s concept of the genera is not necessarily congruent. All major changes are explained in the Discussion or footnotes

Walker (1864)	Cotes & Swinhoe (1887)	Hampson (1892)	Kirby (1892)	Jordan (1907–1909, 1907–1908)	Hering (1922)
–	<i>Cadphises</i>	<i>Cadphises</i>	<i>Cadphises</i>	<i>Cadphises</i>	<i>Cadphises</i>
–		–	–	<i>Hampsonia</i>	<i>Hampsonia</i>
<i>Aglaope</i> ¹		–	<i>Aglaope</i> ¹	–	<i>Aglaope</i>
–	<i>Philopator</i>	<i>Philopator</i>	<i>Philopator</i>	<i>Philopator</i>	<i>Philopator</i>
–		<i>Elcysma</i>	<i>Elcysma</i>	<i>Elcysma</i>	<i>Elcysma</i>
–	<i>Agalope</i>	<i>Agalope</i>	<i>Agalope</i>	<i>Agalope</i> ¹⁷	<i>Agalope</i> ¹⁷
–	<i>Chelura</i>	<i>Chelura</i>	<i>Achelura</i> ⁸	–	–
–	<i>Boradia</i>	<i>Boradia</i> ⁹	<i>Boradia</i>	<i>Boradia</i>	<i>Boradia</i>
–	<i>Campylotes</i>	<i>Campylotes</i>	<i>Campylotes</i>	<i>Campylotes</i>	<i>Campylotes</i>
–	<i>Herpa</i>	<i>Herpa</i>	<i>Herpa</i>	<i>Herpa</i>	<i>Herpa</i>
–		–	–	–	<i>Panherpina</i>
–		–	–	–	<i>Barbaroscia</i>
<i>Corma</i>		<i>Corma</i>	<i>Corma</i>	<i>Corma</i>	<i>Corma</i>
–	<i>Codane</i>	–	<i>Codane</i>	–	–
–		–	–	<i>Eucormiopsis</i>	–
–		–	–	–	<i>Docleomorpha</i>
–		–	–	–	<i>Cryptophysophilus</i>
–		–	–	<i>Anarbudas</i>	<i>Anarbudas</i>
<i>Cyclosia</i>	<i>Cyclosia</i>	<i>Cyclosia</i>	<i>Cyclosia</i>	<i>Cyclosia</i>	<i>Cyclosia</i>
–	<i>Pintia</i>	<i>Pintia</i> ¹⁰	<i>Pintia</i>	–	–
<i>Isbarta</i> ²		<i>Isbarta</i> ¹⁰	<i>Isbarta</i>	–	–
–	<i>Callamesia</i>	<i>Callamesia</i> ¹⁰	–	–	–
–	<i>Epyrgis</i>	–	<i>Epyrgis</i> ¹⁰	–	–
–		–	<i>Klaboana</i> ¹⁰	–	–
–		–	<i>Mimeuploea</i> ¹⁰	–	–
<i>Didina</i>		–	<i>Didina</i> ¹⁰	–	–
–		–	–	<i>Rhodopsona</i>	<i>Rhodopsona</i>
<i>Pidorus</i>	<i>Pidorus</i>	<i>Pidorus</i>	<i>Pidorus</i>	<i>Pidorus</i>	<i>Pidorus</i>
–	<i>Laurion</i>	–	<i>Laurion</i> *	–	–
–	<i>Arbudas</i>	<i>Arbudas</i>	<i>Arbudas</i> *	<i>Arbudas</i>	<i>Arbudas</i>
				–	<i>Eumorphiopsis</i>

Table 1. *Continued*

Walker (1864)	Cotes & Swinhoe (1887)	Hampson (1892)	Kirby (1892)	Jordan (1907–1909, 1907–1908)	Hering (1922)
–		–	–	<i>Hemiscia</i>	<i>Hemiscia</i>
–		–	–	<i>Isocrambia</i>	<i>Isocrambia</i>
–		–	–	<i>Herpolasia</i>	<i>Herpolasia</i>
–		–	–	<i>Clematoessa</i>	<i>Clematoessa</i>
<i>Caprima</i>		–	<i>Caprima</i>	<i>SciODOCLEA</i>	<i>SciODOCLEA</i>
–		–	–	<i>Caprima</i>	<i>Caprima</i>
–		–	–	–	<i>AlloCaprima</i>
–		–	–	<i>Thaumastophleps</i>	<i>Thaumastophleps</i>
–		–	–	<i>Opistoplatia</i>	<i>Opistoplatia</i>
<i>Eterusia</i>	<i>Heterusia</i>	<i>Heterusia</i> ¹¹	<i>Eterusia</i> ¹¹	<i>Eterusia</i>	<i>Heterusia</i>
	<i>Devanica</i>				
<i>Soritia</i>	<i>Soritia</i>	<i>Soritia</i>	<i>Soritia</i>	–	<i>Soritia</i>
–		–	–	–	<i>Mimascaptesyle</i>
–		–	–	–	<i>Prosopandrophila</i>
<i>Trypanophora</i>	<i>Trypanophora</i>	<i>Trypanophora</i>	<i>Trypanophora</i>	<i>Trypanophora</i>	<i>Trypanophora</i>
–		<i>Phlebohecta</i>	–	<i>Phlebohecta</i>	<i>Phlebohecta</i>
–		–	–	–	<i>Pseudoscapesyle</i>
–		–	–	–	<i>Erasmiphlebohecta</i>
–		–	–	<i>Chalcophaedra</i>	<i>Chalcophaedra</i>
–	<i>Erasmia</i>	<i>Erasmia</i>	<i>Erasmia</i>	<i>Erasmia</i> ¹⁸	<i>Erasmia</i>
–		–	–	<i>Eucorma</i>	<i>Eucorma</i>
–	<i>Amesia</i>	<i>Amesia</i>	<i>Amesia</i>	–	<i>Amesia</i>
<i>Chalcosia</i>	<i>Chalcosia</i>	<i>Chalcosia</i>	<i>Chalcosia</i>	<i>Chalcosia</i>	<i>Chalcosia</i>
<i>Milleria</i>	<i>Milleria</i>	<i>Milleria</i>	<i>Milleria</i>	<i>Milleria</i>	<i>Milleria</i>
–		–	–	<i>Pseudonycytemera</i>	<i>Pseudonycytemera</i>
–		–	–	<i>Eusphalera</i>	<i>Eusphalera</i>
–	<i>Canerkes</i>	<i>Canerkes</i> ¹²	<i>Canerkes</i>	<i>Psaphis</i>	<i>Psaphis</i>
–		–	–	–	<i>Scotopais</i>
<i>Histia</i>	<i>Histia</i>	<i>Histia</i>	<i>Histia</i>	<i>Histia</i>	<i>Histia</i>
<i>Gynautocera</i> ³	<i>Gynautocera</i>	<i>Gynautocera</i>	<i>Gynautocera</i>	<i>Gynautocera</i>	<i>Gynautocera</i>
<i>Pompelon</i>		<i>Pompelon</i>	<i>Pompelon</i>	<i>Pompelon</i>	<i>Pompelon</i>
–	<i>Retina</i>	–	<i>Retina</i>	<i>Retina</i>	<i>Retina</i>
–		–	–	–	<i>Boradiopsis</i>
–		–	–	<i>Docleopsis</i>	<i>Docleopsis</i>
–		–	<i>Aphantocephala</i> ¹³	<i>Aphantocephala</i>	<i>Aphantocephala</i>
–		–	–	–	<i>Euxanthopyge</i>
<i>Doclea</i>		–	<i>Doclea</i>	<i>Doclea</i>	<i>Doclea</i>
–	<i>Heteropan</i>	<i>Heteropan</i>	<i>Heteropan</i>	<i>Heteropan</i>	<i>Heteropan</i>
<i>Birtina</i> ⁴		–	<i>Birtina</i>	–	–
–		<i>Callizygaena</i>	–	<i>Callizygaena</i>	<i>Callizygaena</i>
–		–	–	<i>Procotes</i>	<i>Procotes</i>
–		–	–	<i>Hestiochora</i>	<i>Hestiochora</i>
–		–	–	<i>Pollanisus</i>	<i>Pollanisus</i>
–		–	–	–	<i>Procris</i>
–		–	–	<i>Levuana</i>	<i>Levuana</i>
<i>Bintha</i> ⁵		–	–	–	–
–	<i>Arachotia</i>	–	<i>Arachotia</i> ⁵	–	–
–		–	–	<i>Leptozygaena</i>	<i>Leptozygaena</i>
<i>Gingla</i> ⁵		–	<i>Gingla</i> ⁵	–	–
–		–	<i>Dianeura</i> ¹⁴	–	–
–		–	<i>Anomoeotes</i> ¹⁴	–	–
–	<i>Ratarda</i>	–	<i>Ratarda</i> ¹⁵	–	–
–	<i>Epicopeia</i>	–	<i>Epicopeia</i> ¹⁶	–	–
–	<i>Atossa</i>	–	<i>Nossa</i> ¹⁶	–	–
–		–	<i>Schistomitra</i> ¹⁶	–	–
–	<i>Chatamla</i>	–	<i>Chatamla</i> ¹⁶	–	–
–	<i>Scaptesyle</i>	–	<i>Callhistia</i> ⁶	–	–
<i>Arycanda</i> ⁶		–	–	–	–
<i>Balaca</i> ⁷	<i>Thymara</i>	–	–	–	–

Table 1. Continued

Fletcher (1925)	Bryk (1936)	Alberti (1954)	Tremewan (1973)	Endo & Kishida (1999)	Yen (2003a)
<i>Cadphises</i>	<i>Cadphises</i>	<i>Cadphises</i>	<i>Cadphises</i>	<i>Cadphises</i>	<i>Cadphises</i>
<i>Hampsonia</i>	<i>Hampsonia</i>	<i>Hampsonia</i>	<i>Hampsonia</i>	<i>Hampsonia</i>	<i>Hampsonia</i>
	<i>Herpidia</i>	<i>Herpidia</i>	<i>Herpidia</i>	<i>Herpidia</i>	<i>Herpidia</i>
	<i>Aglaope</i>	<i>Aglaope</i>	<i>Aglaope</i>	<i>Aglaope</i>	<i>Aglaope</i>
<i>Philopator</i>	<i>Philopator</i>	<i>Philopator</i>	<i>Philopator</i>	<i>Philopator</i>	<i>Philopator</i>
	–	–	<i>Formozygaena</i>	<i>Formozygaena</i>	<i>Formozygaena</i>
	<i>Atelesia</i>	<i>Atelesia</i>	<i>Atelesia</i>	[neglected]	<i>Atelesia</i>
<i>Elcysma</i>	<i>Elcysma</i>	<i>Elcysma</i>	<i>Elcysma</i>	<i>Elcysma</i>	<i>Elcysma</i>
<i>Agalope</i>	<i>Agalope</i> ¹⁷	<i>Agalope</i> ¹⁷	<i>Agalope</i>	<i>Agalope</i>	<i>Agalope</i>
	–	–	<i>Achelura</i>	<i>Achelura</i>	<i>Achelura</i>
<i>Boradia</i>	<i>Boradia</i>	<i>Boradia</i>	<i>Boradia</i>	<i>Boradia</i>	<i>Boradia</i>
<i>Campylotes</i>	<i>Campylotes</i>	<i>Campylotes</i>	<i>Campylotes</i>	<i>Campylotes</i>	<i>Campylotes</i>
<i>Herpa</i>	<i>Herpa</i>	<i>Herpa</i>	<i>Neoherpa</i> ¹⁹	<i>Herpa</i>	<i>Neoherpa</i>
	<i>Panherpina</i>	<i>Panherpina</i>	<i>Panherpina</i>	<i>Panherpina</i>	<i>Panherpina</i>
	<i>Barbaroscia</i>	<i>Barbaroscia</i>	<i>Barbaroscia</i>	<i>Barbaroscia</i>	<i>Barbaroscia</i>
<i>Corma</i>	<i>Corma</i>	<i>Corma</i>	<i>Corma</i>	<i>Corma</i>	<i>Corma</i>
	<i>Eucormiopsis</i>	<i>Eucormiopsis</i>	<i>Eucormiopsis</i>	<i>Eucormiopsis</i>	<i>Eucormiopsis</i>
	<i>Anarbudas</i>	<i>Anarbudas</i>	<i>Anarbudas</i>	<i>Anarbudas</i>	<i>Anarbudas</i>
	<i>Docleomorpha</i>	<i>Docleomorpha</i>	<i>Docleomorpha</i>	<i>Docleomorpha</i>	<i>Docleomorpha</i>
	<i>Cryptophysophilus</i>	<i>Cryptophysophilus</i>	<i>Cryptophysophilus</i>	<i>Cryptophysophilus</i>	<i>Cryptophysophilus</i>
	<i>Heterusinula</i>	<i>Heterusinula</i>	<i>Heterusinula</i>	<i>Heterusinul[r]a</i>	<i>Heterusinula</i>
<i>Cyclosia</i>	<i>Cyclosia</i>	<i>Cyclosia</i>	<i>Cyclosia</i>	<i>Cyclosia</i>	<i>Cyclosia</i>
<i>Rhodopsona</i>	<i>Rhodopsona</i>	<i>Rhodopsona</i>	<i>Rhodopsona</i>	<i>Rhodopsona</i>	<i>Rhodopsona</i>
<i>Pidorus</i>	<i>Pidorus</i>	<i>Pidorus</i>	<i>Pidorus</i>	<i>Pidorus</i>	<i>Pidorus</i>
	–	–	–	<i>Heteropanula</i>	<i>Heteropanula</i>
	–	–	–	<i>Pseudarbudas</i>	<i>Pseudarbudas</i>
	<i>Kubia</i>	–	<i>Kubia</i> ²⁰	–	–
<i>Arbudas</i>	<i>Arbudas</i>	<i>Arbudas</i>	<i>Arbudas</i>	<i>Arbudas</i>	<i>Arbudas</i>
	<i>Eumorphiopais</i>	<i>Eumorphiopais</i>	<i>Eumorphiopais</i>	<i>Eumorphiopais</i>	<i>Eumorphiopais</i>
	<i>Hemiscia</i>	<i>Hemiscia</i>	<i>Hemiscia</i>	<i>Hemiscia</i>	<i>Hemiscia</i>
	<i>Cyanidia</i>	<i>Cyanidia</i>	<i>Cyanidia</i>	[neglected]	<i>Cyanidia</i>
	<i>Isocrambia</i>	<i>Isocrambia</i>	<i>Isocrambia</i>	[neglected]	<i>Isocrambia</i>
	<i>Herpolasia</i>	<i>Herpolasia</i>	<i>Herpolasia</i>	[neglected]	<i>Herpolasia</i>
	<i>Clematoessa</i>	<i>Clematoessa</i>	<i>Clematoessa</i>	[neglected]	<i>Clematoessa</i>
	–	[not listed]	<i>Hemichrysoptera</i>	[neglected]	<i>Hemichrysoptera</i>
	<i>Hadrionella</i>	<i>Hadrionella</i>	<i>Hadrionella</i>	[neglected]	<i>Hadrionella</i>
	<i>Sciodoclea</i>	<i>Sciodoclea</i>	<i>Sciodoclea</i>	<i>Sciodoclea</i>	<i>Sciodoclea</i>
	<i>Caprima</i>	<i>Caprima</i>	<i>Caprima</i>	[neglected]	<i>Caprima</i>
	<i>Allocaprima</i>	<i>Allocaprima</i>	<i>Allocaprima</i>	<i>Allocaprima</i>	<i>Allocaprima</i>
	<i>Thaumastophleps</i>	<i>Thaumastophleps</i>	<i>Thaumastophleps</i>	[neglected]	<i>Thaumastophleps</i>
	<i>Opisoplatia</i>	<i>Opisoplatia</i>	<i>Opisoplatia</i>	<i>Opisoplatia</i>	<i>Opisoplatia</i>
<i>Eterusia</i>	<i>Eterusia</i>	<i>Eterusia</i>	<i>Eterusia</i>	<i>Eterusia</i>	<i>Eterusia</i>
	<i>Soritia</i>	<i>Soritia</i>	<i>Soritia</i>	<i>Soritia</i>	<i>Soritia</i>
	<i>Mimascaptesytle</i>	<i>Mimascaptesytle</i>	<i>Mimascaptesytle</i>	<i>Mimascaptesytle</i> ²²	–
	<i>Prosopandrophila</i>	<i>Prosopandrophila</i>	<i>Prosopandrophila</i>	– ²³	<i>Prosopandrophila</i>
<i>Trypanophora</i>	<i>Trypanophora</i>	<i>Trypanophora</i>	<i>Trypanophora</i>	<i>Trypanophora</i>	<i>Trypanophora</i>
<i>Phlebohecta</i>	<i>Phlebohecta</i>	<i>Phlebohecta</i>	<i>Phlebohecta</i>	<i>Phlebohecta</i>	<i>Phlebohecta</i>
<i>Pseudoscaptesytle</i>	<i>Pseudoscaptesytle</i>	<i>Pseudoscaptesytle</i>	<i>Pseudoscaptesytle</i>	<i>Pseudoscaptesytle</i>	<i>Pseudoscaptesytle</i>
	<i>Erasmiphlebohecta</i>	<i>Erasmiphlebohecta</i>	<i>Erasmiphlebohecta</i>	<i>Erasmiphlebohecta</i>	<i>Erasmiphlebohecta</i>
<i>Chalcophaedra</i>	<i>Chalcophaedra</i>	<i>Chalcophaedra</i>	<i>Chalcophaedra</i>	<i>Chalcophaedra</i>	<i>Chalcophaedra</i>
<i>Erasmia</i>	<i>Erasmia</i>	<i>Erasmia</i>	<i>Erasmia</i>	<i>Erasmia</i>	<i>Erasmia</i>
<i>Eucorma</i>	<i>Eucorma</i>	<i>Eucorma</i>	<i>Eucorma</i>	<i>Eucorma</i>	<i>Eucorma</i>
	<i>Amesia</i>	<i>Amesia</i>	<i>Amesia</i>	<i>Amesia</i>	<i>Amesia</i>
<i>Chalcosia</i>	<i>Chalcosia</i>	<i>Chalcosia</i>	<i>Chalcosia</i>	<i>Chalcosia</i>	<i>Chalcosia</i>
	<i>Milleria</i>	<i>Milleria</i>	<i>Milleria</i>	<i>Milleria</i>	<i>Milleria</i>
<i>Pseudonyctemera</i>	<i>Pseudonyctemera</i>	<i>Pseudonyctemera</i>	<i>Pseudonyctemera</i>	<i>Pseudonyctemera</i>	<i>Pseudonyctemera</i>
	<i>Eusphalera</i>	<i>Eusphalera</i>	<i>Eusphalera</i>	<i>Eusphalera</i>	<i>Eusphalera</i>
<i>Psaphis</i>	<i>Psaphis</i>	<i>Psaphis</i>	<i>Psaphis</i>	<i>Psaphis</i>	<i>Psaphis</i>
	<i>Scotopais</i>	<i>Scotopais</i>	<i>Scotopais</i>	<i>Scotopais</i>	<i>Scotopais</i>

Table 1. *Continued*

Fletcher (1925)	Bryk (1936)	Alberti (1954)	Tremewan (1973)	Endo & Kishida (1999)	Yen (2003a)
<i>Histia</i>	<i>Histia</i>	<i>Histia</i>	<i>Histia</i>	<i>Histia</i>	<i>Histia</i>
<i>Gynautocera</i>	<i>Gynautocera</i>	<i>Gynautocera</i>	<i>Gynautocera</i>	<i>Gynautocera</i>	<i>Gynautocera</i>
<i>Pompelon</i>	<i>Pompelon</i>	<i>Pompelon</i>	<i>Pompelon</i>	<i>Pompelon</i>	<i>Pompelon</i>
<i>Retina</i>	<i>Retina</i>	<i>Retina</i>	<i>Retina</i>	<i>Retina</i>	<i>Retina</i>
	<i>Boradiopsis</i>	<i>Boradiopsis</i>	<i>Boradiopsis</i>	<i>Boradiopsis</i>	<i>Boradiopsis</i>
	<i>Docleopsis</i>	<i>Docleopsis</i>	<i>Docleopsis</i>	[neglected]	<i>Docleopsis</i>
	<i>Aphantocephala</i>	<i>Aphantocephala</i>	<i>Aphantocephala</i>	[neglected]	<i>Aphantocephala</i>
	<i>Euxanthopyge</i>	<i>Euxanthopyge</i>	<i>Euxanthopyge</i>	<i>Euxanthopyge</i>	<i>Euxanthopyge</i>
	–	–	–	<i>Pseudopidorus</i>	<i>Pseudopidorus</i>
	–	–	–	<i>Neochalcusia</i>	<i>Neochalcusia</i>
	<i>Doclea</i>	<i>Doclea</i>	<i>Cleoda</i> ²¹	[neglected]	<i>Cleoda</i>
<i>Heteropan</i>	<i>Heteropan</i>	<i>Heteropan</i>	<i>Heteropan</i>	[neglected]	<i>Heteropan</i>
	–	–	–	–	<i>Inouela</i>
<i>Callizygaena</i>	<i>Callizygaena</i>	[<i>Callizygaenini</i>]	[<i>Procridinae</i>]	[not included]	[<i>Callizygaeninae</i>]
<i>Procotes</i>	<i>Procotes</i>	–	–	–	–
	<i>Hestiochora</i>	–	–	–	–
	<i>Pollanisia</i>	[<i>Procridini</i> , <i>Procridinae</i>]	–	–	–
	<i>Adscita</i>	–	–	–	–
	<i>Levuana</i>	–	–	[not included]	–
<i>Procris</i>					
<i>Zygaenoprocris</i>	<i>Leptozygaena</i>	–	–	–	–
	<i>Neoprocris</i>	–	–	–	–
	<i>Alloprocris</i>	–	–	–	–
	<i>Theresimima</i>	–	–	–	–
	<i>Ischnusia</i>	–	–	–	–
	<i>Pollanista</i>	–	–	–	–
	<i>Chalcosiopsis</i>	<i>Chalcosiopsis</i>	<i>Chalcosiopsis</i>	[neglected]	<i>Chalcosiopsis</i>

¹*Aglaope* Latreille, 1809 was placed in Ctenuchidae (now Arctiidae, Arctiinae, Ctenuchiini) by Walker and Adscitinae (= Procridinae) by Kirby (1892).

²*Isbarta* Walker, 1856 was not included in 'Chalcosiidae' *sensu* Walker (1864).

³*Gynautocera* Guerin-Meneville, 1831 was placed in Lithosiidae (now Arctiidae, Lithosiinae) by Walker (1854), but not included in 'Chalcosiidae' *sensu* Walker (1864).

⁴ = *Heteropan* Walker, 1854.

⁵*Bintha* Walker, 1864 (= *Artona* Walker, 1854), *Arachotia* Moore, 1879 and *Gingla* Walker, 1864 are presently placed in Procridinae by (Fletcher & Nye, 1982).

⁶*Arycanda* and *Callhistia* (= *Milionia*) are geometrid genera.

⁷*Balaca* is presently placed in Arctiidae.

⁸*Achelura* Kirby, 1892 is an objective replacement name for *Chelura* Hope, 1841.

⁹*Boradia* was associated with Phaudinae by Hampson (1892).

¹⁰These genera have been lumped with *Cyclosia* Hübner by several authors.

¹¹*Heterusia*, derived from Doubleday (1844: 468), is an incorrect spelling of *Eterusia* Hope, 1841

¹² = *Psaphis* Walker, 1854.

¹³*Aphantocephala* Felder, 1861 was placed in 'Pyromorphinae' (= Procridinae) by Kirby (1892).

¹⁴These two genera belong to Anomoetidae.

¹⁵*Ratarda* Moore, 1879 was established in 'Chalcosiidae', transferred to Liparidae (now Lymantriidae) (Hampson, 1892 and Ratardidae (Dudgeon, 1901) and now belongs to Ratardinae of Cossidae.

¹⁶These genera were always placed in Epiplemidae (now as epipleminae of Uraniidae) and Chalcosiinae. Minet (1986) transferred them to Epicopeiidae.

¹⁷These authors considered that *Agalope* Walker included *Achelura* Kirby.

¹⁸*Amesia* Duncan was included in *Erasmia* Hope by Jordan.

¹⁹*Neoherpa* Tremewan is an objective replacement name for *Herpa* Walker.

²⁰*Kubia* Matsumura was synonymized with *Arbudas* Moore by Tarmann (1992c).

²¹*Cleoda* Tremewan is an objective replacement name for *Doclea* Walker.

²²*Mimascaptesyale* Hering was treated as a junior synonym of *Soritia* Walker by Yen (2003a).

²³*Prosopandrophila* Hering was included in *Eterusia* Hope by Endo & Kishida (1999).

1809, with two sibling species confined to the west Mediterranean area, demonstrates an intriguing biogeographical disjunction from the other relatives (Fig. 4).

In contrast, unlike the western Palaearctic Zygaeninae (Burnet moths) and Procridinae (Forester moths, Smoky moths), which have been the subject of frequent and close study (e.g. Ebert, 1994; Guenin, 1997; Efetov & Tarmann, 1999; Naumann *et al.*, 1999, De Freina & Witt, 2001), most of the previous studies dealing with the Chalcosiinae have restricted themselves to establishing new taxa and carrying out faunistic surveys.

The first described species, *Chalcosia pectinicornis*, was documented by Linnaeus from 'Asia' (possibly 'southern China') in 1758 (as *Sphinx pectinicornis* Linnaeus = *Sphinx auxo* Linnaeus, 1767 and *Papilio (Heliconius) thallo* Linnaeus, 1767) (see also Honey & Scoble, 2001: 385). Over the subsequent 250 years, the species diversity of this group was explored in the following works: Drury (1773); Cramer (1775–1776), Fabricius (1775), Hübner (1816), Guérin-Ménéville (in Delessert, 1843), Kollar (1844), Herrich-Schäffer (1850–1858), Walker (1854, 1856, 1864), Doubleday (1847), Butler (1877a, b), Moore (1878, 1879a, b, 1880–1887), Snellen (1879), Druce (1888, 1896), Leech (1890, 1898), Hampson (1891, 1892), Swinhoe (1891, 1892, 1904), Kirby (1892), Oberthür (1893, 1894, 1896, 1910, 1923), Aurivillius (1894), Semper (1896–1902), Dohrn (1899, 1906), de Joannis (1902, 1903), Piepers & Snellen (1903), Jordan (1907, 1908, 1912, 1923), Strand (1915, 1916), Eecke (1920, 1929), Hering (1922), Joicey & Talbot, 1922), Mell (1922), Matsumura (1927, 1931), Talbot (1926, 1929a, b), Bryk (1936, 1948), Inoue (1958, 1976a, b, 1982, 1987a, b, 1991, 1992), Lemée & Tams (1950), Kishida (1988, 1989a, b, 1995, 1996), Owada (1989, 1992a, b, 1996, 2001, 2002), Tarmann, 1992b, c), Horie, 1993, 1994a, b, Horie (1995), Yen (1996), Yen & Horie (1997), Yen & Yang (1997, 1998), Owada & Horie (1999, 2002a, b), Owada, Horie & Xue (1999), Endo & Kishida (1999), Horie & Awada (2000) and Horie *et al.* (2000). Nearly all the currently valid genera had been established by the 1940s, with only four genera added subsequently (Yen & Yang, 1997, 1998; Efetov, 1999; Owada & Horie, 2002a).

Hering (1922) was the first to survey the subfamily from a wider geographical perspective. Based largely on wing venation, shape and pattern, he proposed several new genera and provided comments on the relationships between them. His concept of Chalcosiinae included several genera that had already been transferred to the Procridinae (e.g. *Procris* Fabricius, 1807, now a junior synonym of *Adscita* Retzius, 1783) and Callizygaeninae (*Procotes* Butler, 1876). His ambiguous interpretation of characters resulted in some gen-

era being poorly defined (e.g. *Chalcosia* Hübner, 1819 and *Pidorus* Walker, 1854; see Fig. 2). Subsequently, Bryk's (1936) catalogue of Zygaenidae, which enumerated nearly all the synonyms and valid names in the Chalcosiinae known at that time, demonstrated the taxonomic difficulties and problems caused by phenetic and empirical taxonomic treatments since the Linnaean period.

In his world-wide review, Alberti (1954) used many character sets such as wing venation, genitalia and other external characters for grouping the subfamily. In his classification (Fig. 1A), the Zygaenidae were divided into three major groups. Five tribes of the Chalcosiinae (Agalopini, Aglaopini, Cyclosiini, Chalcosiini and Heteropanini) were weakly defined and established for 40 examined genera, with 25 genera remaining unplaced owing to the unavailability of material (Fig. 3). All the generic names of the Zygaenidae published up to 1973, including those of the Chalcosiinae, were revised and verified by Tremewan (1973), whose catalogue was followed by that of Fletcher & Nye (1982). For major changes in the composition of Chalcosiinae during the last 150 years see Table 1.

Since the 1980s, concomitant with the rapid increase in trade in insects within south-east Asia, new taxa have been described and faunal surveys conducted of this diurnally active subfamily. However, since the supraspecific levels of the Chalcosiinae have not been revised using modern techniques, and since none of the postulated synapomorphies has been verified based on an overall survey, species-level studies face considerable problems when attempting to allocate new species to the correct genera. In addition, the mimetic wing patterns and high degree of sexual dimorphism have led to conflict between character sets, making for problematic classification and tentative taxonomic treatment.

Tarmann (1992a) suggested that the hindwing/abdominal androconial system found in the *Arbudas-* complex would make a good starting point for accessing the potential apomorphies of the Chalcosiinae. Following this proposal, Epstein *et al.* (1999; see also Naumann, 1988; Naumann *et al.*, 1999) recognized three potential apomorphies for Chalcosiinae: (1) male with an androconial organ at base of hindwing and abdominal pleurite; (2) female without a pair of secondary accessory glands close to ooporus; (3) terminal segments in female form a functional ovipositor. However, since these three characters have been found to be inapplicable to many genera, using them to support the monophyly of the Chalcosiinae seems to be questionable (Yen & Yang, 1997; Yen, 2003c). While investigating the family-level phylogeny of Zygaenoidea, Naumann & Feist (1987) and Fänger & Naumann (1998, 2001) uncovered several ultrastructural characters that may have considerable phylogenetic signif-

icance, but which need to be surveyed across the whole of Zygaenoidea or Zygaenidae.

PROBLEMS WITH THE TAXONOMY AND SYSTEMATICS OF CHALCOSIINAE

The diurnal Chalcosiinae have attracted much attention from both professional and amateur entomologists, owing to their great morphological diversity, rarity, spectacular coloration and mysterious behaviour. Despite this, their taxonomy, from species to subfamily level, is still beset with problems.

- (1) Previously proposed synapomorphies have not been based on an overall survey of all the valid species and compared with sufficient outgroups. It is necessary to verify the phylogenetic consistency and systematic significance of these characters.
- (2) Alberti's (1954) tribal classification is difficult to follow because it was based on several weakly defined characters, and many genera were not included in his study.
- (3) As with many other diurnal moths (e.g. Syntomiinae and Ctenuchini of Arctiidae), many chalcosiine species exhibit mimetic and aposematic wing patterns (Endo & Kishida, 1999; Owada & Ta, 2002); as a result, most of the so-called 'larger genera' are almost always assemblages of species sharing similar wing patterns and body colour, while smaller or monobasic genera may possibly be derived lineages of other genera. In some genera (e.g. *Soritia* Walker, 1854, *Pidorus*, *Eterusia* Hope, 1841), classification based on convergence of wing patterns has resulted in frequent switches of species amongst genera (Owada & Horie, 2002b; Yen, 2003a, b, c, 2004b).
- (4) Many genera exhibit extreme sexual dimorphism in wing pattern and body size (e.g. *Prosopandrophila* Hering, 1922, *Cyclosia*), resulting in males and females being described as distinct species, or even as different genera. Associating males and females of sexually dimorphic species appears to be very difficult unless both sexes can be reared from eggs produced by a single female, or adults *in copula* can be observed in the field. At present, several genera are known only from one or other sex, and some 'marriages' proposed by previous authors have yet to be confirmed.
- (5) The species-level taxonomy is currently in a chaotic state, due to the following: (i) colour polymorphism in sexually dimorphic species (e.g. *Eusphalera multicolor* Jordan, 1925) has made it difficult to associate males and females; (ii) clinal variation in genitalia and wing patterns in species complexes (e.g. *Neoherpa subhyalina*-complex) has misled traditional taxonomists, who

have tended to describe new taxa on the basis of sparse material; (iii) there are species with polymorphic continental and oceanic monomorphic subspecies (e.g. *Eterusia aedea*-complex), some of which have been treated as distinct species; alternatively, the species has been treated as paraphyletic and polytypic; (iv) in some species complexes (e.g. *Arbudas submacula*, *Chalcosia nympha* and *Elcysma dohertyi*), the morphology of immature animals may provide significant evidence when establishing taxonomic status; however, the immature stages of the Chalcosiinae remain poorly known.

AIMS OF THE PRESENT STUDY

This is the first phylogenetic investigation of the Chalcosiinae; it tests the validity of all potential apomorphic characters proposed in previous studies. Its goals are as follows:

- (1) To clarify the relationships between the Chalcosiinae and the other zygaenid subfamilies and zygaenoid families.
- (2) To assess the monophyly of Chalcosiinae and test the consistency and distribution of previously recognized apomorphies.
- (3) To elucidate the phylogenetic relationships amongst the major lineages within the subfamily.
- (4) To provide a phylogenetic framework within which hypotheses about the biogeography and evolution of hostplant use, origin of mimetic wing patterns, and the intriguing androconial and copulatory systems can be tested.

MATERIAL AND METHODS

SOURCES

Some thousands of adult and larval specimens, both newly collected and borrowed from various institutions and private collections, were examined. The studied taxa are listed in Appendix 1, together with their geographical origins.

Institutional abbreviations

AKCB	Axel Kallies Collection, Berlin, Germany
BMNH	The Natural History Museum, London, UK
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA
CTC	Colin Treadaway Collection, Limbach-Wagenschwend, Germany (to be transferred to SNG)
CUC	Cornell University Collection, Ithaca, NY, USA
DEI	Deutsches Entomologisches Institut, Eberswalde, Germany

HUFA	Hokkaido University, Faculty of Agriculture, Sapporo, Japan
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MZB	Museum Zoologicum Bogoriense, Bogor, Java, Indonesia
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden
NMNH	National Museum of Natural History, Smithsonian Institution, Washington DC, USA
NMNS	National Museum of Natural Science, Taichung, Taiwan
NSMT	National Science Museum, Tokyo, Japan
OXUM	Hope Entomological Collections, University Museum, Oxford, UK
RNHN	Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
SHYC	Shen-Horn Yen Collection, Taipei, Taiwan
SMD	Staatliches Museum für Tierkunde, Dresden, Germany
SNG	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany
TARI	Taiwan Agriculture Research Institute, Wufeng, Taichung, Taiwan
TLMN	Tiroler Landesmuseum Ferdinandeum, Naturwissenschaften, Innsbruck, Austria
WMM	Thomas Witt Museum, München, Germany
YKCT	Yasunori Kishida Collection, Tokyo, Japan
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany
ZMCD	Zoologisk Museum, Copenhagen, Denmark
ZMCS	Zoological Museum, Chinese Academy of Sciences, Beijing, China
ZMHB	Zoologisches Museum für Naturkunde, Humboldt University, Berlin, Germany
ZSM	Zoologische Staatssammlung, München, Germany

COLLECTING AND BREEDING

Most chalcosiines are encountered relatively rarely in the field and holdings in museum collections are not extensive. A few species have long been regarded as pests, e.g. *Eterusia aedeia sinica* on tea (*Camellia* sp.) (Zhu, Wang & Fang, 1979; Wang, 1983), *Pseudopidorus euchromioides* on *Symplocos chinensis* (Shen, Xue & Zhu, 1991; Xue & Kallen, 1998), *Histia flabellicornis* on *Bischofia javanica* (Yang & Hu, 1987; Huang, 1992), *Elcysma westwoodi* on *Prunus* and *Malus* (Wang, 1983), *Agalope hyalina* on apple (Bhalla, Dogra & Thakur, 1976), *Agalope labasi* on almond (Saba, 1976) and *Soritia pulchella* on *Pinus* spp. (Singh & Singh, 1978; Su, 1992).

Some species are known only from a unique type specimen (e.g. all species of *Isocrambia* Jordan, 1907) or from just a single sex (e.g. *Cyanidia* Jordan, 1925,

Allocaprima Hering, 1922). Furthermore, several peculiar characters are effectively only discernible in living material (e.g. chemical defence mechanism and eversibility of abdominal pleural pouches in the male scent organ). Field collecting and observation necessary for a thorough understanding of Chalcosiinae has been carried out by the senior author in various countries in Asia since 1993. In general, adults were collected during the day by netting individuals that flew above the tree canopy or bush layer, or occasionally at night using mercury vapour lights. Usually, light-trapping was carried out using a vertical white sheet hung behind the lamp. Specimens were collected individually in small plastic or glass vials and kept alive in dark and, if possible, cool conditions, to reduce the moths' activity until they were ready for egg-laying, pairing or to be killed and set. During setting, care was taken not to destroy the delicate androconial hair bristles.

The morphology of the immature stages may be more informative than that of the adult in clarifying phylogenetic relationships in the Zygaenoidea (Fänger & Naumann, 1998, 2001; Fänger, Owada & Naumann, 2002). Rearing involved searching for larvae in the field or inducing females to lay eggs in the laboratory. In the latter case, females were kept alive, together with several branches or bark of different 'predicted' host-plants, in plastic containers of appropriate size until eggs were laid. Small caterpillars were transferred with a fine brush to other plastic boxes to avoid overcrowding and being infested by pathogens. As many potential host-plants as possible were provided as multiple choices for polyphagous species (e.g. *Eterusia taiwana* Wileman, 1911) or for species that perform host-shifts related to season and developmental stages (e.g. *Agalope trimacula* Matsumura, 1927). Several larvae of each instar, if available, were killed in boiling water to protrude their retractile heads and then preserved in 70% ethanol for further morphological study.

Since several groups of Chalcosiinae have a very long prepupal stage due to summer diapause (Gomi & Takeda, 1992; Wipking & Naumann, 1992; Xue & Kallen, 1998; Wei *et al.*, 2001), any disturbance during this period will lead to very high mortality. Pupae were only preserved in ethanol at the end of diapause. Cocoons and pupal cases were preserved in 80% ethanol. The chemical secretions of adults and larvae were gathered separately in capillary tubes and preserved in acetone for further analysis.

PREPARATIONS FOR MORPHOLOGICAL STUDIES

The whole body of at least one specimen of both sexes of each analysed species-group was dissected to study the thoracic and head structures, antennae, legs and

genitalia, except for those represented only by a unique specimen (type) (e.g. *Caprima chryosoma* Prout, 1918) or rare specimens (e.g. *Herpolasia* Rothschild & Jordan, 1905). Protocols follow Landry (1995).

Genitalia were prepared following the general method described by Holloway *et al.* (1987) with slight modifications. After maceration of the abdomen in 10% KOH and subsequent cleaning, male genital capsules were carefully removed from the abdomen and preserved in 70% ethanol for drawing before mounting on slides. The eighth tergite and sternite were not separated from the anterior abdominal segments. Abdominal segments 1–7 were opened along the caudocephalic axis from the right side to uncover the scent organ situated in the lateral folds of the first abdominal segment, with the hair brushes inserted from the bases of the hindwings.

Female genitalia were removed entirely from the abdomen, cleaned and mounted ventral side uppermost. All the membranous genital tubes and bursae derived from the genital openings were preserved. Genitalia and abdominal skins of both sexes were stained with Chlorazol Black (Bioquip) and mounted in Euparal (Bioquip).

Musculature studies were attempted to elucidate the pattern of attachment of each muscle to sclerites or apodemes. For large and robust species (e.g. *Erasmia pulchella* Hope, 1840), preparation of musculature followed De Benedictis & Powell (1989) and Fänger & Naumann (1998), while for smaller and more delicate species (e.g. *Aphantocephala solitaria* Jordan, 1907 and *Isocrambia*), the technique used by Landry (1995) for Crambinae was adopted.

Preparation of specimens for SEM (observations of ultrastructure of wing scales, scent and sensory organs of the head) followed Landry (1995). The technique used for preparing larvae for ultrastructure studies of the larval cuticle followed Naumann & Feist (1987) and Fänger & Naumann (1998, 2001). Most of the SEM work was undertaken in the Department of Biology, National Sun Yat-Sen University, Kaohsiung, Taiwan. Line drawings were made using an Olympus SZ11 microscope and drawing tube. Specimens were photographed using a Nikon Coolpix 995 digital camera.

MORPHOLOGICAL MEASUREMENTS

All measurements were made using an ocular micrometer in a dissecting microscope. Whenever possible, specimens were selected from as many different localities as possible. At least three specimens were measured, unless fewer than three were available. Measurements of head structure mainly focused on the relative position and size of the labial palpus, maxillary palpus, compound eyes, fronto-

clypeus, postoccipt, rami of antennal flagellomeres and range of chaetosemata. For the definitions and abbreviations used for measuring the frontoclypeus see Figure 7.

If the distal segment of the labial palpus was absent, measurement of the ratio between the distal and medial segment was not applied. An individual of *Erasmia pulchella pulchella* Hope was used as a model for defining the elements of wing pattern (Fig. 8) because this subspecies exhibits nearly all possible wing patterns observable amongst chalcosiine species. The length of the female ovipositor and its ratio relative to the length of the seventh abdominal segment were measured. When the seventh sternite was considerably shorter than the tergite, the length of the segment was based on the sternite.

TERMINOLOGY

The terminology used for morphological structures of the Lepidoptera varies according to group and author. Some terms (e.g. transtilla, socii) are ambiguous and have been used confusingly for a long period. In this study, the terminology was chosen from different sources based on whether the terms were widely accepted, indicating homologous structures in different taxa and thus widely applicable. When no term was applicable to the structure, a neutral description was proposed.

The following are the sources of terminology for different parts of the body: head capsule (Matsuda, 1965; Eaton, 1988); chaetosemata (Jordan, 1923); proboscis (Walters, Albert & Zacharuk, 1998; Krenn & Kristensen, 2000); thoracic sclerites and legs (Schultz, 1914; Hering, 1958; Matsuda, 1970; Eaton, 1988; Fänger *et al.*, 1999); wing venation (Common, 1990; Scoble, 1992; Heppner, 1998); wing scales (Downey & Allyn, 1975; Tilley & Eliot, 2002); wing pattern (Nijhout, 1991) androconial organ (Tarmann, 1994); genitalia (Klots, 1970); abdomen (Matsuda, 1976); musculature (Kuznetsov & Stekolnikov, 1981; Fänger & Naumann, 1998); larval chaetotaxy (Hinton, 1946; Tremewan, 1985; Stehr, 1987; Fänger & Naumann, 2001); structures relating to chemical defensive mechanisms (Naumann & Feist, 1987) and pupa (Epstein, 1996; Fänger *et al.*, 2002).

METHODS OF PHYLOGENETIC ANALYSIS

Taxon sampling

Insufficient taxon sampling is often cited as a major source of error in phylogenetic analysis (Theriot, 1989; Lecointre *et al.*, 1993; Poe, 1998; Omland, Lanyon & Fritz, 1999; Yoder & Irwin, 1999; Johnson, 2001). We sampled as many taxa as possible in order provide a wide range of morphological information.

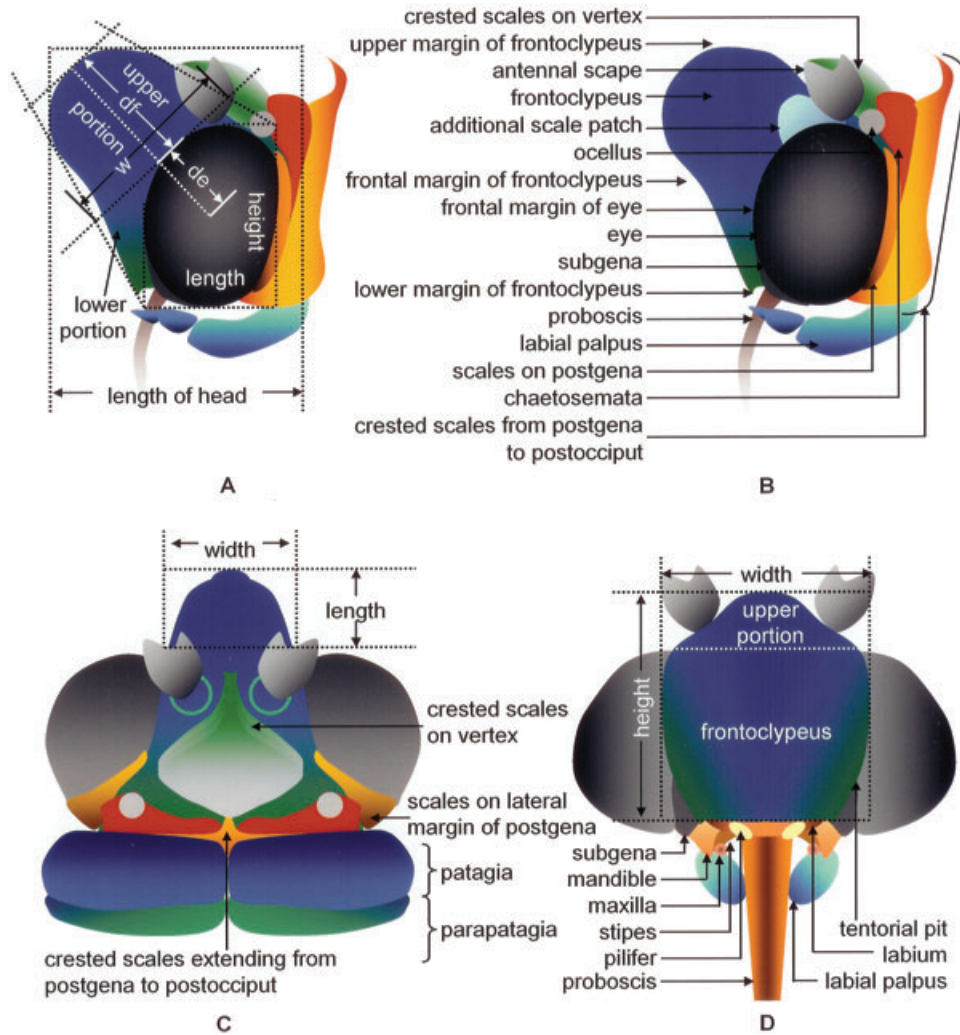


Figure 7. Diagrammatic head of Chalcosiinae. A, lateral view, with reference lines and points for morphometric measurements. B, lateral view. C, dorsal view. D, frontal view.

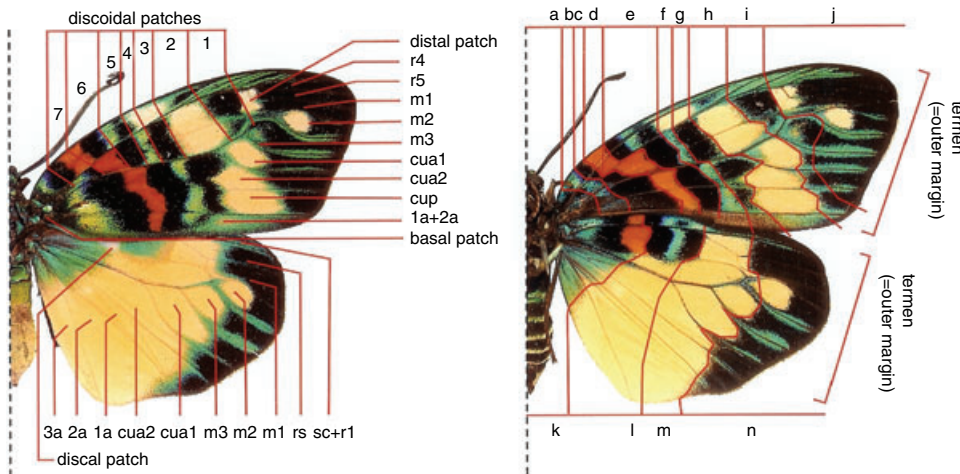


Figure 8. Zonation (right), wing maculation and wing areas (left) defined for morphological analysis of wing patterns of Chalcosiinae.

Owing to the confusion surrounding the taxonomy of Chalcosiinae at both the generic and specific level, ingroup taxon sampling was conducted in two stages: verification of taxon identity, and taxon grouping. Except for *Trypanophora dissimilis* Snellen, of which the type material is possibly missing in RNHN, all of the existing types of available taxa were examined, and we used the nomenclatural treatments of generic names by Tremewan (1973) (followed by Fletcher & Nye, 1982) to verify the type-species of each genus. For species whose types were missing [presumed lost or destroyed, e.g. *Eterusia aedea* (Linnaeus), *Trypanophora semihyalina* (Kollar) and *Pseudonycetmera adalifoides* (Schultze)], identifications were made following consultation of original drawings, descriptions, old specimens derived from the same localities, collections, authors or collectors.

Except for monobasic genera (e.g. *Boradia* Moore, 1879), or genera containing morphologically uniform species (e.g. *Elcysma* Butler, 1881), infrageneric grouping was applied to various genera of which the type species-group carries several character states distinct from the remaining congeneric species-groups. *Pidorus* Walker, 1854, was subdivided into 14 species-groups because it is quite heterogeneous in its copulatory structures and scent organ systems. It is more likely to be an arbitrary assemblage of the species with 'a light-coloured band on the forewing' (Endo & Kishida, 1999) than a monophyletic group.

Although the copulatory structures in the genus *Eusphalera* Jordan, 1907 are relatively uniform amongst species, it was separated into seven species-groups on the basis of wing pattern. We wished to address the question of whether each type of pattern, which may involve many different mimicry rings with other chalcosiine and non-chalcosiine genera, has a significant impact on the phylogenetic structure.

Intraspecific phylogeny is beyond the scope of this study. Therefore, for polytypic species such as *Eterusia aedea* (Clerck, 1759), which has three polymorphic (e.g. *E. a. edocla* from northern India to southern China) and ten non-polymorphic subspecies (e.g. all the subspecies from the Ryukyu Islands of Japan), all subspecies were regarded as a single taxon. In such cases, all major variations in wing pattern of every subspecies were taken into consideration in character coding, and were treated as polymorphism rather than ambiguity in PAUP*. Where the current taxonomic treatment of a potentially polytypic species was doubtful, infraspecific grouping was applied. For example, *Soritia costimacula malaccensis* (Jordan, 1907) was treated as distinct from *S. c. costimacula* Aurivillius, 1894 and *S. c. battakorum* (Dohrn, 1906) because its male has not been discovered, and placement with *costimacula* is still in question. Of the 408 species, including their subspecies and undescribed species, 187

genera and species-groups have been recognized (see Appendix 1). The adults of several representative members of the ingroup are shown in Figure 9 and in part of Figure 10.

Multiple outgroup sampling was considered to be particularly important because monophyly of the Chalcosiinae is doubtful and the sister group is uncertain (Yen, 2003c). Outgroup taxa were selected on the following basis. All the family groups which had hitherto been placed in Zygaenidae or regarded as the sister groups of the Chalcosiinae, viz. Himantopteridae, Anomoeotidae, Heterogynidae and Lacturidae, were included. Only one himantopterid species, *Himantopterus fuscinervis* Wesmael, 1836, was included, because adult characters are rather uniform within the family and information on immature stages is only available for this species. Two anomoeotid species, *Dianeura goochii* Butler, 1888 and *Anomoeotes levis* Felder & Felder, 1874, were selected because they represent the two types of wing venation and wing shape of this family.

The Heterogynidae contain only two genera, *Heterogynis* Rambur, 1837 and *Janseola* Hopp, 1923, and were thought to be closely related to Zygaenidae by Minet (1986), Scoble (1992), Epstein *et al.* (1999) and Fänger & Naumann (2001). Both genera were induced in the analysis, as their individual morphology and ecology are distinct, and their relationships to other zygaenoid groups remain ambiguous. The recently established Lacturidae (Heppner, 1995) were suspected to be related to Zygaenidae (Holloway *et al.*, 2001). However, since the monophyly of this unusual family remains doubtful, only the type species of its type genus, *Lactura dives* Walker, 1854, was included in the analysis in order to avoid misinterpretation of characters based on erroneous taxon sampling.

Although Fänger *et al.* (1999) stated that the Phaudinae are the potential sister group of all other limacodid families rather than being related to the other subfamilies of Zygaenidae, the type genus *Phauda* Walker, 1854, was still included amongst the outgroups. In addition, an exotic and aberrant group, which includes *Burlacena* Walker, 1865 (= *Sesimorpha* Snellen, 1885) and *Cibdeloses* Durrant, 1919, and which has been placed in various families (e.g. Zygaenidae, Glyphipterigidae, Yponomeutidae, Tineidae and Choreutidae; see Heppner, 1981, Fletcher & Nye, 1982), was also compared.

Various zygaenid genera that represent each of the major lineages of different subfamilies were selected from all zoogeographical regions, e.g. Zygaeninae – *Pryeria* Moore, 1877 (east Palaearctic) and *Zygaena* Fabricius, 1775 (west Palaearctic); Procrinae *s.l.* – *Artona* Walker, 1854 (east Palaearctic & Indo-Malaya), *Theresimima* Strand, 1917 (west Palaearctic), *Adscita* Retzius, 1783 (west Palaearctic), *Pollanisus* Walker,



Figure 9. Ingroup (part) and outgroups. From top to bottom, left to right. Row I: (Ingroup) *Chalcosiopsis variata*, *Heteropan* sp. (left), *Heteropan appendiculata* (right), *Inouela* sp., *Doclea syntomoides*, (outgroups from here) *Callizygaena ada* (Callizygaeninae). Row II: *Artona gracilis*, *Clelea formosana*, *Theresimima ampellophaga* (Procridinae), *Dianeura jacksoni* (Anomoetidae). Row III: *Himantopterus fuscineris* (Himantopteridae), *Janseola titaea* (placed in Heterogynidae by Scoble, 1992), *Burlacena* sp. (Zygaenidae, subfamily unassigned), *Saliunca* sp. (Procridinae). Row IV: *Harrisina* sp., *Pollanisus viridipulverulenta*, *Adscita statices*, *Illiberis pruni* (Procridinae), *Staphylinochrous* sp. (Anomoetidae). Row V: *Pryeria sinica*, *Zygaena fausta* (Zygaeninae), *Heterogynis* sp. (Heterogynidae), *Lactura dives* (Lacturidae), *Phauda* sp. (Phaudinae).

1854 (Australia), *Illiberis* Walker, 1854 (east Palaearctic), *Clelea* Walker, 1854 (Indo-Malaya), *Homophylotis nigra* (Hampson, 1892) (Oriental), *Harrisina* Packard, 1864 (Nearctic), *Pyromorpha* Herrich-Schäffer, [1854] 1850–1858 (Neotropical); Callizygaeninae – *Callizygaena* Felder, 1874 (Indo-Malaya) and *Saliunca* Walker, 1864 [1865] (Africa).

Except for monobasic genera, all the characters coded for outgroups were based on their type-species or allies. When any of the outgroups exhibited variable or polymorphic character states in one trait, only the characters of the type species or nominotypical subspecies were utilized. Thus, a total of 21 outgroups was used in this study.

Selection, organization and coding of characters

Since one of the aims of the present study is to reconstruct the generic relationships of the ingroup, characters that only exhibit subtle continuous variation between the study taxa (e.g. tibial spurs) or are only present in outgroups (e.g. apterous female in *Heterogynis* spp., ‘tergal cap’ in *Phauda* spp.) were excluded from the analysis.

There is no doubt that immature stages can be rich sources of characters for phylogenetic analysis. Explicit cladistic analyses incorporating data from immature stages have been undertaken on various groups of Lepidoptera, most notably Geometridae (Choi, 1997), Notodontidae (Miller, 1991, 1992), Nymphalidae (Kitching, 1984; Penz, 1999), Riodinidae (Hall, 2002a, b, 2003; Hall & Harvey, 2001a, b, 2002a, c), Sphingidae (Kitching, 2002, 2003) and New World Saturniidae (Balcázar-Lara & Wolfe, 1997; Peigler, 1993). In the present study, characters of immature stages were collected from every available species. However, problems can arise if there is a high proportion of missing data in one or more of the data subsets.

In general, characters of wing pattern are not favoured in character selection because, especially in a group which demonstrates high sexual dimorphism, polymorphism and diverse mimicry patterns, convergence of patterns is expected to increase homoplasy and decrease resolution and reliability of the phylogeny. However, including characters derived from wing pattern provides an opportunity to detect their impact on traditional classification and to test the relative



Figure 10. Chalcosiine moths (ingroup). From top to bottom, left to right. Row I: *Eterusia sublutea*, *Soritia major* s.l. (female), *Eusphalera milionioides*, *Aglaope labasi* (left), *Arbudas submacula* (right), *Psaphis azurea*, *Psaphis euschemoides*, *Philopator basimaculata*, *Cyclosia papilionaris* (male), *Trypanophora hosemanni*, *Cyclosia pieridoides* (female). Row II: *Rhodopsona costata*, *Cadphises moorei*, *Agalope harutai*, *Amesia sanguiflua viriditincta*, *Gynautocera philomera pavo*, *Campylotes kokotzechi*, *Histia flabellicornis flabellicornis*, *Elcysma delavayi*. Row III: *Pidorus* sp., *Soritia major* (male), *Pseudonyctemera adalifoides*, *Aphantocephala fragilis* (left), *Caprima gelida* (right), *Eusphalera pernitens*, *Cyclosia pieroides* (female), *Chalcosia pretiosa*, *Eusphalera semiflava*, *Papuaphlebohecta bicdora* (female), *Cyclosia midama* (female).

performance compared with the non-colour pattern characters. Wing pattern characters were therefore included in selected analyses.

For this study, 412 characters were studied and partitioned into the following character sets according to their morphological correlation and function:

1. Adult head – general features of cranium, mouthparts and the associated appendages, sensory organs.
2. Adult thorax (excluding scent organ) – thoracic sclerites and appendages, wing coupling device, wing venation, wing shape, wing patterns, wing scales (excluding androconial scales).
3. Adult abdomen – pregenital abdominal segments 1–7, the eighth abdominal segment, male genitalia (subdivided into uncus, subscaphium, tegumen, aedeagus and its supporting apparatus, valva, vinculum and saccus, genitalic musculature), female genitalia (subdivided into ovipositor, eighth tergite and sternite, ostium and the surrounding region, intersegmental membrane, outgroup of A6 and A7, shape of tergum A7, shape of sternum A7, ductus seminalis, pseudobursa, accessory gland, ductus bursae, corpus bursae and signa).
4. Scent organs – intersegmental eversible coremata, genital coremata, androconial scales, metathoracic scent organ, hindwing–abdominal scent organ, female eversible pheromone gland and tergal gland of female.
5. Immature stages – general shape and coloration, internal structure of larva, larval chaetotaxy and other cuticular structure, structures relevant to locomotion, pupa, cocoon.
6. Chemical defence systems – adult and larval systems, chemical compounds.

The following references provided information about characters that were not accessible during the study: Horsfield & Moore (1858–1859), Moore (1878, 1879a, b, 1880–1887), Snellen (1879), Semper (1896–1902), Piepers & Snellen (1903), Gardner (1942), Hwang (1956), Inoue (1958, 1976, 1982, 1987a, b, 1991, 1992), Hattori (1969) Nakamura (1978, 1993), Bode & Naumann (1987, 1988), Nakajima (1987), Sugi (1987), Zilli (1987), Naumann (1988), Zilli *et al.* (1988), Owada (1989, 1992a, b, 1996, 1998a, b, 2000, 2001, 2002), Okubo (1991), Nishihara (1992, 1995), Efetov & Tarmann (1995, 1996), Yen (1995), Barlow & Carter (1996), Epstein (1996), Efetov (1997a, b, 1999), Hallberg & Subchev (1997), Geertsema (1998, 2000), Efetov *et al.* (2000), Kishida (1998, 1989a, b, 1996), Kishida & Endo (1999), Tarmann (1992b, c), Horie (1993, 1994a, b, 1995), Yen (1996), Yen, Jean & Yang (1996), Yen & Horie (1997), Yen & Yang (1997, 1998), Owada & Horie (1999, 2002a, b).

Multistate characters were coded as unordered and without a priori weights applied. Since there are many

different ways of coding characters and the outcome of different coding schemes can dramatically affect hypotheses of relationships (Kitching *et al.*, 1998) different methods of coding were attempted for multistate morphological characters, as explored by Forey & Kitching (2000). Taxa with more than one state for a given trait were scored as polymorphic (e.g. the forewing pattern of *Eusphalera multicolor*). When characters were inapplicable to taxa, they were coded as missing (Strong & Lipscomb, 1999; Lee & Bryant, 1999). The data matrix (see Appendix 3) was constructed, stored and manipulated using MacClade 4.0 (Maddison & Maddison, 1992).

CHARACTER ANALYSIS OF CHALCOSIINAE

A critical review of all the characters used in the cladistic analysis is provided below. For each character we discuss the observed variation, states recognized and distribution of the character states among the ingroup and outgroups. Due to the large number of characters included, their recognized states and descriptions are not given in this section but enumerated in Appendix 2.

ADULT HEAD

General features of cranium

Scales covering the head (characters 1, 2): in most macrolepidopteran taxa, these are uniform in shape and appressed so that the head is described as ‘smooth-scaled’, in contrast with the situation described as ‘rough-scaled’ in microlepidopteran taxa (Scoble, 1992). In the majority of chalcosiine genera, the head belongs to the ‘smooth-scaled’ type (Scoble, 1992; Epstein *et al.*, 1999) (1: 0) (Figs 11A, 13A) except for the genera *Cadphises* (1: 1) (Fig. 11B), *Campylotes* (1: 2) (Fig. 11C), *Hampsonia*, *Watermenia* and *Herpidia*, where a filiform, semi-erect and piliform scale type is mixed with the appressed scales. The heads of all Procridinae, Callizygaeninae and Lacturidae (Fig. 13F) are ‘smooth-scaled’. In Phaudinae, Zygaeninae, Heterogynidae, Anomoeotidae and Himantopteridae, the frontoclypeus is often covered by filiform scales, but their ultrastructure is different from those of the five chalcosiine genera mentioned above. Sexual dimorphism is present in the scale covering of *Hampsonia*, *Watermenia* and *Herpidia* (Owada & Horie, 2002a), so we treated the features of male and female as separate traits.

Frontoclypeus (ch. 3–22): the phylogenetic significance of frontoclypeal structure has been discussed for several lepidopteran families, e.g. Notodontidae (Miller, 1991) and Crambidae (Landry, 1995). A frontoclypeus that has the frontal margin parallel to the

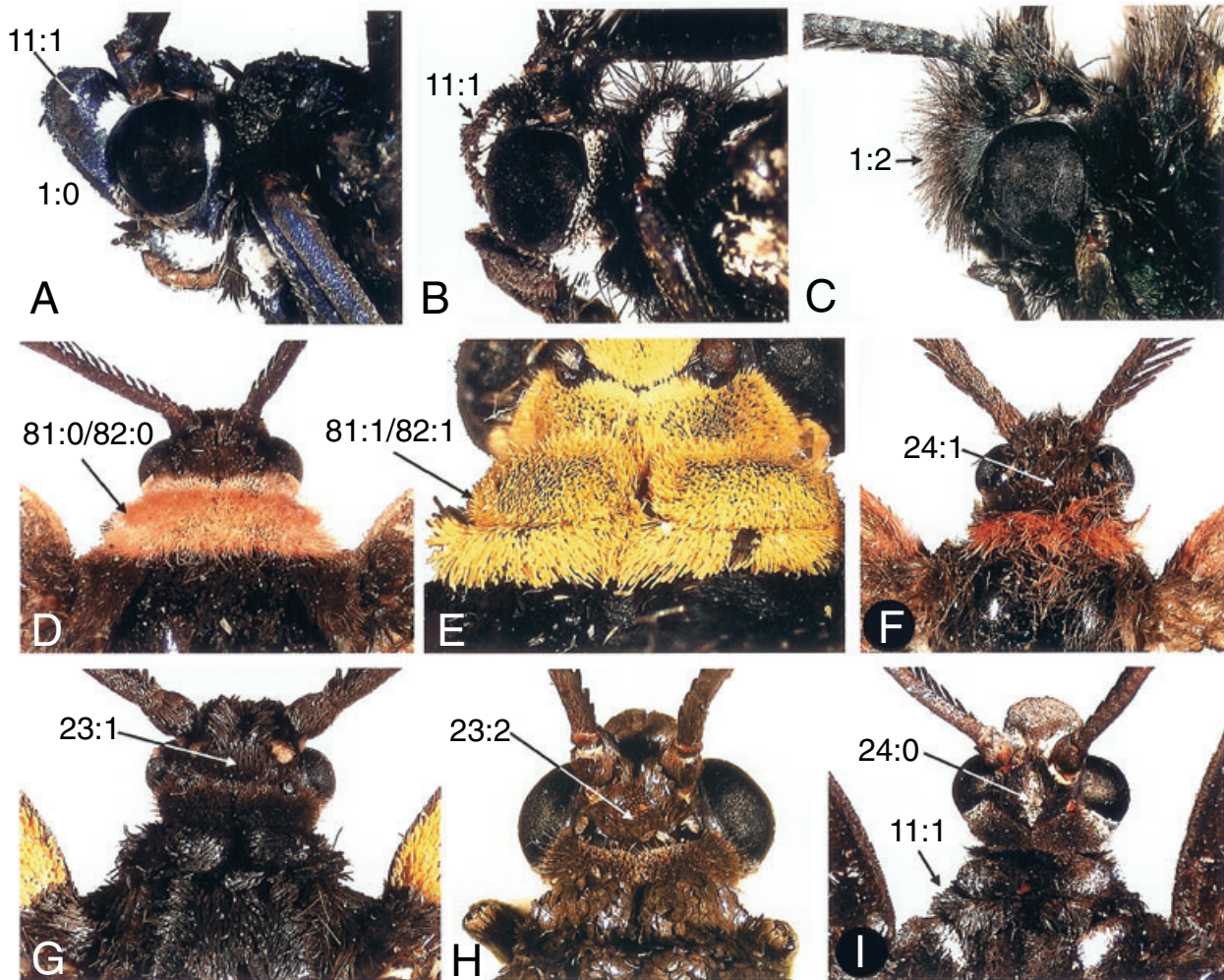


Figure 11. Characters of frontoclypeus, vertex and prothorax. A, *Cyclosia midama*. B, *Cadphises* sp. cf. *moorei*. C, *Campylothes histrionicus taliensis*. D, *Phlebohecta fuscescens*. E, *Eterusia vitessa*. F, *Aglaope infausta*. G, *Agalope harutai*. H, *Elcysma dohertyi*. I, *Amesia aliris*.

anterior margin of the compound eyes is a normal condition in Lepidoptera. Miller (1992) reported that, in Notodontidae, the morphology of the frons is 'variable, without or with frontal projections'. In the chalcosiine zygaenids, the shape of the frontoclypeus is rather complex. A character state described as 'projected head' (e.g. Figs 11A, 13A) by Epstein *et al.* (1999) is currently used to diagnose the Chalcosiinae. Landry (1995) stated that the produced frontoclypeus of snout moths is believed to be an adaptation to dry habitats with hard soil. This character state in Chalcosiinae, however, is unlikely to be related to humidity of the habitats because the 'projected head' and 'non-projected head' can be found in the same habitats, which are usually tropical or temperate rain forests. In Hemiptera, the development of the frontoclypeus is probably related to the feeding mechanism, such that the 'pumping'

system within the frontoclypeus enhances the ability of the proboscis to pierce the substrate of food sources (Novotny & Wilson, 1997); however, this functional correlation has not been revealed in the Lepidoptera. Although most characters of the frontoclypeus are apparently not constant, several traits still provides practical diagnosis for some genera (e.g. *Soritia* and *Cyclosia*). To provide a precise description and character coding, measurements of the frontoclypeus were conducted from three dimensions, viz. dorsal, lateral and frontal (see Figs 7, 12A–I), and compared with the surrounding cranial areas. Variations in the frontoclypeus in this subfamily seem to be correlated to those in the size of the sexually dimorphic compound eyes and the relative position of the antennal bases, so these adjacent organs of the frontoclypeus were considered when describing the character states.

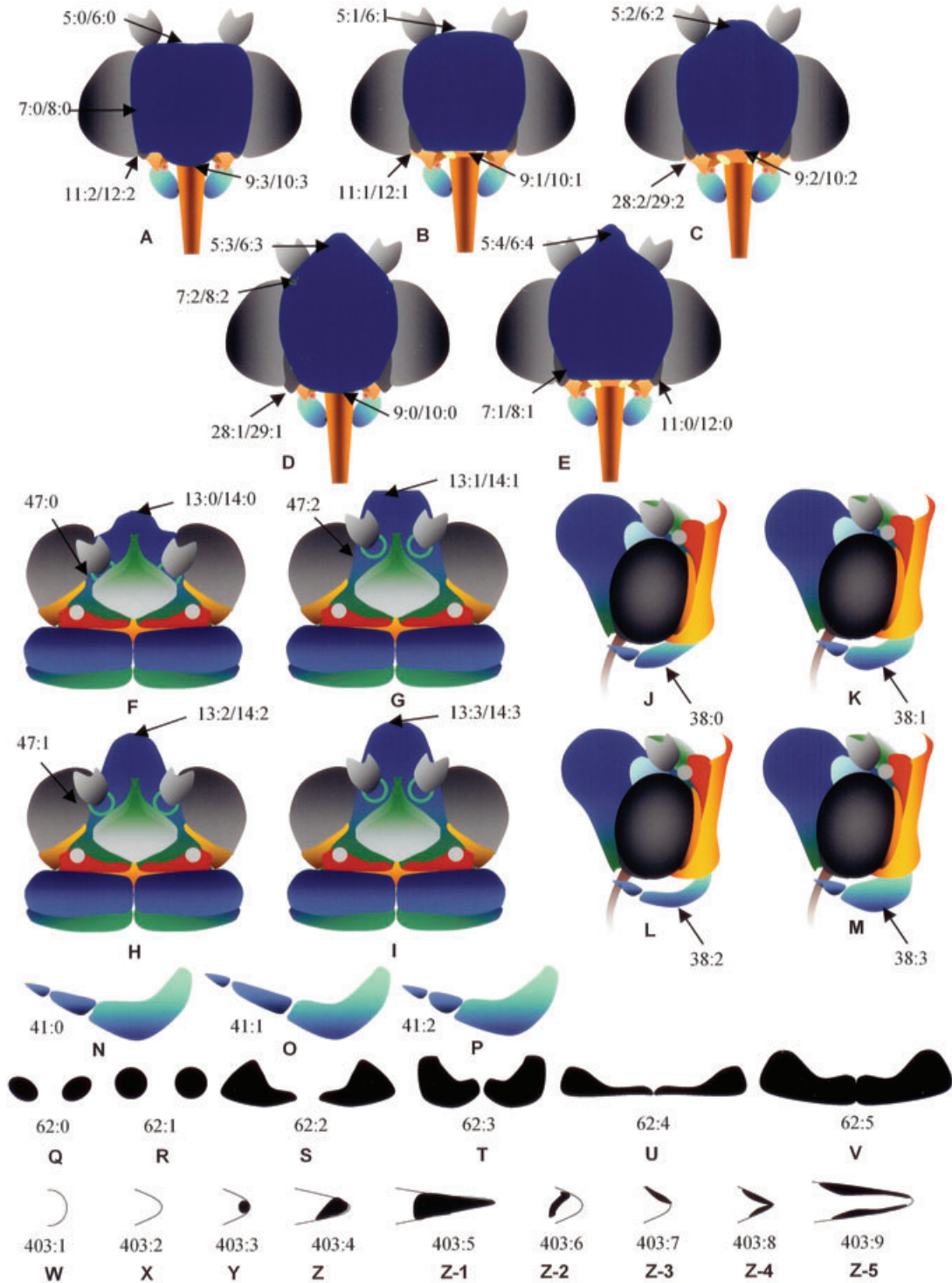


Figure 12. Stylized drawings of selected characters of adult head. See Appendixes 2 and 3 for character descriptions and their distributions. A–E, frontal view. F–I, dorsal view. J–M, lateral view. N–P, labial palpus. Q–V, dorsal view of chaetosemata. W–Z-5, mandibular lobes.

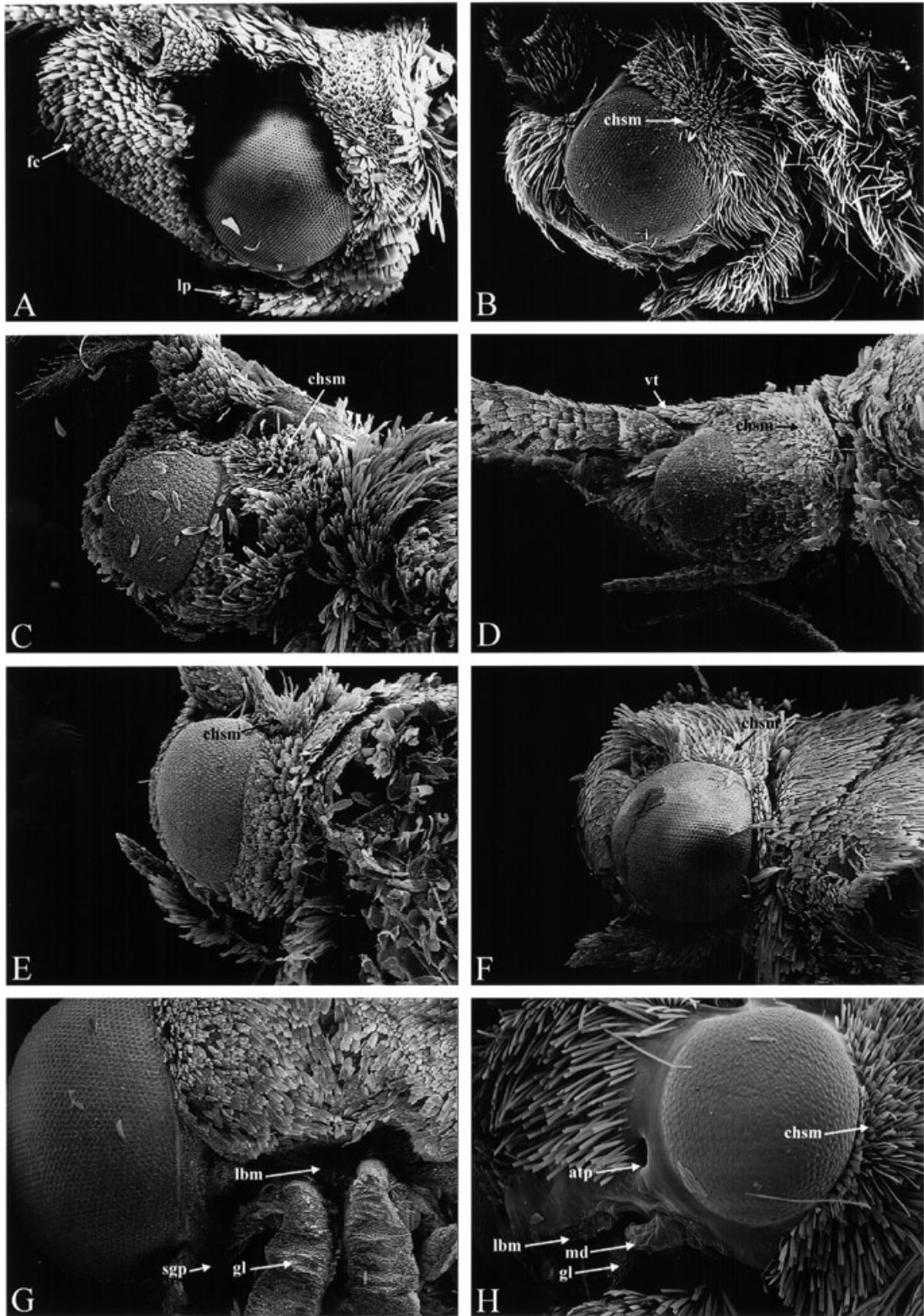


Figure 13. Heads of adults. A, *Soritia strandi*. B, *Agalope trimacula*. C, *Inouela formosensis*. D, *Heteropan* sp. E, *Chalcosiopsis variata*. F, *Lactura dives*. G, *Erasmia pulchella hobisoni*. H, *Aglaope infausta*. Abbreviations: atp, anterior tentorial pit; clsm, chaetosemata; fc, frontoclypeus; gl, galea; lbm, labrum; lp, labial palpus; md, mandible; sgp, subgenal process.

Vertex (ch. 23–27): the ‘crested’ condition of the vertex is considered to be diagnostic for Chalcosiinae by Epstein *et al.* (1999). However, this condition is found in several unrelated taxa, and three character states can be recognized (ch. 27). The ‘crested’ and ‘pillow-like’ condition *sensu* Epstein *et al.* (1999) may possibly refer to the projection on the vertex of *Cyclosia*, and the *Eterusia* + *Soritia*- and *Erasmia* + *Eucorma* + *Amesia*-genus complexes. This structure can be interpreted as the posterior part of the protruded frontoclypeus, but we tend to attribute this trait to the vertex because the presence or absence of the projection on the vertex is not correlated to the degree of development of the frontoclypeus. In *Aglaope*, *Elcysma* and allied groups, a ‘verruca-like’ projection is present on the vertex medially (Fig. 11F–I), and is treated as a different character state. As with the frontoclypeus, the scale-covering of the vertex has two conditions, ‘smooth’ (24: 0) (Fig. 11F) or ‘rough’ (24: 1) (Fig. 11I). In the ingroup and vast majority of outgroups the scales on the vertex arise medially from the dorsal surface of the postocciput and extend towards the antennal bases (25: 1) (Fig. 11H), while in *Burlacena* and *Lactura*, the scale tufts originate from the dorso-lateral sides of the postocciput and extend towards the middle axis (25: 0) (Fig. 13F). The latter condition is often observed in other lower ditrysian families, e.g. Ypomoneutidae, Tineidae and Psychidae. In some taxa (e.g. *Chalcosia*, *Gynautocera*, *Histia*), the colours of the scale covering on the vertex contribute greatly to the formation of aposematic and mimetic patterns. The colours of this region are often concolorous with those on the patagia (ch. 75, 76), parapatagia (ch. 77, 78) and the ‘scale crests’ in front of the patagia (ch. 68).

Subgena (ch. 28, 29) (Fig. 12C, D): except in primitive clades (e.g. Micropterigidae and Neopseustidae), the morphology of the subgena is less significant in phylogenetic studies of Lepidoptera. In the ingroup and outgroups, there are three character states for the relative position of the subgena and lower margin of the compound eyes. Because of sexual dimorphism in the size of the compound eye, the relative position of the subgena and the lower margin of the compound eye is treated as two characters.

Postocciput (ch. 30, 31): the postocciput has seldom been used in phylogenetic studies of Lepidoptera. In the present study, the length of the postocciput was measured and compared with the diameter of the compound eye.

Mouthparts and associated appendages

Proboscis (ch. 32–35): the degree of development of the proboscis has been used to define several zygaenid groups in the earlier literature. For instance, Hamp-

son (1892) brought several ‘mouthpart-wanting zygaenid’ genera into ‘Phaudinae’, which included *Boradia*, *Anomoeotes*, *Alophogaster*, *Phauda* and *Himantopterus*. Length of proboscis was also used by Alberti (1954) to suggest separate monophylies for the Procrarinae, Pryerini (Zygaeninae) and Aglaopini (Chalcosiinae). However, Tarmann (1994) argued against the use of this as a defining character for Procrarinae because ‘proboscis reduction is also present in three other ‘zygaenid’ genera, viz. *Boradia*, *Chalcosiopsis* and *Aglaope*’.

In fact, whether the proboscis is ‘functional’ is not easy to judge simply from the length of the specialized galea; it depends as much on the interaction of various internal muscles (Scoble, 1992). Furthermore, proboscis development may involve morphological adaptations to specific nectar resources (Krenn, 1990; Krenn & Penz, 1998; Corbet, 2000; Krenn & Kristensen, 2000; Krenn, Zulka & Gatschnegg, 2001; Kitching, 2002) and may, therefore, have evolved independently in different lineages. Except in several unusual cases where the galeae are completely absent, the length of proboscis is expressed relative to the height of the frontoclypeus.

The condition of ‘reduced proboscis’ can be separated into three character states (see states 3–5 of ch. 33 and 34). The first state has fused galeae but is rather short and concealed by the labial palpus. This type is found in females of *Cleoda syntomoides*, *Boradia*, *Hadriionella*, *Pidorus latifasciatus*, *Neoherpa subhyalina*-complex, etc. Since the feeding behaviour of these genera has not been observed in the field the function of such a short proboscis is still unclear. The second state has the galeae separated and ‘lobe-like’, a condition observed in *Aglaope*, *Herpolasia*, *Cyanidia* and others. These are less likely to be functional in feeding. The third state is a complete loss of galeae, as found in *Inouela*, *Heterogynis* and *Homophylotis nigra*. In addition, the proboscis of *Chalcosiopsis*, reported as ‘reduced’ by Tarmann (1994), is actually developed and functional.

Sexual dimorphism in the length of the proboscis is found not only in the ingroup but also among the outgroups, so the characters of the proboscis were coded separately for both sexes. The lepidopteran proboscis bears numerous sensilla of two main kinds – sensilla basiconica and sensilla styloconica (Faucheux, 1991; Miller, 1991; Walters *et al.*, 1998; Dey *et al.*, 1999). The former occur over the entire length of the proboscis in both ingroup and outgroups, while the latter are restricted to the distal third of the organ. In most of the examined taxa, the sensilla styloconica are not prominent, but are particularly developed in *Chalcosiopsis variata*, which may suggest that the adult *Chalcosiopsis* has a distinct feeding behaviour or food resource.

Maxillary palpus (ch. 36): the maxillae of Zygaenidae are not as developed as those of other ditrysiinae, but not so rudimentary as those of other zygaenoid families. In *Burlacena*, *Chalcosiopsis*, Procridinae and Zygaeninae, the maxillary palpus is usually 2-segmented with a setose apex, while in *Callizygaena*, *Cleoda*, *Heteropan* and all of the Chalcosiinae, the basal segment is usually indistinguishable from the stipes of the maxillae. The maxillary palpus in certain of species-groups of Chalcosiinae is quite rudimentary and not at all setose.

Labial palpus (ch. 37–45) (Figs 12J–M, 13A–F): segmentation, relative length of segments, direction of curvature and scale covering of the labial palpus have been widely used in the classification and phylogenetics of various lepidopteran groups, e.g. Pyralidae (Landry, 1995), Notodontidae (Miller, 1996) and Geometridae (Choi, 1997, 1998). The value of the labial palpus in chalcosiine systematics was first addressed by Yen & Yang (1997). In general, except in *Heteropan* and *Chalcosiopsis*, the labial palpus is 2- or 3-segmented (Chalcosiinae), but not so well developed as in Zygaeninae and Procridinae. The labial palpus of *Inouela* and *Homophylotis nigra* is completely reduced.

Labrum (ch. 46): the labrum is reduced in most Lepidoptera to a pair of bristled, lateral lobes termed pilifers (Scoble, 1992; Krenn & Kristensen, 2000). In general, the more reduced the mouthpart, the more rudimentary the pilifers. However, in *Heteropan* and *Cyclosia*, where the mouthparts are developed, the pilifers are reduced.

Mandible (ch. 403): in general, mandibles are only functional and present in very primitive lepidopteran groups and have not been used for either phylogenetic or taxonomic studies for the higher ditrysiinae clades. However, in most genera of Zygaenidae, the reduced mandibular lobes, which connect to the anterior margin of the subgena by an intersegmental membrane, are still visible and even protrude from the ventrolateral sides of the frons. The lobes are somewhat sclerotized basally in *Zygaena* and Procridinae, but are more membranous and projected in *Callizygaena*, *Heteropan*, *Cleoda* and the Chalcosiinae (except *Chalcosiopsis* and *Inouela*). Epstein *et al.* (1999) stated that adults of Zygaenidae (except Phaudinae) produce a vitreous, whitish-yellow cyanide liquid or foam between 'the inner margin of the eye and the base of the proboscis' when disturbed. In the present study, we show that the foam is excreted from the mandibular lobes. Whether the liquid or foam is released from a chamber formed by the membranized mandibles or from an internal glandular channel with a pore opening at the apices of the lobes requires histological examination of fresh material.

Sensory organs

Antennae (ch. 47–58): characters of antennae are utilized in the classifications of Procridinae by Alberti (1954), Efetov & Tarmann (1995, 1999) and Naumann *et al.* (1999). In the limacodid families (see Epstein, 1996), Anomoeotidae, Himantopteridae, Phaudinae, Heterogynidae, *Inouela*, *Pryeria* (Yen & Horie, 1997), and some Procridinae (e.g. *Clelea*), the sensory setae of the rami are rather long and developed (52: 0) (Fig. 14J). However, in *Callizygaena*, *Cleoda*, *Heteropan* and most genera of the Chalcosiinae, they are very short (52: 1) (Fig. 14A–H). Rami are absent in *Zygaena*, *Chalcosiopsis* and *Lactura* (51: 1) (Fig. 14K), so the antennal sensory setae of these taxa are only distributed on the 'main body' of the flagellomeres. Several distinct character states of the lateral margins and the 'back-bone' of the flagellomeres were recognized. Although the taxonomic value of the 'enlarged' antennal apex of Zygaenidae has been demonstrated by several authors (e.g. Epstein *et al.*, 1999; Naumann *et al.*, 1999), it is here recommended that the source of such enlargement is clarified as being a protuberance of the apical flagellomeres or flattening of the apical rami (Fig. 14D). In *Zygaena*, the 'clubbed' antennal apex is formed by thickening of the flagellomeres at the apex, while in *Pryeria*, *Adscita*, *Callizygaena*, and many genera of Chalcosiinae (e.g. *Eterusia* and *Prosopandrophila*), the 'enlarged' antennal apex is caused by denser arrangement, longer rami and thickening of both rami and flagellomeres.

Ocelli (ch. 60): the presence or absence of ocelli is frequently used as a family-level character in Lepidoptera although the function of this sensory organ remains questionable (Scoble, 1992). Because ocelli are absent in Phaudinae, this character has been considered inconstant within Zygaenidae (see Heppner, 1998; Epstein *et al.*, 1999), but absence of ocelli is also observed in Himantopteridae, Anomoeotidae, *Lactura*, *Heterogynis*, *Chalcosiopsis* and the *Burlacena*-group.

Chaetosemata (ch. 61–67) (Figs 15, 16): these are cuticular and elevated patches found on the heads of many lepidopterans, and also known as Jordan's or Eltringham's organs (Scoble, 1992). They are usually visible on dried specimens where their bristly appearance generally distinguishes them from the surrounding scaled area. In some taxa (e.g. *Pryeria*, *Callizygaena*), large chaetosemata are concealed by dense scale tufts arising from the patagia. In the literature, the very large chaetosemata of Zygaenidae are usually regarded as one of the diagnostic characters (Jordan, 1923; Holloway *et al.*, 1987, 2001; Tarmann, 1994; Epstein *et al.*, 1999; Naumann *et al.*, 1999), and the shape and size are specific to each group (Epstein *et al.*, 1999). For instance, the tribe Artonini

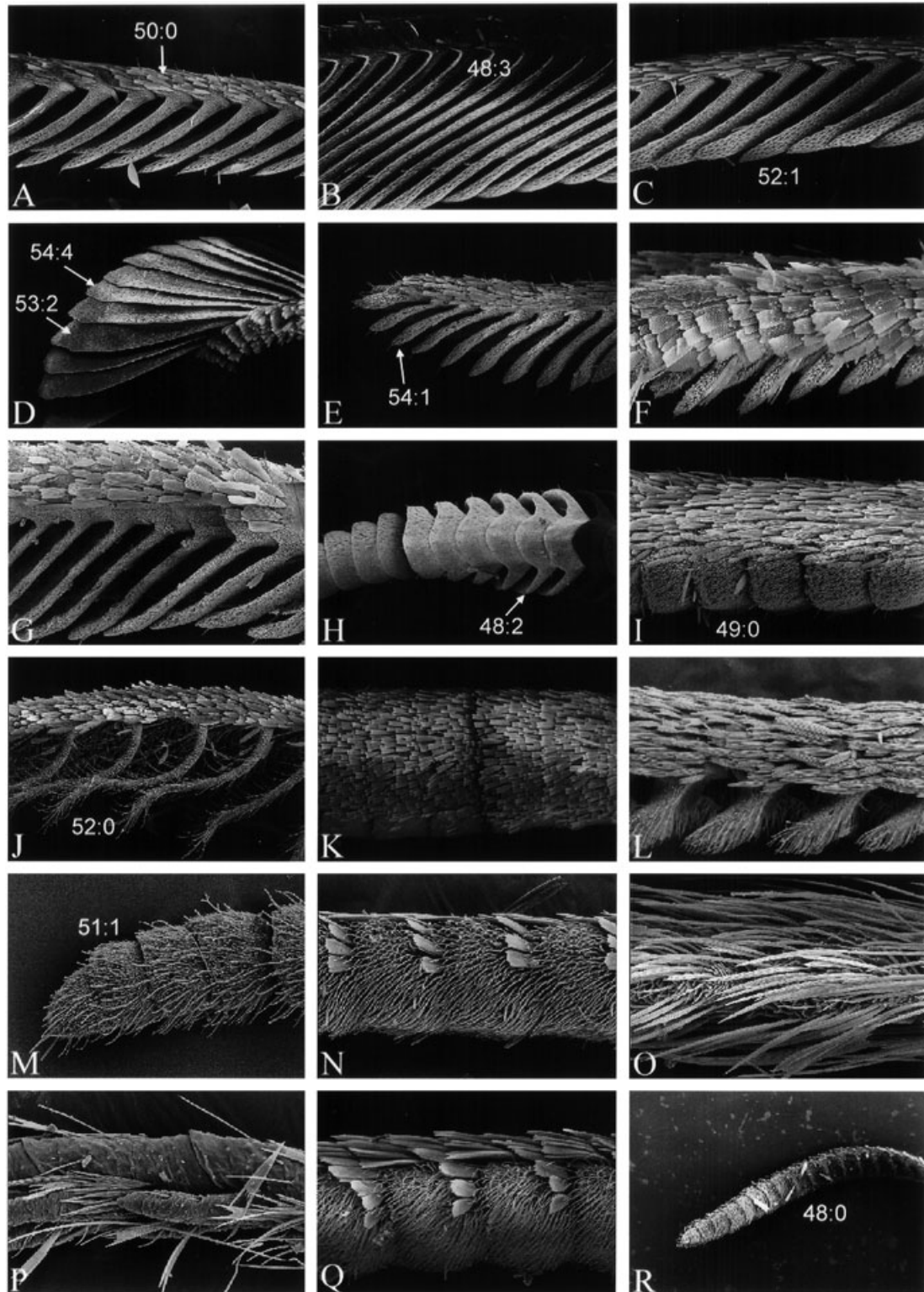


Figure 14. Antennae. A, *Agalope trimaculata*. B, *Rhodopsona rutila*. C, D, *Eterusia aedeae formosana*. E, *Cyclosia midama*. F, *Heteropan scintillans*. G, H, *Callizygaena glacon*. I, *Adscita statives*. J, *Inouela formosensis*. K, *Zygaena filipendulae*. L, *Phauda mimica*. M, N, *Lactura dives*. O, *Anomoeotis levis*. P, *Himantopteus fuscinervis*. Q, R, *Chalcosiopsis variata*.

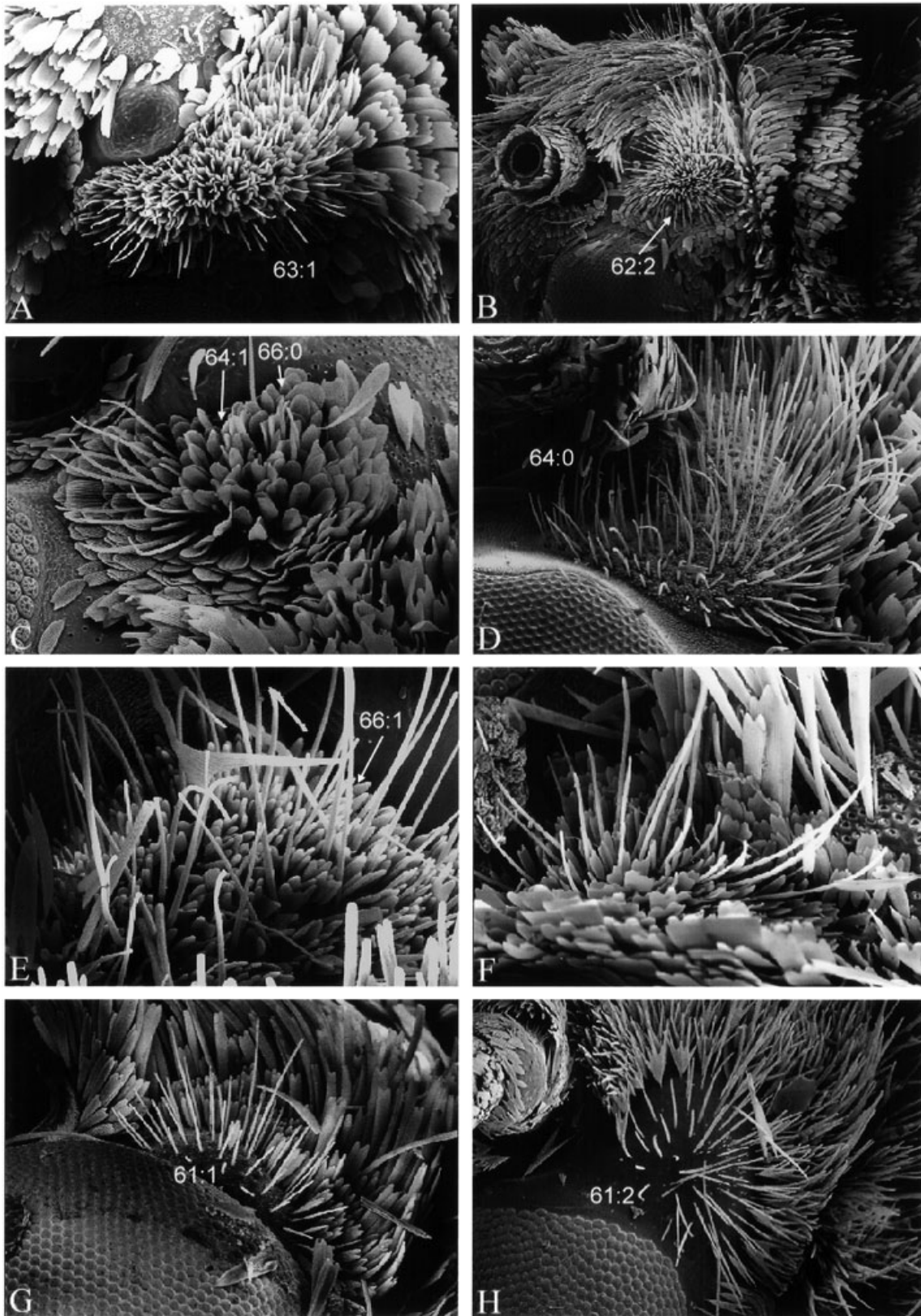


Figure 15. Chaetosemata of different zygaenoid groups. A, *Adscita statices*. B, *Artona hainana*. C, *Inouela formosensis*. D, *Zygaena filipendulae*. E, *Callizygaena glaucon*. F, *Chalcosiopsis variata*. G, *Lactura dives*. H, *Phauda mimica*.

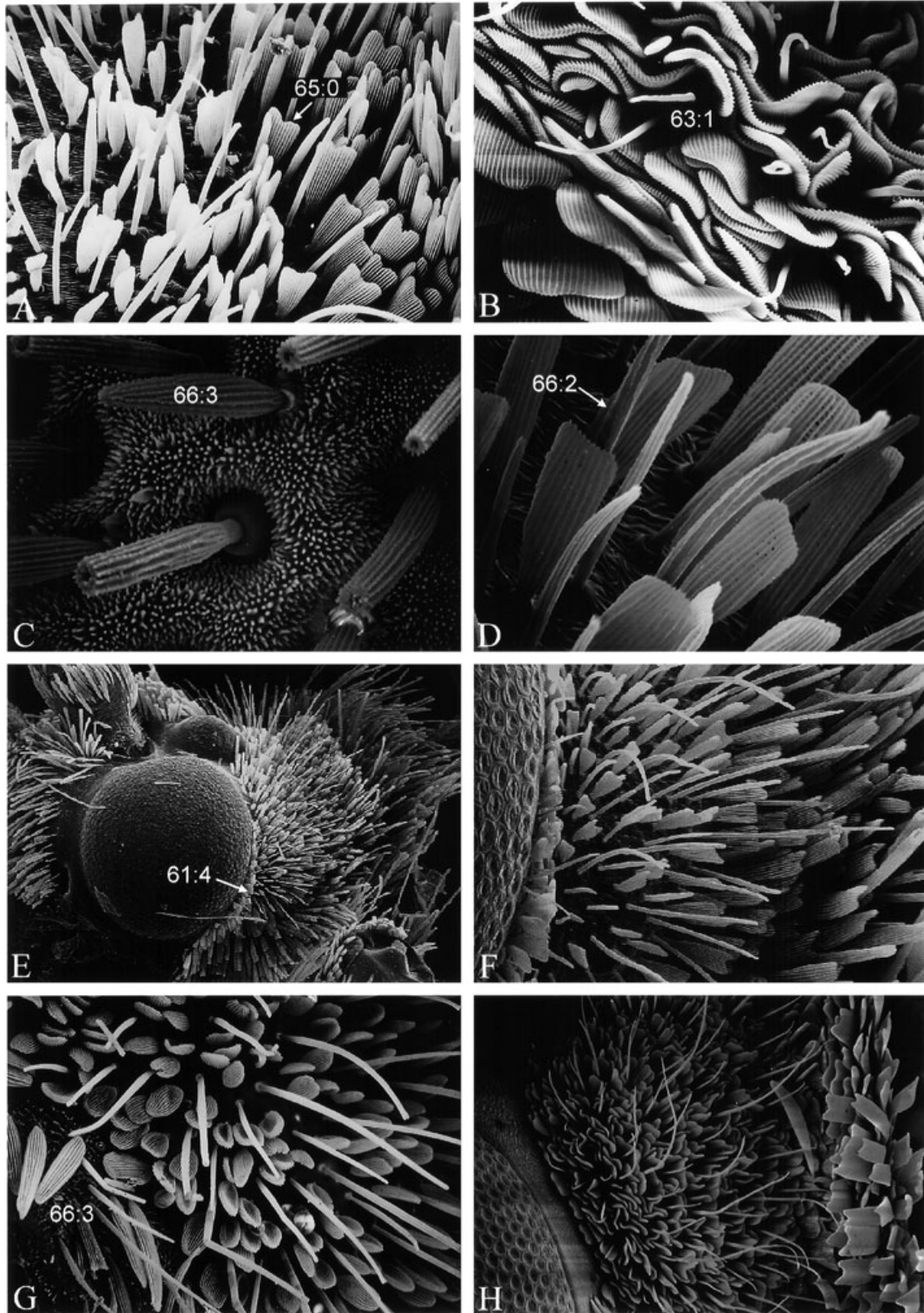


Figure 16. Chaetosemata of different zygaenid subfamilies. A, E, F, *Aglaope infausta*. B, *Cyclosia midama*. C, *Agalope trimacula*. D, *Adscita statices*. G, *Elcysma westwoodi*. H, *Histia flabellicornis ultima*. Chalcosiinae: A–C, G–H; Procridinae: D.

of the Procridae is defined by its peculiar triangularly shaped chaetosemata (Tarmann, 1994). Jordan (1923) reviewed the distribution of this organ among the Lepidoptera, and two major types of chaetosemata were recognized. The first type usually contains many prominent and long sensilla trichodea which are easily distinguishable from other scales and arise from a pair of swollen plates dorsoposterior to the compound eyes or antennal bases. The second has many additional erect specialized scales situated on the plates together with sensilla trichodea. In the present study, the range and shape of this organ on the postocciput, density of sensilla trichodea, distribution, shape and colour of the scales associated with the sensilla were treated as seven characters. In some studies (e.g. Heppner, 1998; Epstein *et al.*, 1999; Holloway *et al.*, 2001), chaetosemata were regarded as 'absent' in Heterogynidae, but Scoble (1992) stated that this organ was present in this family. In the present study, occurrence of chaetosemata in *Heterogynis* and *Janseola* are confirmed, while the former has the first type of chaetosemata and the latter has Jordan's second type.

ADULT THORAX (EXCLUDING SCENT ORGANS)

Thoracic sclerites and appendages

Prothorax (ch. 68–82) (Fig. 17C–O): in more advanced clades, the prothorax is reduced to a 'collar-like' structure, which contains a thin dorsonotal plate, lateral anepisternum and anteroventral laterocervicale. The majority of the studied taxa have a sclerotized dorsonotal plate (69: 1) (Fig. 17D), while this structure is less developed and sclerotized (69: 0) (Fig. 17C) in *Chalcosiopsis variata*, *Phauda*, *Anomoeotes*, *Dianeura* and *Himantopterus*. Patagia are thought to be homologous with the lateral warts in primitive Lepidoptera (Scoble, 1992) and are usually membranous, flap-like structures of various shapes (Schultz, 1914). Posterior to the patagia, paired parapatagia are sometimes present in Lepidoptera. One of the striking features of Chalcosiinae (except *Inouela*, *Chalcosiopsis* and *Cleoda*, unknown in *Heteropan*) is the capability to release a large amount of cyanic fluid or foam from the membrane between the patagia and parapatagia. This behaviour (ch. 403) (Fig. 53B) seems to be correlated with development of patagia and parapatagia, but whether the 'cavity' formed by the enlarged sac-like patagia or parapatagia is used to store the cyanic fluid has not been investigated. A similar chemical defensive mechanism has been reported from several noctuid groups, e.g. Arctiinae (Häuser & Boppré, 1997; Weller, Jacobson & Conner, 1999; Kitching & Rawlings, 1999) and Aganainae (Compton, 1987, 1989). But, unlike the chalcosiines, the thoracic secretion in noctuid groups is released near or below the base of

the tegula, and thus is of pterothoracic derivation and not homologous with that in the Chalcosiinae.

Mesothorax (ch. 83–87) (Fig. 17A, B): in all of the outgroups and in the ingroup, most regions of the mesothorax are rather uniform morphologically except for the shape of the tegula. This sclerite has been thought to play a role assisting wing coupling with a frenular-retinacular system (Scoble, 1992, following Hering, 1958). In both the out- and ingroup, the tegula is quite developed but less extended posteriorly in some weak-fliers like Anomoeotidae, Himantopteridae and Heterogynidae. In *Chalcosiopsis*, the tegula is much more prolonged than in the other groups.

Metathorax (ch. 88): the shape of the metascutellum is uniform among outgroups and ingroup except in the *Burlacena*-group and *Neoherpa* of Chalcosiinae. The tergal phragmata occurring in the dorsal thoraco-abdominal junction were considered phylogenetically informative among the ditrysian clades by Fänger (1999). It was found that the shapes of the lower margin of the tergal rim are distinct at family level. Epstein *et al.* (1999) indicated that an elongated area with many microtrichia is present on the metascutum of Heterogynidae and Zygaenidae, and is involved in locking the microtrichia on the underside of the proximal part of the forewings. However, this type of forewing–thorax locking device has already been reported from various families by Common (1969), Kuijten (1974), Minet (1991) and Sattler (1991a); it has also been described by Scoble (1992) as a commonly shared character among Ditrysia. Microtrichia either on the metascutum or on the forewings were found uniformly throughout the out- and ingroup, so this feature is not phylogenetically informative.

Dorsal thoraco-abdominal junction (ch. 89): the phylogenetic significance of the dorsal thoraco-abdominal junction of Ditrysia was investigated by Fänger (1999). In his research, a fully developed euphragma was considered to be a potential synapomorphy of the Obtectomera *sensu* Minet (1991), although this feature is also shared by Choreutidae, Sesiidae and Brachodidae. In the present study, this character state was only observed in *Chalcosiopsis*.

Legs (ch. 90–93): presence or absence of epiphysis, tibial spur formula and the relative length of the tibial spurs have conventionally been used to diagnose the procridine zygaenids (Efetov, 1997a, b, 1999; Efetov & Tarmann, 1995, 1996, 1999). Tibial spur formation has been used to subdivide the western Palearctic Procridae (e.g. Tarmann, 1994; Efetov & Tarmann, 1995), but this character seems not to be constant from species to family level as stated by Heppner (1998). On the other hand, in the previous literature

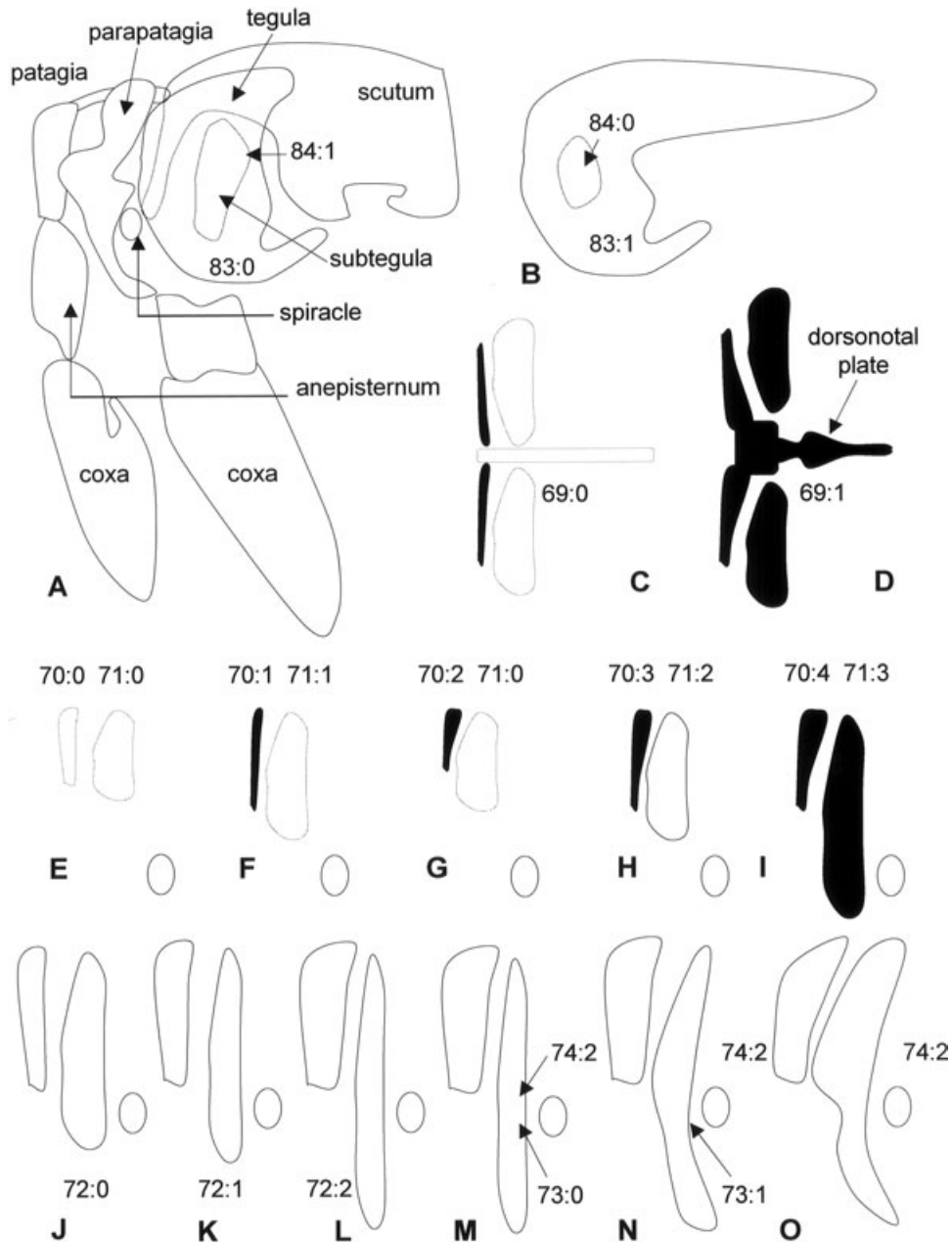


Figure 17. Stylized drawings of selected characters of adult thorax. A, generalized diagram of prothorax and mesothorax. B, tegula and subtegula. C, D, dorsal view of pronotum. E–O, various combinations of patagia and parapatagia.

(e.g. Heppner, 1998) three character states of tibial spur formation were usually recognized, viz. 0-0-0, 0-2-2 and 0-2-4, for Zygaenidae. However, in the present study, the 0-0-0 condition was not found in Zygaenidae, and the record of its presence may be based on an earlier concept of the family, which included Anomoetidae and Himantopteridae. Among most species-groups of Chalcosiinae, tibial spur formation is rather uniform in 0-2-2, while the tibial spurs are longer and more prominent in the genera *Cadphises*, *Campylotes*,

Hampsonia and *Herpidia*. In Epstein's (1996) phylogenetic study of the limacodid-group families, the sensilla on the ventral surface of the 5th tarsomere of the female were included. These characters, however, have no noticeable variation in either the out- or ingroup, so they were not considered here.

Wing coupling device

Wing coupling device (ch. 94): the coupling device in Zygaenidae is the typical frenulum–retinaculum sys-

tem. There is no obvious difference in the shape of the male frenulum and retinaculum among the studied groups, while the number of bristles in the female frenulum, which varies in different taxa, may provide some phylogenetic information (Yen & Yang, 1997). The number of female frenular bristles in the outgroups and ingroup ranges from 0 to 6, with only the Himantopteridae and Anomoeotidae having none. This character is treated as inapplicable in *Heterogynis*, which has an apterous female. The microtrichia on the underside of the forewing, implied as synapomorphic for the supposed monophyly of Heterogynidae + Zygaenidae by Epstein *et al.* (1999), is not considered reliable because this character is in fact shared by many lepidopteran groups (Common, 1969; Scoble, 1992).

Wing venation

Venational patterns were used extensively in the classification of the Chalcosiinae by Hampson (1891, 1892) and Hering (1922), and are more diverse in this subfamily than in Procridinae, Zygaeninae, Callizyginae or any of the outgroups.

Surface of veins (ch. 95): the condition of the underside of the wing veins being slightly hairy is shared by many lepidopteran clades, but no comprehensive survey of the distribution of hairs or wing veins has been carried out across the order. Among the studied taxa, long hairs are found in different wing regions in two species-groups. In the *Heteropan appendiculata* species-group, the anal veins in the hindwing have a hairy region on the underside. This feature, however, is not found in other species-groups of *Heteropan*.

Forewing costal (C) to subcostal (Sc) veins (ch. 96, 97): a series of cross-veins between C and Sc of different density are found in all the species-groups of *Cyclosia*, *Eucormopsis*, *Gynautocera*, *Pompelon* and *Histia*. In addition, a proximal series of cross-veins is also present in the anomoeotid genus *Dianeura* Butler, 1888 and the zygaenine *Pryeria* (96: 1) (Figs 19A, 21B). The distal end of Sc is separate from that of R1 in most Lepidoptera (97: 0) (Fig. 19B), while another two alternative character states are found in the present study.

Branches of forewing radial (R) veins (ch. 98–102): except in Himantopteridae, Anomoeotidae, *Cleoda*, *Atelesia*, *Sciodoclea*, *Pseudonyctemera*, *Boradiopsis* (Fig. 21C), *Phlebohecta jordani*, *Aphantocephala*, *Docleopsis sulaensis*, *D. stigma* and *Euxanthopyge*, all the taxa studied have five radial branches. The stalking and forking patterns of R-veins were treated as occurring among three major components: R1, R2 and R3–5.

Discal cell (ch. 105–107): the discal cell of the forewing of Lepidoptera is usually separated into two subcells (here termed subcells 1 and 2) by a medial stem. Sclerotization of the medial stem varies with different taxa and sometimes the trace is barely visible. The 'chorda' is an area bordered by the distal end of the forked medial stem and the distal end of the discal cell. Presence of a chorda is not rare among the limacodid-group families (Epstein, 1996), but rather unusual among the outgroups and ingroup taxa. A chorda has only been observed in *Chalcosiopsis variata* and several species-groups of *Cyclosia*, e.g. *C. midama*. The ratio between the lengths of subcells 1 and 2 is not consistent among the studied taxa.

Forewing cubital (Cu) and anal (A) veins (ch. 108–110): in Zygaenoidea these are less variable than the vein sets discussed above. Two unusual conditions of cross-veins present between the posterior cubital and anal veins have been found during the present study. A cross-vein between the posterior cubital vein (CuP) and 1A + 2A has been observed in *Pryeria* and the *Cyclosia midama* species-group. In *Thaumastophleps*, CuP is forked submedially, crossing CuP and ending at the middle of 1A + 2A. Presence of a basal fork of 3A is variably present among the outgroup taxa.

Hindwing Sc + R1–Rs veins (ch. 111, 112) (Figs 18, 21): the configuration between Sc + R1 and Rs can be separated into four conditions. The condition in which a short cross-vein connects Rs to Sc + R1 (111: 3) (Fig. 21A) was used to diagnose the *Arbudas* complex (*sensu* Tarmann, 1992a), and has been found inconsistently distributed within the ingroup. Rs and M1 are usually separated in Zygaenoidea, but in this study, stalked Rs and M1 have been uniquely observed in *Chalcosiopsis*.

Wing shape and size

Sexual dimorphism (ch. 119, 120): in the present study, sexual dimorphism in wing shape usually involves the male having a much narrower or longer forewing than the female (119: 1) (Fig. 22C, D). However, dimorphism in wing size (120: 1) is not necessarily correlated with dimorphism in wing shape. Both features are widely distributed in the studied taxa.

Forewing shape (ch. 124, 125) (Fig. 22A, F–M): in the earlier literature (e.g. Hampson, 1892; Hering, 1922) the 'broad wing' condition was often used to distinguish Chalcosiinae from the other zygaenid subfamilies, and to merge Chalcosiinae and Anomoeotidae (as Anomoeotinae) into a single group 'Hauptstamm II' (*sensu* Alberti, 1954). The so-called 'rounded wing' has never been scientifically defined although it usually refers to a forewing shape with the outer and inner

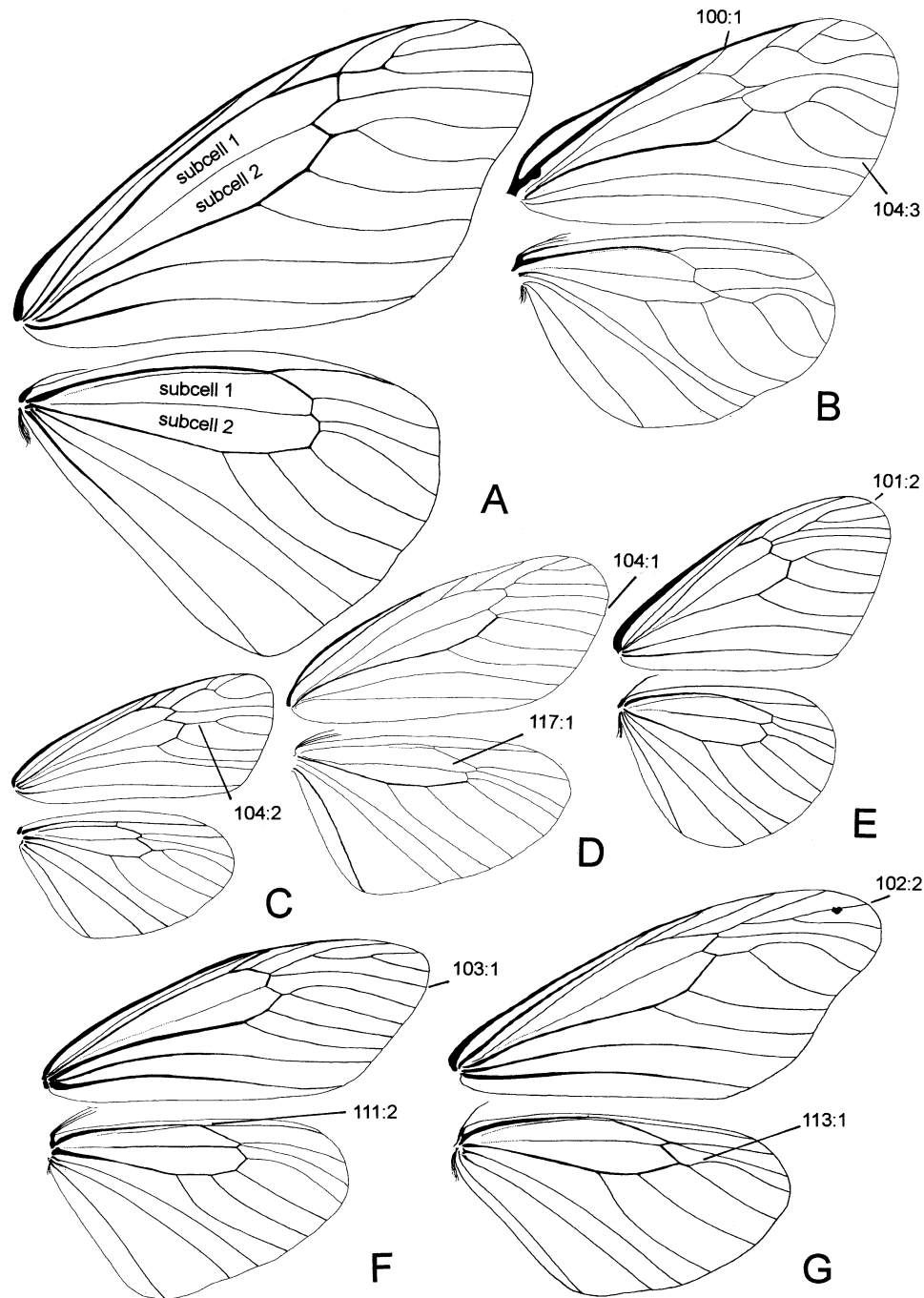


Figure 18. Wing venation of Chalcosiinae. A, *Cadphises moorei*. B, *Campylotes maculatus*. C, *Campylotes sikkimensis*. D, *Panherpina basiflava*. E, *Philopator rotundata*. F, *Watermenia bifasciata*. G, *Hampsonia pulcherrima*.

margins almost equal in length, the termen slightly protruded and the angle formed by the costal margin and the inner margin ranging from 40 ° to 45 °. On the other hand, the so-called ‘elongated forewing’ in descriptions of many taxa covers a multitude of sins. A forewing can be elongated in two ways: (1) elongated termen plus contracted hind margin (e.g. *Elcysma*), or

(2) contracted termen plus elongated hind and costal margins (e.g. *Cleoda*). Longitudinal compression of the first type may give the elongated forewing of *Gynaetocera* and the *Histia flabellicornis* species-group. In the present study, the shape of the forewing was treated as eight character states and coded for male and female separately.

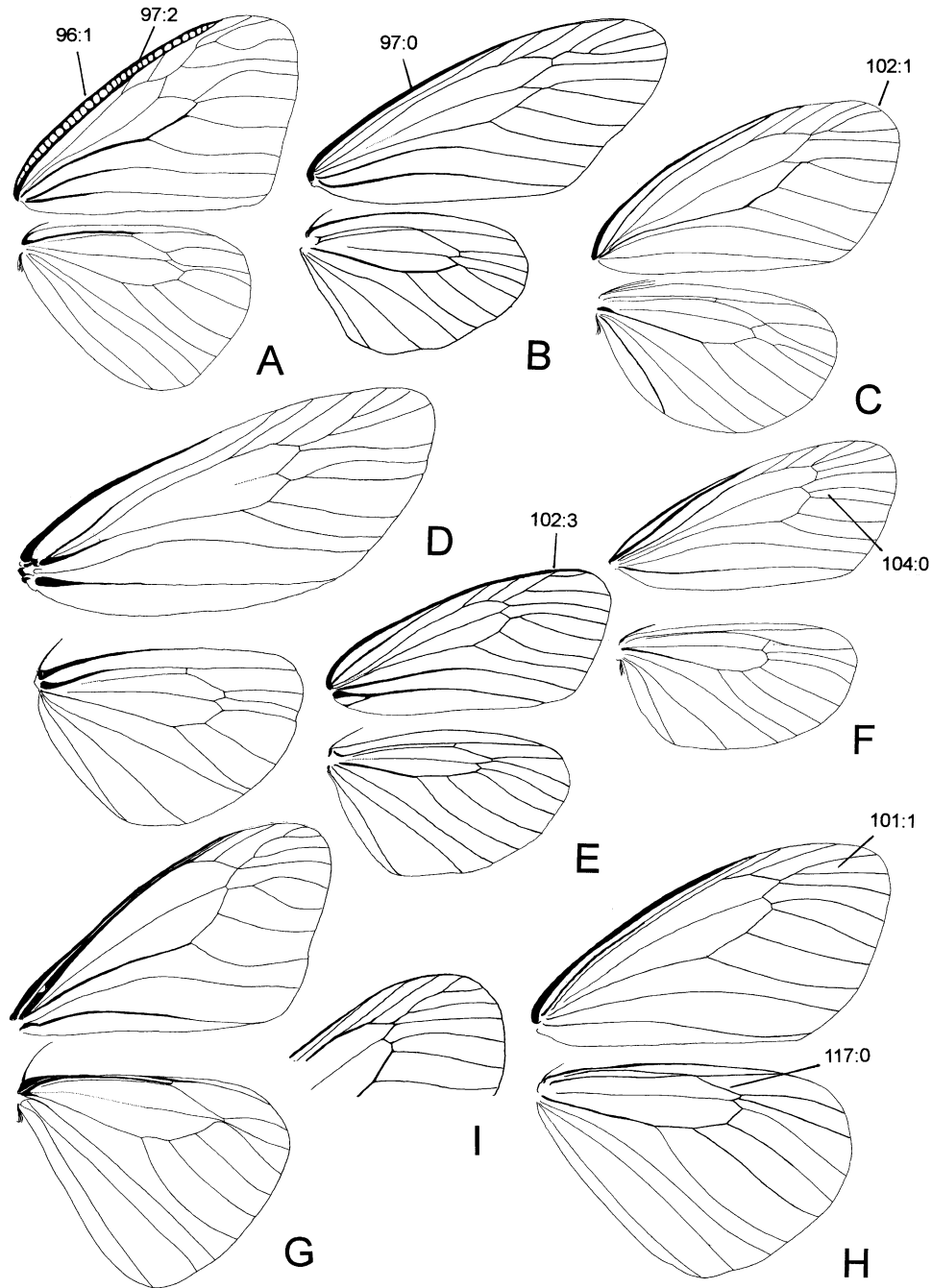


Figure 19. Wing venation of Chalcosiinae. A, *Cyclosia pagenstecheri*. B, *Corma maculata*. C, *Corma zenotia*. D, *Docleomorpha boholica*. E, *Neoherpa nevosa*. F, *Aglaope infausta*. G, *Agalope trimacula*. H, I, *Agalope immaculata* (I shows variation of R veins).

Hindwing shape (ch. 127–129): in general, the shape of the hindwings is quite uniform among the zygaenoids. Three major aspects of hindwing modification were focused upon in this study. Reduction of the hindwing has been categorized into four levels (Sattler, 1991b) and reported from various lepidopteran families including the Zygaenidae (Sattler, 1991b;

Heppner, 1991). However, the reduction of the hindwing reported for Zygaenidae was likely based on an earlier concept of this family, which included Himantopteridae, a family with reduced venation of the hindwing. Although Heppner (1991) reported a case of hindwing reduction in *Thyrassia*, a procridine genus belonging to the *Clelea*-group (*sensu* Efetov &

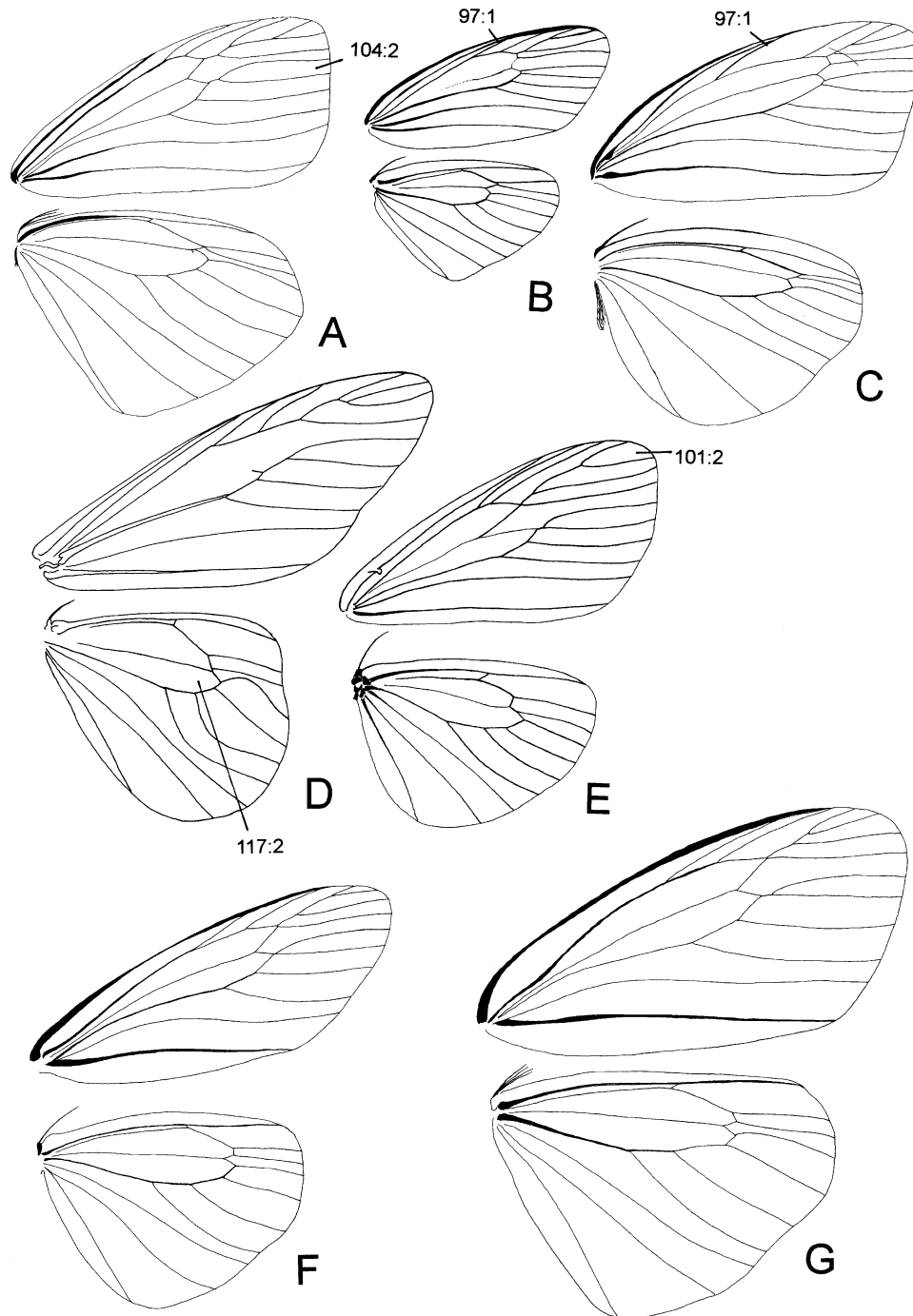


Figure 20. Wing venation of Chalcosiinae. A, *Chalcophaedra zuleika*. B, *Pseudoscaptesytle bicolor*. C, *Barbaroscia amabilis*. D, *Psaphis euschemoides*. E, *Clematoessa virgata*. F, *Chalcoscia zehma*, male. G, Ditto, female.

Tarmann, 1995), our observations based on all the known species of *Thyrassia* do not reveal any reduction either in venation or length. The small hindwings of 'wasp-mimic' or 'Syntominiinae-mimic' Zygaenidae (e.g. *Trypanophora* and *Thaumastophleps* of Chalcosiinae, *Thyrassia* and *Ischnusia* of Procridiinae) are easily misinterpreted as having a reduced

condition. In three unrelated taxa, *Elcysma*, *Histia* and Himantopteridae, the hindwings are extended into long tails by elongation of the M veins. In *Elcysma*, the tail is formed by extension of Rs, M1 and M3 (127: 1) (Fig. 22M), while the elongated hindwing of *Histia* is caused by extension of Sc + R1, M1, M2 and M3 (128: 1) (Fig. 22L). The long tail of

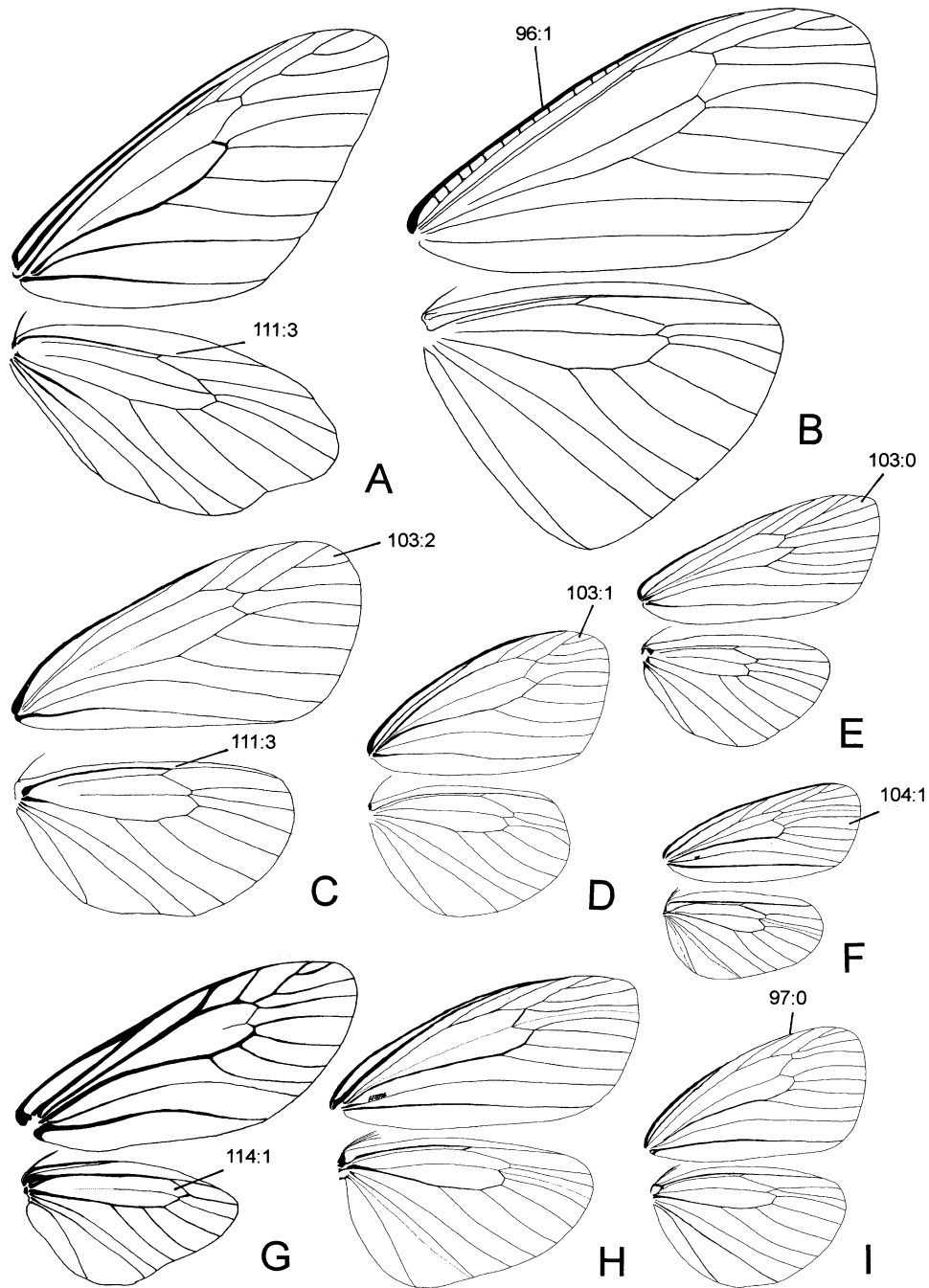


Figure 21. Wing venation of Chalcosiinae. A, *Hestia libelluloides*. B, *Pompelon marginale*. C, *Boradiopsis grisea*. D, *Chalcoscia thaivana*. E, *Allocaprima duganga*. F, *Pseudopidorus fasciatus*. G, *Trypanophora semihyalina*. H, *Neochalcoscia remota*. I, *Pidorus atratus*.

Himantopteridae involves elongated M veins, but this feature was not coded because it is phylogenetically uninformative.

Wing patterns and mimicry types

The models of wing patterns of and their developmental mechanism in butterflies have been well surveyed

(e.g. Nijhout, 1991). However, except for some recent studies (Hall & Harvey, 2001a, b, 2002a, b, c; Nylin *et al.*, 2001; Hall, 2002a, b, 2003; Willmott, 2003) the diverse features of wing patterns have often been ignored by morphologists attempting to reconstruct the supraspecific phylogeny of Lepidoptera. Essentially, the wing patterns of butterflies and other mac-

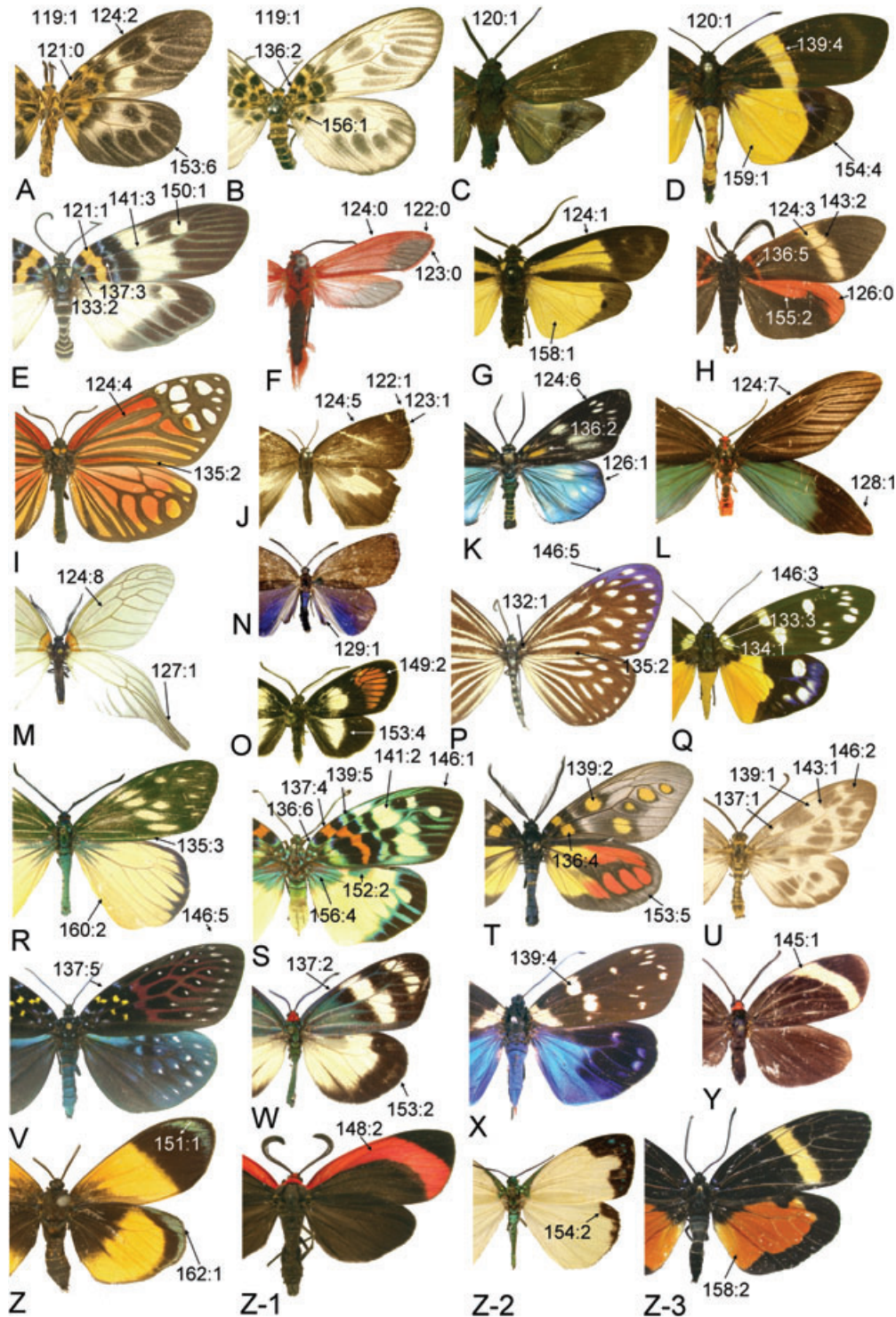


Figure 22. Selected character states of wing shapes and wing patterns. A, *Philopator basimaculata*, male. B, ditto, female. C, *Eterusia angustipennis*, male. D, ditto, female. E, *Erasmiphlebohecta picturata*. F, *Phauda kantonensis*. G, *Soritia major*. H, *Watermenia bifasciata*. I, *Campylotes kotzechi*. J, *Chalcosiopsis variata*. K, *Psaphis azurea*. L, *Histia flabellicornis*. M, *Elcysma doherlyi*. N, *Heteropan appendiculata*. O, *Caprima gelida*. P, *Cyclosia midama*. Q, *Eterusia tricolor*. R, *Milleria dualis*. S, *Erasmia pulchella*. T, *Hampsonia ueharai*. U, *Corma maculata*. V, *Amesia sanguiflua*. W, *Chalcosia pectinicornis*. X, *Eterusia subcyanea*. Y, *Pidorus cyrtus*. Z, *Eusphalera cadamium*. Z-1, *Rhodopsona costata*. Z-2, *Cyclosia hecabe*. Z-3, *Eucorma obliquaria mindanaoensis*.

rolepidopterans can be classified into several fundamental elements (e.g. Nijhout, 1991; Willmott, 2003). Although a model of wing pattern has been proposed to discriminate among sibling taxa of *Zygaena* (e.g. Naumann *et al.*, 1999), the model of wing pattern used in the present study generally follows the 'butterfly system', but with slight modification by integrating the wing pattern of *Erasmia pulchella pulchella* (Fig. 7), a taxon bearing possibly the greatest degree of wing maculation and zonation among the Chalcosiinae.

In the present study we sought to include various kinds of characters from wing patterns, examining phylogenetically significant elements in order to recover a phylogeny that accurately reflected the diversification of pattern in chalcosiines. However, there are some problems in homology assessment and coding of wing patterns; these include whether to code similar pattern elements in different wing cells as single or multiple characters (Willmott, 2003), and whether to code 'forewing band' at different wing zones as 'one character with multiple states' or 'several binary characters'. Forey & Kitching (2000) demonstrated different methods of coding multistate characters and the impacts of these on systematic and evolutionary conclusions. They suggested that there was reason to believe that there is a biological and/or logical dependency between individual observations that are coded as states within a character.

In the present study, to avoid a priori assignment of homology and subjective judgement, we coded most wing pattern elements in different wing cells and wing zones as distinct characters, and thus their homology and correlation can be corroborated by further statistical tests. Compared with the Chalcosiinae, most of the selected outgroups have rather uniform and dull colour patterns so that the characters obtained from the ingroup are not applicable to the outgroup taxa. A total of 33 wing pattern characters (about 8% of the total characters) was coded.

Sexual dimorphism (ch. 130): the degree of sexual dimorphism is often judged subjectively by the researcher. In many cases, the sexual dimorphism of body size can be statistically estimated, while that of colour patterns may not be so easy to quantify, especially when polymorphism and clinal variations are common. In the present study, the boundary between dimorphic and non-dimorphic patterns is judged based on ground colour, size and arrangement of specific elements of wing pattern. If the size of a specific stripe or spot is correlated with size difference in the two sexes, this kind of variation is not regarded as sexual dimorphism.

Upperside and underside (ch. 131): most taxa have similar upper- and underside wing patterns, although

the latter usually have more blurred maculation and lighter ground colour. Four species-groups, *Pseudonyctemera dissimulata*, *Eucormiopsis lampra*, *Rhodopsona matsumotoi* and *Cyclosia pieroides*, exhibit different upperside and underside wing patterns.

The wing patterns of Chalcosiinae can be roughly classified into several mimetic or aposematic types, named here after the lepidopteran taxa which dominate as models. These taxa, either sympatric or allopatric, are suspected to be involved in mimicry complexes with Chalcosiinae. These major mimicry 'types' are summarized but not coded as characters to maintain independence of data.

(A) *Translucent/semi-translucent type* (Fig. 22M): characterized by the white or creamy white background of forewings and hindwings and a basal or sub-basal band (ch. 138, 141, 142). This type was used to define several genera of the tribe 'Agalopini' by Alberti (1954). The 'translucent' effect is caused by un-overlapped, flattened or needle-like scales (see ch. 164 and 165). The taxa demonstrating this pattern include *Elcysma*, *Agalope*, *Achelura*, *Boradia*, *Neoherpa*, *Panherpina* and *Boradiopsis grisea*. They appear to be less aposematic or mimetic than other 'non-Agalopini' groups, while some species of the *Agalope bieti* species-complex may form different mimicry complexes with the diurnal lymantriid genera *Laelia* and *Pantana*, the nymphalids *Calinaga* and *Parantica*, and the pierid *Aporia*. The defensive chemical compounds involved in these potential mimicry complexes are diverse. In addition to the cyanoglucosides utilized by chalcosiines, pyrrolizidine alkaloids (PAs) are well-known as being sequestered by danaines and *Aporia* (Nishida, 1995, 2002). No information about chemical defence in diurnal lymantriids is known, but their urticating hairs in abdomen may make them unpalatable to predators (Holloway *et al.*, 2001).

(B) *'Danainae' type* (Fig. 22P): suggested by the extraordinary similarities between various groups of danaine butterflies found in the tropical rain forests of South-east Asia. Alberti (1954) accommodated all the 'danaine butterfly-mimic' species in the genus *Cyclosia*, although their monophyly has yet to be tested. The long generic synonymy of *Cyclosia* (e.g. *Callamesia*, *Didina*, *Epyrgis*, *Isbarta*, *Klaboana*, *Mimeuploea* and *Pintia*) reflects how wing patterns in this genus have intrigued entomologists for over 200 years.

Four types of 'Danainae' mimetic wing patterns are recognized. The first is exhibited by the female of the insular subspecies of *Cyclosia pieridoides*, which is very similar to *Ideopsis gaura* (Horsfield, 1829) in wing pattern and size. This wing pattern is also predominant in *Idea* Fabricius, 1807 (Danainae) and shared by several papilionid species in *Graphium* Sco-

poli, 1777 and *Papilio* Linnaeus, 1758. The male of *C. pieridoides* seems to be aposematic but not mimetic with *Ideopsis*. The wing pattern of the continental subspecies of *C. pieridoides* is not assigned to any type because it appears to be an intermediate form between *Delias* pierids and *Ideopsis* danaines.

The second is called the *Ideopsis* type (not including *gaura*). This wing pattern is characterized by the long transverse stripes in each wing cell. The representative *Cyclosia* species with this wing pattern are *C. curiosa*, *C. pagenstecheri*, *C. imitans* and *C. papilionaris*.

The third type is dominated by *Parantica sita*, a large danaine species ranging throughout north-east India, Indochina, Luzon, Taiwan, southern Korea and the Japanese archipelago. *Cyclosia notabilis* from south-west China and northern Indochina is the only chalcosiine species mimicking this butterfly. This wing pattern is also shared by several sympatric Papilionidae (*Chilasa*), Nymphalidae (*Hestinalis*, *Calinaga*) and Pieridae (*Aporia*).

The fourth type refers to the diverse *Euploea* butterflies. Colour forms of *Cyclosia imitans* and *C. inornata* are possibly co-mimics with the *Euploea* core group in Thailand. *C. danaides* and its potential co-mimetic *Euploea diocletianus* are sympatric in Malaysia. The sexually dimorphic *C. midama* and *C. terpsichrois* are very accurate co-mimics with the sexually dimorphic *Euploea mulciber* in all of their sympatric areas. Interestingly, a non-*Euploea mulciber* mimetic form of *C. midama* may join another mimicry complex with *Amesia aliris* from India to Vietnam. *C. midama dolosa* is sympatric with *Euploea modesta* in Java and Bali. In addition, Endo & Kishida (1999) suspected that *Amesia apoensis* from Mindanao and Luzon may form a mimicry complex with *Euploea blossomae*.

(C) '*Delias*'-mimic type (Fig. 22R): the *Delias* pierid butterflies, with more than 200 species distributed in the Oriental and Indo-Australian regions, are among the most diverse lepidopteran genera. Their adults and larvae exhibit aposematic and mimetic colour patterns and have volatile compounds sequestered from their hostplants (e.g. Loranthaceae). Yagishita, Nakano & Morita (1993) recognized 22 species-groups of *Delias*. Of these, four are involved in mimicry complexes with chalcosiine moths. *Cyclosia pieroides* is sexually dimorphic. The male resembles some *Appias* or *Cepora* butterflies (Pieridae), while the female is extremely similar to the *Delias pasithoe* species-group. Their distributions in South-east Asia are generally congruent, but *C. pieroides* is not present in southern China and Taiwan. The male of *C. pseudospargens* is not known, while the female is very likely mimetic with *Delias blanca* in Mindanao Island. A third type of

Delias mimicry is found in the *Cadphises maculata*, *Milleria rehfoysi*, *M. okushimai* and *M. adalifa* species-groups. Their wing patterns are all characterized by black ground colour, white spots in each cell and a bright yellow inner part of the hindwing (ch. 160, 161). These chalcosiine species are mostly sympatric with the *Delias lativitta* species-group from north-east India across south-west China to Indochina. However, this type of mimicry is not present in Taiwan, where two species of this *Delias* group occur. Females of the *Pseudonyctemera dissimulata* species-group may be involved in another *Delias*-mimicking pattern. However, the male wing pattern resembles some diurnal lymantriid genera.

(D) '*Eurema*' type (Fig. 22Z-2): there are no reports of chemical defence in *Eurema* butterflies; however, this wing pattern is dominated by this genus and shared by various lepidopteran groups. Among chalcosiines, females of *Cyclosia inclusus* and *C. inclusoides* are remarkably similar to *Eurema* butterflies, while their males are mimics of some other chalcosiine groups (e.g. *Pidorus constrictus*). *Barbaroscia amabilis* has a similar wing pattern to *Eurema*, but its basal and sub-apical forewing spots and distinctive colour pattern from vertex to thorax suggest it may not belong to this mimicry complex. *Soritia zelotypia*, *Pseudoscaptisyle*, *Cryptophysophilus* and *Heterusinula* also exhibit the 'yellow/black' wing pattern. Their inner margin of forewing zone j lacks an incised notch, which is characteristic of *Eurema*, so we suspect these taxa may form another complex with Immidae, Lithosiinae (Arctiidae), Tortricidae & Noctuidae in various areas of South-east Asia.

(E) '*White-bank*' type (Fig. 22Y): this wing pattern, which is characterized by a black ground colour and a white (or light yellow) band in the forewing, is very commonly shared by various lepidopteran families in all the biogeographical regions. Within the Chalcosiinae, various species have this feature but they do not necessarily participate in the same mimicry complex because of their allopatric distribution and polymorphism. Among these groups, the so-called *Pidorus* is the best known assemblage of this wing pattern. Kishida (1989a) suggested that this wing pattern in Chalcosiinae may have mimicry relationships with some diurnal lymantriids, geometrids or noctuids, but this assumption has yet to be proved.

(F) '*Milionia-mimic*' type (Fig. 22Z): the range of the diurnal *Milionia* (Geometridae, Ennominae) extends throughout South-East Asia, New Guinea and tropical Australia. They are well-known for their diverse wing shapes, colour patterns and specific host association with Podocarpaceae and Araucariaceae (Holloway *et al.*, 2001), which produces secondary compounds

with molecular structures similar to insect juvenile hormones. Each species of *Milionia* forms a different mimicry complex with various lepidopteran groups, especially Chalcosiinae and Agaristinae (Noctuidae). All species of *Eusphalera* are co-mimics with *Milionia* in Wallacea, while in Sundaland, *Milionia* mimicry is participated in by *Eucorma millionioides* and *Pidorus splendens*. *Hemiscia meeki xenia* is also an excellent mimic of an undescribed *Milionia* species from Halmahera.

(G) 'Agaristinae' type (Fig. 22Z-3): Owada & Ta (2002) suggested that *Eterusia aedea* and *E. sublutea* may form a mimicry complex with the agaristine *Scrobiger aematrix*. The wing pattern shared by them is characterized by the prominent forewing white/light yellow spots in zone e–g (ch. 139, 140) or the band in zone h (ch. 141, 142) and a broad yellow/orange area in zone k–m (ch. 158, 159). As well as in the polymorphic *Scrobiger aematrix*, this pattern is very common in other diurnal agaristine genera in South-east Asia, e.g. *Fleta* and *Crinocula*, and they all form different regional mimicry complexes with different chalcosiines. From north-east India to north Indochina, *Scrobiger aematrix* is sympatric with *Eterusia sublutea*, *E. aedea aedea*, *E. tricolor* and *E. nobuoi*. In the Malay Peninsula, Borneo, Sumatra and Java, this mimicry type is participated in by *Eucorma obliquaris*, *Fleta*, *Crinocula* and *Scrobiger proxima*. In the Philippines, *Eucorma obliquaris mindanaoensis*, an undescribed subspecies of *Eterusia risa* and an undescribed *Eusphalera* species share the same wing pattern. Adults of diurnal agaristines release pungent fluids from the prothorax and the tips of the legs when captured. The compounds, however, have not been analysed, so we have no indication as to how many chemical defensive mechanisms are involved other than cyanoglucosides in Chalcosiinae.

(H) 'Nyctemera' type: this type of wing pattern resembles that of the diverse arctiid genus *Nyctemera*. The *Corma zenotia* species-group resembles the *Nyctemera adverta* species-group in the white ground colour and black spots in zone f–g and zone j of the forewing, and the yellow abdomen with black pleural spots. Other mimicry with *Nyctemera* is exhibited by the *Pseudonyctemera marginale* and *Chalcosia nyctemeroides* species-groups from the Philippines, Java, Sumatra and Lesser Sunda Islands. The female of *Psaphis azurea* may also participate in this mimicry complex.

(I) 'Dysphania' type: *Dysphania* is a relatively diverse geometrid genus in South-East Asia. The *Psaphis euschmoides* species-group has extremely similar size, wing shape and wing pattern to *Dysphania*. In north-east India, south-west China and north Vietnam, these two genera are sympatric with another co-mimic

genus, *Chamtala* of Epicopeiidae. Owada & Ta (2002) suggested that *Gaena maculata* (Cicadidae), *Pyrops astarte* (Fulgoridae), *Nikaea longipennis* (Arctiidae, Arctiinae) and *Episteme maculatrix* (Noctuidae, Agaristinae) belong to the same mimicry complex as *Dysphania militaris*. However, these species lack the large yellow area of the forewing, so their mimicry relationships need further investigation.

(J) 'Lithosiinae-mimic' type: this type occurs in *Phlebohecta* and *Scotopais tristis*, where the forewings are rather elongated and unicoloured and the 'neck' (patagia and parapatagia) is usually orange or yellow.

(K) 'Wasp-mimic' or 'Syntomini-mimic' type: the 'wasp-mimic' pattern is widely shared by many lepidopteran families, but such resemblance apparently has multiple origins. In the Chalcosiinae at least two groups, e.g. *Trypanophora* and *Thaumastophleps*, belong to this type.

(L) 'Asota' type (Fig. 22A, B): *Asota* (Noctuidae s.l., Aganainae) is very abundant in various areas of South-East Asia. This type of wing pattern is characteristic by black spots with yellow ground colour at forewing zone a–b, and black or grey patches scattered in the major wing cells. The only chalcosiine genus demonstrating this pattern is *Philopator*, which has three known species ranging throughout India, south-west China and northern Vietnam. The other lepidopteran groups involved in this mimicry complex are Geometridae (Ennominae) and Crambidae (Pyraustinae).

(M) 'Damias' type (Fig. 22O): the diurnal *Damias* (Arctiidae, Lithosiinae) comprises about two dozen species widely distributed in Wallacea, the Philippines and Melanesia. Their wing patterns vary with species-group; all are characterized by several large bright colour patches (red, yellow, white) with black or white background colour. Holloway (1984) first noted the potential mimicry complexes dominated by this genus. The chalcosiine groups relevant to this mimicry type are *Hadriionella*, *Caprima* and *Aphantcephala*. Additionally, various species of Geometridae (Ennominae), Callidulidae and Immidae may participate in these complexes and are sympatrically distributed in New Guinea and its surrounding islands.

(N) 'Herpidia' type (Fig. 22H): this is characterized by a white/light yellow forewing band and a red/orange stripe running from the tornus to base of hindwing. The males of the sexually dimorphic *Herpidia* and *Watermenia* and the monomorphic *Pidorus miles* share this type of wing pattern from north-east India to north Indochina.

(O) 'Rhodopsona' type-I (Fig. 22Z-1): *Rhodopsona costata* and *R. bocki* are partly sympatric in north Indochina, while *R. bocki* extends into the Malay Pen-

insula. Their prominent red costal stripe running from the subapical termen along the costa to the wing base may suggest a mimicry group with the unrelated *Retina* from southern China to Indochina.

(P) '*Rhodopsona*' type-II: the wing pattern of *Rhodopsona rubiginosa* has a distinct black transverse line from the wing base to the middle of the CuA2 cell, red forewing ground colour and a wholly black hindwing. This type is shared by several sympatric diurnal lithosiine arctiids and pyraustine crambids in eastern China.

(Q) '*Rhodopsona*' type-III: in the subalpine mountains of Taiwan, *Rhodopsona marginata* and *R. rutila* are locally common. Both have a reddish orange forewing and hindwing with black margins. This wing pattern is shared by the sympatric *Formozygaena shibatai* and *F. kishidai*.

(R) '*Troidini*' type: the *Gynautocera papilionaris* species-group is often considered to be co-mimic of *Troides* birdwing butterflies. However, this is doubtful because the moths lack the characteristic yellow hindwings of *Troides*. However, several *Atrophaneura* species in north-east India, north Thailand and south-west China may possibly be candidates as the co-mimics of *Gynautocera* because of their similar colour patterns and flight in forests. *Troides dohertyi* (= *T. rhadamanthus dohertyi*), a small birdwing with a wholly black colour pattern, may form a mimicry group with the subspecies of *Gynautocera philomera* on Talaut Island.

(S) '*Unassigned*' type: *Histia libelluloides nivosa* in northern Borneo looks very similar to the diurnal eupterotid genus *Melanothrix*. It is still questionable whether they are co-mimics because *Histia* moths are usually diurnal fliers in the canopy layer, while the biology of these eupterotid species is poorly known.

Wing scales (excluding androconial scales)

The ultrastructure of scales has phylogenetic significance in the higher systematics of Lepidoptera. Notable differences have been found between the wing scales of primitive moths (non-Glossata and Eriocraniidae) and those of other Lepidoptera (Scoble, 1992, following Kristensen, 1970). At the infra-familial level, the phylogenetic importance of scale ultrastructure has been less frequently investigated except for the iridescent scales in butterflies (Ghiradella, 1984), androconial scales in various macrolepidopteran families (summary by Scoble, 1992; Hall & Harvey, 2002b) and some specific taxa, for instance, acentropine crambids (Speidel, 1998) and lycaenid butterflies (Tilley & Eliot, 2002). In Zygaenidae, the ultrastructure of wing scales was first figured by Naumann *et al.* (1999: text-fig. 29) based on several western Palaearctic species.

Having examined the scales of the studied taxa, 12 characters assigned to the following four categories were coded.

Surface sculpture (ch. 163): the surface of the upper lamina of the scale is usually more complex than that of the smooth lower lamina. The sculpture of the upper lamina is correlated with the shape of the scale. In general, needle-like scales have no series of windows formed by longitudinal ridges and transverse cross ribs, while flat scales usually have more developed windows. Three character states are recognized. All non-zygaenid groups (including Phaudinae), *Pryeria* and *Chalcosiopsis* have no windows on the scale surface (163: 0) (Fig. 23G). The procridine outgroups, *Inouela* and *Zygaena*, have internal reticulate lamellae (163: 1) (Fig. 23C); the scales of the majority of the ingroup plus *Callizygaena* exhibit windows but not reticulate lamellae (163: 2) (Fig. 24F).

Sockets (ch. 164): scales usually arise from stalked sockets. The degree of erection of scales largely affects the degree of transparency and the overlapping of scales. Three character states are expressed by the scale socket type. The repressed type (164: 0) (Figs 23F, G, 24H–J) is widely distributed among groups. The semi-erect type (164: 1) (Fig. 23J–L) is found in various groups, e.g. Himantopteridae, Anomoetidae, *Callizygaena*, *Cadphises*, *Hampsonia*, *Watermenia*, *Herpidia*, '*Soritia*' *sevastopuloi*, *Philopator*, *Agalope*, *Formozygaena*, *Atelesia*, *Neoherpa*, *Hemichrysoptera*, *Scioclelea*, *Cyanidia*, *Thaumas-tophleps*, *Pseudopidorus*, *Anarbudas bipartita*, *Boradiopsis grisea*, *Aphantocephala* and *Euxanthopyge*. Among them, the erect type is only present in the *Agalope* genus-complex (164: 2) (Fig. 24A, B), *Thaumas-tophleps* and the *Trypanophora hyalina* species-group.

Scale arrangement (ch. 165): the wing scales of ditrysian lepidopteran groups are usually arranged in overlapping series (Fig. 24I, K). In the present study, 25 species-groups were found to have a non-overlapped wing scale arrangement (165: 1) (Fig. 24E), which makes the wing texture thinner and translucent.

Shape of scales (ch. 166–174): scales vary in shape. Downey & Allyn (1975) grouped them into three categories: piliform or hair-like, lamellar or blade-like, and 'other (variable form)'. The shape of lamellar scales (166: 0) (Fig. 24C–L) is often described as ovate, obovate, or lanceolate in the literature. Spindle-like scales (166: 1) (Fig. 24A, B) are restricted to the species-groups of *Agalope*, *Elcysma*, *Boradia* and *Achelura*. Piliform scales (Fig. 23L) are round or elliptical in cross section (166: 2). This type of scale is found in Himantopteridae, Anomoetidae, Heterogynidae and *Pryeria*. In the present study, scales are classified into two types: type I refers to the narrower lamellar scales

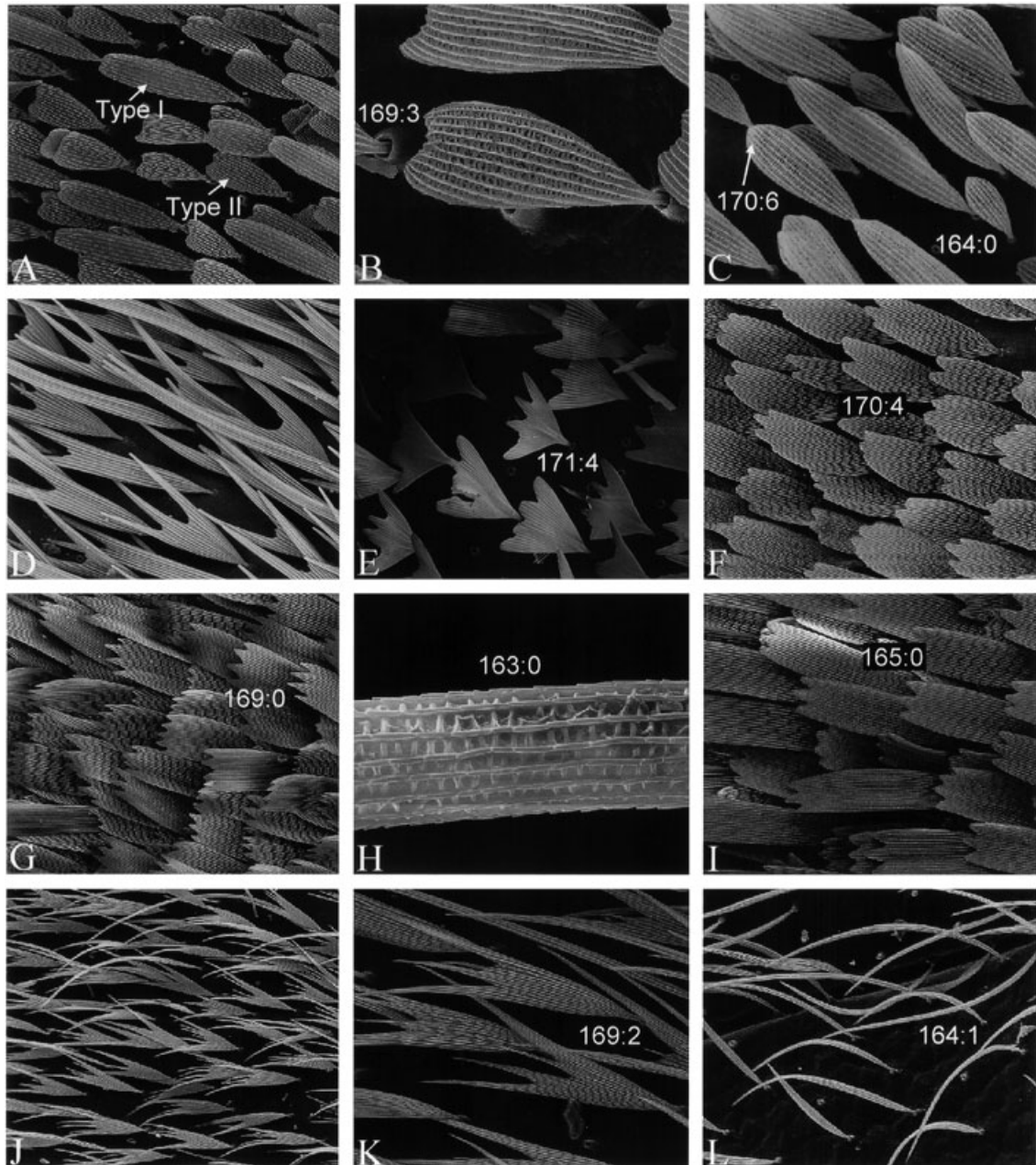


Figure 23. Scale morphology. A, B, *Adscita statices*. C, *Inouela formosensis*. D, *Phauda mimica*. E, *Callizygaena auratus*. F, *Callizygaena splendens*. G, H, *Chalcosiopsis variata*. I, *Lactura dives*. J, K, *Himantopteris fuscinervis*. L, *Anomoetes levis*.

and type II to the broader lamellar ones (see Fig. 23A). For taxa which have non-lamellar scales, both types were treated as indistinguishable. The distribution and the shapes of the two types were coded separately. In most of the studied taxa scale shape tends to be constant, while in some taxa, e.g. *Neoherpa*, *Panherpina*, *Rhodopsona*, *Herpolasia*, *Clematoessa*, *Pidorus Chalybeatus*, *Pidorus constrictus*, *Retina*, *Thaumastophleps* and the *Phlebohecta fuscescens* species-group, it varies between individuals and is not correlated with the

wing area, so that character states were treated as polymorphic.

ADULT ABDOMEN

Pregenital abdominal segments 1–7

Outgrowth of tergum (ch. 175): in most of the lepidopteran groups, the tergum of the pregenital abdomen is usually covered by dense scales. In Himantopteridae and Anomoetidae (175: 1)

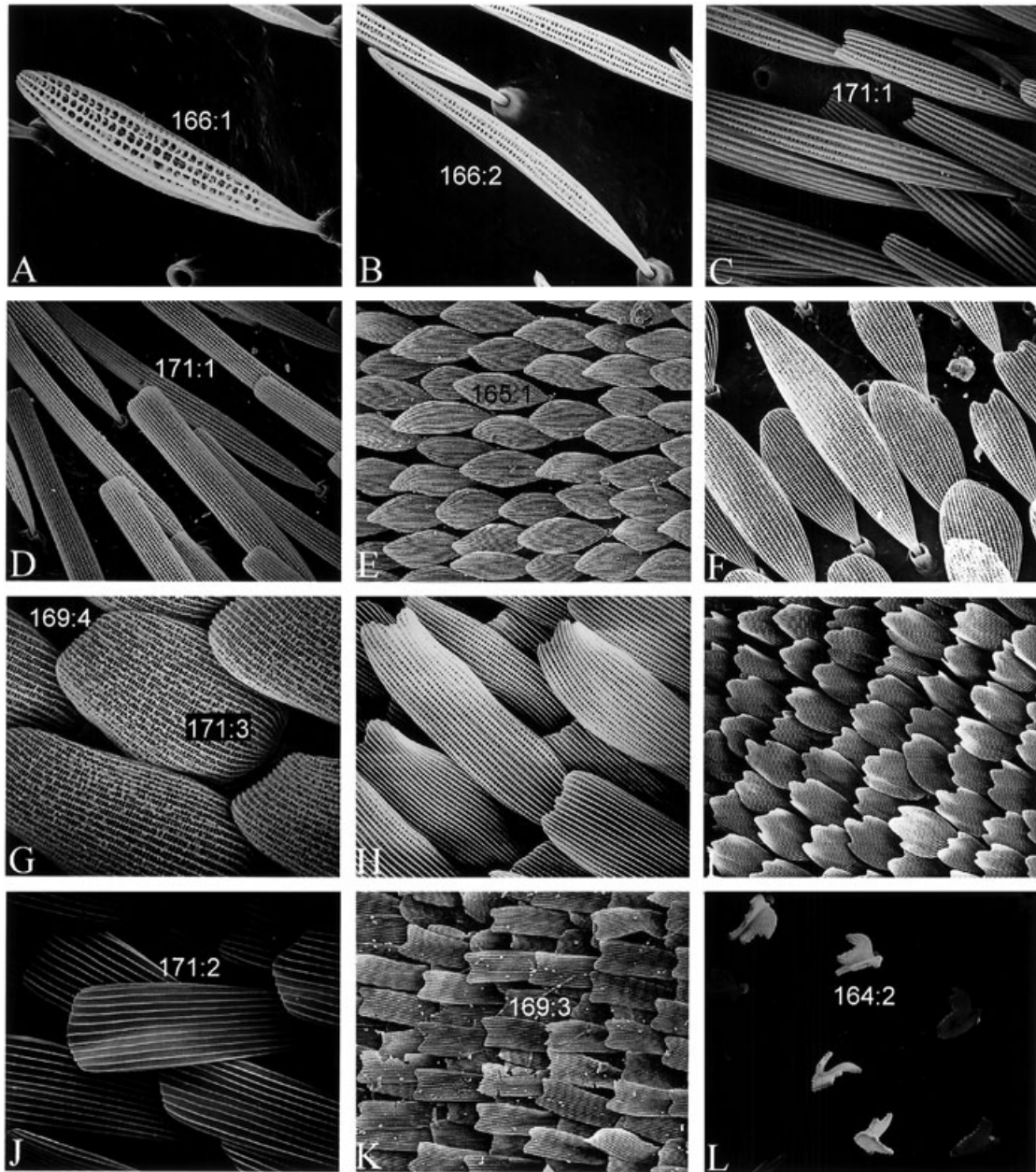


Figure 24. Scale morphology. A, *Agalope trimaculata*. B, *Elcysma westwoodi*. C, D, *Aglaope infausta*. E, *Formozygaena shibatai*. F, *Campylotes maculosus*. G, *Histia flabellicornis ultima*. H, *Pidorus atratus*. I, *Cyclosia midama*. J, *Clelea formosana*. K, *Heteropan lycaenoides*. L, *Trypanophora semihyalina*.

(Fig. 25A), tergal spinulets are consistently present in most species in the form of multiple rows. This character state is also shared by the African endemic Somabrachyidae (Fänger, 2001; H. Fänger, pers. comm., 2002).

Sternal modifications (ch. 176, 177) (Fig. 26A–F): characters of the sternal apodemes have seldom been used in phylogenetic reconstruction for generic phylogenies. In the present study, two multistate charac-

ters were obtained from the sternal apodemes and anterolateral processes (= anterosternal syndesial processes).

Sclerotization of tergum A2 (ch. 178) (Fig. 25B–H): the anterior margin of tergum A2 in the ditrysiinae is usually more sclerotized than that of the following segments, slightly ridged and firmly linked to the posterior ring of tergum A1 (= neoterium). On the dorsolateral surface of the anterior

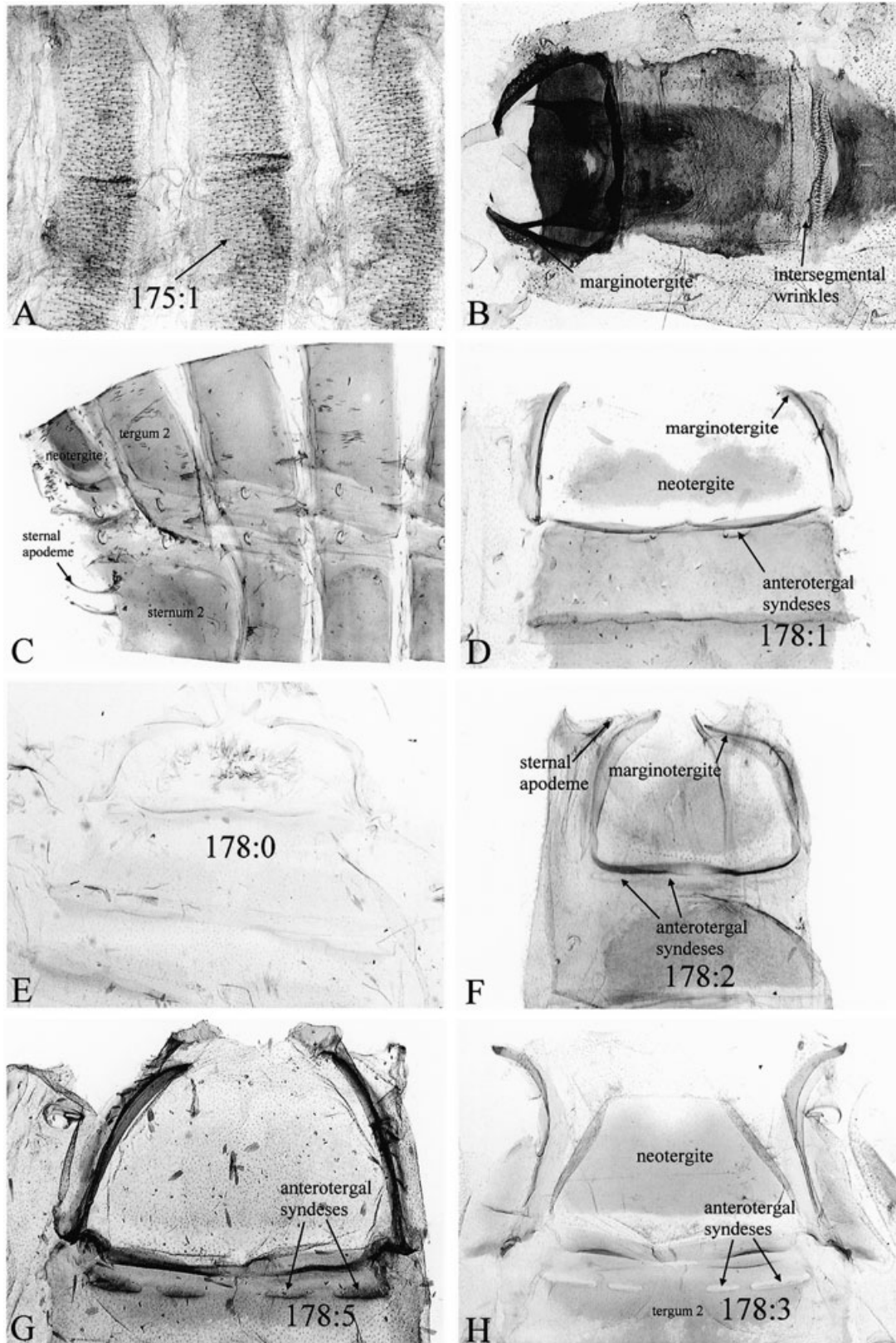


Figure 25. Anterolateral syndesemes. A, *Anomoetes levis*. B, *Heterogynis* sp. C, *Saliunca styx*. D, *Pollanisus viridipulverulenta*. E, *Cleoda syntomoides*. F, *Heteropan alberti*. G, *Pompelon marginale*. H, *Chalcosia* sp. cf. *argentata*.

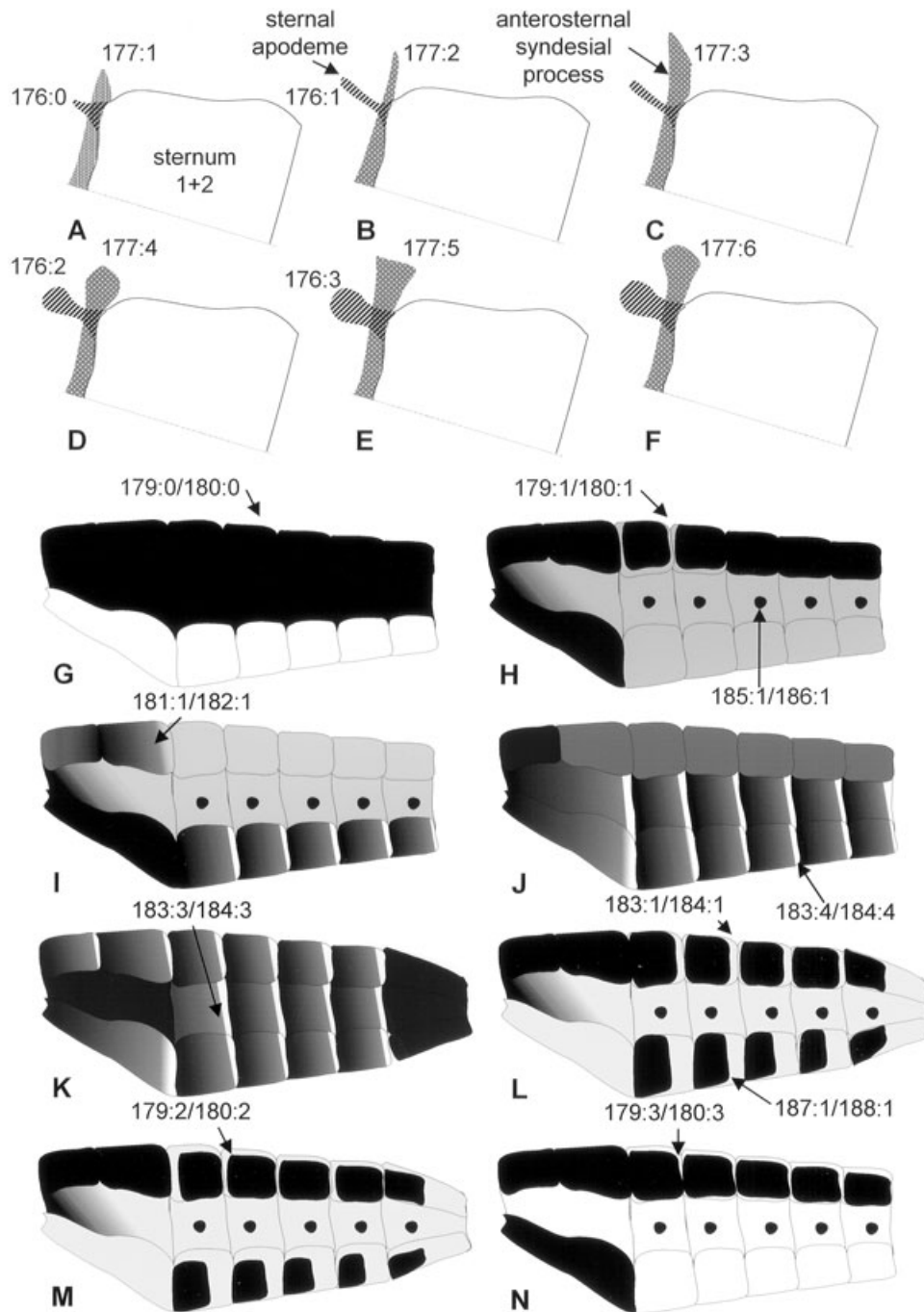


Figure 26. Stylized drawings of the characters of pregenital abdominal segments. A–F, sternal apodemes and anterosternal syndesial process. G–N, colour patterns of abdomen (ch. 179–188).

margin of A2, a paired semi-translucent structure which is the result of weaker sclerotization, termed the 'anterotergal syndesis' (Fänger *et al.*, 2002; H. Fänger, unpubl. data), is found in most taxa of the ingroup with several different character states. The function of these syndeses in Zygaenidae is not yet clear.

Colour patterns of abdomen (ch. 179–188) (Fig. 26G–N). Like many other aposematic and mimetic Lepidoptera, the colour pattern on the abdomens of Chalcosiinae is particularly interesting due to the variations caused by sexual dimorphism, polymorphism and high diversity. According to their disposition on the abdominal segments, the colour patterns

can be separated into tergal, pleural and sternal elements. Each of the elements can be further divided into anteromedial and posterior regions.

The eighth abdominal segment

The majority of lepidopteran insects have a rather simple eighth abdominal segment; that is, the posterior margins of eighth tergite and the sternite are attenuate, retuse or truncate and without special modifications. The taxonomic value and phylogenetic significance of various kinds of modification of this segment have been reported from various lepidopteran families, e.g. Riodinidae (Hall, 2002a, b; Hall & Harvey, 2001a, b, 2002a, b, c), Notodontidae (Miller, 1991), Drepanidae (Holloway, 1998) and Saturniidae (Nässig, 2002; Decaëns & Herbin, 2002). The eighth abdominal segment of chalcosiine moths was first reported by Hampson (1892: 247); however, he mis-interpreted the structure of the 'clasper' due to the extraordinary similarity between the specialized sternite and the typical valval shape of the male genitalia. Bethune-Baker (1915), having examined a *Eusphalera* species, correctly described the copulatory organ of this genus as incorporating the specialized sternal arms. More recently, the systematic value of the specialized eighth abdominal segment has been amply demonstrated (e.g. Inoue, 1987b, 1991; Owada, 1989, 1992b, 1996; Owada & Horie, 1999, 2002b; Owada *et al.*, 1999; Yen, 1996, 2002, 2003a, b; Yen & Yang, 1997, 1998). In this section, the characters obtained from this segment are partitioned into the following categories.

Relative position between A8 and male genitalia (ch. 189): relative positions of the male genitalia and the eighth abdominal segment have four observed conditions: completely exposed (especially part of the valvae) (189: 0), partly exposed (189: 1), concealed by a 'normal' eighth segment (189: 2) and completely concealed by the specialized eighth segment (189: 3). Nevertheless, the condition in which the genitalia are concealed by the abdominal segment is more likely derived independently via two evolutionary routes. The first hypothesis is that the genitalia are completely covered by the elongated eighth abdominal segment, and that the valval part of the genitalia can be everted to conduct copulation. This hypothesis is based on observations on *Cyclosia*, *Rhodopsona* and related taxa. The second hypothesis is that the genitalia might have been greatly reduced, the whole structure thereby concealed by the elongated and specialized eighth tergite and sternite. These two hypotheses lead to the division of the 'concealed' condition into two different character states.

Relative length of the eighth tergite and sternite (ch. 190): it is difficult to judge the real length of a segment

when various projections or emarginations are inconsistently present. To 'standardize' the estimation, we excluded any caudal projections of tergite or sternite in measurements. Six character states are recognized for this character.

Shape of the eighth tergite (ch. 191–195): characters obtained from the tergite are very complex. We have created five, describing the variations of the hind margin and all the modifications derived from this sclerite. Nine character states are recognized for the medial part of the hind margin (191) (Fig. 27A). Among these, single projection (191: 7), two projections (191: 8) and multiple projections (191: 9) are defined for *Soritia moerens*, the *Trypanophora semihyalina* species-group and *Pidorus circinata* and *P. yayoiiae*, respectively. These projections are not immediately derived from the posterolateral margin so they were treated separately as part of ch. 193 and 194.

In *Campylotes*, *Neoherpa* and *Panherpina*, a large posterior extension from the tergite is present (192: 1) (Fig. 27D). This usually has a bifurcate, downcurved and pointed apex that is similar to the uncus of the male genitalia. Nine types of latero-posterior projection (193) (Fig. 27D) are found in the ingroup, defined by the degree of arching. Character 194 (Fig. 27A) accommodates six states that describe the relative length of the bilobed projections to the tergite. Unlike the projections defined in character 193, these are not derived from the posterolateral corners of the tergite.

Character 195 (Fig. 27A) includes seven character states describing the general outline (dorsal view) of the tergite. All of the outgroups and many members (e.g. *Aglaope*, *Achelura* and the *Soritia pulchella* species-group) of the ingroup have the most generalized type, in which the tergite is attenuated towards the caudal end (195: 0). The second type (195: 1) is defined for the rectangular tergite found in many ingroup members, e.g. *Cadphises*, *Watermenia*, *Herpidia*, *Campylotes*, *Amesia* and *Eterusia repleta*. The third type (195: 2) tends to narrow towards the caudal end but with a retuse hind margin. Six species-groups of *Pidorus* (e.g. *P. glaucopis*, *P. circinata*, *P. splendens*, *P. cyrtus*, *P. chalybeatus*) and *Eterusia binotata*, *Chalcosia zehma*, *Pseudopidorus*, *Neochalcosia* and *Gynaetocera* share this feature. The fourth type (195: 3) is similar to the third but with a more prominent concave margin. The taxa which bear this character state are *Pidorus culoti*, *P. constrictus*, *Retina*, *Erasmia*, *Eucorma*, *Phlebohecta*, *Soritia moerens* and *Allocaprima duganga*. The fifth type (195: 4) is unique to the *Trypanophora semihyalina* species-group, in which the tergite has a paired auriculate process in addition to the medial bifurcate projection. The genus *Pompelona* has a unique tergal shape, in which the lat-

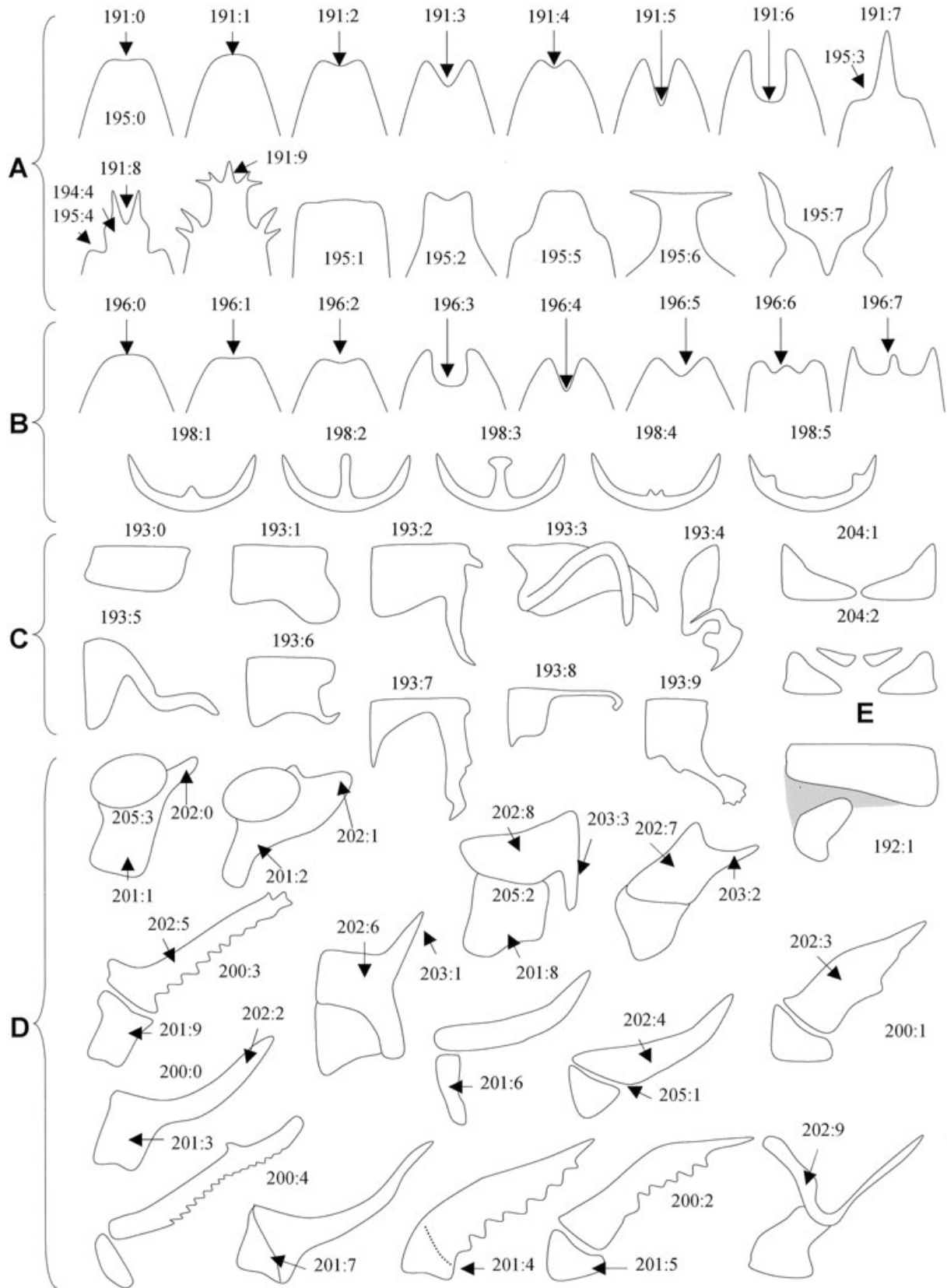


Figure 27. Stylized drawings of selected character states of the eighth abdominal segment. A, C, tergite. B, D, E, sternite.

eral margins are incised and the caudal margin is truncate (195: 5). The sixth type, in which the lateral margins of the tergite are usually incised near the anterior end (195: 6), is widely distributed among the ingroup taxa, e.g. *Rhodopsona marginata*, *R. matsumotoi*, *Pidorus fasciatus*, *Soritia bicolor*, *Barbaroscia*, *Eterusia vitessa*, *Milleria adalifa* and *Histia*. The seventh type is only represented by the *Eterusia tricolor* and *E. subcyanea* species-groups. Their tergal shape is in general narrower towards the caudal end, while the incision of the lateral margins is much stronger than in 195: 5.

Hind margin of the eighth sternite (ch. 196) (Fig. 27B): compared with those of the tergite, the 13 characters obtained from the sternite are even more complex. Like character 191, definition of the hind margin is restricted to the middle part of the caudal end.

Serration of inner margin of the eighth sternal arms (ch. 200) (Fig. 27D): sternal arms are only present in 62 species-groups of the ingroup, so lack of this character in the other taxa is treated as an inapplicable character, and coded using '?'.

Orientation of medial process of sternal extension (ch. 203) (Fig. 27D): this feature is the process which arises from the middle of posterior margin of sternal arms.

MALE GENITALIA

Various components of the male genitalia of Lepidoptera are not fully homologized. In particular, it has been difficult to assign several sclerotized parts to the particular segments from which they might have been derived. In this section, the characters of male genitalia (ch. 209–271) are separated into the following categories.

Uncus and subscaphium

Articulation between uncus and tegumen (ch. 209) (Fig. 29A): articulation and fusion between uncus and tegumen varies between different lepidopteran groups. We coded the articulated type as '0' because this condition is most widely shared by the outgroup taxa and part of the ingroup. In the partly fused type the boundary between uncus and tegumen is visible, and the laterobasal angles of the uncus are not fused with the tegumen.

Apex of uncus (ch. 212, 213) (Fig. 29B, C): an uncus with a long, slender, setose, curved main body with a pointed apex was considered apomorphic for Cyclosiini (Alberti, 1954). However, this kind of uncus is also shared by most species of Procridinae and a part of the *Agalope*-genus complex (e.g. *Elcysma*). It is not comparable with the unci of the majority of taxa, so we did

not code the whole shape of the uncus as a character. Features of the apex are treated as two distinct characters for taxa which have an articulated uncus and those with a partly fused and fused uncus and tegumen (see below). In total, six states are recognized for the articulated unci, and nine for the fused uncus + tegumen.

Socii (ch. 217): Owada & Horie (2002b) considered that in *Pidorus*, *Soritia* and *Eterusia* the uncus is reduced and the bilateral protuberances with long setae should be interpreted as 'tegumen and socii' or 'socii'. According to Klots's (1970) definition, the socius is a structure that is weakly sclerotized, paired, hairy, sometimes petiolate, on the caudal margin of the tegumen and ventrad of the base of the uncus. He also indicated that the so-called socii of various lepidopteran groups may not be homologous. We do not consider the post-tegumenal membranous structure as socii because transformation series of the related characters (209–216, 291–223) have shown that the 'socii' claimed by Owada & Horie are more likely to be a very membranous and fused tegumen and uncus. In the present study, the only recognized socii are found in *Chalcosiopsis melli* (see Diakonoff, 1978, Fig. 27).

Subscaphium (ch. 218): Klots (1970) defined the subscaphium as 'sclerotization of [the] ventral part of the tuba analis'. We therefore included all the conditions of sclerotization into this character.

Tegumen, its apodemes and derived sclerites

General outlines of dorsum of tegumen (ch. 219–221) (Fig. 29D): the general outline and shape of the dorsum of the tegumen are allocated three characters. Four states are recognized for the connection between both sides of the tegumen. In the outgroups and in most of the ingroup, the tegumen is a continuous, ring-like structure (219: 0).

General outline of hind margin (ch. 222) (Fig. 29D): this character focuses on the shape of the medial part of the posterior margin and is dependent upon the general outline of the tegumen linked to an articulated uncus. Therefore, all taxa with a fused tegumen and uncus were coded as '?'.

Posterior tegumenal projections (ch. 224): all the posterior tegumenal projections are treated within two distinct characters (see also ch. 225) according to their derivation and position relative to the inner margin of the tegumen. Ch. 224 is defined for a transformation series observed from the *Cadphises*–*Aglaope*–*Agalope* assemblage. *Cadphises* has paired, wrinkled and weakly sclerotized protuberances arising from the interior fold of the tegumen (224: 1) (Figs 30B, 32A), described as the 'fultura inferior' by Owada & Horie

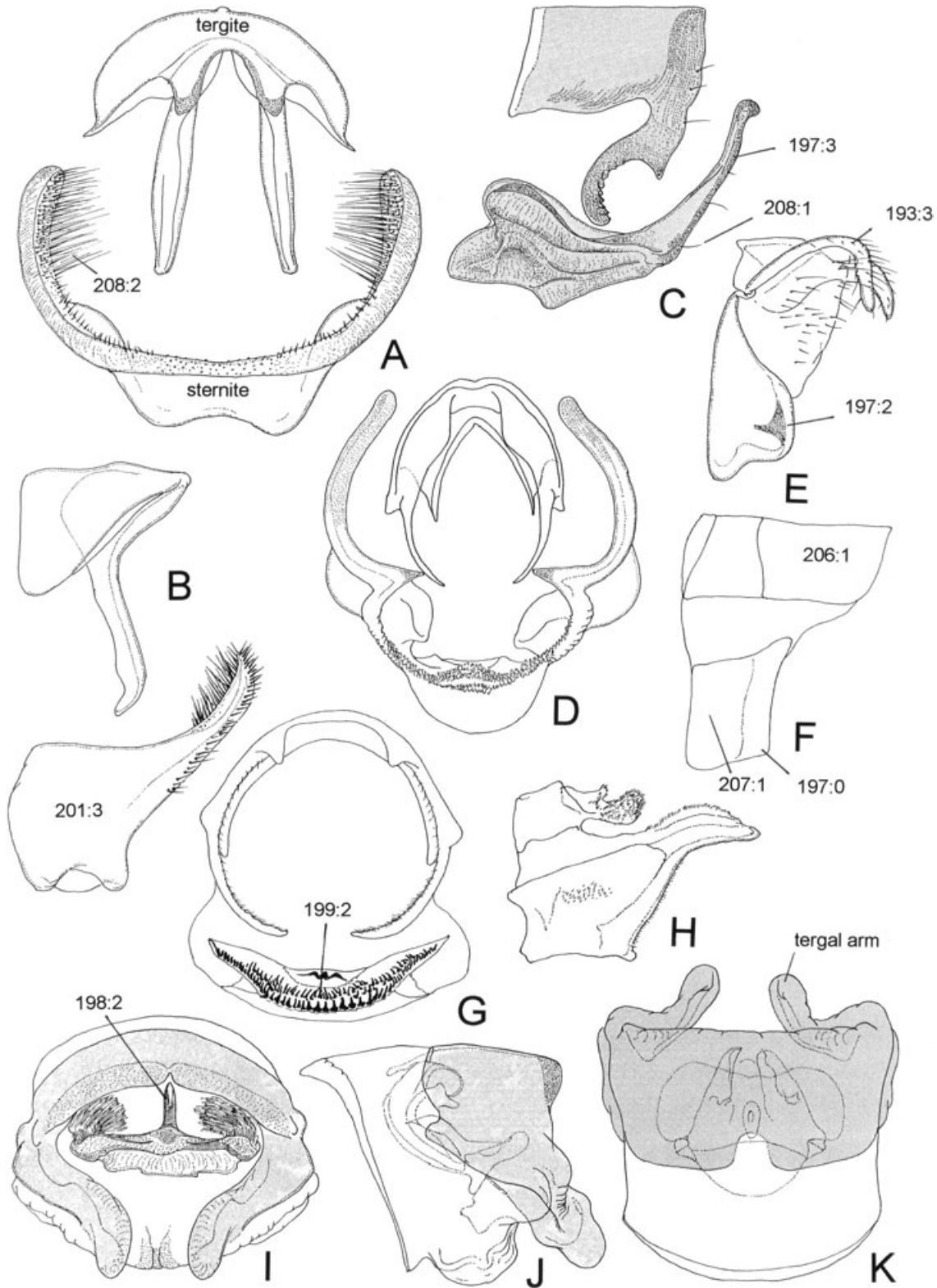


Figure 28. Eighth abdominal segment in the males of Chalcosiinae. A, *Soritia azurea*, posterior view. B, ditto, lateral view. C, *Eusphalera regina*, lateral view. D, ditto, posterior view. E, '*Pidorus*' *fasciatua*, lateral view. F, *Herpidia eupoma*, lateral view. G, *Retina rubrivitta*, posterior view. H, *Pidorus chalybeatus*, lateral view. I, *Amesia sanguiflua*, posterior view. J, ditto, lateral view. K, ditto dorsal view.

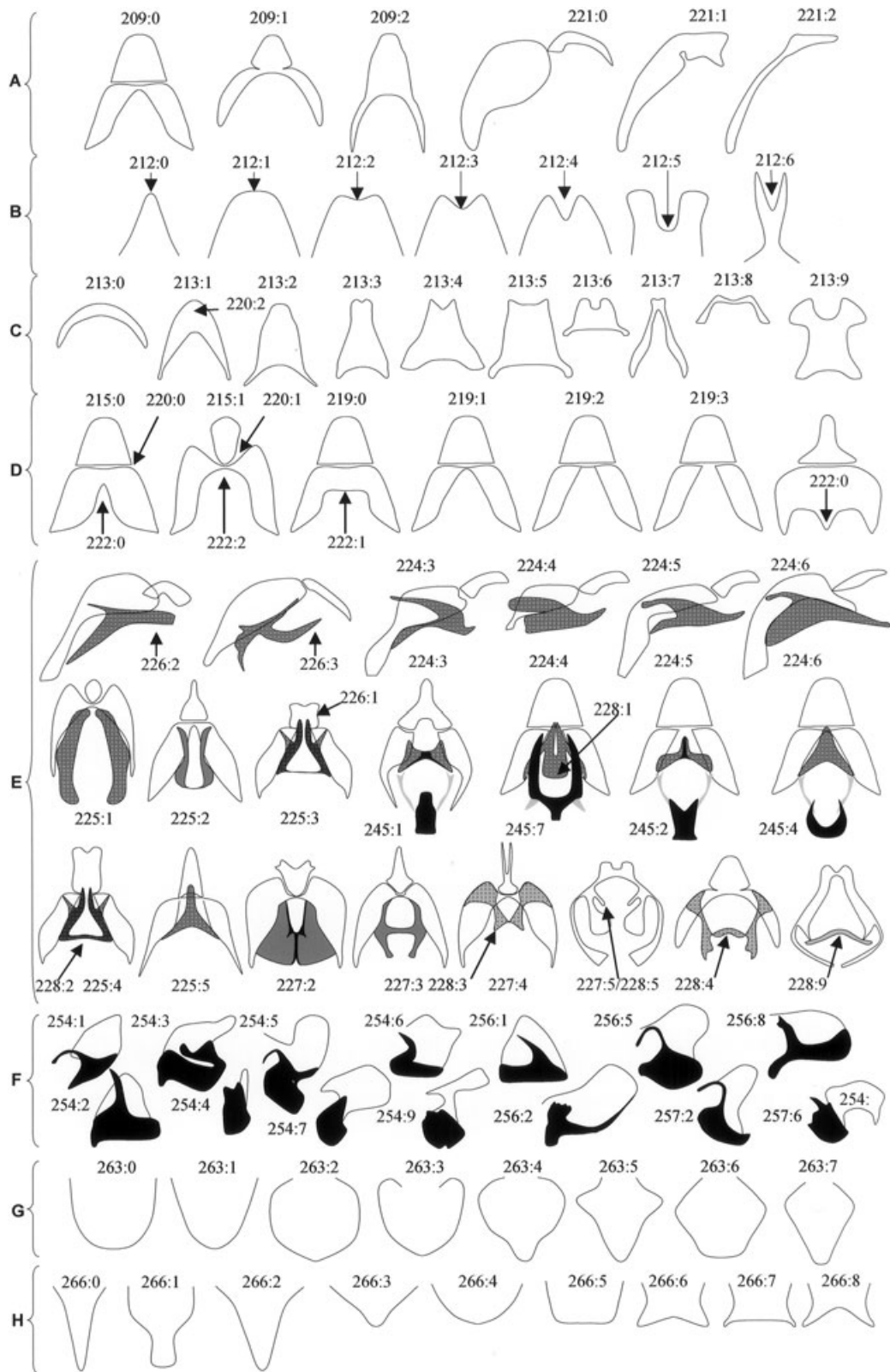


Figure 29. Stylized drawings of selected characters of male genitalia. A–D, uncus–tegumen complex. E, tegumen (white), derived protuberances (light grey), apodemes (dark grey) and juxta (black). F, valvae (black: sacculus; white: cucullus). G, vinculum. H, saccus.

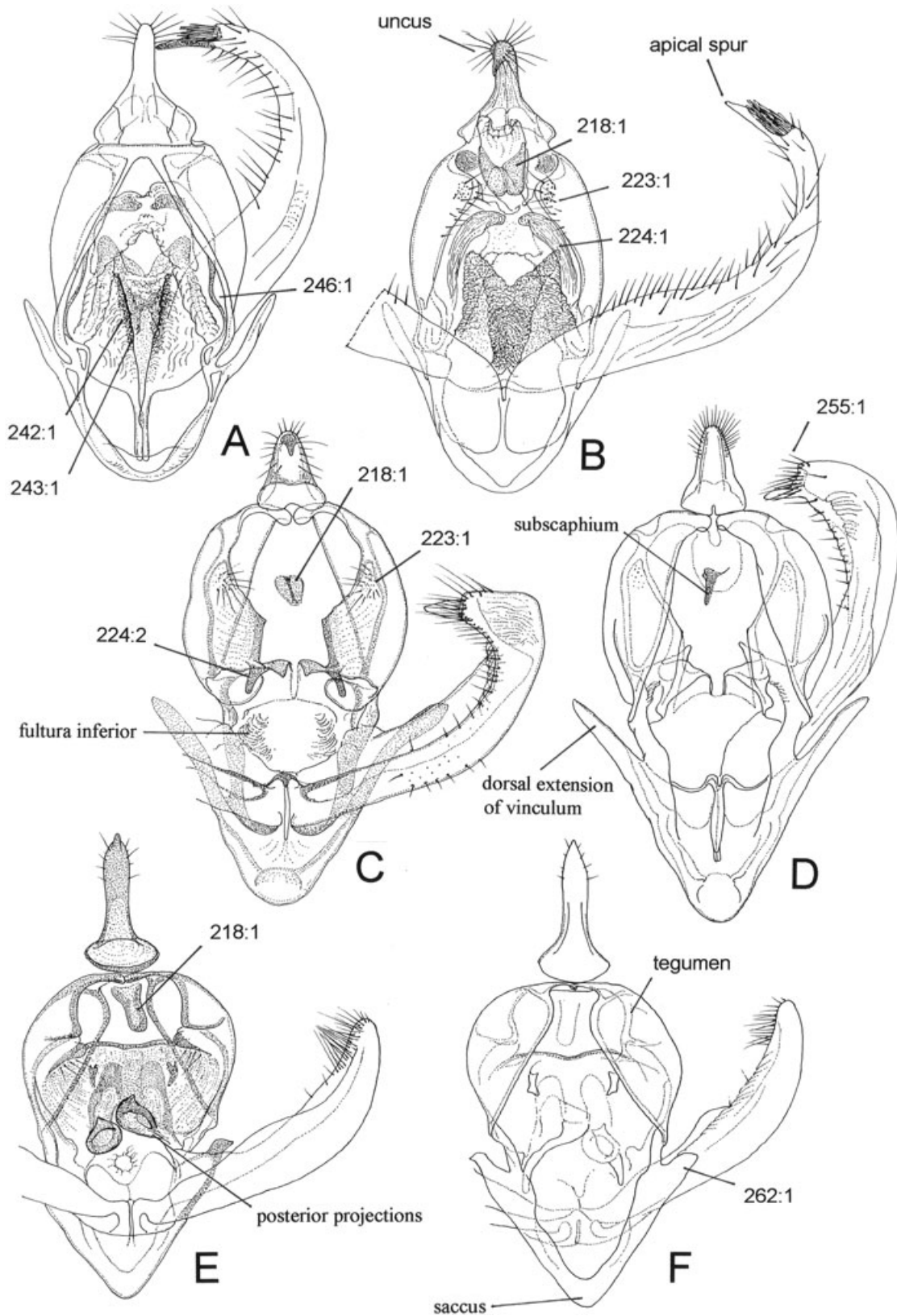


Figure 30. Male genitalia of Chalcosiinae (aedeagus removed). A, *Cadphises moorei*, dorsal view. B, ditto, ventral view. C, *Watermenia bifasciata*, ventral view. D, ditto, dorsal view. E, *Soritia sevastopuloi*, ventral view. F, ditto, dorsal view.

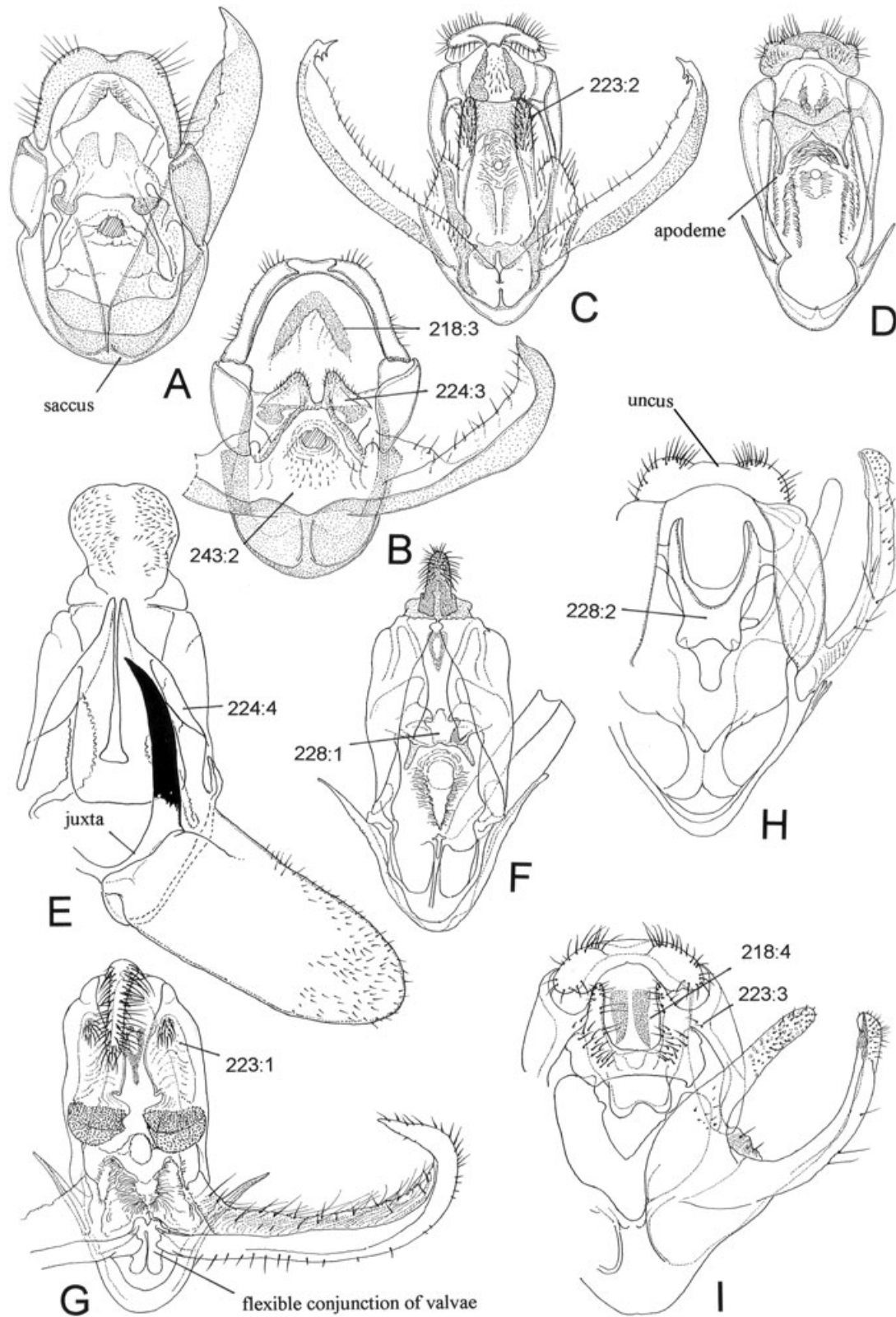


Figure 31. Male genitalia of Chalcosiinae (aedeagus removed). A, *Aglaope infausta*, dorsal view. B, ditto, ventral view. C, *Philopator basimaculata*, ventral view. D, ditto, dorsal view. E, *Boradia carneola*, ventral view. F, *Hampsonia ueharai*, dorsal view. G, ditto, ventral view. H, *Atelesia nivosa*, dorsal view. I, ditto, ventral view.

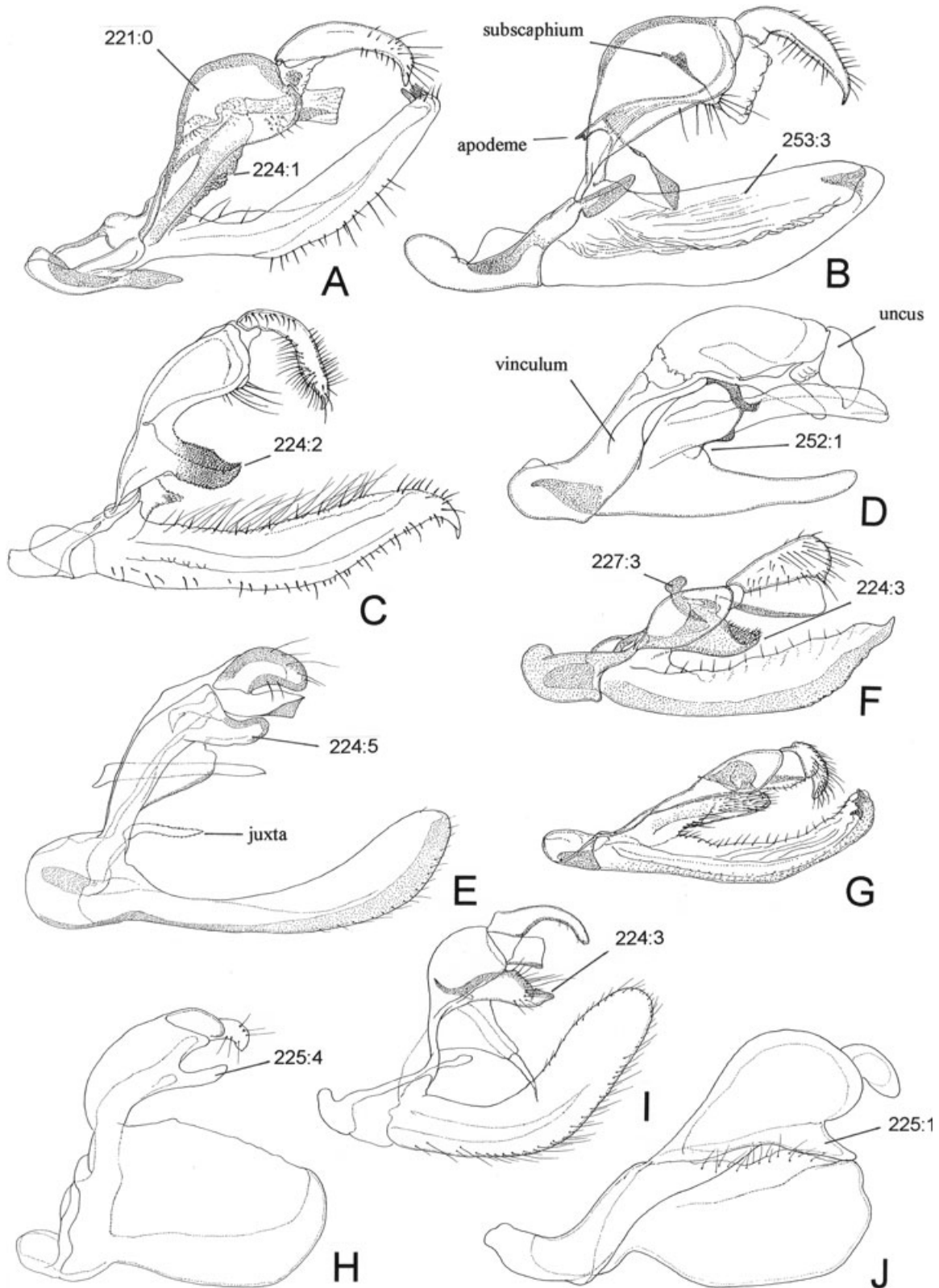


Figure 32. Male genitalia of Chalcosiinae (lateral view). A, *Cadphises moorei*. B, *Herpidia eupoma*. C, *Hampsonia ueharai*. D, *Atelesia nivosa*. E, *Elcysma westwoodi*. F, *Aglaope infausta*. G, *Philopator basimaculata*. H, *Panherpina basiflava*. I, *Aglaope trimacula*. J, *Campylotes maculosus*.

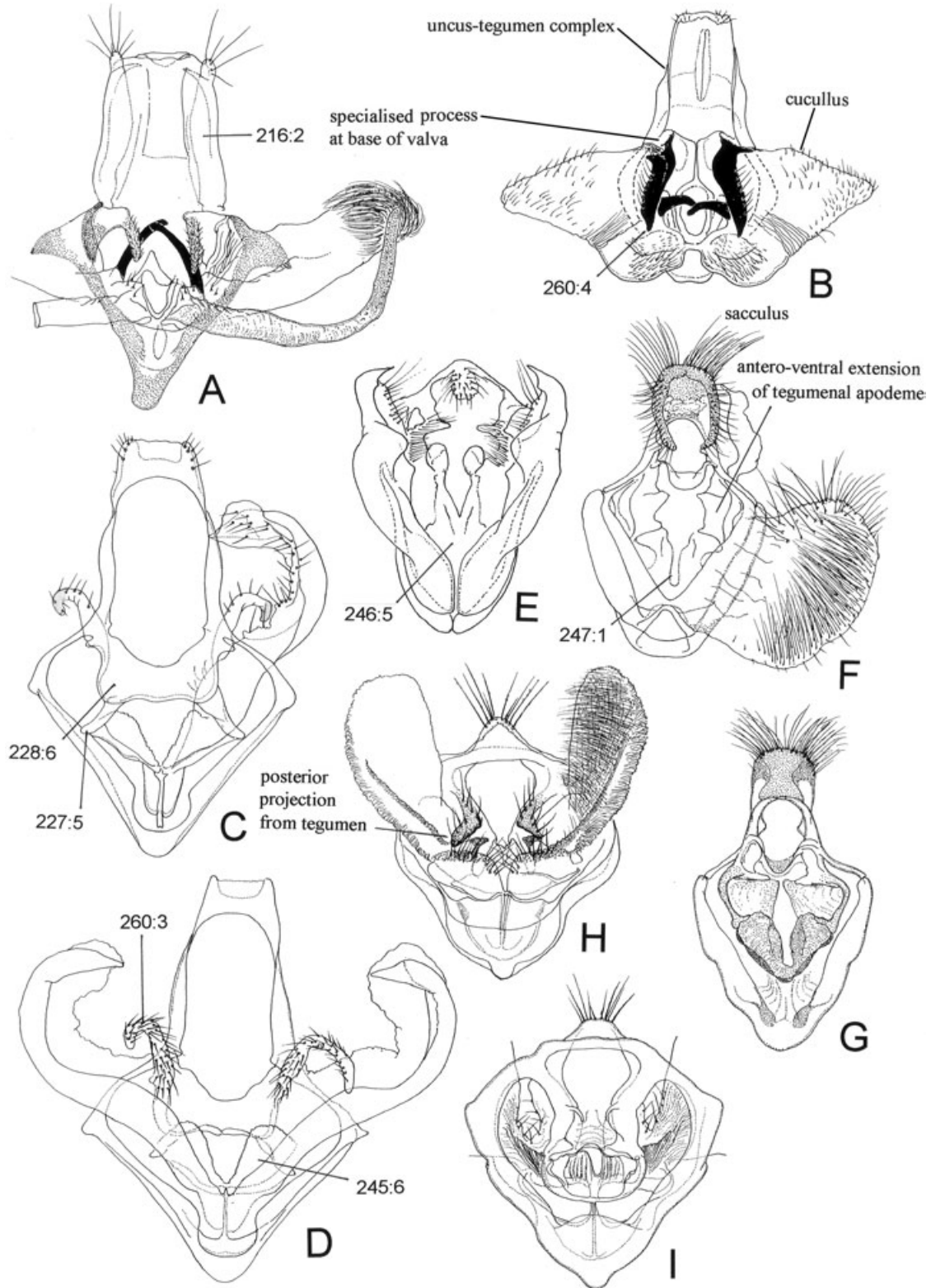


Figure 33. Male genitalia of Chalcosiinae. A, *Thaumastophleps expansa*, ventral view with left valva removed. B, *Sciodoclea modesta*, ventral view. C, *Hadrionella spectabilis*, dorsal view. D, ditto, ventral view. E, *Herpolasia augarra*, ventral view. F, *Phlebohecta fuscescens*, ventral view. G, ditto, dorsal view with valvae removed. H, *Retina rubrivitta*, ventral view. I, ditto, dorsal view with valvae omitted.

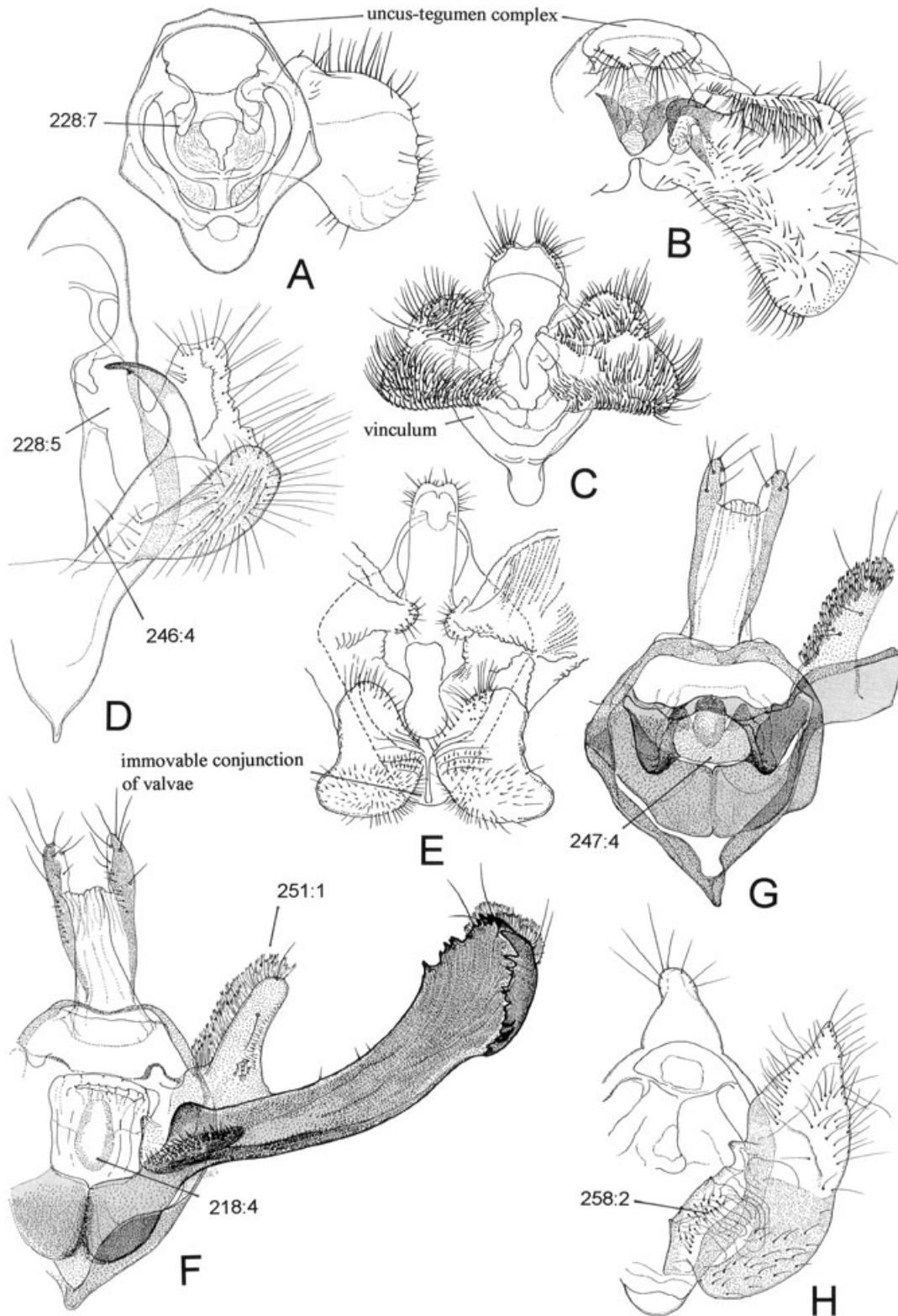


Figure 34. Male genitalia of Chalcosiinae. A, *Amesia sanguiflua*, dorsal view with right valva removed. B, ditto, ventral view. C, *Amesia aliris*, ventral view. D, *Pidorus atratus*, ventral view. E, *Gynautocera papilionaris*, ventral view with valvae omitted. F, *Eterusia repleta*, ventral with left valva removed. G, ditto, dorsal view with valvae omitted. H, *Pseudopidorus fasciatus*, ventral view.

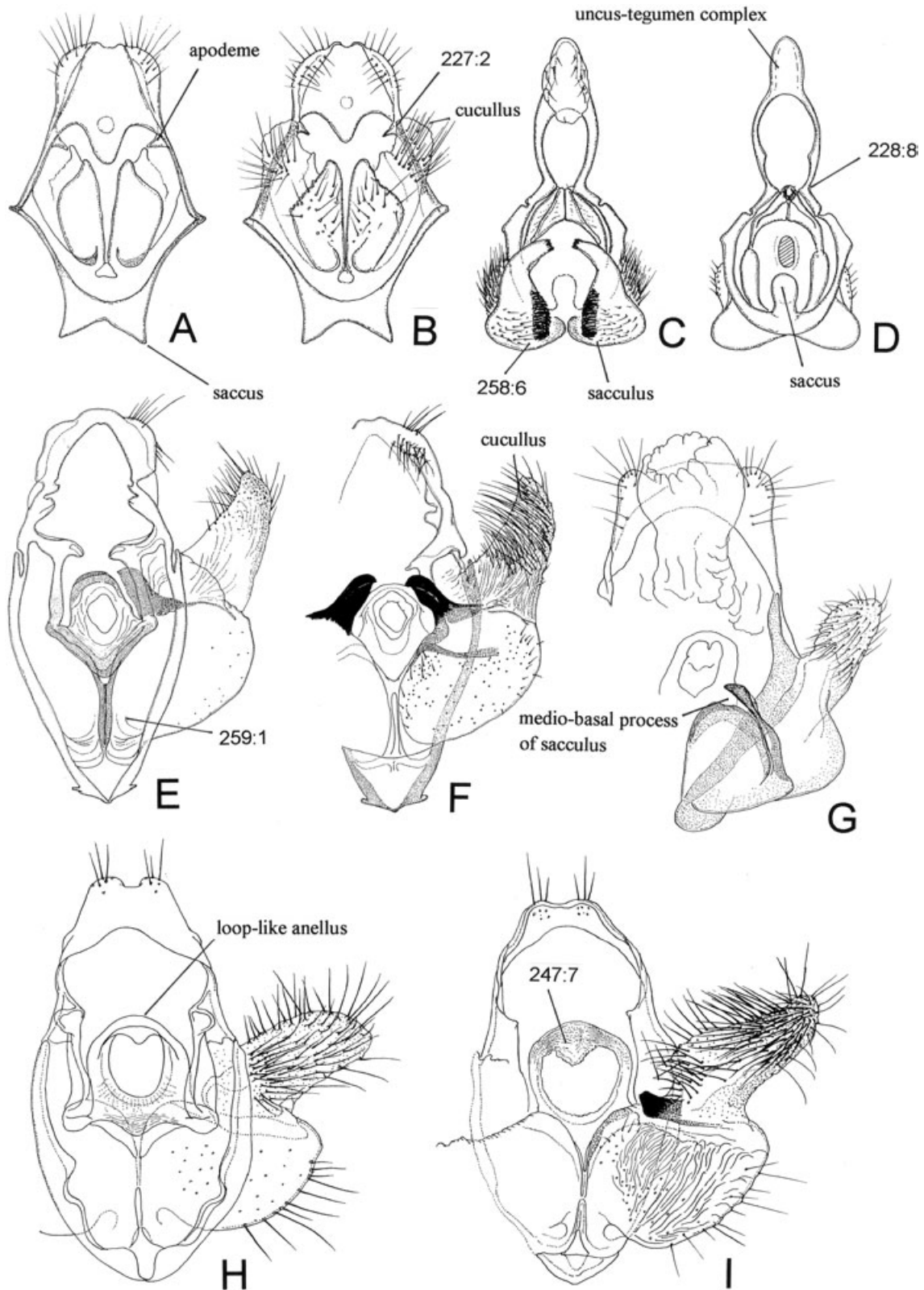


Figure 35. Male genitalia of Chalcosiinae. A, *Soritia propimarginata*, dorsal view. B, ditto, ventral view. C, *Soritia elizabethae*, ventral view. D, ditto, dorsal view. E, *Eterusia vitessa*, dorsal view. F, ditto, ventral view. G, *Eterusia aeda formosana*, ventral view. H, *Eterusia risa*, dorsal view. I, ditto, ventral view.

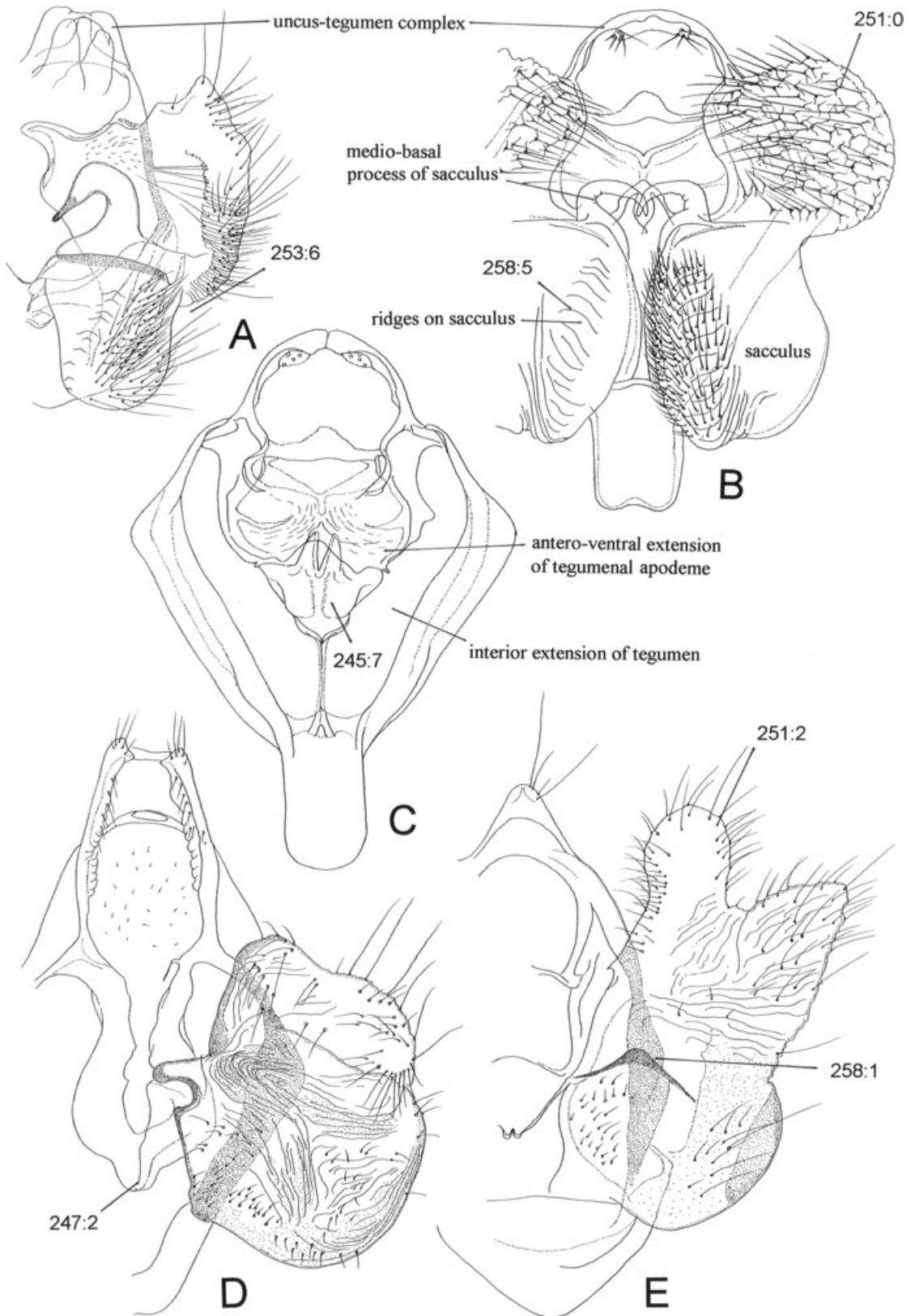


Figure 36. Male genitalia of Chalcosiinae. A, *Chalcosia diana*, ventral view. B, *Eusphalera regina*, ventral view. C, ditto, dorsal view. D, *Neochalcosia remoata*, ventral view. E, *Chalcosia zehma*, ventral view.

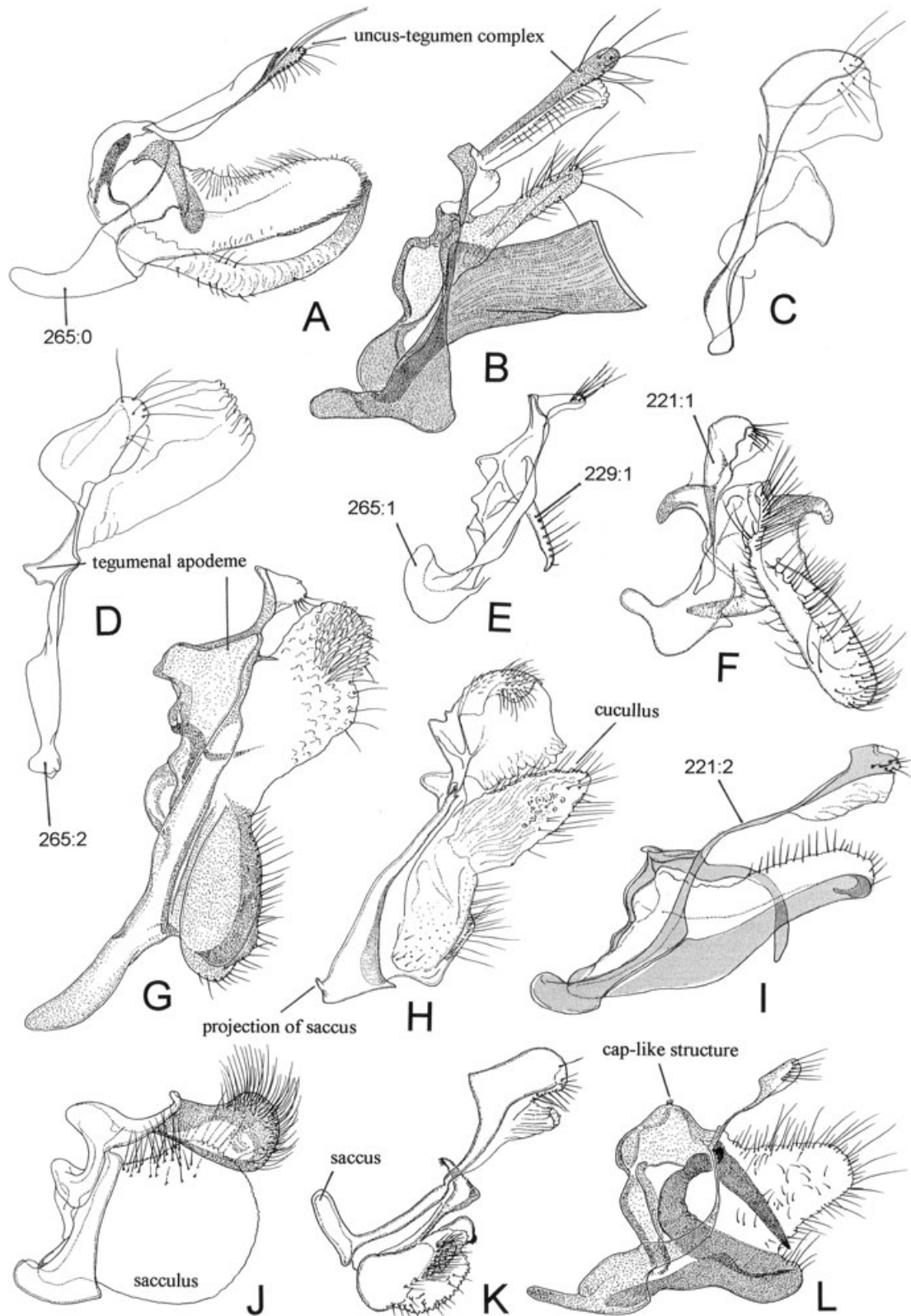


Figure 37. Male genitalia of Chalcosiinae (lateral view). A, *Thaumastophleps expansa*. B, *Eterusia repleta*. C, *Pseudopidorus fasciatus*. D, *Eterusia aedeae formosana*. E, *Retina rubrivitta*. F, *Amesia sanguiflua*. G, *Eusphalera regina*. H, *Eterusia vitessa*. I, *Hadrionella spectabilis*. J, *Phlebohecta fuscescens*. K, *Soritia elizabethae*. L, *Caprima gelida*.

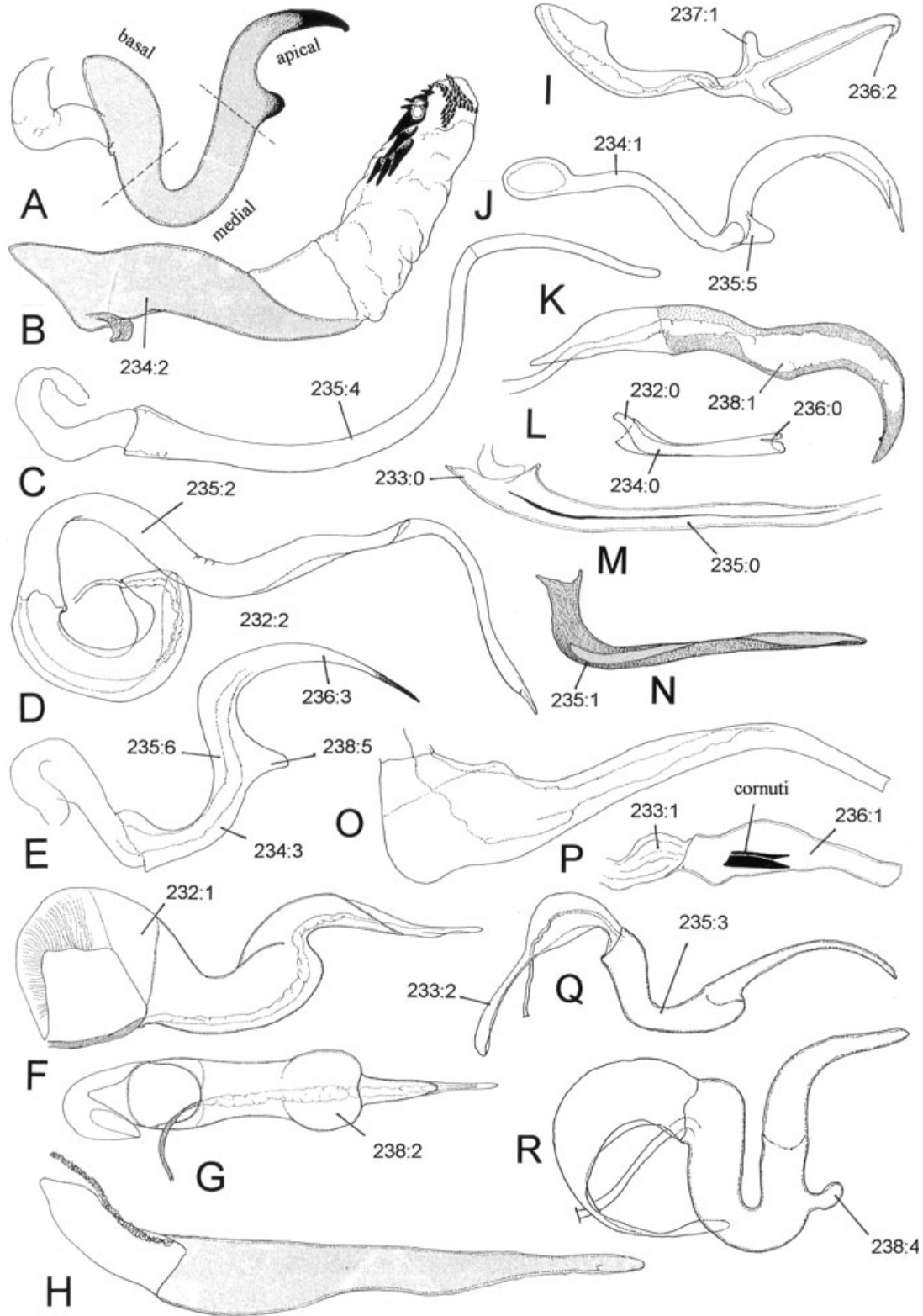


Figure 38. Aedeagus of Chalcosiinae. A, *Eusphalera regina*. B, *Eterusia repleta*. C, *Chalcosia zehma*. D, *Amesia sanguiflua*. E, *Chalcosia diana*. F, *Eterusia vitessa*, lateral view. G, ditto, ventral view showing the swollen part. H, *Cyclosia pagenstecheri*. I, *Retina rubrivitta*, dorsal view. J, ditto, lateral view. K, *Pseudopidorus fasciatus*. L, *Aglaope infausta*. M, *Panherpina basiflava*. N, *Caprima gelida*. O, *Pidorus atratus*. P, *Corma zenotia*. Q, *Soritia proprimarginata*. R, *Eterusia raja*.

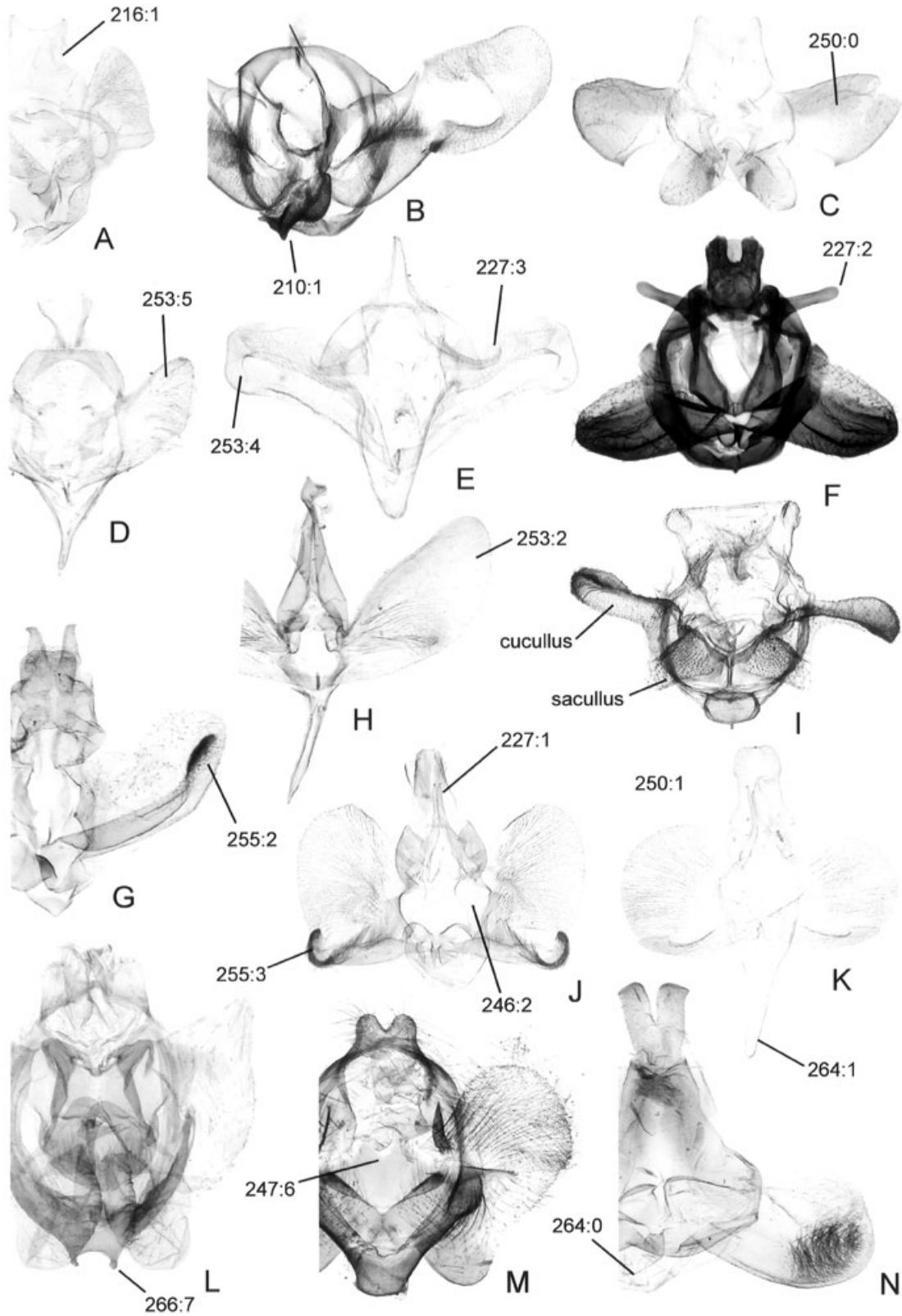


Figure 39. Male genitalia of Chalcosiinae. A, *Arbudas bicolor*. B, *Chalcosiopsis variata*. C, *Boradiopsis grisea*. D, *Heteropanula flavimacula*. E, *Cyclosia* sp. F, *Neoherpa subhyalina*. G, *Chalcosia syfania*. H, *Heteropan alberti*. I, *Anarbudas bipartita*. J, *Docleomorpha* sp. K, *Anarbudas insignis*. L, *Cyclosia notabilis*. M, *Pompelon marginata*. N, *Cleoda syntomoides*.

(2002a). In *Hampsonia*, *Watermenia*, *Herpidia* and *Soritia sevastopuloi*, these protuberances are more prominent and well separated (224: 2) (Figs 30C, 32C) and described by the same authors as the 'fultura superior'. In *Agalope*, *Philopator*, *Formozygaena*, *Atelesia*, and the *Chalcosia thibetana*, *Chalcosia alpherakyi*, *Agalope bieti* and *Agalope pica* groups, the bilateral protuberances are narrower and connected by a medial plate (224: 3) (Figs 29E, 31B, 32F, I). The medial plate of *Achelura* and *Boradia* is completely fused with the bilateral protuberances, and a bifurcate posterior projection is present (224: 4) (Figs 29E, 31E). This structure was interpreted as 'bifurcate processes of the gnathos' by Owada *et al.* (1999).

In *Elcysma*, *Agalope immaculata* and *Agalope glacialis*, the medial plate and posterior projection form a gnathos-like structure with an inner ridge (224: 5) (Figs 29E, 32E). Owada (1992) used 'gnathos + transtilla' to describe this structure. The gnathos-like structure without an inner ventral ridge (224: 6) (Fig. 29E) is only found in the *Agalope hyalina* and *A. eronioides* groups; it was treated as a true gnathos by Owada (1992). We doubt that 224: 1 and 224: 2 can be regarded as a 'fultura' because the true 'fultura inferior' and 'fultura superior' are defined as the sclerotized diaphragma ventrad and dorsad of the aedeagus (Klots, 1970). Both 224: 1 and 224: 2 are lateral structures derived from the inner margin of the tegumen. Nor can we agree with Owada's inference that 224: 3, 224: 5 and 224: 6 are relevant to the gnathos because the true gnathos is an articulated structure and ventrad to the anal tube and articulated at the upper margin of the tegumen (Klots, 1970). Maes (1997) and Solis & Maes (2002) suggested using 'pseudognathos' for the non-articulated gnathos-like structure in Crambidae. Since the homology of the pseudognathos is uncertain and this term has never been used with regards to the Zygaenoidea, we prefer not to use 'pseudognathos' to describe this character.

Posterior bilateral projections (ch. 225) (Fig. 29E): this character is superficially similar to 224, but the projections extend from the lateral rather than inner margins of the tegumen. The general features of the male genitalia of *Eucormiopsis* and *Docleomorpha* are very similar, so we infer that the bilateral projections of the former and the gnathos-like structure of the latter can be included as one character.

Tegumenal apodemes (ch. 227) (Fig. 29E): the internal apodemes which serve as attachments for the M2 and M4 muscles are located at various positions on the tegumen with different taxa. Because not all the taxa have prominent apodemal processes, recognition of an apodeme and its location was gauged by presence of the M2 and M4 muscles. In all of the outgroups (except

for *Callizygaena*), *Chalcosiopsis* and *Inouela*, the inner margins of the tegumen lack prominent apodemes (227: 0).

Posterior projections from tegumenal arms (ch. 229) (Fig. 37E): peculiar structures found only in *Retina* and *Pidorus constrictus*. They are very similar in appearance to 260: 4, which is a beak-like process arising from the valval base. The processes in these two groups are apparently not derived from the valvae but are derived from anterior tegumenal arms.

Transtilla (ch. 230): Owada (1992) considered that a transtilla was present in the *Achelura*–*Agalope*–*Elcysma* complex, but as indicated in the discussion for 224, a true transtilla should be a transverse sclerite connecting the valval apodemes. By this definition, a transtilla is present in five outgroups, *Artona*, *Theresimima*, *Illiberis*, *Saliunca*, *Janseola* and in two ingroup members, *Heteropan* and *Pidorus miles*.

Aedeagus and its supporting apparatus (Fig. 38)

Phallobase (ch. 241): Klots (1970) defined the phallobase as the proximal part of the phallus, in contrast to the aedeagus, while we use it to indicate the elongated/protruded region anterior to the inception of the ductus ejaculatorius. A phallobase (241: 0) is only found in the outgroups (except for *Callizygaena*), *Chalcosiopsis* and *Inouela*.

'*Juxta*' (ch. 244, 245) (Figs 29E, 33): the broad definition of a juxta by Klots (1970) has long been followed by lepidopterists. He included within his definition both the independent sclerite ventrad to the aedeagus, together with the sclerite fused with the vinculum. We have chosen to allocate two separate characters to these two types of juxta because they are found in unrelated groups and unlikely to be homologous, as judged by their position relative to other structures such as the vinculum, saccus and tegumenal extensions. An independent juxta is present mostly in the outgroup taxa; however, an ellipsoidal juxta (244: 1) is also found in *Neoherpa eleonora*, *Panherpina basiflava* and *Pseudarbudas ochrea*. The derived juxta in which the sclerite is connected to the base of the vinculum is confined to the *Agalope* genus-complex.

Anteroventral extensions of the tegumenal apodemes (ch. 246) (Fig. 34): the juxta is not the only aedeagus-supporting apparatus of the ingroup members (except for *Chalcosiopsis*, *Cleoda*, *Inouela* and *Heteropan*). In the majority of them, the anteroventrally extended apodemes and derived sclerites serve a similar function of supporting the aedeagus. A pair of band-like sclerites arising from the conjunction between the valval bases and posterior tegumenal projections (246: 1) (Fig. 30A) is present in 29 species-groups.

Basal region of interior extension of tegumen (ch. 247) (Figs 35, 36): although the basal region of this extension is sometimes indistinguishable from the inner margin of the vinculum or medial ridge of the saccus, it is treated as distinct because its derived protuberances are not relevant to the development of the ventral sclerites.

Valva

Scaling on valva (ch. 248, 249): two types of scaling are found on the valvae in the ingroup and they are treated as two binary characters. In *Herpolasia augarra*, *Clematoessa virgata*, *Hemichrysoptera*, *Papuaphlebohecta*, *Sciococlea*, *Hadrionella*, *Caprima* and *Hemiscia albivitta*, the cucullus of the valvae has scale tufts developed along the margin (248: 1). The second type of scale tuft, present in *Rhodopsona*, *Corma*, *Docleomorpha* and *Eucormiopsis*, is more concentrated around the valvula (249: 1).

Vinculum and saccus (Figs 37, 39)

Position of articulation between tegumen and vinculum (ch. 261): the proportional length of the tegumen and vinculum varies between taxa so we measured it according to the position of the articulation from a ventral view. Six states are recognized.

Shape of saccus (ch. 266) (Fig. 29H): the shape of this structure was observed in posteroventral view. Nine states are recognized.

Genitalic musculature

Kuznetsov & Stekolnikov (1981) examined the musculature of five zygaenid species, which represent three subfamilies: *Zygaena filipendulae* and *Pryeria sinica* (Zygaeninae), *Artona octomaculata* (as *Balataea octomaculata*) and *Illiberis pruni* (Procridinae, the latter misplaced in 'Agalopinae'), and *Elcysma westwoodi* (Chalcosiinae, as Agalopinae). Their observations of genitalic musculature were re-interpreted in a phylogenetic study of the 'tortricoid-grade moth families' by Kozlov, Kuznetsov & Stekolnikov (1998). Meanwhile, Fänger & Naumann (1998) described detailed observations of the genitalic musculature and copulatory mechanism of *Z. filipendulae*. However, the terminology and character interpretation used in these studies are slightly different (see Table 2). Fänger & Naumann's (1998) terminology and concept of each muscle, and the five characters obtained are adopted here.

FEMALE GENITALIA

The phylogenetic significance of features of the female genitalia of zygaenids was first noted by Naumann (1988). Following his observations, a developed ovipositor and absence of Peterson's gland are currently considered to be apomorphic characters of the Chalcosiinae (Tarmann, 1994; Epstein *et al.*, 1999). The distribution and phylogenetic value of these characters, however, were not tested cladistically based on an overall survey of the whole group.

Table 2. Comparison of terminology for the main male genitalic muscles. Kuznetsov & Stekolnikov (1998) and Kozlov *et al.* (1998): m, intrinsic muscle; mt, tergal muscles of abdominal segment viii; ms, sternal muscles of abdominal segment viii; m1, musculus tergalis intersegmentalis ix-x; M2, gonopodalis externus dorsolateralis; M3, laminae mediale anterior; M4, gonopodalis externus dorsomedialis; m5, phallicus externus posterior; m6, m7, gonopodalis externus medialis. Fänger & Naumann (1998): g, intrinsic genital muscle; pg, postgenital muscle; t, tergal extrinsic muscle; s, sternal extrinsic muscle

Kuznetsov & Stelnikov (1998)	Kozlov <i>et al.</i> (1998)	Fänger & Naumann (1998)
m1	m1	g1
	-	pg1
m10	m10	g2
M2	M2	g3
M4	M4	g4
m7	m7	g5
m5	m5	g6
m6	m6	g7
M3	M3	g8
	mt8-9 (1)	t1
	mt8-9 (2) & (3)	t2
	ms8-9 (3)	s1
	ms8-9 (2)	s2
	ms8-9 (1)	s3

Ovipositor

Length of ovipositor (ch. 272): we used the length of the seventh tergite to standardize the length of the ovipositor, as the latter varies between taxa. The length of the seventh sternite was not compared with that of the ovipositor because its variable shape and the specialized structure surrounding the ostium may reduce the value of measurements. All the included taxa were measured and eight character states recognized; these are not consistently distributed within the specific groups. Discovery of an extended ovipositor in non-chalcosiine taxa, e.g. *Saliunca styx* (272: 2), *Homophylotis nigra* (272: 3) and *Callizygaena ada* (272: 1), contradicts the prior hypothesis that the developed ovipositor is a unique synapomorphy of the Chalcosiinae.

Ostium and the surrounding region

Ostium (ch. 286, 287): the sclerotized area surrounding the ostium is usually called the 'sterigma', consisting of a *lamella antevaginalis* and a *lamella postvaginalis* (see ch. 288, 289). This term, however, is not used because the homology of various types of 'sterigma' is still uncertain.

Lamella antevaginalis (ch. 288): this is defined as a sclerotized region immediately anterior to the ostium. No ingroup members display this structure. In *Zygaena*, it is separated from the ostium (288: 0), while in *Illiberis*, *Clelea* and *Pryeria*, it is fused with the ostium (288: 1).

Lamella postvaginalis (ch. 289): this sclerite is immediately behind the ostium. In *Zygaena*, *Illiberis*, *Clelea*, *Theresimima* and *Adscita*, it is separated from the ostium (289: 0), but fused in *Pryeria* and *Pollaniscus*. As with 288, this feature is not present in the ingroup and both are informative for outgroup relationships.

Specialized cuticular structure posterior to ostium (ch. 290): there are two types of post-ostium cuticular structure which cannot be assigned to the preceding characters because they do not surround the ostium. In *Papuaphlebohecta*, the area between the ostium and the base of the ovipositor is slightly sclerotized and wrinkled (290: 0). In *Chalcosiopsis melli* and *Allocaprima duganga*, this area is strongly sclerotized and well separated from the ostium (290: 2).

Paired sclerites posterior to ostium (ch. 291) (Fig. 40G): in the *Chalcosia tibetana* species-group, a pair of small sclerites is present behind the ostium (291: 1). This character is not treated as a state of character 290 because the paired sclerites are small and far from the ostium.

A6–A7

Scaling of sternites A6–A7 (ch. 297, 298): Owada & Horie (2002a) were the first to note that A6 of *Cadphises* is smooth (297: 1), not scaled (297: 0) as in most of the zygaenoid groups. In *Cadphises*, sternite A7 is also smooth (298: 1) as in the species-groups of *Agalope*, *Elcysma*, *Achelura* and *Boradia*.

General outline of tergite and sternite A7 (ch. 300, 301) (Fig. 40E, F): the shape of these two sclerites was assessed in lateral view.

Marginal features of sclerites in A7 (ch. 302–306) (Fig. 40E, F): these characters describe the sclerotic invaginations or notches at different locations on tergite A7 and sternite A7. These structures may correspond to 'locking devices' for the valvae, tergal or sternal arms of the male.

Internal ducts and glands

Pseudobursa (ch. 314) (Figs 40B, 41, 42): based on examination of only *Elcysma* and *Agalope*, the presence of a pseudobursa was considered to be a potential synapomorphy of the Chalcosiinae (Naumann, 1988). In the present study, a pseudobursa (314: 1) was found in *Callizygaena* and throughout the Chalcosiinae, but was absent in *Chalcosiopsis*, *Heteropan*, *Inouela* and in all of the outgroups.

Accessory gland (ch. 315): Epstein *et al.* (1999) considered the absence of the accessory gland to be a potential synapomorphy of the Chalcosiinae because of its presence in the Zygaeninae and part of the Procridiinae (e.g. *Artona*, *Adscita*, *Pollaniscus*, *Illiberis*) (315: 1, 315: 2). We included this character to see if its absence represents secondary loss, as the above authors suspected.

Surface of corpus bursae (ch. 321, 322): modifications of the surface of the corpus bursae are treated as characters different from the signa, which is usually heavily sclerotized and has a particular shape and arrangement. In the majority of taxa, the corpus bursae may have transverse or irregular wrinkles. In *Formozygaena*, it has a granular surface (321: 1), absent in all other groups. In several groups, the wrinkles and pleats are slightly sclerotized laterally (322: 1); in the *Pseudoscaptisyle*, *Eusphalera* and *Psaphis* species-groups they are more aggregated and form a single band-like structure (322: 2).

Signa (ch. 323–328) (Fig. 42E): the shape and location of the signa in the corpus bursae are extremely variable, and it is hard to determine whether all the types can be included in one multistate character. Here, except for the pea-shaped signa, all other shapes are treated as different binary characters.

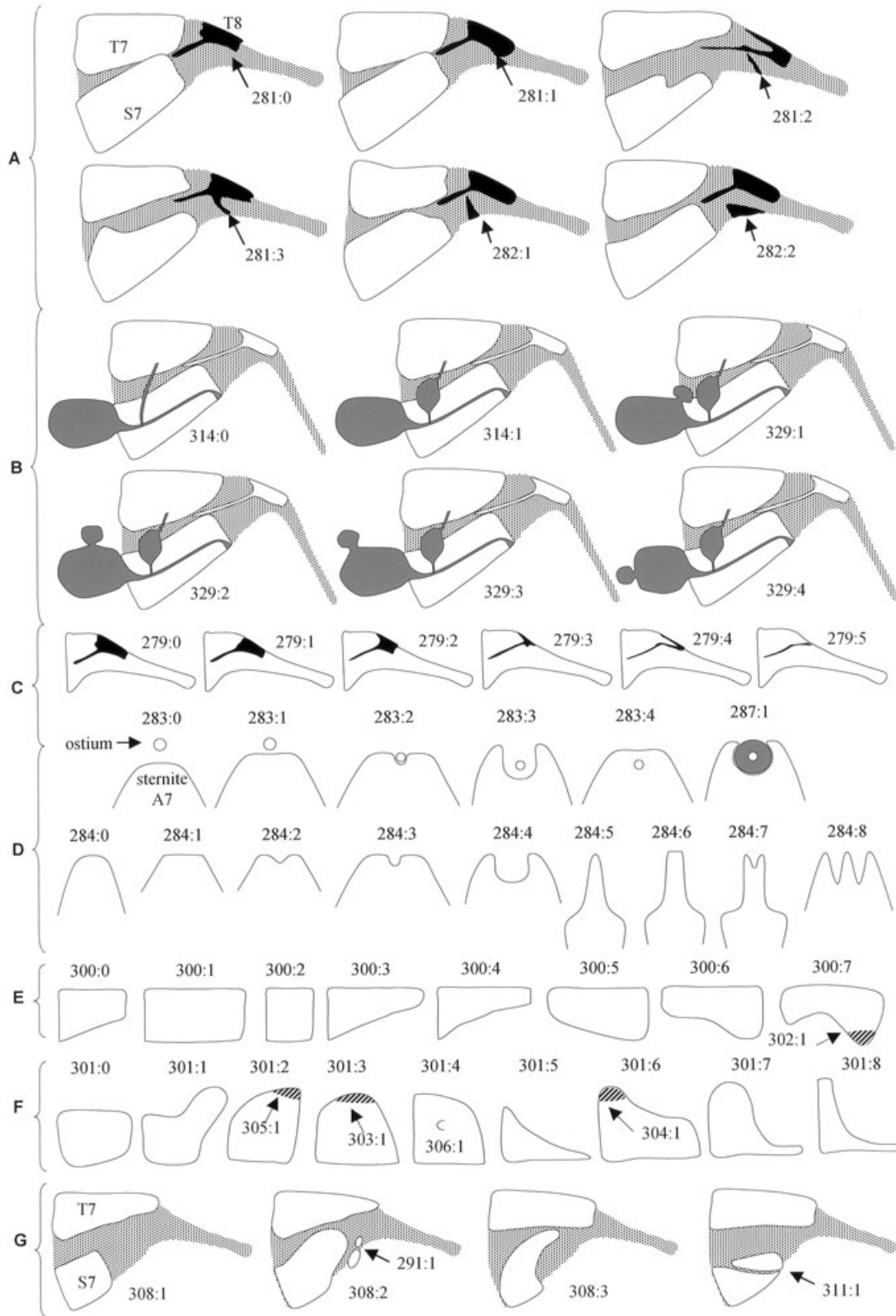


Figure 40. Stylized drawings of selected characters of female genitalia and the associated sclerites. A, C, modifications of 8th tergite. B, internal ducts. D, sternite 7, ventral view. E, tergite 7, lateral view. F, sternite 7, lateral view. G, modifications of the 7th sternite and sclerites posterior to ostium.

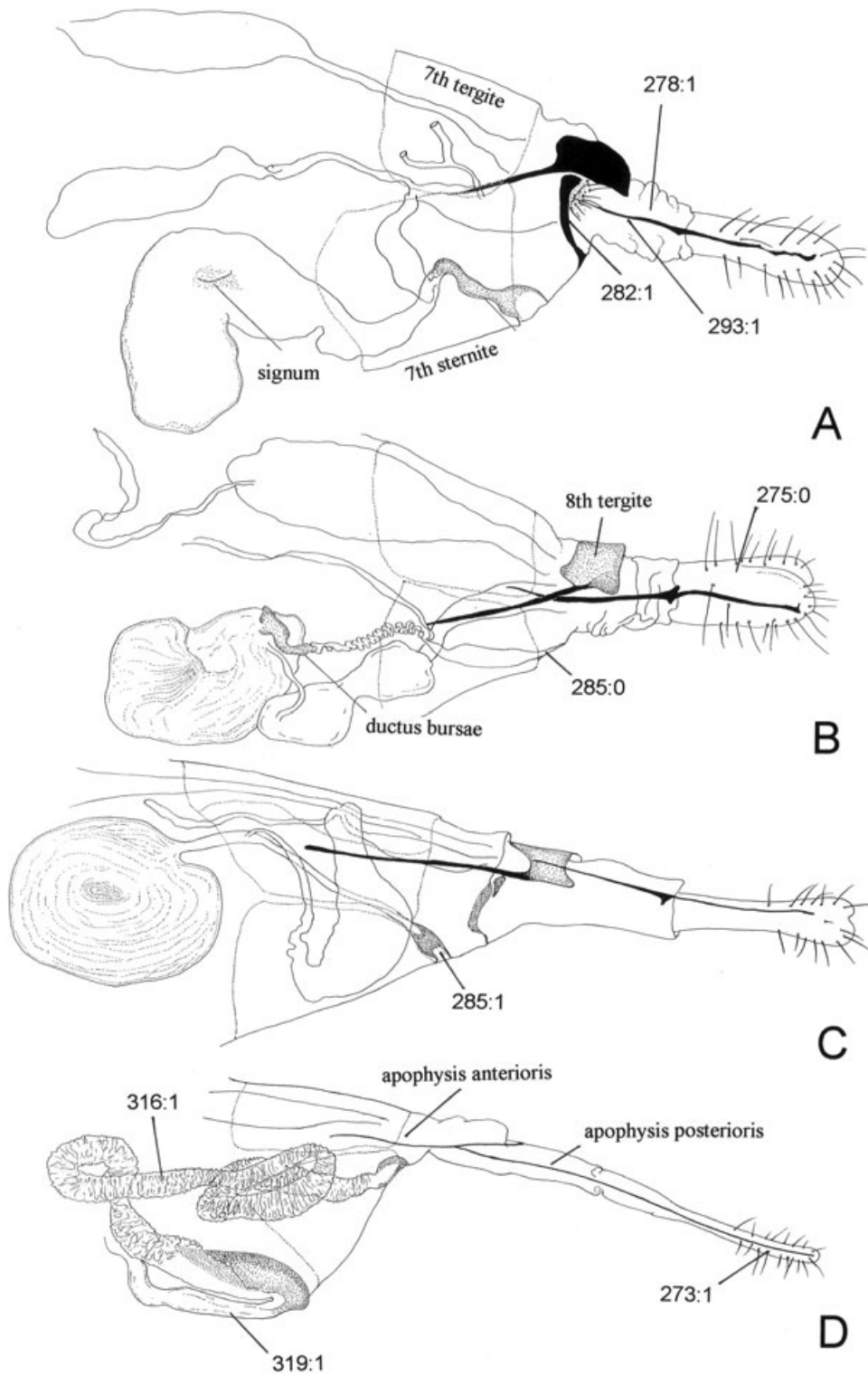


Figure 41. Female genitalia of Chalcosiinae. A, *Campylotes maculosus*. B, *Panherpina basiflava*. C, *Rhodopsona marginata*. D, *Cyclosia pagensteheri*.

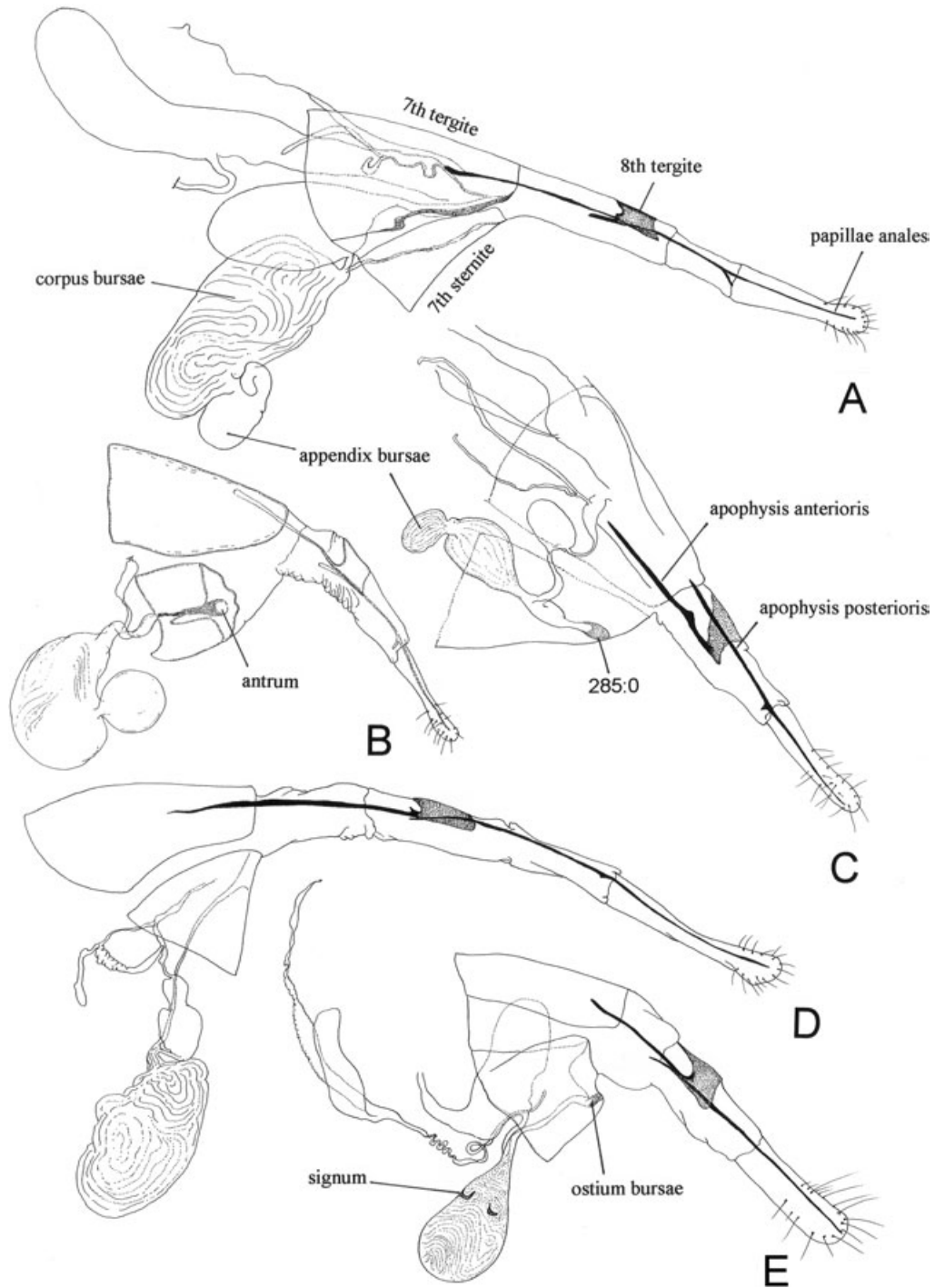


Figure 42. Female genitalia of Chalcosiinae. A, *Eterusia aedeae formosana*. B, *Soritia elizabethae*. C, *Pidorus atratus*. D, *Chalcosia zehma*. E, *Pseudopidorus fasciatus*.

SCENT ORGANS

Eversible coremata between segments A8 and A9 in males (ch. 330): eversible coremata are one of commonest type of scent organs among the Lepidoptera.

In *Zygaena*, a pair of short coremata is present between A8 and A9 (330: 1) (see Naumann *et al.*, 1999, plate 9, fig. 3). This organ has much longer hair tufts in *Pryeria* (330: 2) (Fig. 44C). The scent organs of *Harrisina* and *Cleoda* have long eversible protuberances

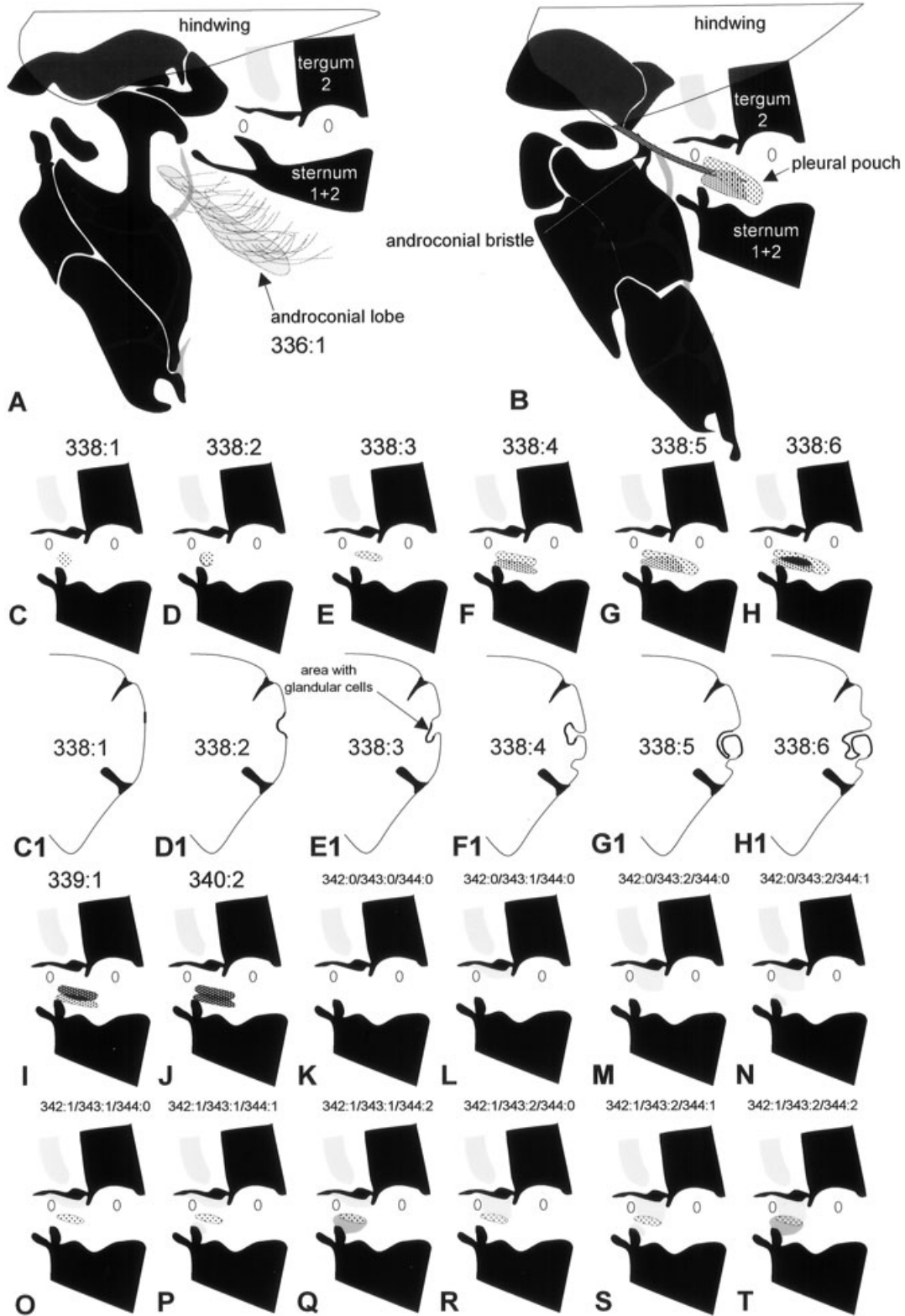


Figure 43. Stylized drawings of scent organs. A, *Chalcosiopsis variata*. B, 'typical' hindwing–abdominal scent organ in Chalcosiinae. C–H1, different types of male pleural modifications (C–H: lateral view. C1–H1: frontal view of cross section of A1 + A2). I, J, pleural sclerotization in male. K–T, ten types of female pleural modifications with different combinations of characters.

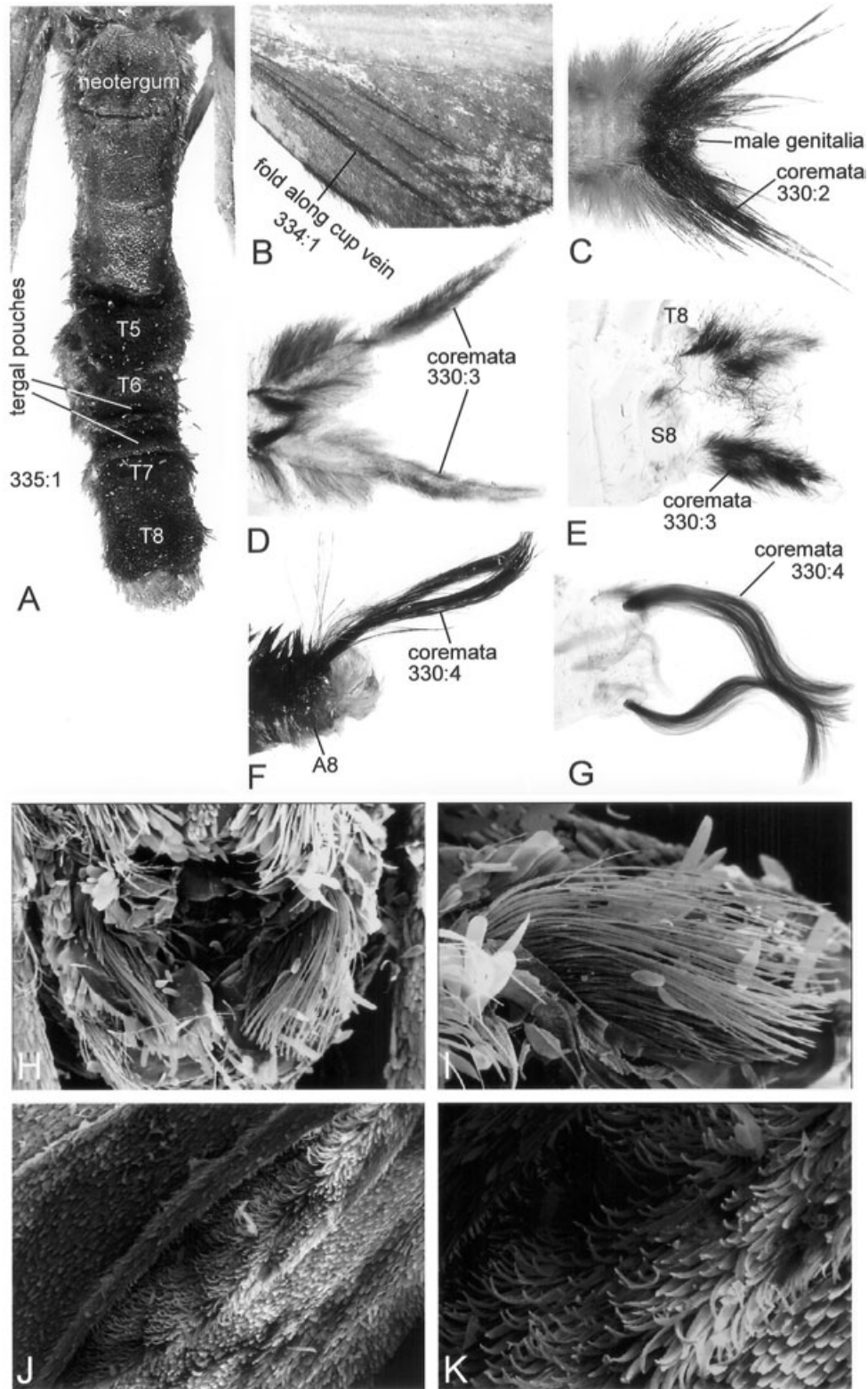


Figure 44. Non-hindwing-abdominal scent organs. A, abdominal androconial scales: *Heteropan appendiculata*. B, J, K, hindwing androconial scales: *Heteropan scintillens*. C, abdominal hair tufts without long eversible coremata: *Pryeria sinica*. D, long coremata between A8 and 9: *Harrisina americana*. E, ditto: *Cleoda syntomoides*. F, G, long eversible coremata attached on sclerites: *Phauda flammans*. H, I, metathoracic scent organ: *Chalcosiopsis variata*.

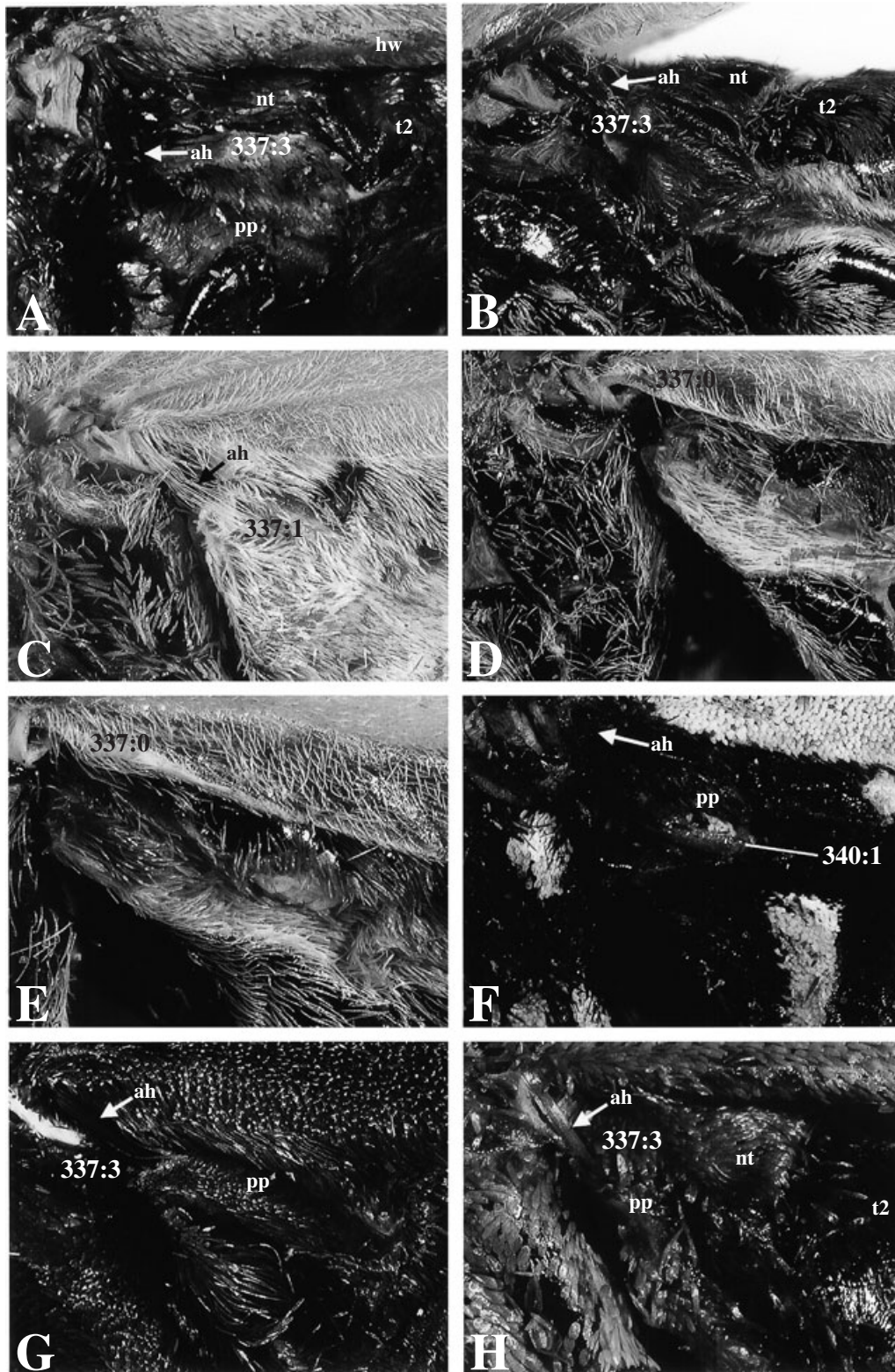


Figure 45. Hindwing-abdominal scent organ in males of Chalcosiinae. A, *Achelura sanguifasciata*. B, *Agalope davidi*. C, *Agalope immaculata*. D, *Agalope pica*. E, *Agalope trimaculata*. F, *Cadphises* sp. cf. *moorei*. G, *Rhodopsona costata*. H, *Rhodopsona marginata*. Abbreviations: ah, androconial hairs; hw, hindwing; lps, lower pleural sclerite; nt, neotergite; pp, pleural pouch; t2, tergite 2; ups, upper pleural sclerite.

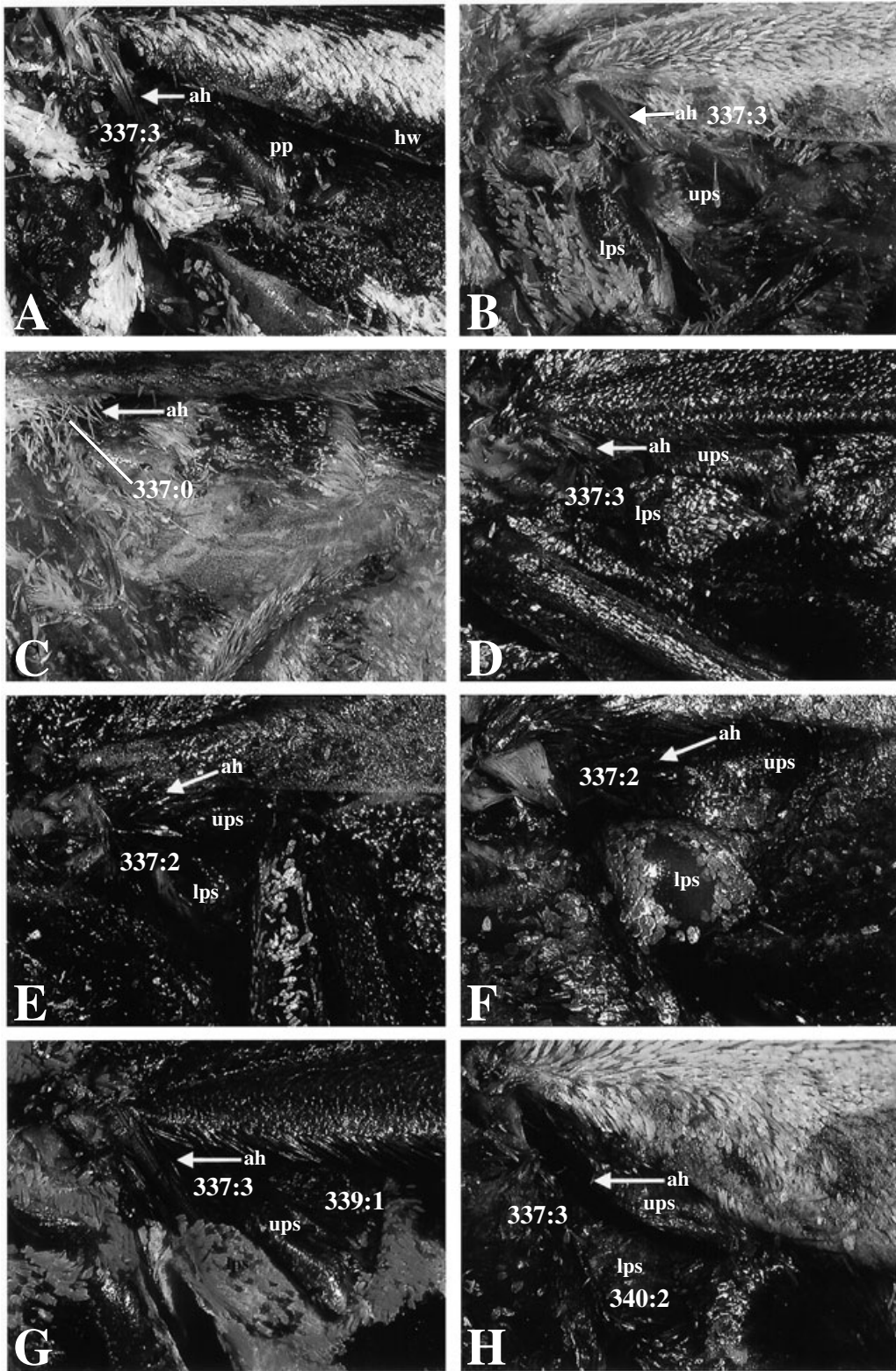


Figure 46. Hindwing-abdominal scent organ in males of Chalcosiinae (continued). A, *Cyclosia imitans*. B, *Corma zenotia*. C, *Corma zelica*. D, *Erasmia pulchella hobsoni*. E, *Eterusia taiwana*. F, *Eterusiella repleta*. G, *Histia flabellicornis ultima*. H, *Neochalcosia remota*. Abbreviations: ah, androconial hairs; hw, hindwing; lps, lower pleural sclerite; pp, pleural pouch; ups, upper pleural sclerite.

and long hairs (330: 3) (Fig. 44D, E). A similar long and hairy scent organ is found in *Lactura* and *Phaуда*, but these coremat hairs are attached to a small sclerite on the intersegmental membrane between A8 and A9 (330: 4) (Fig. 44F, G).

Androconial scales of males (ch. 334, 335): the morphology of androconial scales on the hindwings is often used in the classification of lycaenid (Eliot, 1973) and riodinid (Hall & Harvey, 2002) butterflies, but is less utilized in moth taxonomy and systematics. In the present study, two types of androconial scale were found in the genus *Heteropan*. In the *Heteropan scintillans* and *H. alienus* species-groups, the hindwings bear a rough scale patch near the anal angle (334: 1) (Fig. 44B, J, K), similar to that in *Atrophaneura* spp. (Papilionidae) and several neotropical epiplemines (Uraniidae). In the *H. appendiculata* species-group, a peculiar androconial system is found in the tergum of A3–6; it comprises three pairs of invaginated pouches, with numerous androconial scales inside, situated in the intersegmental membrane (335: 1) (Fig. 44A).

Male metathoracic scent organ (ch. 336) (Fig. 44H, I): a specialized metathoracic androconial system was found in *Chalcosiopsis variata*. The long and curved androconial hairs are densely attached to a pair of spatulate membranous protuberances arising from the interscleritic membrane between the metathoracic epimeron and postnotum. Eversibility of this organ has yet to be proved. A similar type of metathoracic androconial organ has been found in Adelidae from Africa (Wojtusiak, 1999), although it is formed by densely arranged specialized scales which do not arise from a petiole.

Hindwing–abdominal scent organ (ch. 337–344): Hasse (1888) classified the scent organs of the Lepidoptera into seven major types. The scent organ of Chalcosiinae (as Chalcosidae [sic]), based on *Chalcosia*, was assigned to ‘group vii’, together with a nymphalid genus, *Prothoe* Hübner, 1824. Hasse mentioned that the scent organ of Chalcosiinae involves the A2 sternite (*hinterleib*) and [hind]wing (*flügel*). Tarmann (1994) re-examined the scent organ of the *Arbudas*-complex (*Arbudas*, *Eumorphiopais*, *Pseudarbudas* and *Heteropanula*), and suggested that its presence could be a potential synapomorphy of the Chalcosiinae. The organ investigated by Hasse and Tarmann comprises two major structures, a pleural pouch in the 1st to 2nd abdominal segment and a bundle of hair tufts that arises from the anal axillary sclerite of the hindwing and inserts into the pleural pouch (Fig. 43B). The combinations of hair tuft types and pleural evaginations were found to be very complex so we separated the features of this scent system into eight distinct characters. Male (ch. 337–340, A–C)

and female (ch. 341–344, D–F) scent organs are discussed separately.

(A) *Androconial hair brush in male hindwing* (ch. 337): the hair tufts, scales or hairs of the hindwing are treated as a single multistate character because all of these structures are attached to the anal axillary sclerite of the hindwing base. In all of the outgroups and some ingroup taxa (see data matrix), this sclerite is smooth, without specialized scales or hairs (337: 0); in other ingroup taxa, a bundle of short and filiform scales arises from the sclerite (337: 1) (Figs 45F, 46C), its function unknown. In some groups, a bundle of short and oblong scales arises from the sclerite (337: 2) (Figs 45C, 46E, F). An androconial brush inserting into a pleural pouch (337: 3) (Figs 45A, B, G, H, 46A, B, D, G, H) is present in various groups. A similar type of ‘hindwing scent bristle’ was reported by Whalley (1974) from *Strigilina castaneata* Hampson (Thyrididae); this type of bristle does not arise from the sclerite, inserting instead into the pleural pouch.

(B) *Invagination of pleural membrane* (ch. 338): the pleural pouch varies in shape, size (Tarmann, 1994) and degree of sclerotization (Yen, 2002c) among groups. A simple pouch, which has only one shallow interior fold (338: 3) (Fig. 43E, E1), is present in *Rhodopsona* (except for *R. rubiginosa*) and the *Hemiscia meeki*, *Hemiscia* sp. ‘Luzon’ and *Pidorus gemina* species-groups. The double-fold type (338: 4) (Fig. 43F, F1) figured by Tarmann (1992a: pl. 9, fig. 42, pl. 10, figs 43, 44), has more developed internal folding. About 42% of the ingroup members have this structure. An elongated type (338: 5) (Fig. 43G, G1) is present in a few groups, such as *Cyclosia* (except for *C. notabilis*), *Eucormiopsis*, *Docleomorpha* and the *Corma maculata* and *C. zenotia* species-groups. This type of pouch has its posterior part elongated anteriorly and looks longer than the preceding type. The complex type (338: 6) (Fig. 43H, H1) has much interior folding.

(C) *Sclerotization of pleural pouch* (ch. 339, 340): the pleural pouch comprises the upper pleural sclerite (derived from the tergal margin) and lower pleural sclerite. In c. 46% of ingroup members the upper pleural sclerite is not sclerotized (339: 0), while in the remainder it is (339: 1) (Fig. 43I); however, sclerotization is not necessarily correlated with the presence of a developed pouch (e.g. most species groups of *Eterusia* and *Soritia*). The strongly sclerotized lower pleural sclerite (340: 2) (Fig. 43J) is only present in the *Phlebohecta fuscescens* and *P. lithosina* species-groups.

(D) *Female hindwing base scaling* (ch. 341): the presence of scales and hair brushes has not been discussed by the previously mentioned authors. A bundle of hair-like scales arises from the anal axillary sclerite of the

hindwing (341: 0) in four outgroups and about a quarter of the ingroup. Spatulate scales are found in about a quarter of the ingroup taxa. In *Prosopandrophila mirifica*, a spatulate scale bundle longer than A1 is present (341: 4). Although all of these types of scales or hairs are homologous with the male ones, none of them has been proved to be a scent organ.

(E) *Pleural pouch in female* (ch. 342): half the ingroup members have a pleural pouch between A1 and A2 (342: 1) (Fig. 43O–T), but its presence does not necessarily correspond to the presence of any of the scales or hairs discussed above.

(F) *Sclerotization of pleural pouch in female* (ch. 343, 344) (Fig. 43K–T): besides the outgroups, about a third of the ingroup taxa lack any sclerotization in the pleural region (343: 0) while half lack lower pleural sclerotization (344: 0). In a few taxa the tergal arms are laterally extended (343: 1). A complete pleural sclerite derived from the tergal arm (343: 2) is present in the majority of the ingroup.

Eversible gland between segments A8–A9 in female (ch. 345): a pair of eversible putative pheromone glands is present only in *Zygaena* (see Naumann *et al.*, 1999, plate 9, fig. 1) and *Pryeria*, and absent in all the other examined groups.

Female tergal gland (ch. 346): this gland has been found only in *Theresimima*, *Illiberis* and *Clelea*. Although a similar calling behaviour, in which the female expands and contracts the abdominal segments to release the pheromone, has been observed in some chalcosiines (e.g. *Aglaope*), this gland has not been found in any chalcosiine species.

IMMATURE STAGES

The literature on Chalcosiinae includes very limited information on immature morphology except for the studies by Gardner (1942) and Hwang (1956), Nishihara (1992), Yen & Yang (1997, 1998), Fänger *et al.* (1999, 2002), Fänger & Naumann (2001) and Suzuki (2001). Although Tremewan (1960) and Tarmann (1992b) have reviewed most of the available records in the literature, little of the information could be used in the phylogenetic analysis.

The head of Zygaenidae was regarded as prognathous for a long time (e.g. Tremewan, 1985; Epstein *et al.*, 1999) until Fänger *et al.* (1999) stated that when everted to its maximum extent it is actually hypognathous. The retractile head has been thought to be apomorphic for the entire Zygaenoidea (Minet, 1986; Epstein, 1996; Epstein *et al.*, 1999). However, Heppner (1999) argued that such resemblance is due to convergent evolution, and Fänger *et al.* (1999) suggested replacing the description of the 'retractile head' by the

more clearly defined character 'AF2, L1, MD1, 2 and P1, 2 shifted ventrad'.

In the present study, only 72 (including 14 outgroups) of the 207 species-groups have available data on immatures.

General shape and coloration of larva

Body shape (ch. 347, 348): the majority of the examined larvae have a cylindrical (347: 0) or stout (348: 0) body shape (e.g. Fig. 47A–O). However, larvae of the *Arbudas bicolor*, *A. submacula* and *A. leno* species-groups have a very flattened (347: 1) and attenuated (348: 1) body shape (Fig. 48D).

Segmentation of A8–A9 (ch. 352): reduction of A8 and A9 (352: 1) in zygaenoid larvae was noted by Epstein (1996) and Fänger *et al.* (1999, 2002). This character is only exhibited in *Himantopterus*, *Lactura* and *Phauda*.

Internal structure of larva

Internal muscles of larva (ch. 353): Naumann *et al.* (1999: 39, text fig. 41) were the first to report that, in larvae of Zygaenidae, a pair of specialized crossed muscles is present around the foregut. This structure possibly contributes to the transport of food particles into the midgut. In the present study, this structure was found in all the examined larvae of Chalcosiinae.

Larval chaetotaxy and other cuticular structures

Cervical gland (ch. 354): in lepidopteran larvae, a pair of cervical glands occurs in various families, e.g. Nymphalidae (Osborn, Sánchez & Jaffé, 1999), Noctuidae, Pieridae, Hesperidae, Yponomeutidae (Nakamura, 1998) and Notodontidae (Miller, 1991). Although the shape of the paired organ varies in different families, its function has been thought to be chemical defence (Miller, 1991; Nakamura, 1998; Osborn *et al.*, 1999). Fänger & Naumann (2001) first reported it as an 'eversible prothoracic s[ub]v[entral] tube' from *Aglaope*, but could not discern its function. It has been found in all the examined larvae and also in the Nearctic procridine genus *Harrisina* (Stehr, 1987) and Oriental *Artona* (Yen *et al.*, 1996). Histological examination in the present study has revealed that in Chalcosiinae the gland does not contain muscles to manipulate it, while those of the procridine genera contain several simple muscles. The cervical glands of Chalcosiinae and Procridinae are therefore treated as different character states.

Prothoracic shield (ch. 355): the prothoracic shield is where the D, SD and XD setae are situated. In Phaudinae, Lacturidae, all genera of Procridinae and Zyg-

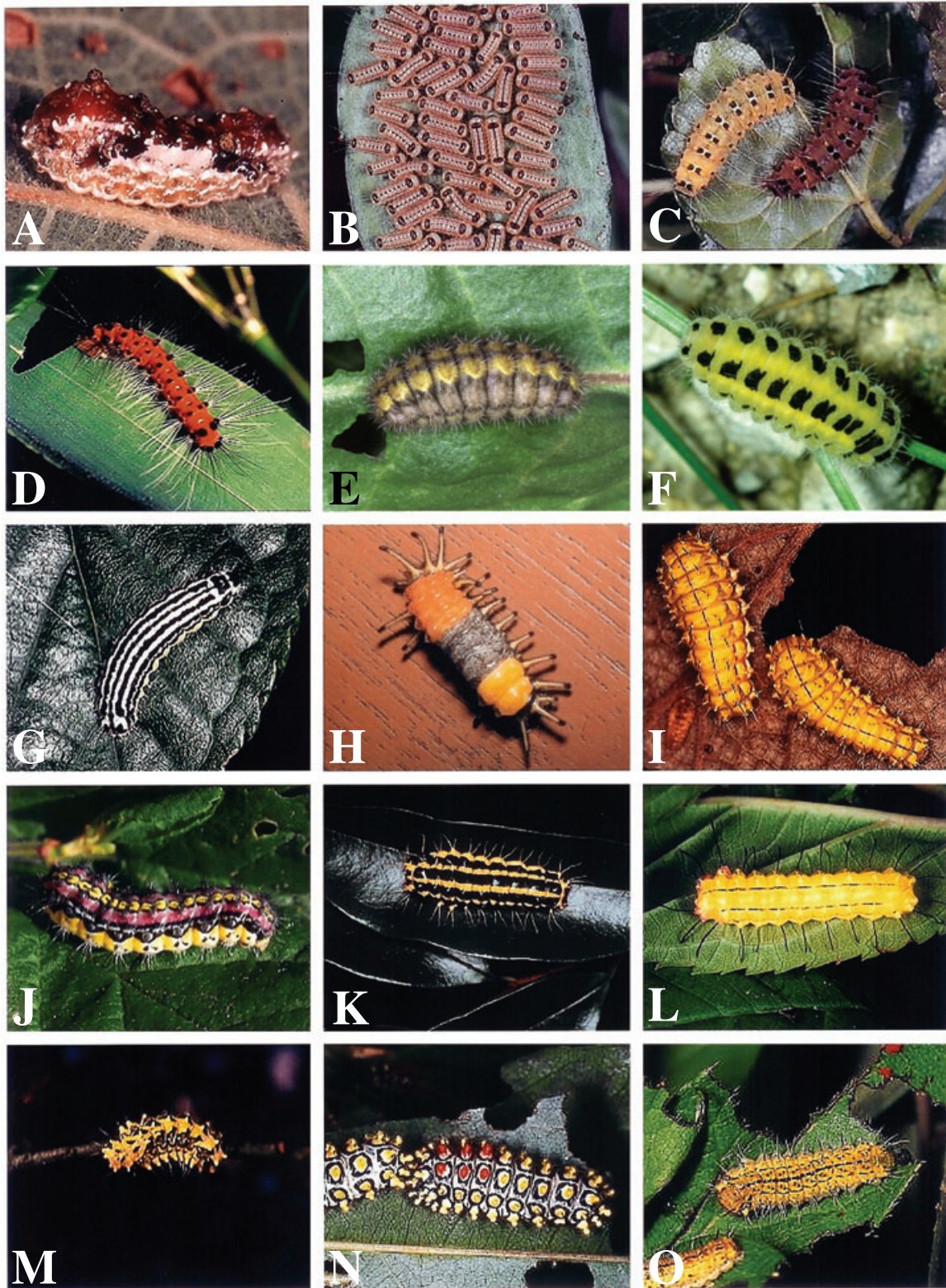


Figure 47. Larvae of different zygaenoid groups. Phaudinae: A, *Phauda arikana*. Procridinae: B, *Clelea formosana*. C, *Illiberis silvestris*. D, *Artona martini*. E, *Adscita statice*. Zygaeninae: F, *Zygaena filipendulae*. G, *Pryeria sinica*. Callizygænae: H, *Callizygæna ada* (courtesy of Hans Malicky). Chalcosiinae: I, *Formozygaena shibatai*. J, *Aglaope infausta*. K, *Achelura sanguifasciata*. L, *Elcysma delavayi*. M, *Agalope trimacula*. N, *Cyclosia papilionaris*. O, *Rhodopsona marginata*.

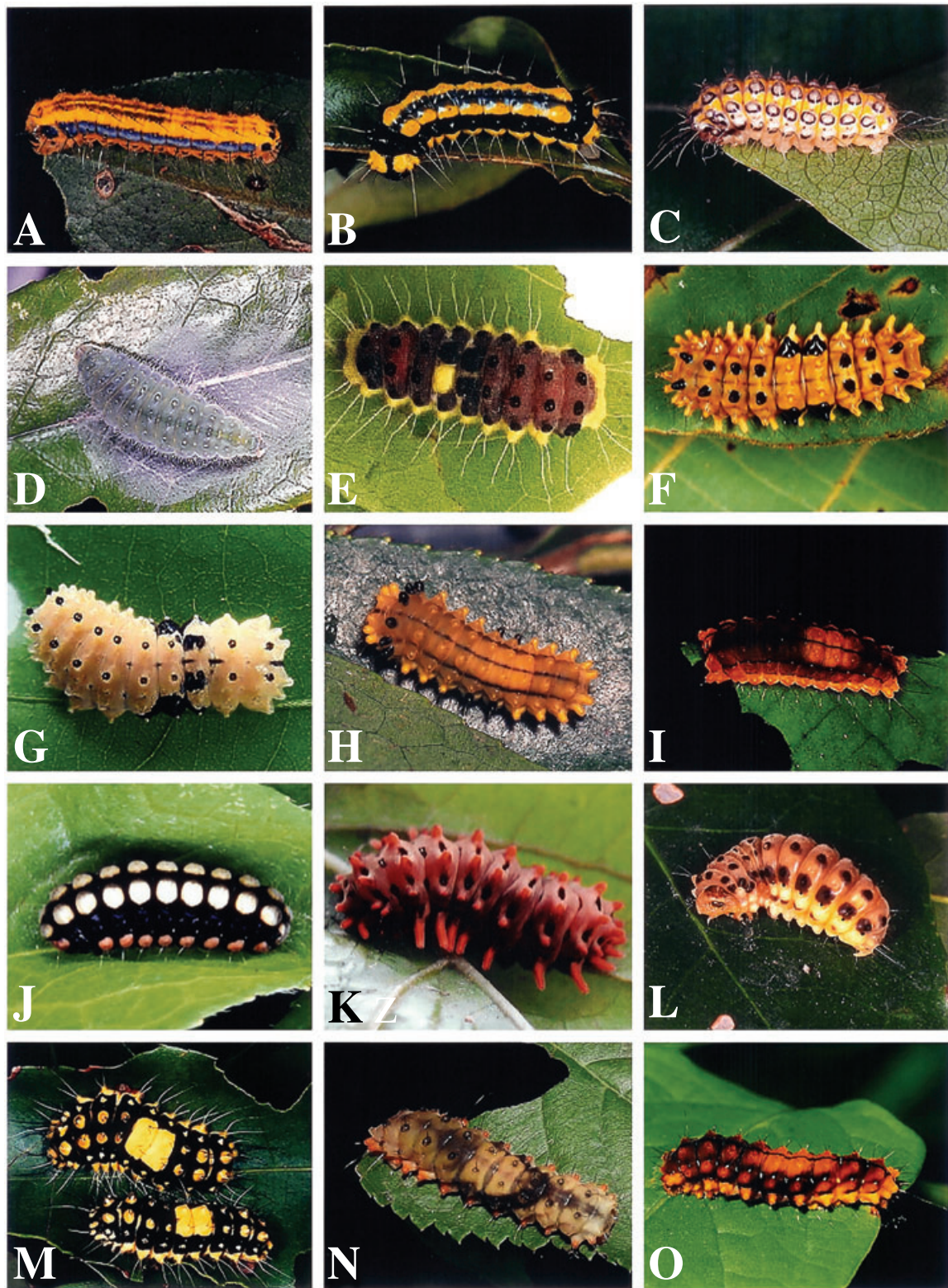


Figure 48. Larvae of Chalcosiinae. A, *Pidorus* sp. B, *Pidorus atratus*. C, '*Pidorus*' *gemina*. D, *Arbudas leno*. E, *Retina rubrivitta* (courtesy of David L. Mohn). F, *Gynautocera papilionaria*. G, *Pompelon marginata*. H, *Chalcosia suffusa*. I, *Chalcosia formosana contradicta*. J, *Neochalcosia remota*. K, *Histia flabellicornis ultima*. L, *Erasmiphlebohecta picturata picturata*. M, *Erasmia pulchella chinensis*. N, *Eterusia aedea formosana*. O, *Soritia strandi*.

aeninae have a weakly developed shield (355: 0), whereas the Himantopteridae, Callizygaeninae and Chalcosiinae have a well-developed shield with a clearly defined margin (355: 1) (Fig. 49E).

Cuticular groove (ch. 356): the term cuticular groove is defined here to describe a concave cuticular structure of the dorsum. In larvae of *Cadphises*, *Histia* (Fig. 48K) and *Gynautocera*, a transverse groove is present between the D verrucae on all the thoracic and abdominal segments (356: 1). This feature is absent in all other examined larvae.

Secondary setae (ch. 358): the presence of secondary setae is usually considered a derived trait in the Lepidoptera, and it is widely distributed in most of the higher lepidopteran groups. Compared with other non-obtectomeran groups, the larvae of Zygaenoidea usually have more developed secondary setae (358: 1) (Fig. 47C–F) and specialized cuticular structures (e.g. Epstein, 1996; Fänger *et al.*, 1999). All Chalcosiinae otherwise have only primary setae (358: 0) (Fig. 49A–D, F) except for *Aglaope* (Fig. 49E) and *Arbudas*, which develop secondary setae in the second instar.

Tonofibrillary platelet (ch. 359) (Fig. 51G): the ‘composite tonofibrillary platelet’ is a simple cuticular structure, to which a number of internal muscles are attached. Fänger & Naumann (2001) first reported it in *Aglaope infausta* and suspected its phylogenetic significance within the Zygaenoidea. Among the examined taxa, one platelet is present on the SD verrucae in all the chalcosiine groups plus *Callizygaena ada*, while this feature is absent in other taxa.

Colour of setae (ch. 365, 366): the phylogenetic implications of setal colour were first noted by Efetov *et al.* (2000). In the present study, we recognize two characters of setal colours for SD and L setae. For details of distribution of each character state see Appendices 2 and 3.

‘Scar-like’ structure (ch. 371): a ‘scar-like’ structure is present in the lateral region of larvae of *Himantopterus*. It is not known in any other zygaenid, but is well developed in the larvae of Somabrachyidae (Geertsema, 1998, 2000; Fänger & Fänger, 2000).

Surface of setae (ch. 380, 381): Fänger & Naumann (2001) reported that the surface of the larval setae of *Aglaope infausta* was ‘plumose’. These plumose setae are in general distributed in the SD, L and SV regions. The SD plumose seta (380: 1) (Fig. 51D) is found not only in *Aglaope*, but also in *Cadphises*, *Elcysma*, *Agalope* and *Achelura*. Distribution of L and SV plumose setae (381: 1) among the group is the same as 380: 1, while in *Erasmia* and *Eucorma*, the L and SV setae are sparsely plumose (381: 2) (Fig. 51A).

Anal plate (ch. 382): Fänger *et al.* (1999) stated that a reduced anal plate may be a potential synapomorphy of limacodid family-groups + Phaudinae. This feature (382: 1) was also found in Lacturidae and Himantopteridae in the present study, while all the remaining outgroups and the ingroup have a developed anal plate (382: 0).

Structures relevant to locomotion

Thoracic legs (ch. 383): paired spatulate setae (383: 2) (Fig. 51J) are present in all the examined zygaenid groups (except *Phauda*) and Heterogynidae (see also Fänger *et al.*, 1999). In *Lactura* and *Phauda*, only one spatulate tarsal seta is found (383: 1). The function of such setae is not yet known, but their phylogenetic significance and distribution among the Lepidoptera was discussed by Miller (1991).

Crochets arrangement (ch. 384–386). Among the studied taxa, only the larvae of Heterogynidae have uniserial and uniordinal crochets (384: 0, 385: 0), while all the other taxa have biserial and biordinal ones (384: 1, 385: 1) (Fig. 51K). The lateral penellipse type (386: 0) is only observed in Heterogynidae. Except for Himantopteridae, Lacturidae and Phaudinae, where the crochets are in a bipartite mesoseries (386: 2), all zygaenid groups have crochets in a mesoseries (382: 1). Fänger & Naumann (2001) noted that an additional row of processes present at the base of the crochets (Fig. 51K) was possibly a synapomorphy of Zygaenoidea.

Proleg (ch. 387): studies by Epstein (1996, 1995) and Fänger *et al.* (1999) inferred that the reduced length of the prolegs may provide a synapomorphy for the limacodid family-groups + Phaudinae + Himantopteridae. In the present study, this condition (387: 1) is observed in *Himantopterus*, *Lactura* and *Phauda*, but not seen in other examined taxa.

Pupa

Pupal morphology has often been shown to have phylogenetic significance in Lepidoptera (e.g. Chapman, 1893; Nakamura, 1970; Miller, 1992; Willmott, 2003). Epstein (1996) investigated the pupal morphology of the limacodid family-groups, focusing on variations in the eye-piece, labial palpus and maxilla. More recently, Fänger *et al.* (1999, 2002) reviewed the pupal characters of various zygaenoid groups, and some characters of interest are discussed below:

General shape (ch. 388): chalcosiine pupae are classified as pupae incompletae, i.e. they are incomplete, obtect, adecticous, the appendages are loosely fused to the body and articulated mandibles are absent. Their coloration is usually yellowish brown. The majority of the examined pupae have a circular cross-section

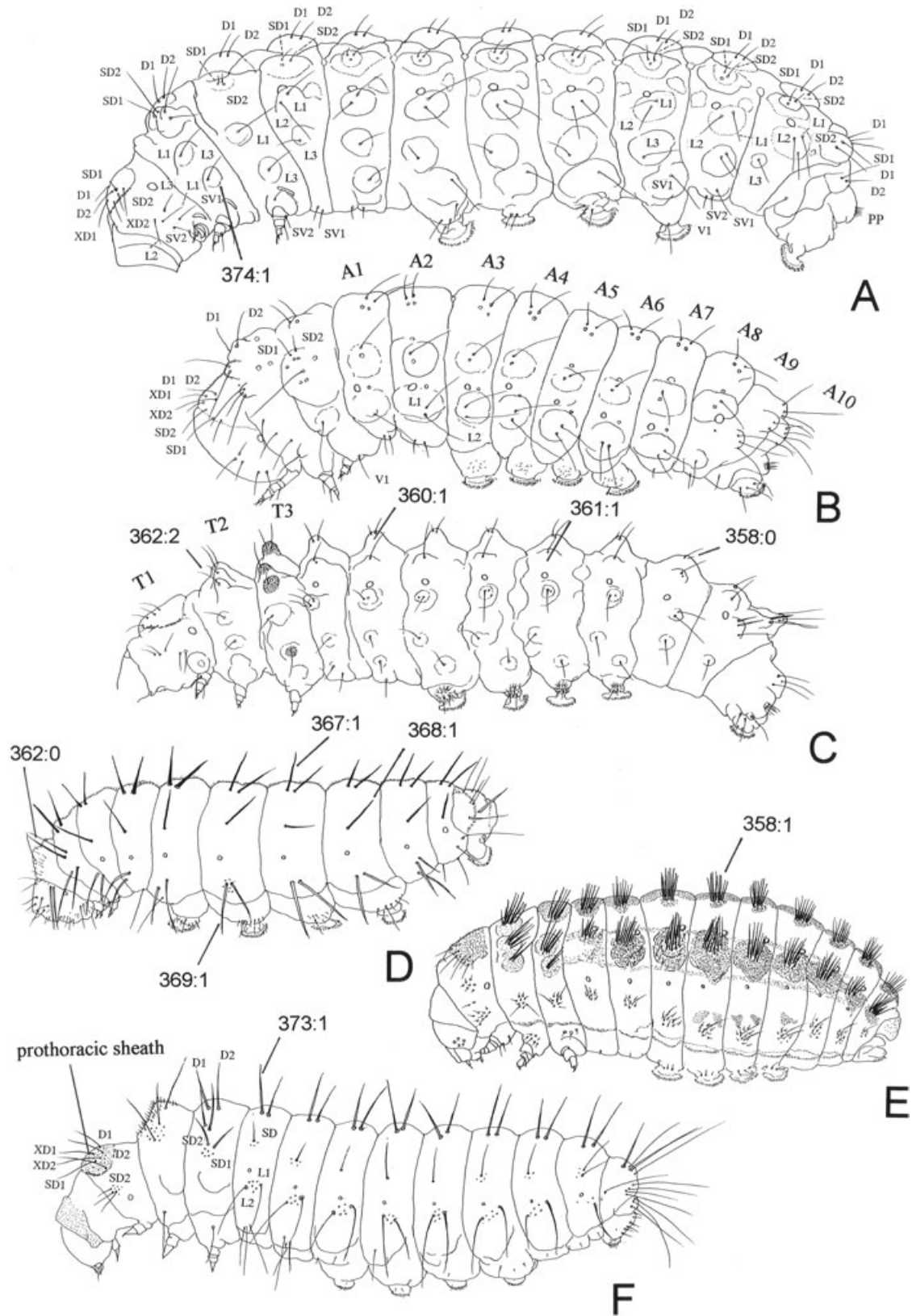


Figure 49. Larval chaetotaxy of Chalcosiinae. A, *Neochalcosia remota*. B, *Soritia strandi*. C, *Chalcosia diana*. D, *Rhodopsona rutila*. E, *Aglaope infausta*. F, *Formozygaena shibatai*.

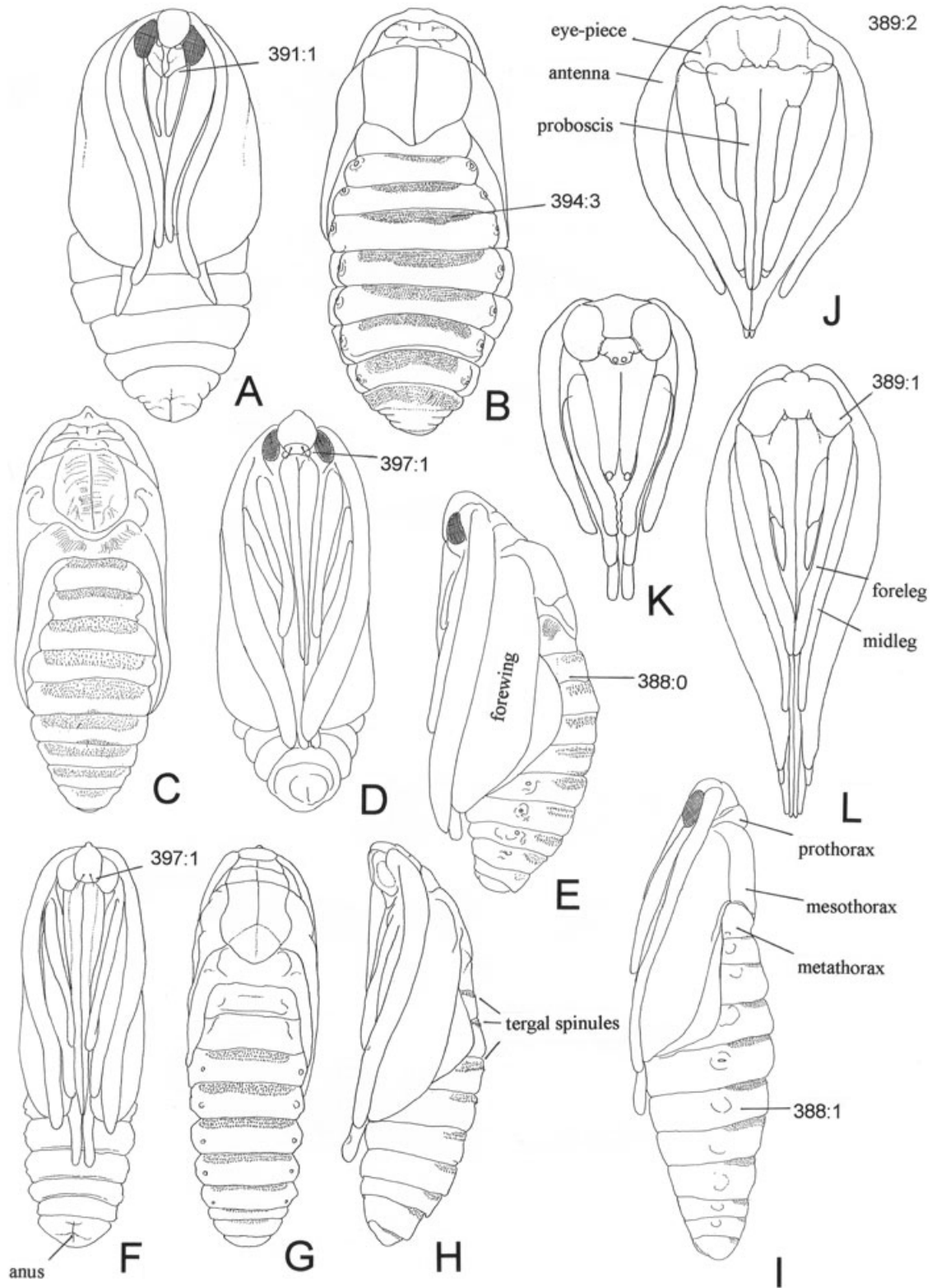


Figure 50. Pupal morphology of Chalcosiinae and the outgroup taxa. A, *Aglaope infausta*, ventral view. B, ditto, dorsal view. C, *Formozygaena shibatai*, dorsal view. D, ditto, ventral view. E, ditto, lateral view. F, *Soritia strandi*, ventral view. G, ditto, dorsal view. H, ditto, lateral view. I, *Agalope trimacula*, lateral view. J, head, antennal and leg sheaths of *Callizygaena ada*. K, ditto, *Himantopterus fuscinervis*. L, ditto, *Zygaena filipendulae*.

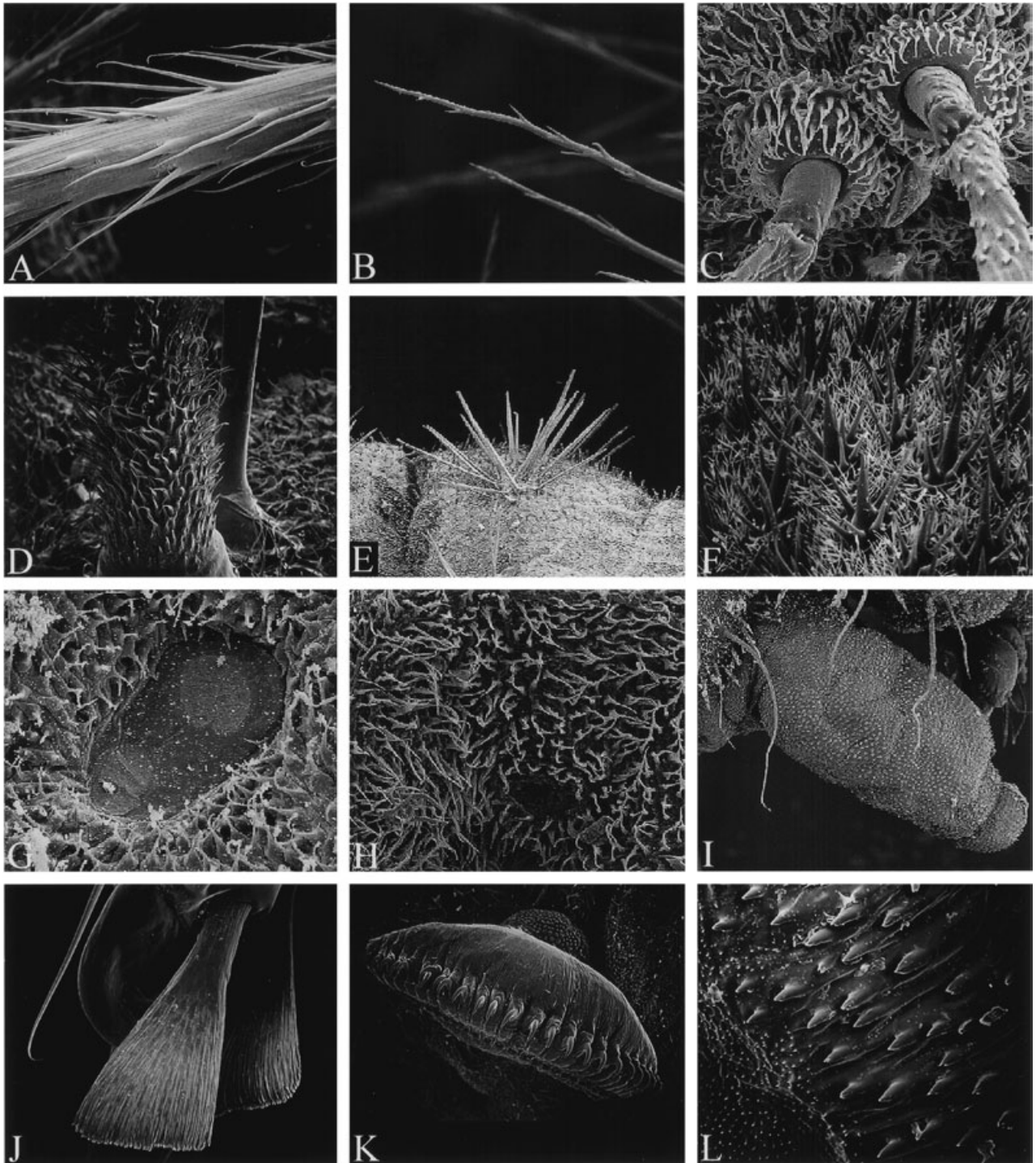


Figure 51. Ultrastructure of larval and pupal cuticle. A, loosely plumose setae (381: 2), *Erasmia pulchella hobsoni*. B, secondary setae of *Zygana filipendulae*. C, base of setae, *Pidorus atratus*. D, plumose setae (381:1), *Elcysma westwoodi*. E, dorsal setae of *Adscita statices*. F, setae of *Heterogynis* sp. G, tonofibrillary platelet (359: 1), *Arbudas submacula*. H, spinules on dorsum, *Histia flabellicornis*. I, retractile cervical gland (354: 2). J, paired spatulate setae (383: 2). K, crochets, *Pidorus atratus*. L, multiple rows of spinules on the terga of pupa (394: 3), *Callizygana ada*.

(388: 0) (Fig. 50E), while the pupae of *Artona*, *Clelea*, *Cadphises*, *Aglaope*, the *Agalope-complex*, *Campylotes*, *Cyclosia* and *Arbudas* are more compressed dorsoventrally (388: 1) (Fig. 50I).

Eye-piece (ch. 389): a sculptured flange to the eye-piece was considered to be a synapomorphic character of the limacodid family-groups, absent in Zygaenidae (Epstein, 1996). However, Fänger *et al.* (2002) showed that the flange is actually present in Zygaenidae, though often concealed by the antennal base. We recognize two states of the flange in the studied groups. A small flange (389: 1) (Fig. 50K, L) is present in Himantopteridae, all genera of Procridinae and Zygaeninae. A larger flange (389: 2) (Fig. 50J) is observed in *Callizygaena*. The eye-piece of chalcosiine groups is treated as 'simple' and coded as '0'.

Proboscis (ch. 391): the absence of a proboscis case (391: 1) (Fig. 50A, K) can possibly, but not necessarily, be linked to reduction of the proboscis (ch. 32–34). Four taxa lack a proboscis case: *Himantopterus*, *Heterogynis*, *Pryeria* and *Aglaope*.

Thoracic furrow (ch. 392): the intersegmental furrow between the pro- and mesothorax is surrounded by a smooth anterior rim (392: 0) or a sculptured rim. Fänger *et al.* (2002) found the sculptured condition (392: 1) in the pupa of *Eterusia aedea*. The outgroups and several chalcosiine genera including *Cadphises*, *Campylotes*, *Agalope*, *Aglaope*, *Cyclosia* and *Corma* have the smooth anterior rim while the remaining chalcosiine genera have the sculptured rim.

Abdomen (ch. 394, 395): the arrangement of spinules on abdominal terga 3–8 is considered to be of phylogenetic significance (Fänger *et al.*, 1999, 2002). In the advanced zygaenoid families (e.g. Epstein, 1996: fig. 311), as well as in the Phaudinae, these spinules, which are generally thought to facilitate emergence of the pharate adult from the cocoon, are arranged in large fields, their presence correlating with a decrease in the thickness of the pupal cuticle. In the taxa examined, the himantopterid pupa lacks a spined field (394: 0). The single row condition (394: 1) (Nielsen & Common, 1991: figs 41, 60c) is observed in all outgroup taxa except *Phauda* and *Callizygaena*, where two rows are found (394: 2) (Fig. 50). Multiple rows are restricted to chalcosiines (394: 3) (Fig. 50B, C, E, G; Yen & Yang, 1998: fig. 4h, i). Except for *Callizygaena*, which has some spinules loosely arranged behind the anterior spined band (395: 1), all the other outgroups have their spinules confined to the anterior row (395: 0). In the chalcosiines examined, the spinules are spread all over the terga (395: 2).

Tuberculate band of A10 (ch. 396): an elevated and transverse tuberculate band (396: 1) has been

reported from the pupa of *Eterusia aedea* by Fänger *et al.* (2002). This feature is shared by all the chalcosiine taxa examined but not seen in any outgroup.

Pupal chaetotaxy (ch. 397): unlike other non-obtectomeran pupae, zygaenoid pupae usually lack primary setae except for those on the frons. Paired C1 and C2 setae are present (397: 1) in *Callizygaena* and chalcosiines, but absent from other outgroups.

Cocoon

Structure (ch. 398): the structure of zygaenid cocoons can be separated into an inner layer and an outer layer (cf. 'inner chamber' of Dalceridae by Epstein, 1996). Among the studied taxa, only the procridine genera currently assigned to Procridini (e.g. *Theresimima*, *Pollanisus*, *Illiberis*, *Clelea*, *Harrisina*, *Pyromorpha*) have such a type of cocoon (Fig. 52A), while those of all other taxa (Fig. 52B–J) do not have separate inner and outer layers.

Crystallites (ch. 399): the crystallites produced in the Malpighian tubules are densely arranged on the outer surface of the cocoons (see also Naumann *et al.*, 1999: 22), but in Phaudinae such crystallites are not found on either the outer or inner surface.

Attachment to substrate (ch. 400): there are three different types of attachment of cocoons to the substrate. In Himantopteridae, Lacturidae and Phaudinae (Fig. 52J), the cocoons are built among plant litter and have irregular shapes (400: 0). The cocoons of Heterogynidae, *Zygaena filipendulae* and *Aglaope* are loosely attached to plant stems or leaves (400: 1). All the remaining taxa have cocoons enclosed by leaves or firmly attached to other substrates (400: 2) (Fig. 52A–I).

Shape (ch. 401): Naumann *et al.* (1999) classified the shapes of zygaenid cocoons into three major types: ovoid, spindle-shaped and bluntly fusiform. We define six types of cocoon shape in the present study. A fusiform (401: 0) (Fig. 52J) cocoon is present in Himantopteridae, *Lactura* and *Phauda*. An ovoid form (401: 1) is only observed in *Aglaope* and *Pseudopidorus*. The cocoons of *Artona* and *Pryeria* are rather flattened, compressed dorsoventrally and rounded (401: 3) (Fig. 52B). The majority of chalcosiines and *Callizygaena* have a peculiar cocoon shape which is formed by a crescentic lateroventral part and an upper 'cover' which is attenuated at the caudal and cephalic ends (401: 4) (Fig. 52H). This upper 'cover' of the cocoon is more rhomboid in *Cyclosia* (404: 5).

Texture (ch. 402): the texture of the cocoon is largely influenced by the quality and quantity of the silk and also the crystallites coating the cocoon. Cocoons of *Callizygaena* and the chalcosiine groups examined are firm to the touch (402: 1).

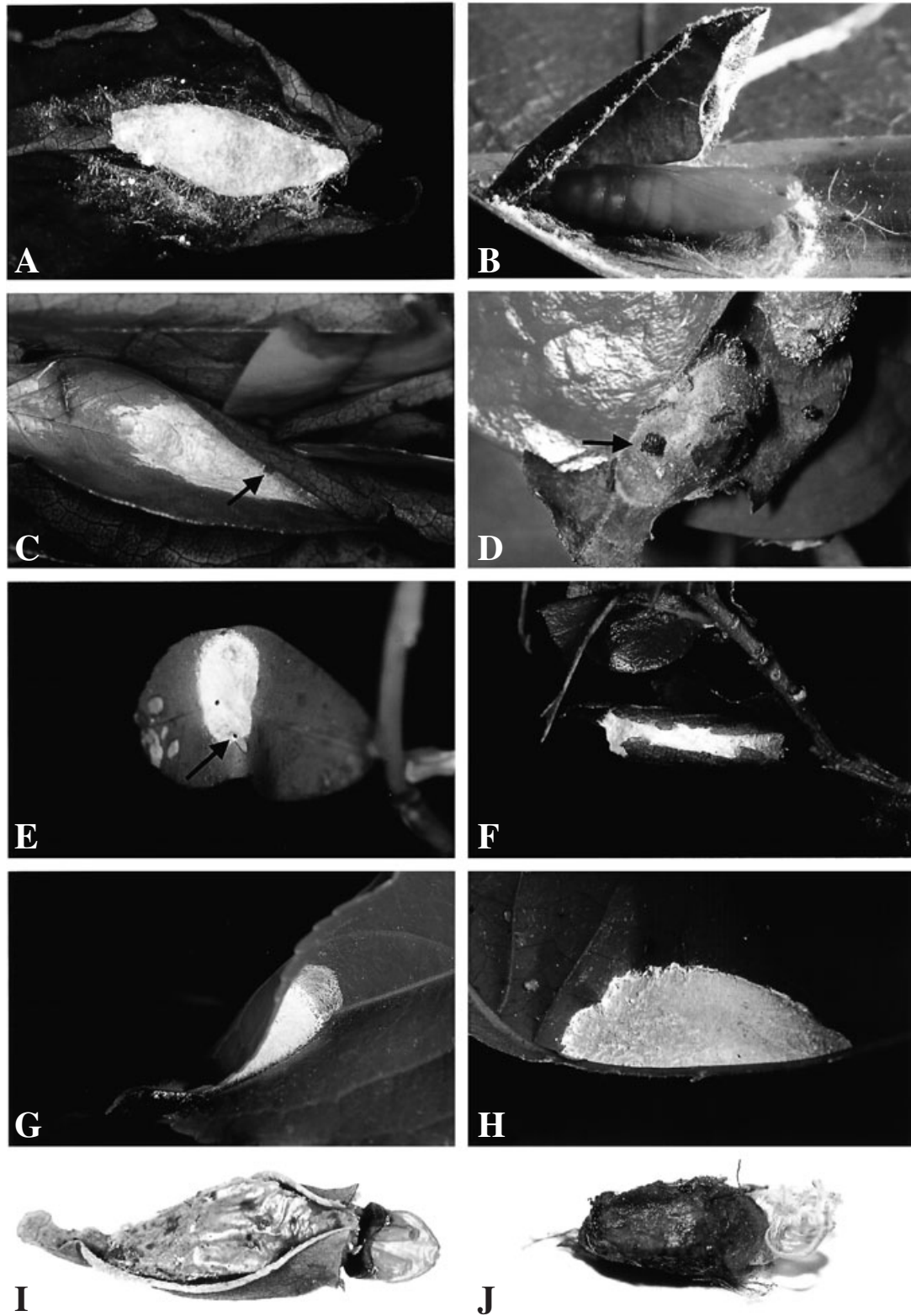


Figure 52. Cocoons of Procridinae (A, B), Chalcosiinae (C–H), Callizygaeninae (I) and Phaudinae (J). A, *Illiberis horni*. B, *Artona martini*. C, *Achelura sanguifasciata*. D, *Rhodopsona rutila*. E, *Arbudas submacula*. F, *Chalcosia diana*. G, *Histia flabellicornis ultima*. H, *Erasmia pulchella hobsoni*. I, *Callizygaena splendens*. J, *Phauda mimica*. Arrows indicate the 'last piece of frass' left on the cocoons.

In addition, except for Phaudinae, all the examined cocoons of Chalcosiinae and *Callizygaena* have the 'final piece of frass' attached to the cocoons (Fig. 52C–E). This feature requires further study.

CHEMICAL DEFENCE SYSTEM

Adult system

Epstein *et al.* (1999) reported that the adults of zygaenids (except for Phaudinae) release cyanic foam from the 'lower margin of the compound eyes'. In the present study we determined the exact location where the foam is released to be the intersegmental membrane between the subgena and the rudimentary mandibular lobe, although no significant orifice has been located. Mandibular lobes are totally absent in some outgroups, such as *Burlacena*, Himantopteridae, Anomoeotidae, Lacturidae, Phaudinae, Heterogynidae, *Janseola*, *Homophylotis nigra* and three species-groups of the ingroup, *Inouela*, *Chalcosiopsis variata* and *Chalcosiopsis melli*. The apex of the reduced mandible is usually concealed by the lower margin of the frontoclypeus and sclerotized to varying degrees.

The feature of a completely membranous mandibular lobe was separated into two character states

(403: 1 and 403: 2) (Fig. 12W, X). In *Theresimima*, *Pryeria*, *Arbudas*, *Eumorphiopais* and some other groups, this lobe protrudes only slightly from the lower margin of the subgena, while it is more prominent in several unrelated groups, e.g. *Corma*, *Erasmia* and some species-groups of *Soritia*. In many of the genera of Procridinae examined, the lobe protrudes slightly, but has a sclerotized tip (403: 3) (Fig. 12Y). A type of lobe, half sclerotized, was observed in *Zygaena*, *Callizygaena ada* and *Artona* (403: 4) (Fig. 12Z). In all species-groups of *Rhodopsona*, *Eucormopsis* and *Anarbudas insignis*, the lobe is more than two-thirds sclerotized (403: 5) (Fig. 12Z-1). Band-like sclerotization on the mandible is shared by various species-groups currently placed in the *Cadphises*, *Agalope*, *Aglaope*, *Campylotes* and *Neoherpa* genus-complexes (403: 6) (Fig. 12Z-2). Character states 403: 7–9 represent progressive degrees of sclerotization along the length of mandible (Fig. 12Z-3–5). In total, nine character states were coded for this feature. The ability to release cyanic foam from the mandibular lobe was coded as well (404: 1) (Fig. 53A).

In the Chalcosiinae, another foam-releasing structure is found between the patagia and parapatagia (405: 1) (Fig. 53B). The morphology of the patagia and

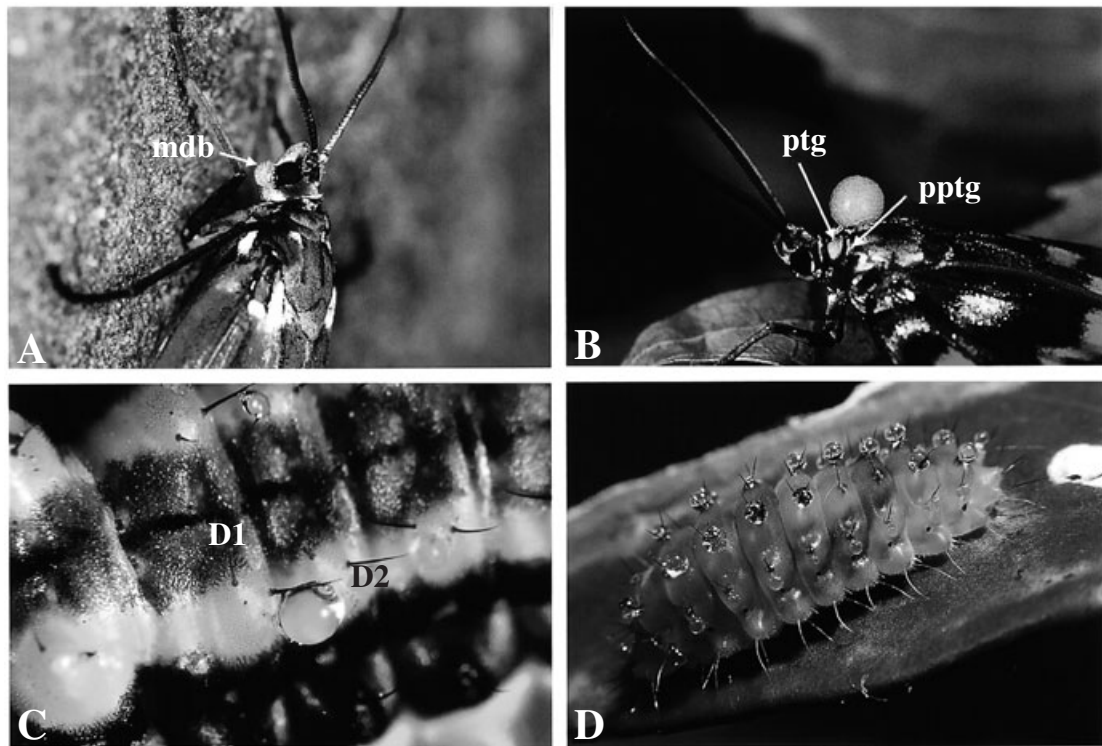


Figure 53. Adult and larval chemical defence of Chalcosiinae. A., cyanic foam released from the membranized mandibles (mdb) of *Eterusia aedeiformosana*. B., cyanic foam released from the intersegmental membrane between patagia (ptg) and parapatagia (pptg) of *Erasmia pulchella hobsoni*. C., cyanic fluid released from dorsal (D) cuticular cavities of *Pidorus atratus*. D., a larva of *Eterusia aedeiformosana* Jordan releases cyanic fluid from the dorsal and subdorsal cuticular cavities.

parapatagia has been discussed in the section dealing with the prothorax. In this section, only the features relevant to chemical defence are considered.

In addition, one distinct but unidentified compound has been detected from the *Agalope* genus-complex (*Agalope*, *Achelura*, *Elcysma*). This feature is tentatively coded as 'presence of cyanoglucoside-A' (406: 1).

Larval system

Based on the western Palaearctic *Zygaena trifolii* and the eastern Palaearctic *Pryeria sinica* (both belonging to Zygaeninae), two types of cuticular cavity (Franzl & Naumann, 1984, 1985, 1987; Franzl, Naumann & Nahrstedt, 1988) and their opening mechanisms for storing and releasing cyanic secretions were recognized by Naumann & Feist (1987). Type I has a large chamber beneath the dorsal integument with a simple opening pore, but no sensory setae, while type II (Fig. 54E, H) has smaller and more densely distributed pores and a single sensory seta. The cavities are thought to provide a graded response to different degrees of attack from natural enemies or any other alien disturbance. Epstein *et al.* (1999), regarded the presence of these storage chambers and opening mechanisms as synapomorphic characters of Zygaeninae and Chalcosiinae, and their absence in Procrarinae was considered to be a secondary loss.

However, following the morphological survey in this study, only one type of storage cavity and opening mechanism is recognized. Unlike *Zygaena* and *Pryeria*, the distribution of cuticular cavities in Chalcosiinae is confined to each of the verrucae. The opening mechanism has 1–3 openings (Fig. 54A–D, G) located on the tip of each verruca, but has no accessory sensory setae situated beside the pore(s). Fänger & Naumann (2001) reported that the larva of *Aglaope infausta* has cuticular cavities for storing cyanic fluids but the opening mechanism is absent.

A similar larval chemical defence system is present in Heterogynidae. The structure of the opening mechanism in *Heterogynis* (Fig. 54F) was found to be different from that of zygaenids. In Zygaeninae, the opening pores are usually surrounded by microtrichia, and the pores in chalcosiine larvae are surrounded by a circular sclerite. In Heterogynidae, all the opening pores are located on a short, aristate knob and bordered by a granular surrounding area.

The two major compounds of the cyanoglucosides linamarin and lotaustralin are shared by larvae and adults of zygaenines, procrarines and chalcosiines (Davis & Nahrstedt, 1982; Witthohn & Naumann, 1984a, b; Franzl, Nahrstedt & Naumann, 1986; Witthohn & Naumann, 1987a, b; Naumann *et al.*, 1999). Nishida (1995) reported that lotaustralin is the major component in the secretion of *Elcysma*. Preliminary

examination of chemical compounds gathered from various species of *Agalope*, *Achelura*, *Hampsonia*, *Formozygaena* and *Aglaope* suggests this feature may provide a synapomorphic character for a certain group (S. H. Yen, unpubl. data). Sarmentosin is also reported from the larval secretions of Procrarinae, Zygaeninae, Chalcosiinae (Nishida, 1995; present study) and also Heterogynidae.

PHYLOGENETIC ANALYSIS

PROTOCOLS

Building the most parsimonious trees and character weighting

In the present study, maximum parsimony tree building for all 207 taxa and 414 characters (168 binary, 246 multistate) assigned equal weights (EW) was carried out using PAUP* 4.0b10 (Swofford, 1998). Multistate characters were interpreted as being polymorphic rather than as uncertain. An initial heuristic search was performed with 10000 random additions and with tree bisection reconnection (TBR) branch swapping, but with no more than one tree held during each search. All the shortest trees were found and were then used individually as starting trees for the next search with maxtrees set to 10000.

The searching strategy for estimating large phylogenies followed Quicke, Taylor & Purvis (2001). This strategy uses an interactive searching process of branch swapping with equally weighted characters, followed by swapping with reweighted characters. It increases the efficiency of the search by changing the landscape of 'tree-islands' allowing search to escape local optima.

Successive approximations weighting (SAW) (Farris, 1969, 1989) was conducted. Use of CI as the reweighting factor has been debated (Gauthier *et al.*, 2000; Quicke *et al.*, 2001) and the maximum or the minimum value of RI was suggested as an alternative. In the present study, we used the latter. The results were compared with those based on EW by generating a strict consensus.

Support and confidence statistics for cladograms

We applied three methods to measure the support and confidence statistics for cladograms. Bremer support (Donoghue *et al.*, 1992; Källersjö *et al.*, 1992; Bremer, 1994) was calculated for selected branches.

We also applied both bootstrapping and jackknifing for the whole cladogram and compared their support for each of the clades. For calculating bootstrap and jackknife values, we used 200 replicates of 10000 random additions (maxtrees = 10000). A deletion rate of 36.79% for jackknife resampling, suggested by Farris *et al.* (1996), was adopted.

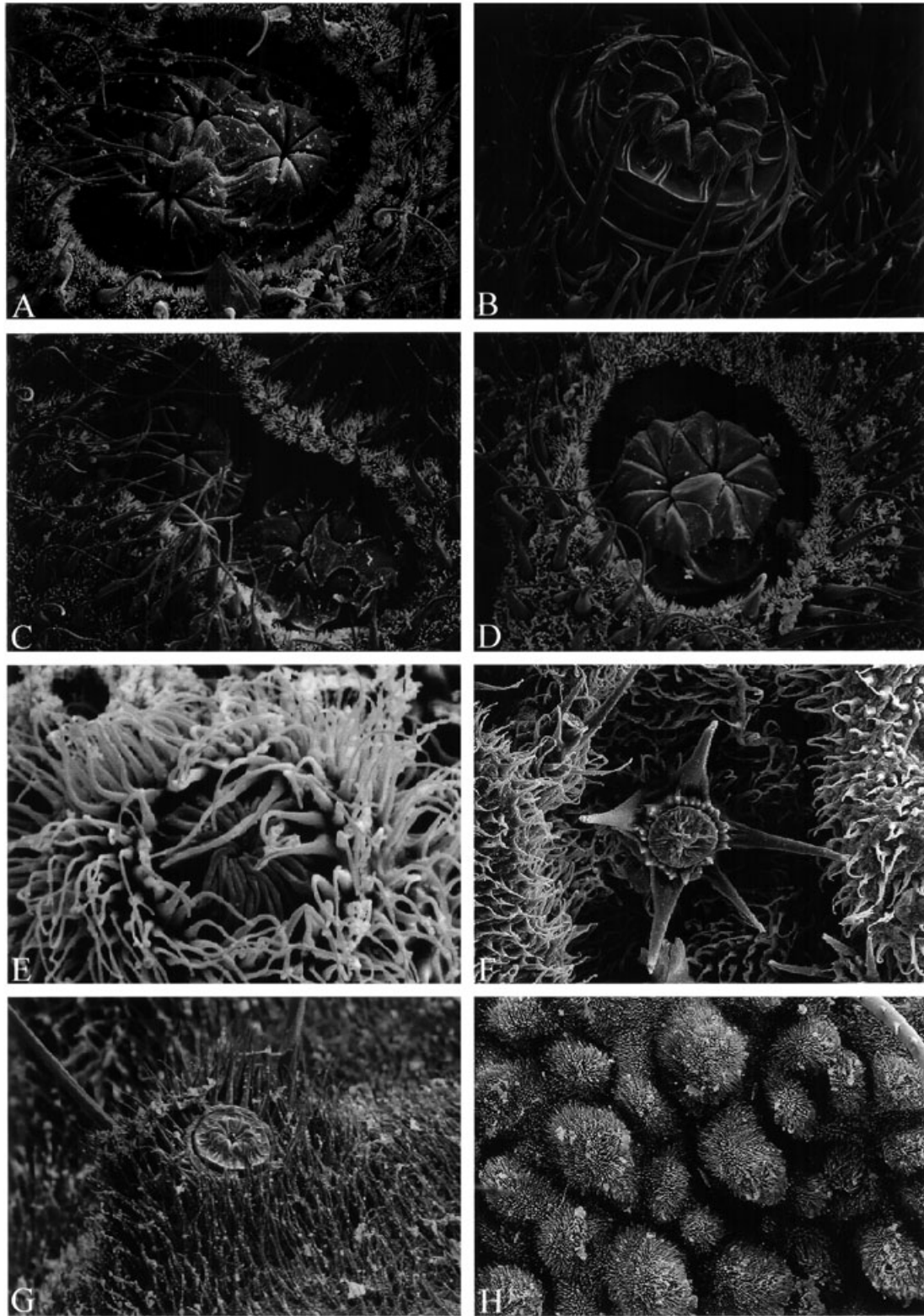


Figure 54. Cuticular structures relevant to chemical defence system. A, several opening pores situated in a cavity (410: 2), *Eterusia aedeae formosana*. B, single pore situated in a cavity (410: 1). C, two pores in a cavity (410: 2), *Pidorus atratus*. D, two pores nearly fused. E, opening pore of *Zygaena filipendulae*. F, the opening pore of *Heterogynis* is located on a star-like verruca. G, opening pores of *Arbudas submacula*. H, in *Zygaena*, one verruca has only one opening pore (409: 1).

Testing incongruence between character subsets

In order to understand the influences of different combinations of data subsets on the phylogeny of Chalcosiinae, we implemented the incongruence length difference (ILD) test as described in Farris *et al.* (1994), Mason-Gamer & Kellogg (1996) and Desalle & Brower (1997). We partitioned the data matrix in two ways. First, because the morphological characters of Chalcosiinae demonstrate extremely strong sexual dimorphism, which has led to very misleading classification at both specific and generic levels, we sought to investigate whether the phylogenies generated by the characters of different sexes told different evolutionary stories. We separated the whole data set into three partitions, e.g. male, female, and non sex-linked (including immature stages), then we tested the phy-

logenetic congruence between each pair of character partitions (see Table 3).

Second, we separated the whole characters into two subsets, adult and immature. This allowed us to examine whether the characters of latter were more informative in the phylogenetic reconstruction of family-level relationships of Zygaenidae/Zygaenoidea (as stated by Fänger *et al.*, 1999; 2002; Fänger & Naumann, 2001). However, since there is a large proportion of missing entries for the immature characters (the immature stages of 66% of the included taxa are unknown), we constructed MPTs based on the 56 immature characters deactivated and then compared them with the initial MPTs based on the whole data set to check whether the topological structure was greatly influenced by this exclusion. Then we excluded

Table 3. The contents of the topological constraints generated for testing monophylies of the groups

Constraints	Contents	Sources of previous hypotheses
<i>Inouela</i> + Chalcosiinae	<i>Inouela</i> , Chalcosiinae s.s.*	Efetov (1999)
<i>Inouela</i> + <i>Arbudas</i>	<i>Inouela</i> and all species-groups of <i>Arbudas</i>	Efetov (1999)
<i>Cleoda</i> + Chalcosiinae	<i>Cleoda syntomoides</i> , Chalcosiinae s.s.	*Bryk (1936); Alberti (1954, Endo & Kishida (1999)
Zygaeninae + Chalcosiinae	the ingroup, <i>Pryeria</i> and <i>Zygaena</i>	Naumann (1987a), (1988); Naumann <i>et al.</i> (1999); Fänger & Naumann (2001)
Chalcosiinae s.l.	the ingroup	Alberti (1954); Endo & Kishida (1999)
Heteropanini <i>sensu</i> Alberti	see Fig. 3	Alberti (1954)
<i>Aglaope</i> + other chalcosiines	<i>Aglaope</i> is the sister-group of the other chalcosiine genera	Fänger & Naumann (2001)
<i>Aglaope</i> + (Zygaeninae + Chalcosiinae)	<i>Aglaope</i> is the sister-group of Zygaeninae + Chalcosiinae	Fänger & Naumann (2001)
Aglaopini <i>sensu</i> Tarmann	see Fig. 3	Alberti (1954); Tarmann (1992)
Agalopini <i>sensu</i> Alberti	see Fig. 3	Alberti (1954)
Cyclosiini <i>sensu</i> Alberti	see Fig. 3	Alberti (1954)
Chalcosiini <i>sensu</i> Alberti	see Fig. 3	Alberti (1954)
<i>Agalope</i>	all the species placed in <i>Agalope</i> **	Bryk (1936); Endo & Kishida (1999)
<i>Pidorus</i>	all the species placed in <i>Pidorus</i> **, <i>Arbudas leno</i> , <i>A. truncatus</i> and <i>Pseudopidorus fasciatus</i>	Bryk (1936); Endo & Kishida (1999)
<i>Eterusia</i>	all the species placed in <i>Eterusia</i> **, <i>Pidorus culoti</i> , <i>Eusphalera venus</i> , <i>E. subnigra</i> , <i>Soritia shahama</i> , <i>Prosopandrophila distincta</i> , <i>Pr. mirifica</i> and <i>Soritia pulchella</i>	Bryk (1936); Endo & Kishida (1999)
<i>Soritia</i>	all the species placed in <i>Soritia</i> and <i>Pidorus circinata</i> , <i>Eterusia risa</i> , <i>E. binotata</i> , <i>Scotopais tristis</i> **	Bryk (1936); Endo & Kishida (1999)
<i>Chalcosia</i>	all the species placed in <i>Chalcosia</i> and <i>Psaphis azurea</i> **	Endo & Kishida (1999)
<i>Trypanophora</i>	all the species placed in <i>Trypanophora</i> **	Bryk (1936); Endo & Kishida (1999)
<i>Docleopsis</i>	all the species placed in <i>Docleopsis</i> **	Bryk (1936); Endo & Kishida (1999)

*The ingroup excluding *Chalcosiopsis*, *Cleoda*, *Heteropan* and *Inouela*.

** See Appendix 1 for details of the taxa defined and included.

the taxa for which data on immature stages are unavailable. Eventually 72 taxa, including 14 of the 21 outgroups, were left on which to test incongruence between the adult and immature characters. We also constructed MPTs based on male, female, non sex-linked (with all taxa included), male and immature characters (with 135 taxa excluded), respectively.

The ILD tests were carried out using 100 replicates with 100 random additions and maxtrees set at 100. All tests were run with uninformative characters excluded, as recommended by Cunningham (1997).

Comparing phylogenies with specific character subsets deactivated

We used another method to compare the phylogenies generated by the data matrix; this involved deactivating different character subsets. We aimed to evaluate the significance of two kinds of subset on the phylogenetic structures of Chalcosiinae: characters which were traditionally not 'favoured' and considered by morphology-based cladistic studies (e.g. colour patterns); and characters which were considered taxonomically or phylogenetically significant. We examined each character individually and assigned it to the following groups: (1) colour patterns; (2) wing shape; (3) wing venation; (4) male eighth abdominal segment; (5) female genitalia; (6) scent organs; (7) chaetosemata; (8) sensory organs; (9) chemical defence systems. We constructed MPTs by using the same protocol described above, based on the whole data set with each of them deactivated, respectively. We compared their topological differences with the initial working MPTs using 'Tree-to-Tree distances' in PAUP* to reveal the symmetrical differences among all pairs of trees; in addition, we calculated their range and mean. We particularly noted whether any part of the topology became unresolved and whether the phylogenetic positions of particular clades were changed in each of the analyses.

Testing monophyly or nonmonophyly

We adopted Templeton's (1983) test as implemented in PAUP* under parsimony tree scores, for comparing the hypotheses of chalcosiine relationships.

RESULTS OF PHYLOGENETIC ANALYSIS

ANALYSES OF FULL DATA SET

The initial heuristic search based on EW characters produced 35 MPTs of 4829 steps (CI = 0.241, RI = 0.741) (see Appendix 7 for character diagnosis). We then performed heuristic searches for each of the trees by using the 'changing the landscape' strategy proposed by Quicke *et al.* (2001). However, we did not

find trees shorter than 4829 steps, so we used the initial 35 trees, the shortest consensus of which is shown in Figure 55. These trees differ only in the interrelationships among seven terminal clades of the ingroup, e.g. ((*Cadphises* + *Hampsonia*) + (*Watermenia* + *Herpidia*) + '*Soritia*' *sevastopuloi*) (*Docleomorpha boholica* + *Cryptophysophilus bicoloratus* + *Heterusinula dichroa*) (*Cyclosia papilionaris* + *C. chartacea*, *C. spargens* + *C. macularia*) (all species-groups of *Rhodopsona* + *Pidorus miles*) ((*Erasmiphlebohecta picturata* + *Chalcophaedra zuleika*) + *Erasmia pulchella* + all species-groups of *Eucorma*), all species-groups of *Eusphalera* and *Gynautocera*.

SAW analysis stabilized after seven iterations and found 54 MPTs of 4836 steps (when characters were reweighted back to unity) (CI = 0.240, RI = 0.740). These 54 trees (Fig. 56) differ among themselves in only four terminal clades of the ingroup, e.g. (*Cyclosia papilionaris* + *C. chartacea* + *C. spargens*) (*Rhodopsona costata* + *R. jordani* + *R. reverdii*) (*Erasmia pulchella* + *Eucorma intercesa* + *Eucorma euphaena*) ((*Eusphalera multicolor* + *E. subnigra*) + *E. picturata*) + (*E. ligata* + *E. regina*) + *E. venus*). Because the general topologies of the MPTs of EW/SAW are only slightly different in 11 clades (Fig. 58), we calculated their consensus. The cladogram is shown in Figure 57.

The Bremer support values of EW/SAW analyses are given in Figure 57. Those for the branches of clades 3–18, 4–18, 8–18 and 9–18 are relatively weak. The topologies generated by bootstrapping and jackknifing analyses are almost identical, so we calculated the consensus of the results based on the whole data matrix (Fig. 59). These two tree-supporting approaches show that the hitherto accepted concept of Zygaenidae, including *Burlacena*, *Chalcosiopsis* and *Phauda*, is not monophyletic, although the interrelationships among the subfamilies are strongly supported. Chalcosiinae is not monophyletic if *Inouela*, *Cleoda*, *Chalcosiopsis* and *Heteropan* are included; in addition, its inter-tribal and inter-generic relationships are poorly supported.

The detailed results are discussed below. First, we consider the relationships among the zygaenoid families brought into the analyses. Second, we examine the subfamilial-level relationships of Zygaenidae and its potential sister group, Chalcosiinae. Third, we discuss the relationships among the major clades of Chalcosiinae. All discussions of these patterns of relationships are based on the EW and SAW analyses. We refer only to unambiguously optimized characters unless specifically stated.

INTERFAMILIAL RELATIONSHIPS OF ZYGAENOIDEA

Although investigating the relationships among the zygaenoid families was not the main scope of the

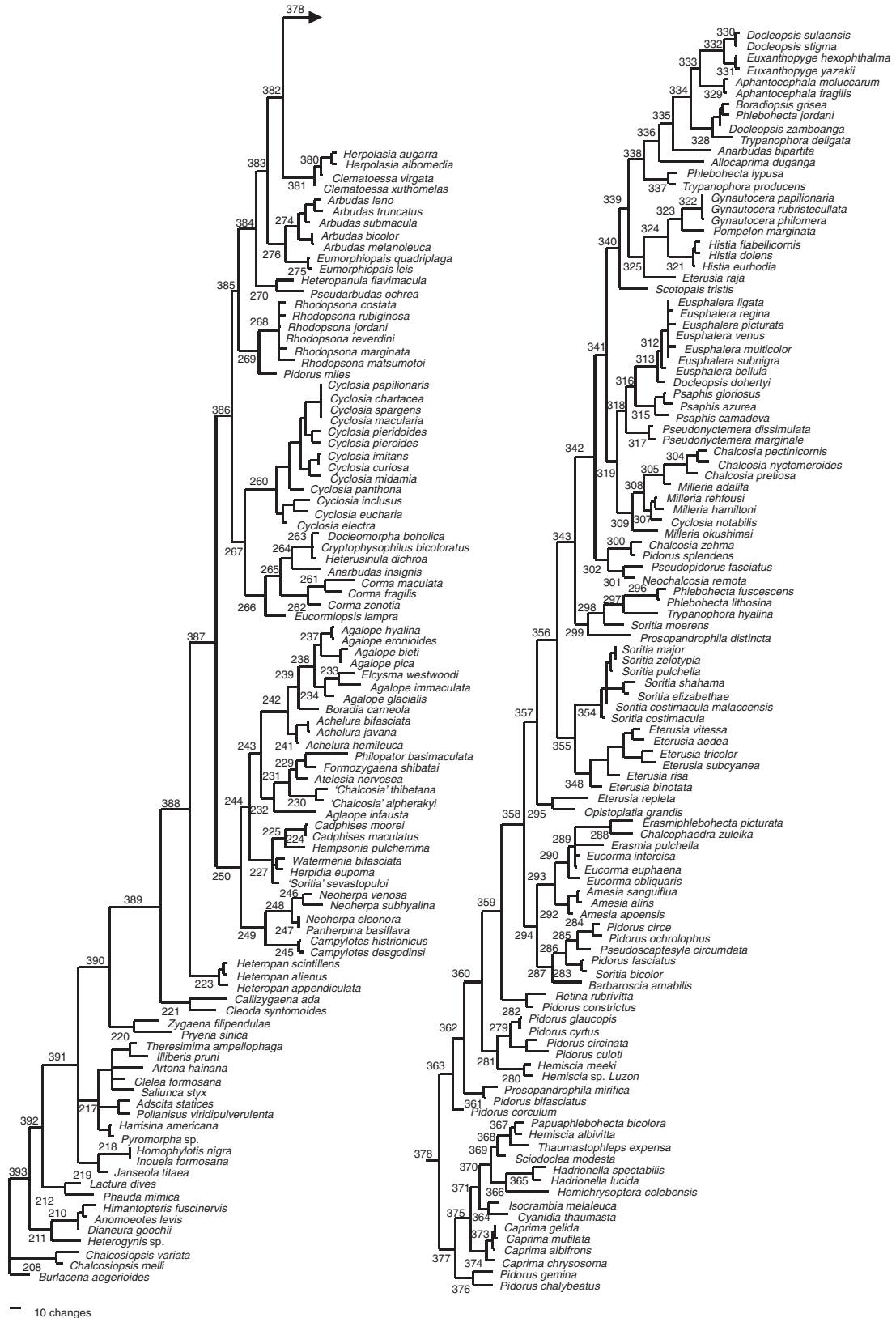


Figure 55. Strict consensus of 35 MPTs based on the whole data set under EW. Numbers correspond to node numbers in Appendix 4.

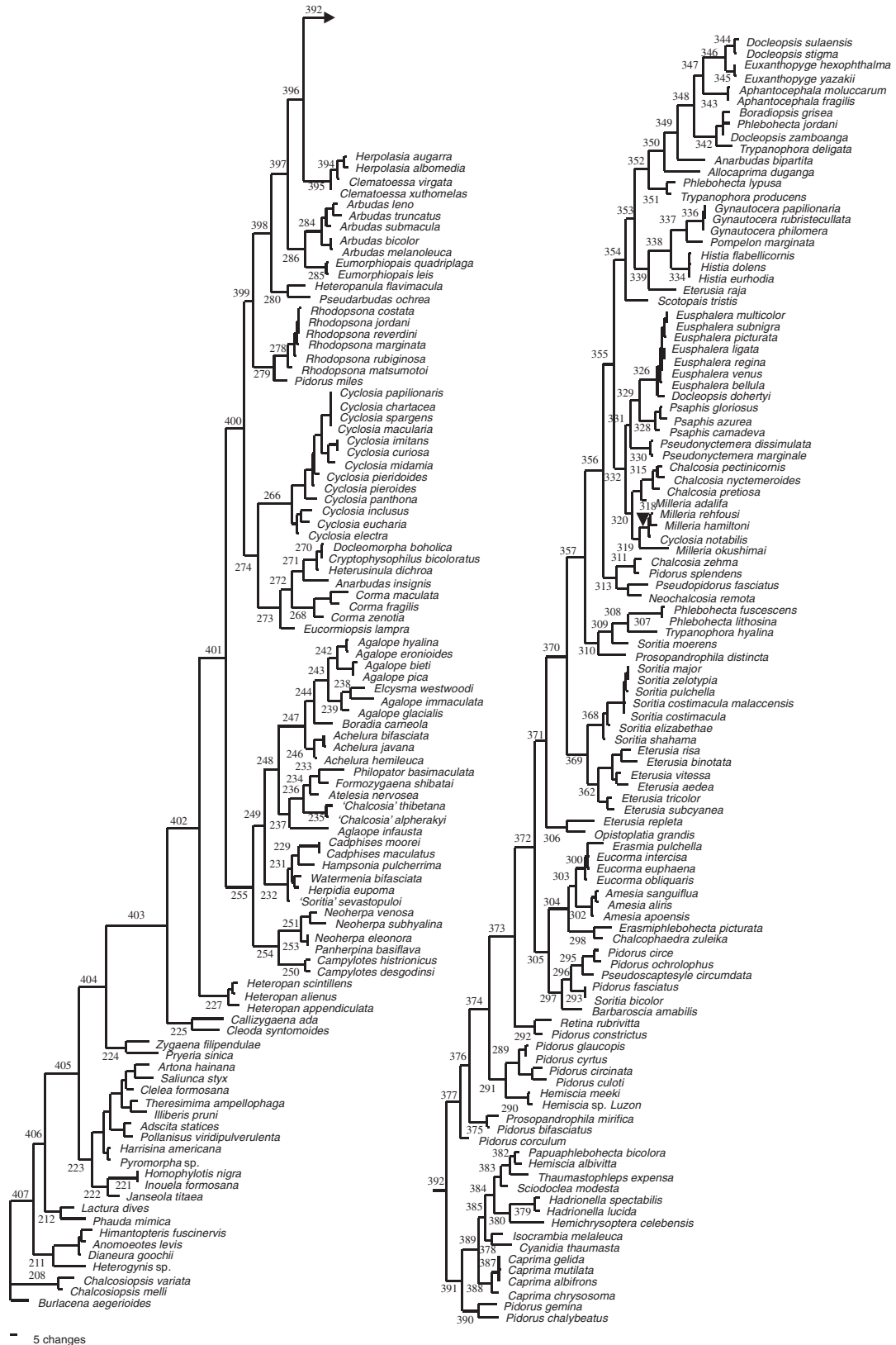


Figure 56. Strict consensus of 54 MPTs (tree length = 2986.5489, CI = 0.2704, RI = 0.7906) based on the whole data set under SAW. Numbers correspond to node numbers in Appendix 5.

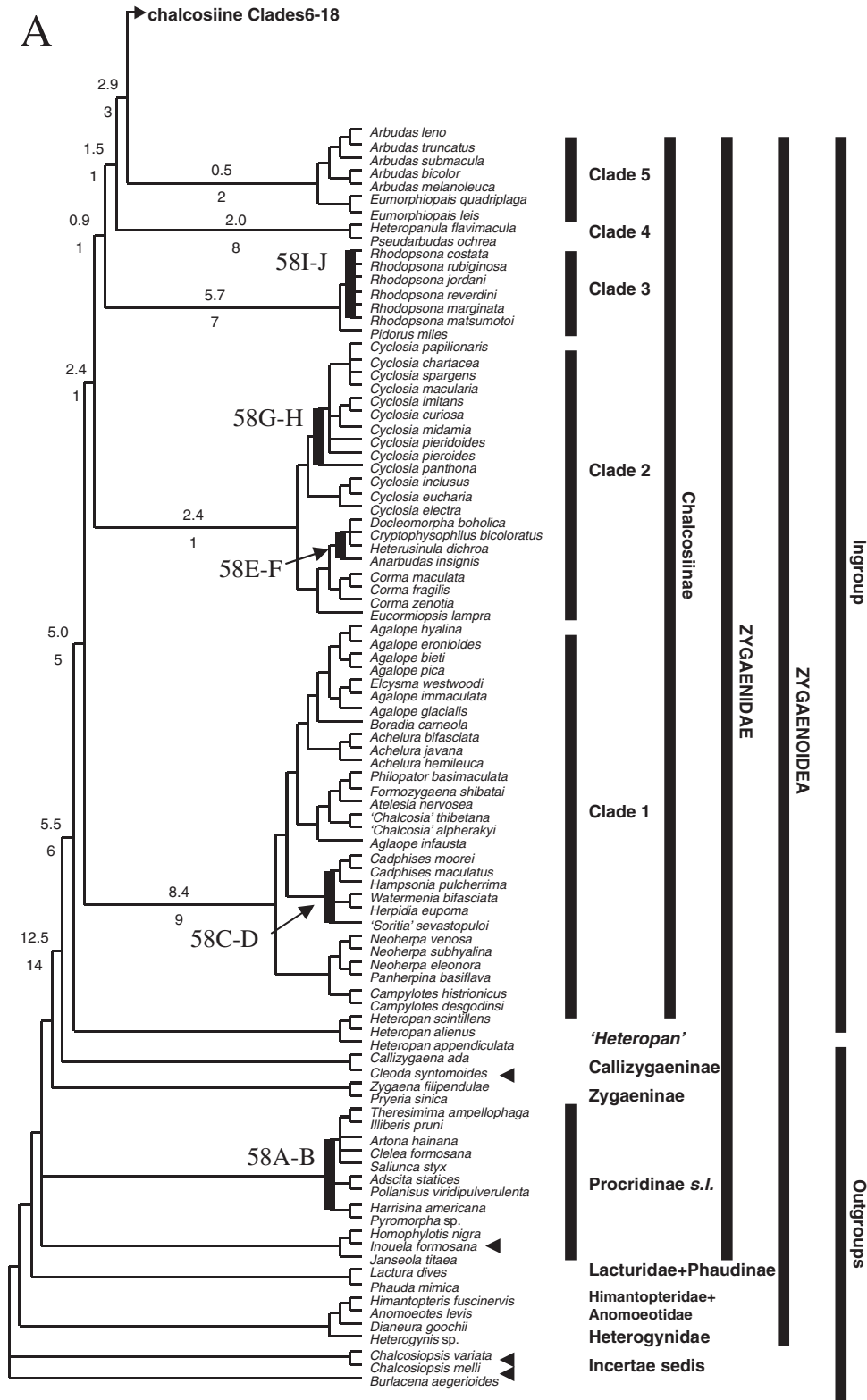
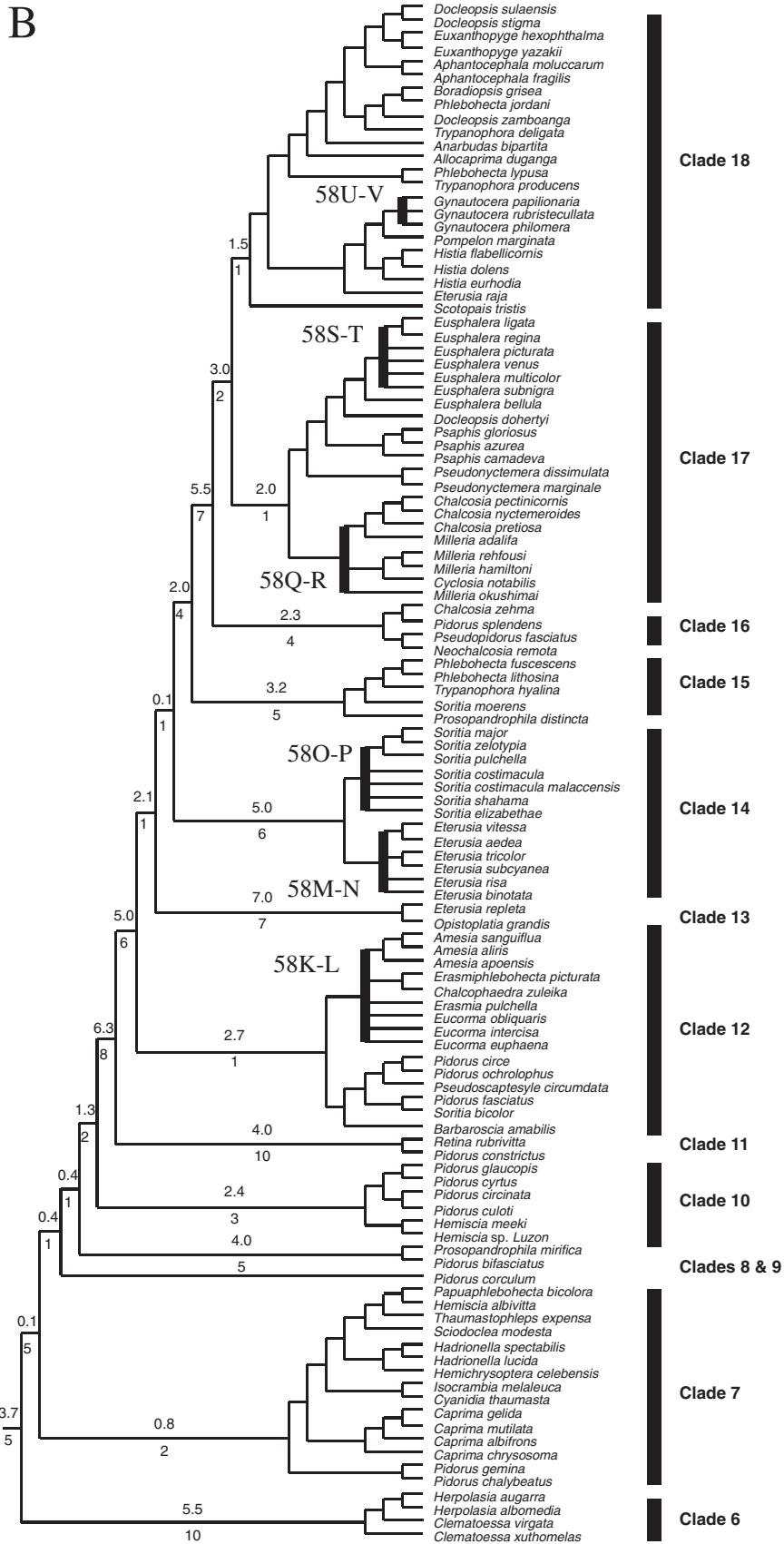


Figure 57. Strict consensus of 35 MPTs under EW (A) and 54 MPTs under SAW (B) based on the whole data set. Topological differences between the trees are indicated by thickened branches. Numbers beside the latter refer to more detailed clades in Fig. 58. Arrows indicate the ingroup taxa that are grouped with the outgroups. Bremer support values for the EW analysis (below branches) and SAW analysis (above branches) are labelled for the major clades.



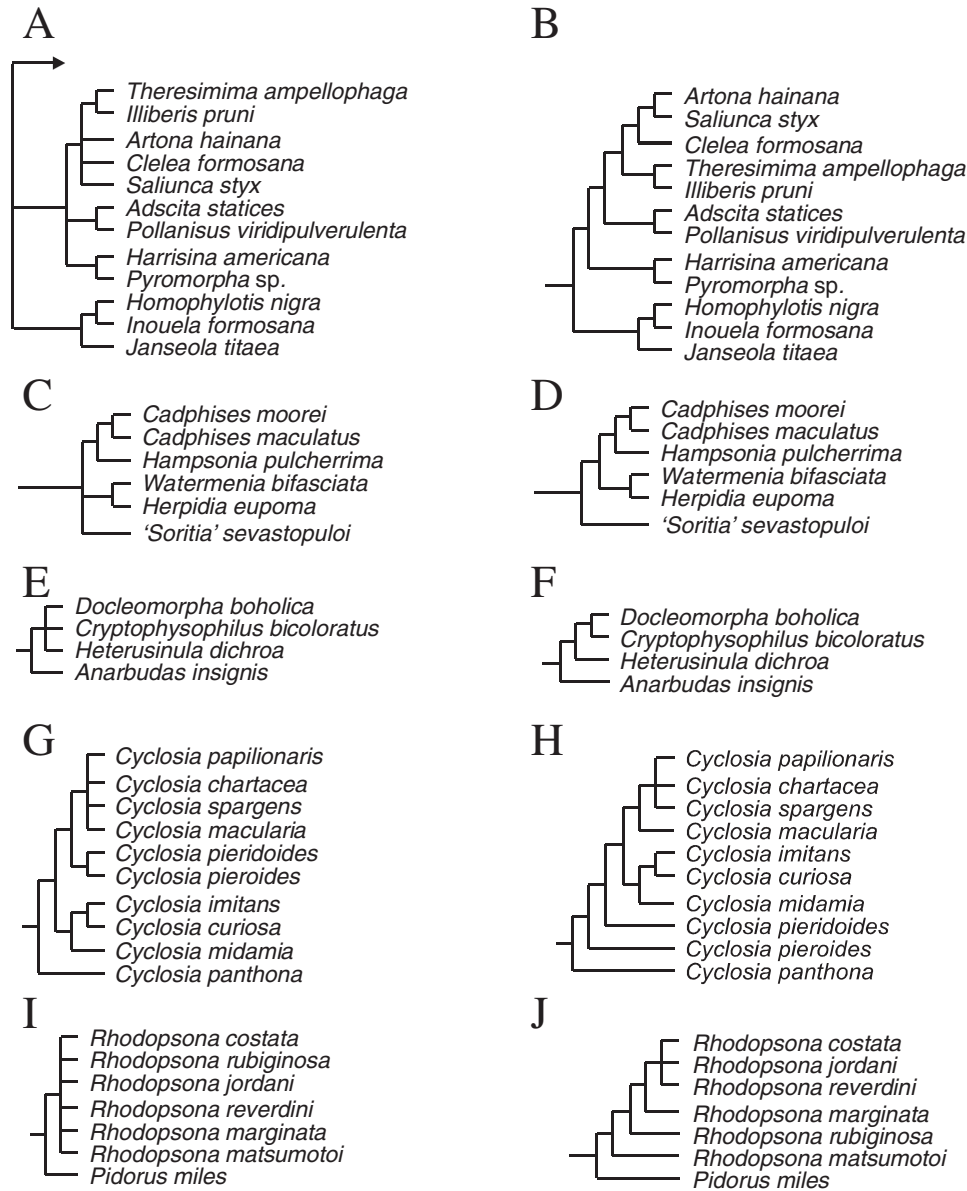


Figure 58. Detailed topological differences between the 35 MPTs under EW (left row) and 54 MPTs under SAW (right row). A–J, differences between the outgroups and 'clade 3'.

present study and the sampling of the family groups was incomplete due to the absence of all the limacodid families *sensu* Epstein, we were interested in whether the relationships of those recovered in the present study agreed with the previous hypotheses (see Fig. 1).

First of all, in both the EW and SAW analyses, *Burlacena aegerioides* and two members of the ingroup, *Chalcosiopsis variata* and *Chalcosiopsis melli*, were not found to be monophyletic with other zygaenoid groups as neither presents any synapomorphies shown by the other zygaenoids. The synapomorphies

which support the zygaenoid taxa in EW include 20 characters (see Appendix 4), although ch. 90: 1 (epiphysis of fore tibia absent) is absent in SAW.

None of these has been proposed as a synapomorphy by previous authors because the lack of immature characters in the majority of included taxa has constrained their apparent phylogenetic signal. Surprisingly, ch. 33: 5 and 34: 5 (proboscis totally absent) become synapomorphic for the Zygaenoidea; that is, redevelopment of a functional proboscis has evolved independently in different lineages of Zygaenoidea. This result is counter-intuitive, but it can only be

tested if all the representative taxa of the superfamily and its potential sister groups (e.g. Sesioidea, Castnioidea, and Cossioidea) are included in an analysis.

A clade, which is supported by 21 characters and contains *Heterogynis*, *Dianeura*, *Anomoeotes* and *Himantopterus*, is recovered by both EW and SAW. The Anomoeotidae are paraphyletic with respect to Himantopteridae, as the striking forewing venation of *Dianeura* (96: 1, cross veins present between C and Sc) distinguishes it from *Anomoeotes* and *Himantopterus*. In both analyses, *Phauda* and *Lactura* form a monophyletic group which in turn forms the sister group to all of the zygaenid clades. *Phauda* + *Lactura* is supported by 21 characters in EW, with two characters (72: 1, patagia as developed as parapatagia; 90: 1, epiphysis of fore tibia absent) absent in SAW.

The remaining outgroups and the ingroup, strongly supported by 33 and 31 characters in EW/SAW respectively, form a monophyletic clade (see Appendices 4 and 5). This clade is regarded as the 'redefined' Zygaenidae. Among these apomorphies, ch. 353: 1 (larva with cross-muscle around mid-gut) is unique to Zygaenidae, as suspected by Naumann *et al.* (1999). Three characters relevant to chemical defence, e.g. release of cyanic foam from mandibular lobes by adults (404: 1), larval cuticular cavities with opening mechanism (407: 1), and sarmentosin present in larval defensive secretions (414: 1), also support monophyly of the Zygaenidae. However, the two major compounds of the larval secretion, linamarin (412: 1) and lotaustralin (413: 1), do not appear on this node.

Within Zygaenidae, it is very interesting to notice that *Janseola*, a genus currently associated with Heterogynidae (Scoble, 1992), appears grouped with the female of *Homophylotis nigra* and with *Inouela*. Our morphological research into *Janseola* and *Heterogynis* does not in fact suggest their affinity, as *Janseola* shares more apomorphies with some African genera of Procridinae and lacks all the autapomorphies of *Heterogynis* (Appendices 4, 5). We therefore suggest transferring *Janseola* to Zygaenidae, although its association with Procridinae remains questionable.

INTERSUBFAMILIAL RELATIONSHIPS OF ZYGAENIDAE

Within the Zygaenidae, five major clades, viz. Procridinae, Zygaeninae (Callizygaeninae + *Cleoda*), *Heteropan* and Chalcosiinae (excluding *Chalcosiopsis* and *Inouela*), are recovered by both EW and SAW, although the monophyly of Procridinae is uncertain. In EW the clade (*Janseola* + (*Homophylotis nigra* + *Inouela*)), the remaining nine outgroup taxa of Procridinae, and the clade (((Zygaeninae + ((Callizygaeninae + *Cleoda*) + (*Heteropan* + Chalcosiinae)))) form an unsolved trichotomy (Fig. 58A), while in SAW the clade (*Janseola* + (*Homophylotis nigra* +

Inouela)) becomes the basal lineage of Procridinae (Fig. 58B), supported by 12 apomorphies.

The presence of accessory glands in the female genitalia was supposed to be the synapomorphy for Procridinae (Naumann, 1988; Epstein *et al.*, 1999; Naumann *et al.*, 1999), but this feature is neither found among the apomorphies at node 217 in EW nor at node 223 in SAW. The genus *Inouela*, originally erected in the Chalcosiinae (Efetov, 1999), is grouped with the female of *Homophylotis nigra* in both EW (29 characters) and SAW (27 characters). This result does not necessarily mean that *Inouela* and *Homophylotis* are synonymous or closely related, because the type species of the latter (type species: *Homophylotis thyridotata* Turner, 1904; type locality: N. Queensland) is more closely related to *Turneriprocris* Bryk, 1936, another Australian procridine genus presumably related to Artonini (Tarmann, 1994). The monophyly of *Homophylotis* thus remains questionable. Efetov (1999) considered that the thorn-like aedeagus, ventral process and membranous cucullus of valvae, slender tegumen and tegumen-uncus complex of the male genitalia of *Inouela* may suggest an affinity with the *Arbudas* complex *sensu* Tarmann (1992c). However, this is not corroborated by the present study because all of these characters (e.g. uncus and tegumen fused, costal process present on valva, presence of transtilla-like structure) are shown to be convergent with those of the *Arbudas* species.

Monophyly of the Zygaeninae, represented by *Zygaena* and *Pryeria* in the present study, is supported by 24 apomorphies in both EW and SAW. This clade forms a monophyletic group with the remaining zygaenid groups based on 28 (EW) and 23 (SAW) synapomorphies. As suspected by Naumann (1987a, b; Naumann *et al.*, 1999), characters relevant to chemical defence, e.g. presence of membranous mandibular lobe (403: 1), larval cuticular cavities with opening mechanism (408: 1), mature larvae with only one opening mechanism on each of SD verrucae (409: 1), one opening mechanism with single pore (410: 1) and linamarin (412: 1) and lotaustralin (413: 1) present in the secretion, strongly support this grouping. Fänger *et al.* (1999) and Fänger & Naumann (2001) assumed that absence of a cuticular cavity for storing cyanic fluids in procridine larvae was due to secondary loss, while the present result suggests that absence of this structure is plesiomorphic. Minet (1986) suspected that Heterogynidae might be a 'degenerated taxon of Zygaenidae' because its larvae have a similar cuticular structure for storing cyanic fluids, and Fänger & Naumann (2001) assumed that Heterogynidae could possibly be a derived taxon in Zygaenidae. However, both of these hypotheses are rejected by the present result.

A group comprising *Callizygaena* and *Cleoda*, the latter an extremely rare genus that has been placed in

A

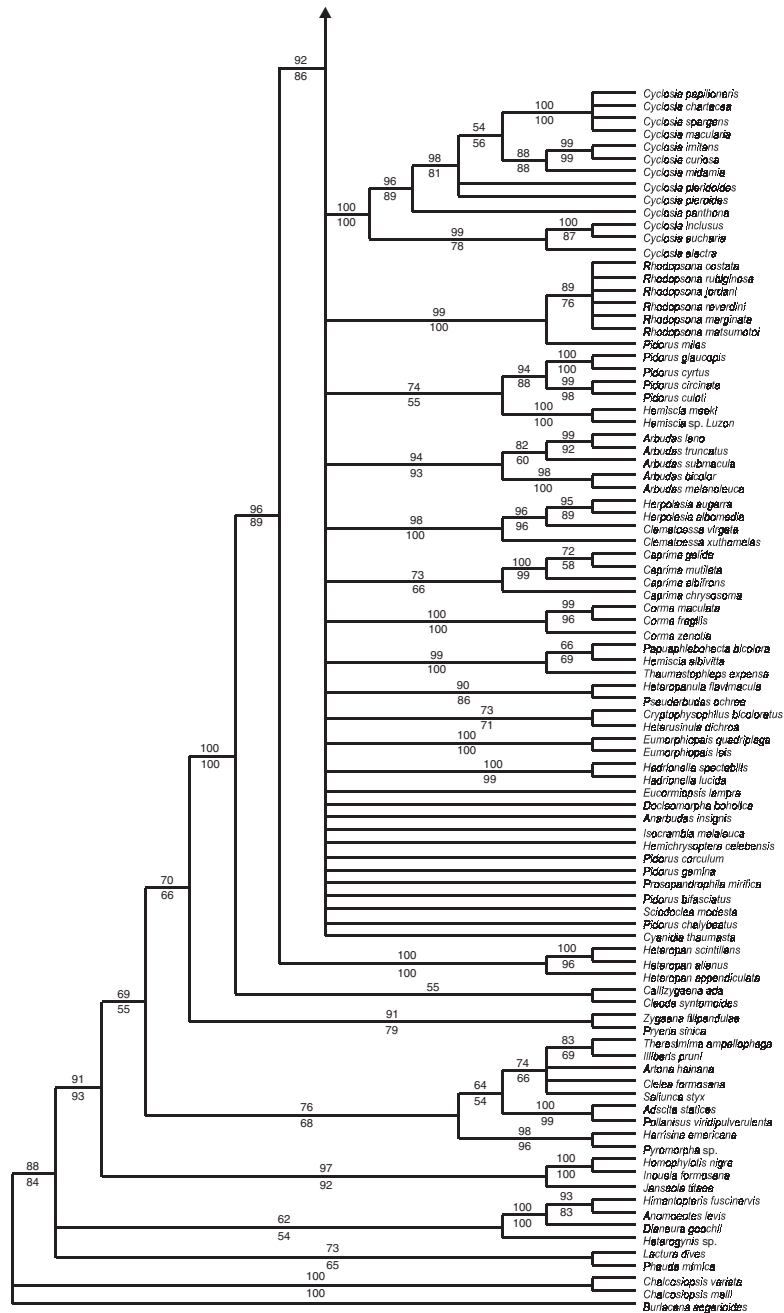
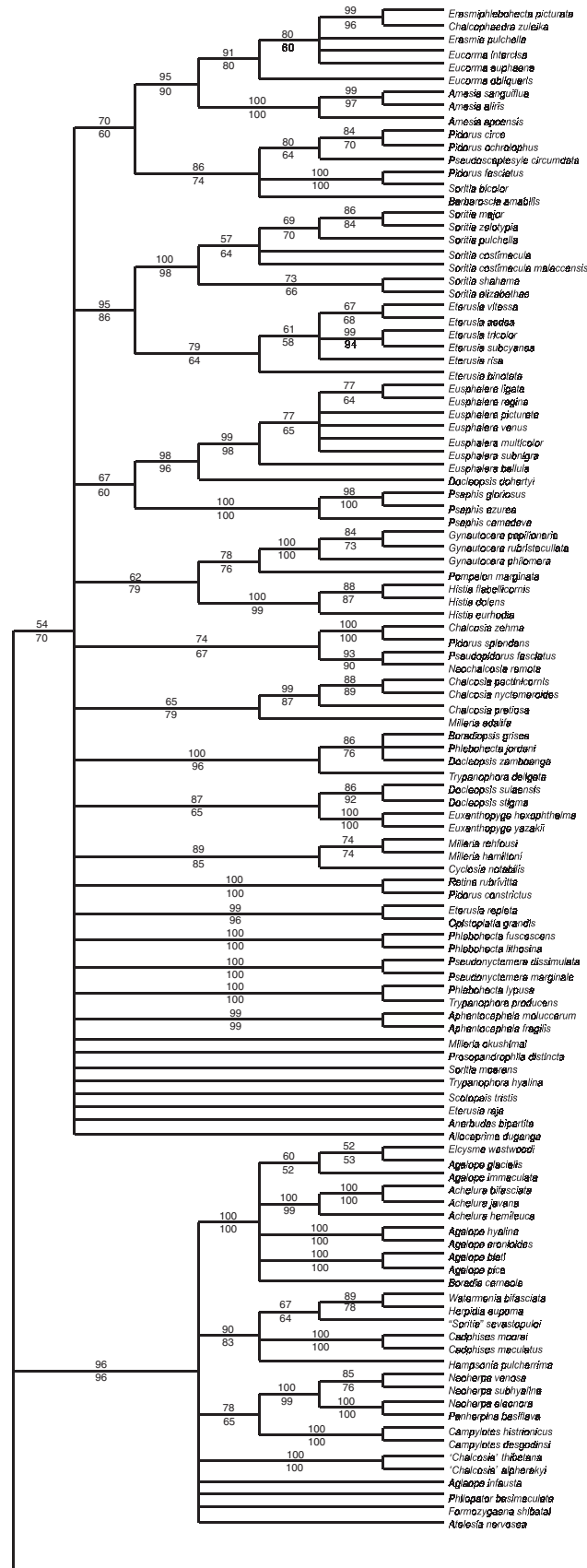


Figure 59. Strict consensus of jackknife (A) and bootstrap (B) trees (values above and below branches, respectively) based on the whole data matrix.

Chalcosiinae for a long time, is recovered as a strongly supported clade based on 27 (EW/SAW) characters. Six characters are unique to this clade: scales on chaetosemata deeply forked (65: 1), ‘type I’ apex and scales on both forewings and 4-toothed hindwings (169: 2, 170: 2, 173: 2, 174: 4) and L1 verrucae tubercle-like (361: 1). The clade forms a monophyletic group

with *Heteropan* and the Chalcosiinae, based on 48 apomorphies, of which 18 are unique: most basal segment of labial palpus swollen laterally (39: 1), terminal labial palpal segment shorter than the second one (44: 2), chaetosemata developed and extending from vertex beyond lower margin of compound eyes (61: 4), chaetosemata obliquely reniform (62: 5), subdorsal

B



and lateral anterotergal syndeses along front margin of tergum 2 (178: 2), papillae analis weakly bilobed (273: 1), papillae analis disc reduced (276: 1), sensory setae of papillae analis sparse and longer (277: 1), pseudobursae present (314: 1), tonofibrillary plate present on SD verrucae (359: 1); D1 and D2 setae situated before/hind each other (373: 1), one group trisetose on T1 (374: 1), SD group of T2 bisetose (375: 1), SD2 of T3 bisetose (376: 1), SV group of T2–3 unisetose (377: 1), SD2 and SV2 of A3–6 absent (378: 1; 379: 1), terga A3–8 of pupae with 2–3 rows of spined field (394: 2), and spined field with some spinulets loosely arranged behind the band (395: 1).

Heteropan and Chalcosiinae are always placed as sister groups, based on 27 synapomorphies (EW/SAW). Of these, seven characters are unique to this clade: patagia strongly sclerotized and sac-like (70: 4), patagia more developed than parapatagia (72: 2), T1 of larva with retractile cervical gland (354: 2), thoracic spiracles not concealed by 'spiracle access' (393: 1), terga 3–8 with multi-rowed spinulets (394: 3), spinulets occupying the whole terga of pupa (395: 2), and A10 of pupa with an elevated transverse tuberculate band (396: 1). The three taxa of *Heteropan* are grouped by 27 apomorphies (EW/SAW), but, of these, only 56: 2 (lateral margin of flagellomeres ridged and undulated, 57: 2 (back bone of flagellomere cirstate or keeled long the whole antennae) are unique.

Monophyly of Chalcosiinae is supported by 24 (EW) or 23 (SAW) characters. Among them, only two characters, scales on patagia bending downwards (81: 1), subdorsal and lateral syndeses located posterior to front margin of tergum 2 (178: 3), are unique. Tarmann (1992c), Epstein *et al.* (1999) and Naumann *et al.* (1999) suspected that the hindwing–abdominal androconial organ, developed ovipositor and absence of accessory glands in female genitalia provide the synapomorphies of Chalcosiinae. However, the present study shows that only two uncontradicted characters relevant to the scent organs [a bundle of long hair-like bristles inserting into the pleural pouch (337: 3) and presence of 'normal type' of pleural pouch (338: 4)] support the monophyly of Chalcosiinae. An elongated ovipositor, found in the majority of the studied taxa was, however, not recovered as a synapomorphy of the subfamily. In addition, a long mandibular lobe with sclerotization from the subbasal to apical part (403: 5), an uncontradicted character relevant to the chemical defence system, also supports monophyly.

RELATIONSHIPS OF THE MAJOR CLADES OF CHALCOSIINAE

Excluding *Cleoda syntomoides*, *Inouela*, *Chalcosiopsis variata* and *Chalcosiopsis melli*, which are grouped

with different outgroup taxa, 18 large clades of Chalcosiinae are recovered in both EW and SAW analyses (see Figs 55, 56, 58). Of these, seven have different topologies of their terminal taxa (Fig. 58) but this does not affect the relationships of the main clades.

Clade 1, which comprises most of the genera currently placed in Agalopini *sensu* Alberti (1954) (except for *Chalcophaedra*, *Corma* and *Rhodopsona*), Agalopini *sensu* Tarmann (1992) and some taxa placed in Cyclosiini and Chalcosiini, is recovered based on 23 (EW) and 22 (SAW) apomorphies. Of these, only one character, scales not overlapping each other (165: 1), is unique.

Within the clade, four generic complexes (the *Campylotes*, *Cadphises*, *Aglaope* and *Agalope* genus-groups) are recovered. The *Campylotes* group, supported by 31 apomorphies, is always considered the most basal lineage. *Cadphises* forms a monophyly with *Aglaope* + *Agalope* based on 22 (EW) and 21 (SAW) apomorphies, which include four unique characters: fultura inferior folded structure ridged and scobinate (242: 1), surface of fultura inferior granulate (243: 1), sternite A8 present in form of a complete sternite (282: 2), and intersegmental membrane between sternites A6 and A7 tightly linked (294: 1). EW and SAW produce alternative topologies; in the former (*Watermenia* + *Herpidia*) forms a trichotomy with (*Cadphises* + *Hampsonia*) and *Soritia sevastopuloi*, while in the latter (*Watermenia* + *Herpidia*) is sister to (*Cadphises* + *Hampsonia*).

Monophyly of the *Aglaope* and *Agalope* groups is based on 11 (EW/SAW) and 24 (EW/SAW) apomorphies, respectively. Of those supporting the *Agalope* group, 281: 1 (tergite A8 extended lateroventrally) and 406: 1 (adult thoracic secretion with an unidentified cyanoglucoside are unique. Clade 1 and its internal grouping (except for the *Aglaope* group) are well supported by all measures used (Figs 57, 59).

Monophyly of clade 2, which includes some members of the Cyclosiini (*Cyclosia*), Agalopini (*Corma*) and Chalcosiini (*Anarbudas*) *sensu* Alberti (1954), is supported by 12 apomorphies, in which 225: 2 (tegumen of male genitalia with paired projections arising from base) and 226: 3 (posterior projection of tegumen with apex sharp) are unique to this clade.

Within clade 2, two major groups, here termed the *Cyclosia* and *Corma* genus-groups, are supported by 29 (EW/SAW) and 20 (EW/SAW) apomorphies, respectively, but none of these is unique. EW and SAW produce two alternative topologies of the *Cyclosia* group. In both EW and SAW, the *Cyclosia panthona* species-group is always found to be the most basal lineage, and the monophyletic group comprising *Cyclosia papilionaris*, *C. macularia*, *C. chartacea* and *C. spargens* is always recovered. However ((*C. imitans* + *C. curiosa*) + *C. midama*) is the second most basal

lineage to the remaining species-groups in EW, while turning out to be the sister group of *C. papilionaris* and *C. macularia*. The internal relationships of *Cyclosia* uncovered by the present study are not consistent and require further investigation.

The topologies of the *Corma* genus-group obtained from EW (Fig. 58E) and SAW (Fig. 58F) are slightly different in the relationships between *Docleomorpha*, *Cryptophysophilus* and *Heterusinula*. These genera form a sister group to *Anarbudas insignis* in both analyses. Their relationships are unsolved in EW but well resolved in SAW. The sister-group relationship of clade 2 and the remaining clades (3–18) is supported by 15 apomorphies (EW/SAW).

Clade 3, comprising *Pidorus miles* and *Rhodopsona*, is sister to the monophyletic group in clades 4–18; monophyly is supported by 19 apomorphies (EW/SAW), including two unique ones, D (367: 1) and SD (368: 1) setae of mature larvae much longer. Although EW (Fig. 58I) and SAW (Fig. 58J) produced two alternative patterns of relationships within this clade, *P. miles* is always found to be the sister taxon to the remaining *Rhodopsona* species.

Monophyly of clade 4, comprising two small genera, *Pseudarbudas* and *Heteropanula*, is supported by 18 (EW) and 16 (SAW) apomorphies. Monophyly of clades 4–18 is supported by 18 apomorphies (EW/SAW), of which the pupal character 392: 1 (intersegmental furrow between the pro- and mesothoracic segment with outgrowths along the anterior rim) is unique to this group.

Monophyly of clades 5–18 is supported by ten apomorphies (EW/SAW). Clade 5, including *Arbudas* and *Eumorphiopais*, is supported by 13 apomorphies (EW/SAW), of which two are unique: 347: 1 (larval body flattened dorsoventrally) and 348: 1 (larval body attenuated at both ends).

Clades 6–18 are strongly supported as a monophyletic group, based on 14 uncontradicted characters (EW/SAW). Clade 6 comprises only two, atypical, genera, *Clematoessa* and *Herpolasia*, but is recovered on the basis of 28 uncontradicted characters (EW/SAW).

Clades 7–18 form a monophyletic group supported by 13 characters (EW/SAW). Monophyly of clade 7, comprising *Caprima*, *Cyanidia*, *Isocrambia*, *Hadri-onella*, *Thaumastophleps*, *Hemichrysoptera*, *Sci-odoclea*, *Papuaphlebohecta* and several species-groups of *Pidorus* and *Hemiscia*, is supported based on 13 apomorphies (EW/SAW).

Monophyly of clades 8–18 is supported by 12 apomorphies (EW/SAW). Clade 8, comprising only *Pidorus corculum*, is based on ten apomorphies (EW/SAW). The sister-group relationship between clade 9 and clades 10–18 is supported by nine apomorphies, while the monophyly of clade 9, comprising *Pidorus*

bifasciatus and *Prosopandrophila mirifica*, is supported by 19 (EW/SAW).

Retina and *Pidorus constrictus* are always placed in clade 10 based on 14 apomorphies. The sister group of this clade is the combined clades 11–18, based on 17 apomorphies (EW/SAW).

A group comprising *Barbaroscia*, *Pseudoscaptosyle*, *Amesia*, *Eucorma*, *Erasmia*, *Erasmiphlebohecta*, *Chalcophaedra* and several species-groups of *Pidorus* and *Soritia* is recovered as a strongly supported clade (12), based on 13 apomorphies (EW/SAW), of which 320: 1 (anterior end of corpus bursae at the anterior margin of A6) is not found by SAW, and 284: 1 (middle part of hind margin of sternum A7 truncate) is only found by SAW. Within clade 12, two internal subclades are recovered: the *Barbaroscia*–*Pseudoscaptosyle* genus group, supported by 14 apomorphies (EW/SAW) and the *Erasmia*–*Chalcophaedra* genus group, supported by 16 (EW) or 21 (SAW) apomorphies.

Among the latter characters, three are only found by EW: 152: 1 (hindwing with obscure costal patch present at middle of cell), 213: 8 (apex of uncus–tegumen complex emarginated and wide), 250: 0 (cucullus sclerotized) and 381: 2 (larval setae L and SV plumose), while nine are only found by SAW: 17: 6 (w/ d.f. ratio of upper portion of frontoclypeus in male = 1.5), 139: 4 (e–g zone of male forewing with a band formed by five patches), 140: 4 (e–g zone of female forewing with a band formed by five patches), 141: 3 (male forewing with all patches on zone h forming a continuous band), 142: 3 (female forewing with all patches on zone h forming a continuous band), 153: 4 (male hindwing with zone n extended to zone m), 154: 4 (female hindwing with zone n extended to zone m), 266: 4 (posteroventral view of saccus convex) and 284: 7 (middle part of hind margin of sternum A7 caudate and slightly bifurcate at apex). EW (Fig. 59K) and SAW (Fig. 59L) produce two alternative patterns of relationships. The sister-group relationship between clade 12 and clades 13–18 is supported by 19 apomorphies (EW/SAW), none of which is unique. Clade 13 includes only two species, *Eterusia repleta* and *Opistoplatia grandis*, and is based on 13 apomorphies (EW/SAW).

Monophyly of clades 13–18 is supported by 14 apomorphies (EW/SAW). Clade 14, comprising the ‘core’ species-groups of *Eterusia* and *Soritia*, is strongly supported by 17 (EW) or 19 (SAW) apomorphies. Five of these characters are only found by EW analysis: 130: 1 (wing pattern sexually dimorphic), 140: 1 (female forewing with outer margin of zone e–g clearly defined), 153: 6 (male hindwing with zone n extended to inner margin and occupying about one half of hindwing area), 159: 1 (female hindwing with a large yellow area ranging from zone k to zone m), 261: 4 (tegumen/vinculum about 0.4); eight are only found by

SAW: 18: 7 (w/ d.f. ratio of upper portion of frontoclypeus in female = 1), 19: 4 (de/ d.f. in male = 1.5), 54: 1 (rami of terminal segments of antennae in male present, much shorter than medial ones), 139: 2 (male forewing with discal, CuA2 and 1A + 2A patches), 146: 3 (male forewing with patches present on R2–M3 and M2–M3), 147: 3 (female forewing with patches present on R2–M3 and M2–M3), 150: 1 (spot on forewing discoidal end present) and 184: 3 (male abdomen with annular rings extending to sternal area). Within clade 14, two major subclades comprising several species-groups of *Eterusia* and *Soritia*, respectively, are well supported. The 'Eterusia subclade' is supported by 14 (EW) or 18 (SAW) apomorphies. Of these, five are only found in EW: 7: 1 (lateral margin of frontoclypeus in male attenuated towards bottom), 67: 0 (scales on chaetosemata black), 213: 5 (uncus–tegumen complex somewhat rectangular with posterior margin emarginated), 239: 1 (medioventral protuberance (of aedeagus) present near apex), 256: 7 (mediobasal process of sacculus *Eterusia*-type). Nine are only found in the SAW analysis: 137: 1 (outer margin of male forewing with zone d defined, zone b–d not differentiated), 138: 1 (outer margin of female forewing with zone d defined, zone b–d not differentiated), 140: 3 (female forewing with five patches present on cu, discal, CuA2, 1A + 2A and 3A cells), 153: 0 (male hindwing with zone n confined to apex), 154: 4 (female hindwing with zone n extended to zone m), 182: 1 (male abdominal tergites 1–2 with distinct colour from the remaining segments), 183: 5 (male abdomen with annular rings on sternal area only), 184: 5 (female abdomen with annular rings on sternal area only) and 186: 1 (female abdomen with pleural dots present on a1–a7).

EW (Fig. 58M) and SAW (Fig. 58N) produce two alternative internal relationships of this subclade. In EW, *Eterusia binotata* is basal to all the other *Eterusia* species-groups; the *E. risa* species-group is sister to (*Eterusia vitessa* + *E. aedeae*) + (*E. tricolor* + *E. subcyanea*). SAW suggests that (*E. binotata* + *E. risa*) is sister to (*E. vitessa* + *E. aedeae*), and (*E. tricolor* + *E. subcyanea*) is the most basal lineage. The 'Soritia-clade' is well supported by 25 (EW) or 19 (SAW) apomorphies. Only 12 characters support the group in the EW trees: 3: 2 (height/width of frontoclypeus [frontal view] = 1.5), 8: 0 (lateral margin of frontoclypeus in female parallel), 76: 3 (in female, scales on patagia yellow), 78: 4 (in female, scales on parapatagia yellow), 120: 1 (wing size sexually dimorphic), 146: 1 (male forewing with R2–r3 patches present), 150: 1 (forewing with spot of discoidal end present), 201: 3 (sternite with ventral part rectangular and lateral part not swollen), 227: 2 (tegumen with a pair of spatulate apodemes each side), 257: 9 (sacculus *Soritia*-type), 263: 5 (anterior view of vinculum

rhomboid), 341: 2 (female hindwing with a bundle of short spatulate scales present at anal plate). Six characters are only found in SAW: 17: 7 (w/ d.f. ratio of upper portion of frontoclypeus in male = 1), 20: 6 (de/ d.f. in female = 1/1.5), 67: 2 (scales on chaetosemata yellow), 68: 4 (crested scales in front of patagia yellow), 261: 1 (tegumen/vinculum = 2.5) and 265: 1 (sacculus extending antero-upwards). Alternative topologies are produced by EW (Fig. 58O) and SAW (Fig. 58P). In EW (*Soritia shahama* + *S. elizabethae*) is sister to ((*S. major* + *S. zelotypia*) + *S. pulchella*). In SAW the *S. shahama* and *S. elizabethae* species-groups appear as the basal lineages, and the paraphyletic species *S. costimacula* forms a monophyletic group with ((*S. major* + *S. zelotypia*) + *S. pulchella*). Owada & Horie (1999) inferred that enlargement of terminal antennal segments in the female serves as a diagnostic character distinguishing *Eterusia* from *Soritia*. However, this character state does not appear to support either the monophyly of *Eterusia* or of *Soritia*. The sister clade to clade 14 is the monophyly of clades 15–18, based on 18 apomorphies (EW/SAW), none of which is unique.

In the MPTs obtained from both EW and SAW, the *Phlebohecta fuscescens*, *Phlebohecta lithosina*, *Trypanophora hyalina*, *Soritia moerens* and *Prosopandrophila distincta* species-groups are recovered as a clade (clade 15), based on 12 apomorphies. Clade 15 and clades 16–18 comprise a sister group based on 17 apomorphies (EW/SAW).

Clade 16 (the *Neochalcosia*, *Pseudopidorus*, *Chalcosia zehma* and *Pidorus splendens* groups) is recovered based on 13 apomorphies (EW/SAW). It always appears as the sister group of clades 17 + 18 supported by 18 apomorphies (EW/SAW).

Clade 17 is one of the most diverse groups of Chalcosiinae, and is well supported by ten (EW) or 11 (SAW) apomorphies. Of these, ch. 67: 3 (scales on chaetosemata white) is only found in reconstruction on the EW trees, while ch. 78: 1 (in female, scales on parapatagia green) and 154: 2 (male hindwing with zone n ending at CuA2) are only obtained from SAW. This clade has three major internal groups: the *Chalcosia*–*Milleria*, *Pseudonyctemera* and *Psaphis*–*Eusphalera* genus-groups. *Chalcosia*–*Milleria* comprises three species-groups of *Chalcosia* and four of *Milleria* plus *Cyclosia notabilis*. Monophyly is based on 13 apomorphies (EW/SAW), although EW (Fig. 58Q) and SAW (Fig. 58R) produce two alternative topologies. In EW, *Milleria okushimai* is the most basal taxon but in SAW it is sister to ((*Milleria rehfoosi* + *M. hamiltoni*) + *Cyclosia notabilis*). Both EW and SAW place *Pseudonyctemera* as sister to *Psaphis*–*Eusphalera*, based on seven uncontradicted characters; 25 characters (EW/SAW) support monophyly of the two species-groups of *Pseudonyctemera*. *Psaphis*–*Eusphalera* includes all

the species-groups of *Psaphis* and *Eusphalera* plus *Docleopsis doherityi*. Monophyly is recovered with ten supporting apomorphies, none of them unique. EW analysis fails to resolve the inter-relationships of *Eusphalera* (Fig. 58S). The topology obtained from SAW is more resolved, although (*Eusphalera ligata* + *E. regina*) still forms a trichotomy with *E. venus* and (*E. multicolor* + *E. subnigra*) + *E. picturata*.

Clade 17 is sister to clade 18 based on 11 apomorphies (EW/SAW). Clade 18 based on 11 (EW) or ten (SAW) apomorphies, of which character 200: 4 (hind margin of sternal arms densely serrate) is only obtained from EW. Four internal monophyletic groups: (1) *Scotopais*, (2) the *Eterusia raja*–*Histia*–*Pompelon*–*Gynautocera* genus-group, (3) *Phlebohecta lypusa* + *Trypanophora producens* and (4) the *Allocaprima*–*Docleopsis* genus-complex – are recovered. Group (1) is the most basal taxon of this clade. Group (2) is supported by 15 apomorphies (EW/SAW) and is sister to (3) and (4). The latter comprises *Allocaprima*, *Boradiopsis*, *Aphantocephala* and *Euxanthopyge*, and the *Anarbudas bipartita*, *Trypanophora deligata*, *Docleopsis zamboanga*, *Phlebohecta jordani*, *Docleopsis stigma* and *Docleopsis sulaensis* species-groups. The results from EW and SAW analyses optimized 15 homoplastic characters on to the branch leading to *Allocaprima*–*Docleopsis*.

INCONGRUENCE BETWEEN DATA SUBSETS

Results of the ILD test for comparing the MPTs from male (1 MPT, tree length = 1919, CI = 0.248, RI = 0.772) (Fig. 60), female (2 MPTs, tree length = 1880, CI = 0.195, RI = 0.681) (Fig. 61) and non sex-linked (1 MPT, tree length = 1584, CI = 0.324, RI = 0.790) (Fig. 62) characters, respectively, shows that the phylogenies generated by these three character systems are significantly incongruent ($P < 0.05$).

Compared with the consensus of EW and SAW MPTs (Fig. 57), the topology of the male-based phylogeny (Fig. 60) differs as follows: (Himantopteridae + Anomoeotidae) and Heterogynidae are placed within the Zygaenidae; clades 1 and 2 form a monophyletic group; *Eumorphiopais* is sister to clades 6–18; clade 8 is monophyletic with the *Papuaphlebohecta*–*SciODOCLEA* genus-group; clade 9 is paraphyletic but forms a monophyletic group with *Hemichrysoptera* + *Aphantocephala fragilis*; (*Chalcosia zehma* + *Pidorus splendens*) is basal to clades 15–18; clade 17 includes the *Eterusia raja*–*Histia*–*Pompelon*–*Gynautocera* genus-group with *Milleria okushimai* forming a monophyly with *Scotopais tristis*; and clade 18 becomes paraphyletic with respect to clade 17. The MPTs based only on female characters are poorly resolved. The monophyly of Zygaenidae, inter-relationships among

the chalcosiine subfamilies and monophyly of Chalcosiinae are not recovered.

A search based on only the 72 taxa with immature data available yielded 48 MPTs (tree length = 2246, CI = 0.420, RI = 0.760) (Fig. 63A). When adult characters were excluded, 1329 MPTs (tree length = 1327, CI = 0.351, RI = 0.675) were obtained (Fig. 63B), while excluding immature characters generated 147 MPTs (tree length = 2253, CI = 0.418, RI = 0.758) (Fig. 63C). The ILD tests for estimating the incongruence between the trees based on adult and immature characters, respectively, show that the phylogenetic patterns generated from these two data subsets are significantly incongruent ($P < 0.05$, Table 4). The consensus cladogram shown in Figure 63A (72 taxa based on the whole data set) does not suggest that the Zygaenidae are monophyletic, and the inter-relationships of the subfamilies shown in Figure 57 are not recovered. However, monophyly of the taxa included in Chalcosiinae is supported by 51 apomorphies (see Appendix 6), including 36 not found in the analysis based on 207 taxa and 12 obtained from immature characters. Of these characters, 15 are unique within the context of this analysis: 43: 2 (terminal segment of labial palpus oval), 55: 2 (rami of terminal segment in female as long as those of other segments), 70: 4 (patagia strongly sclerotized and sac-like), 72: 2 (patagia more developed than parapatagia), 84: 1 (subtegula developed, arm-like), 87: 1 (metascutellum trapezoid/ 'hamlet-like'), 102: 2 (forewing with R3 stalked with R4 + R5), 178: 3 (anterotergal syndesemes present, subdorsal and lateral syndesemes located posterior to front margin of tergum A2), 253: 3 (costal margin between cucullus and sacculus *Eterusia*-type); 373: 1 (D1 and D2 before/behind each other), 374: 1 (L group trisetose on T1), 375: 1 (SD group bisetose on T2), 376: 1 (SD2 bisetose on T3), 377: 1 (SV group with T2–3 unisetose) and 378: 1 (A3–A6 with SD2 absent).

A monophyletic group, comprising the taxa placed in clade 1 (Fig. 57), was recovered based on 30 apomorphies, of which 14 are not found to support the clade as shown in Figures 55, 56 and 57. Two uncontradicted characters, 380: 1 (SD setae plumose), 388: 1 (cross-section of pupa dorsoventrally compressed), are obtained from immatures. The sister-group relationship between *Cyclosia* + *Corma* and the remaining clades is supported by 20 apomorphies, including 11 characters not found in the node which supports clade 2 + clades 3–18 in the original MPTs (Fig. 57), and three unique ones: 73: 1 (parapatagia curved backward), 253: 5 (costal margin between cucullus and sacculus *Corma*-type) and 292: 1 (intersegmental membrane between A7 and A8 with a ring of hairs). However, none of the immature character supports this relationship.

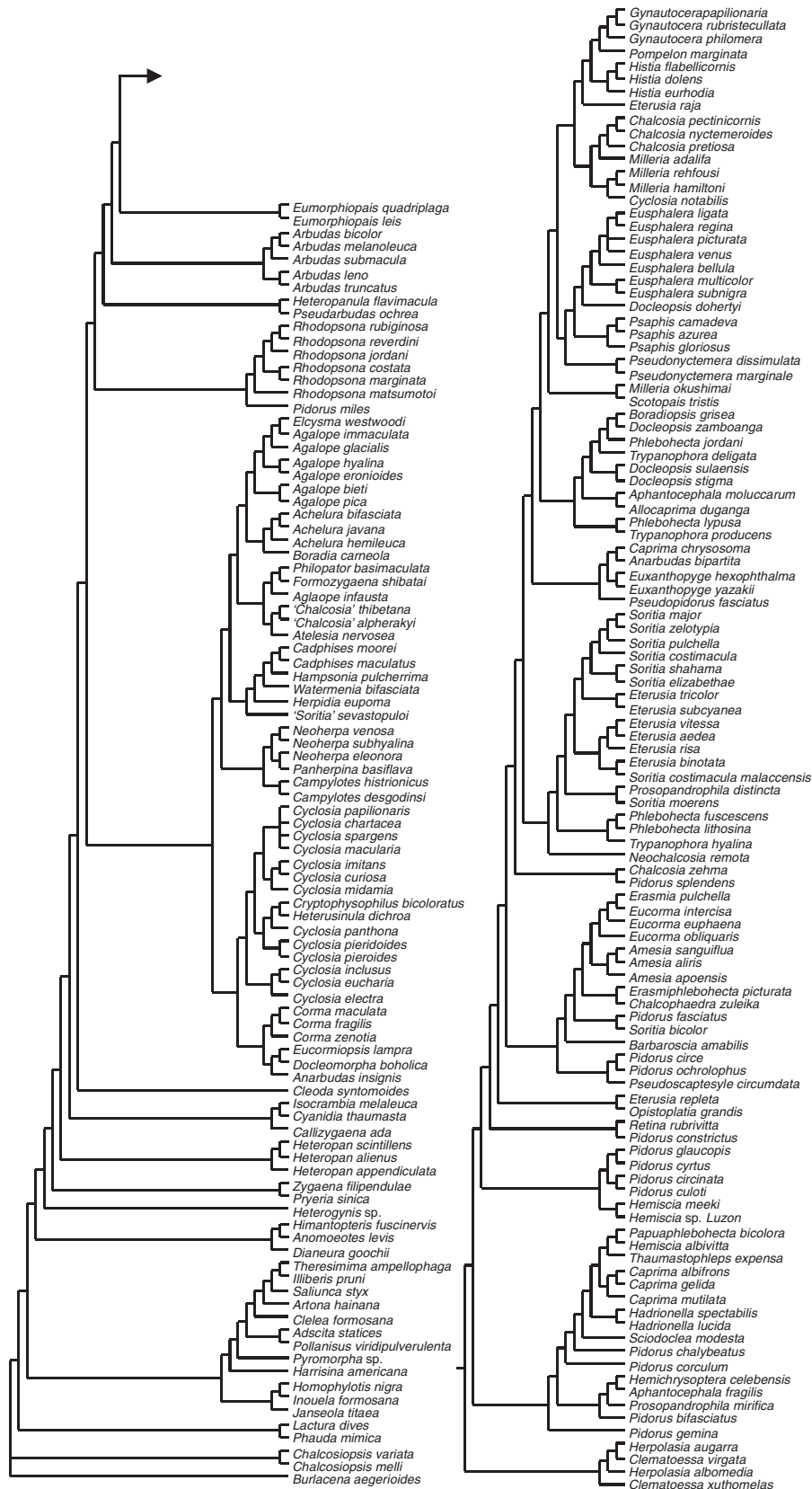


Figure 60. Single cladogram obtained from EW analysis based on male characters.

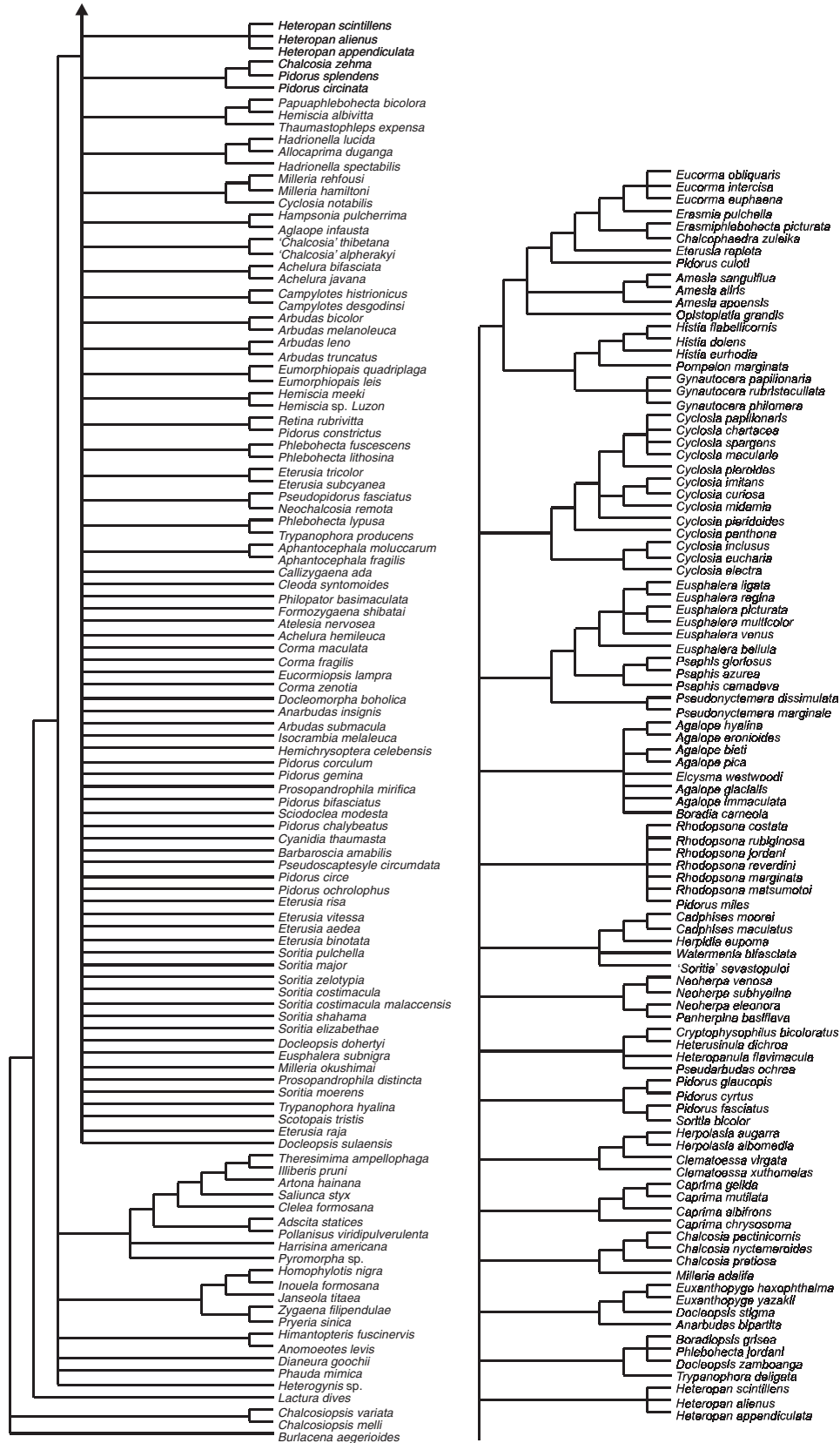


Figure 61. Strict consensus of two MPTs (tree length = 1875, CI = 0.196, RI = 0.681) based on female characters under EW.

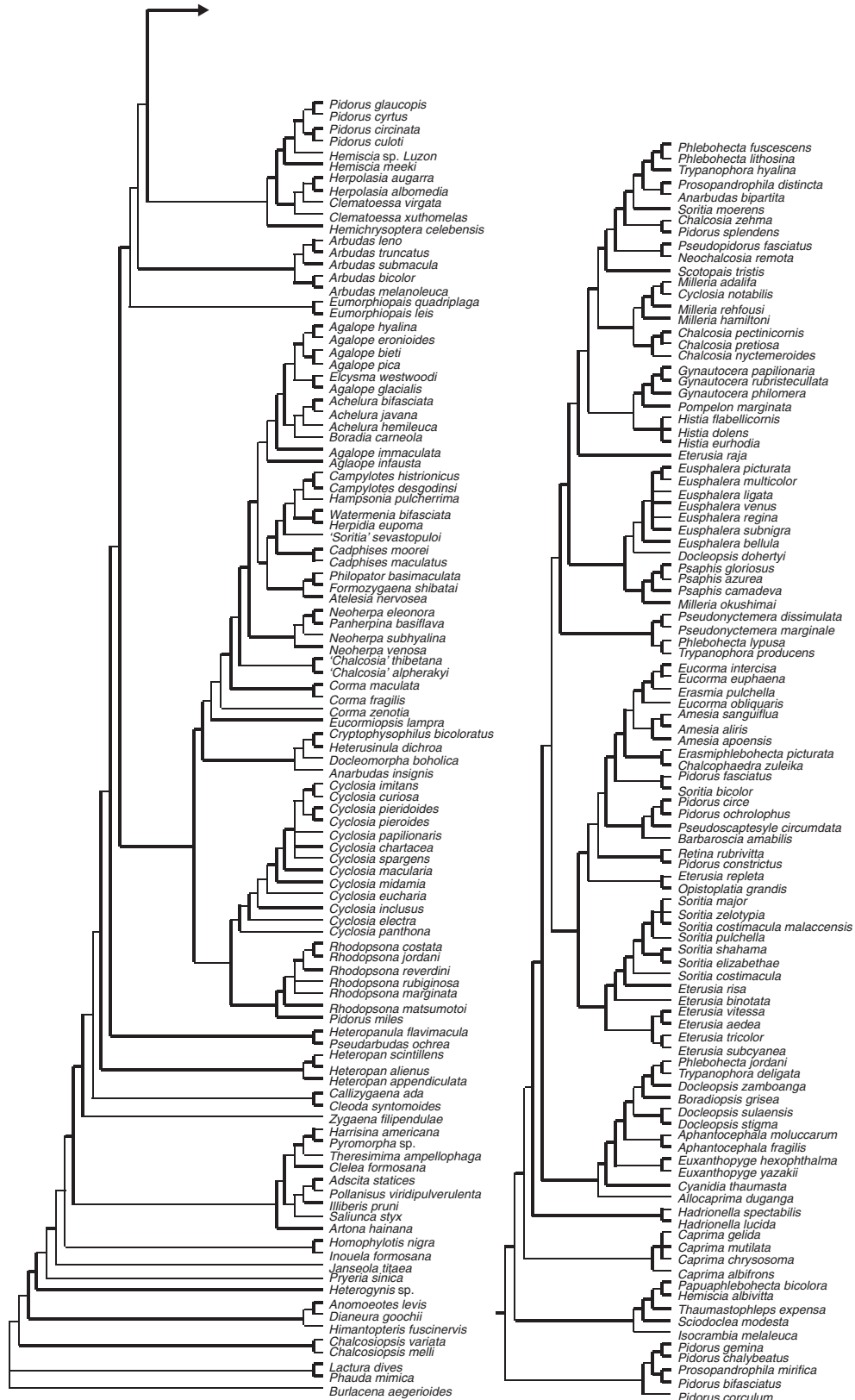


Figure 62. Single cladogram (tree length = 1584, CI = 0.324, RI = 0.791) obtained from EW analysis based on non-sex-linked characters.

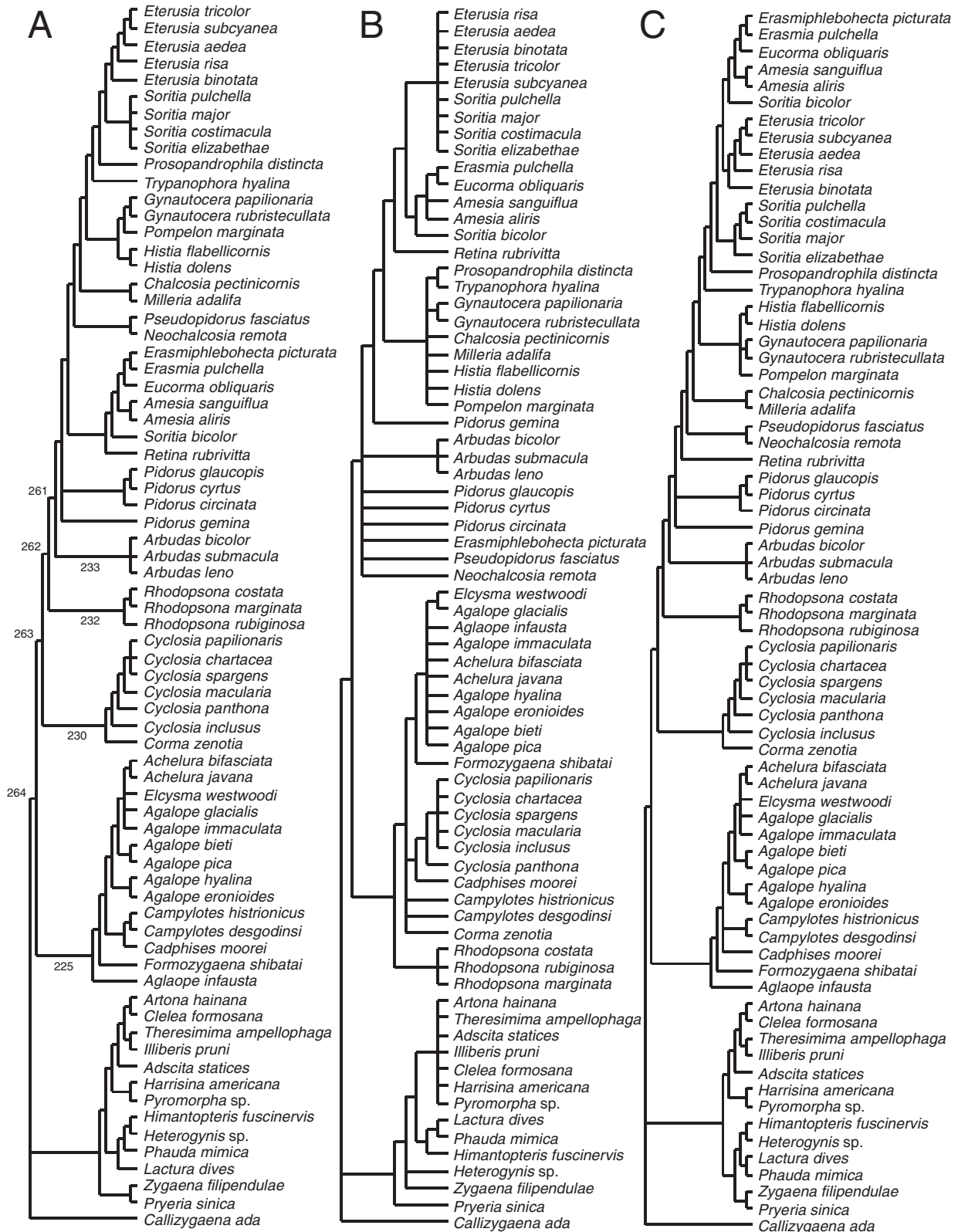


Figure 63. Comparison of three consensus cladograms based on 72 taxa with information on immature stages available: A, adult + immature characters. Numbers correspond to node numbers in Appendix 6. B, adult characters excluded. C, immature stage characters excluded.

Table 4. Results of ILD tests for comparisons of the two data partitions. ILD tests with parsimony-uninformative characters ¹included and ²excluded

Comparison (number of characters)	No. of taxa	<i>P</i> value ¹	<i>P</i> value ²
All characters (414)	207	–	–
1a. Male (110) – 1b. Female (99)	207	0.002*	0.01*
1a. Male (110) – 1c. Non sex-linked (205)	207	0.01*	0.01*
1b. Female (99) – 1c. Non sex-linked (205)	207	0.01*	0.01*
2a. Adult(358) – 2b. Immature (56)	72	0.03*	0.014*

*Statistically significant at the $P < 0.05$ level.

Monophyly of *Cyclosia* + *Corma* is supported by 11 apomorphies, of which six are not found in the original MPTs and three are unique: 225: 2 (male genitalic tegumen with paired projections arising near base), 226: 1 (apexes of posterior bilateral projections stout) and 240: 4 (cornuti slender and thread-like spines).

Monophyly of *Rhodopsona* and the remaining clades is supported by 15 apomorphies. Of these, 13 characters, including two from immature stages, are not found in the node which supports clade 3 (*Rhodopsona* + *Pidorus miles*) + clades 4–18 in Figure 57. The apomorphies backing the monophyly of *Rhodopsona* include 17 characters not found in the cladogram in Figure 57, and include three unique ones: 211: 1 (uncus without sensory setae); 367: 1 (D setae long) and 368: 1 (SD setae long).

A monophyletic group comprising *Arbudas* through to *Eterusia* is well supported by 17 apomorphies, which are all present in the node for clade 5 + clades 6–18 in Figure 57. Four of them turn out to be unique in this analysis: 209: 1 (uncus and tegumen fused medially), 220: 2 (dorsoposterior margin of tegumen forming a ring-like structure by fusing with uncus), 253: 6 (costal margin between cucullus and sacculus Chalcosiini-type); 392: 1 (intersegmental furrow between the pro- and mesothoracic segments with sculptured outgrowths along the anterior rim).

Monophyly of *Arbudas* is based on 21 apomorphies, of which 11 are not found among the 14 apomorphies supporting the five *Arbudas* species-groups in Figure 57, and four are unique: 240: 3 (cornuti as short spines at apex), 327: 1 (band-like signa present); 347: 1 (larval body flattened) and 348: 1 (larval body attenuate at both ends). The taxa above node 261 (see Fig. 63A) are recovered as a monophyletic group based on 35 apomorphies. Of these, 19 characters are not found on the node which supports the monophyly of the 'equivalent' clades 6–18 in Figure 57, including three that are unique: 209: 2 (uncus and tegumen completely fused), 267: 1 (g1 muscle reduced, only with a small bundle of fibre) and 340: 1 (male androconial pouch with lower pleural sclerite sclerotized).

EFFECTS OF DEACTIVATING SPECIFIC CHARACTERS ON PHYLOGENIES

Table 5 and Figures 64–70 demonstrate results which address the effects of deactivating specific character subsets on the phylogenetic structures. Results of the *t*-test for comparing the symmetrical-difference distances (SDD) between the trees based on the whole data set and those based on one deactivated character subset show that only exclusion of 'wing scale' characters produces trees that are not significantly different from the whole data set trees. The consensus cladogram of this treatment (Fig. 66) differs from that of Figure 57 as follows: *Cleoda* and *Callizygaena* become paraphyletic; *Heteropanula* + *Pseudarbudas* (clade 4) becomes sister to clades 2–3 and 5–18, and clade 6 appears as sister to clade 7, while clade 7 becomes paraphyletic by insertion of clades 8 and 9.

Of all the treatments, the trees obtained from exclusion of 'colour' characters achieve the highest significant difference ($P = 1.154 \times 10^{-48}$). The consensus cladogram (Fig. 64) differs from that in Figure 57 in the following features: the internal groupings of clade 1 are collapsed to form a polytomy, in which the *Aglaope* genus-complex is not recovered as monophyletic; clades 2–4 form a polytomy; clade 5 becomes paraphyletic; clade 6 forms a monophyletic group with the *Caprima* genus-complex of clade 7; clades 8–9 are placed as the basal lineages of clade 7; the relationship between clades 7 and 10 is not resolved; the *Erasmiphlebohecta*–*Chalcophaedra* genus-complex of clade 11 switches from a terminal to a basal position; the *Chalcosia*–*Milleria* genus-complex of clade 17 is paraphyletic; and *Scotopais* becomes sister to the *Allocaprima*–*Docleopsis* genus-group.

Exclusion of 'wing shape' characters generated 124 MPTs. The consensus cladogram (Fig. 65A) only differs from the whole data set cladogram in two places within the basal lineage: *Cleoda* and *Callizygaena* are placed in a trichotomy with *Heteropan* + *Chalcosiinae* and the internal relationships of clade 1 are collapsed. In contrast, the phylogenetic patterns based on the exclusion of 'wing venation' (Fig. 65B), are only differ-

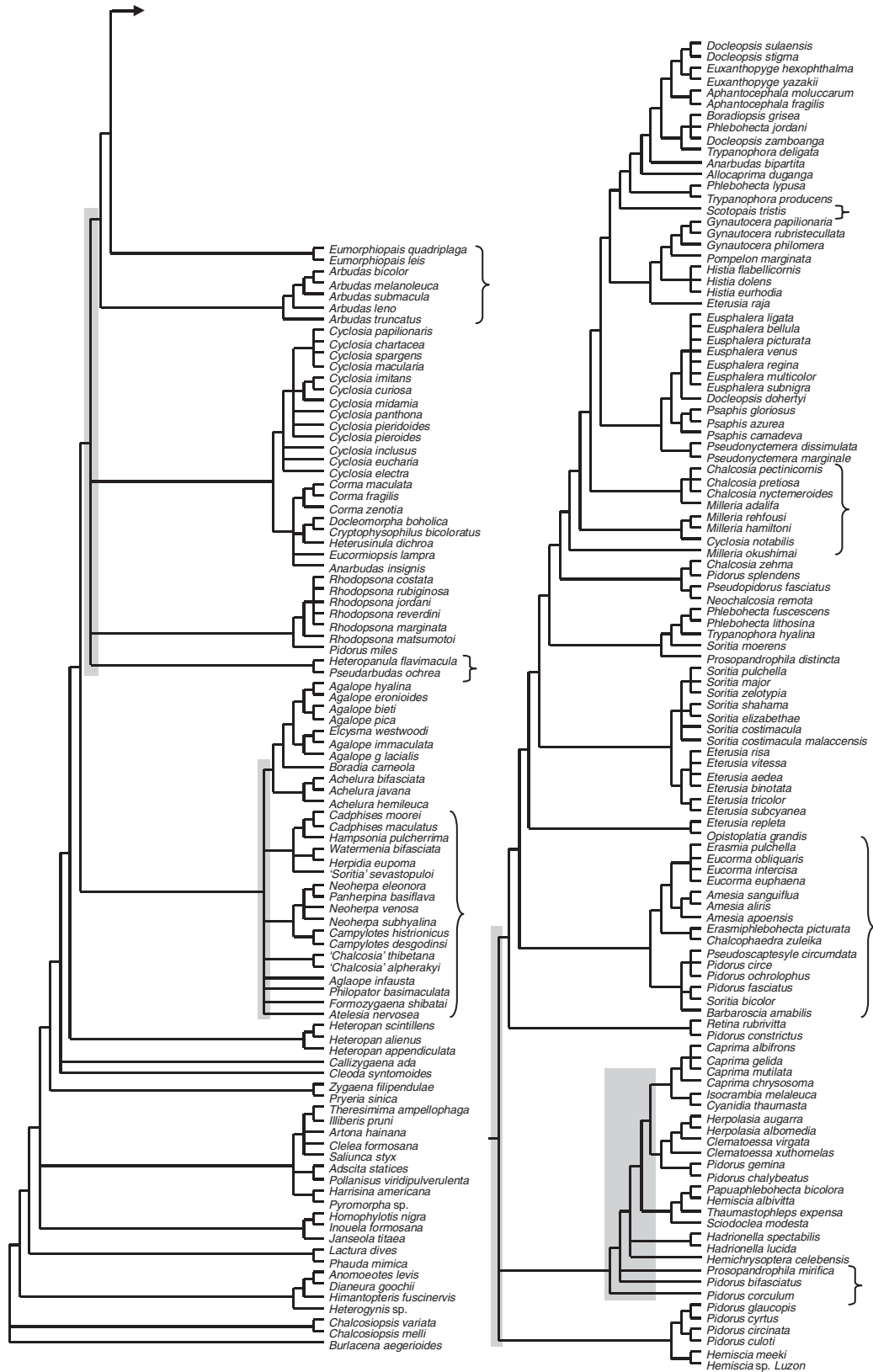


Figure 64. Strict consensus of 45 MPTs (tree length = 3658, CI = 0.264, RI = 0.786) based on the whole data set, but with 'coloration' characters inactivated, under EW. Tinted boxes indicate the main topological differences from Fig. 57.

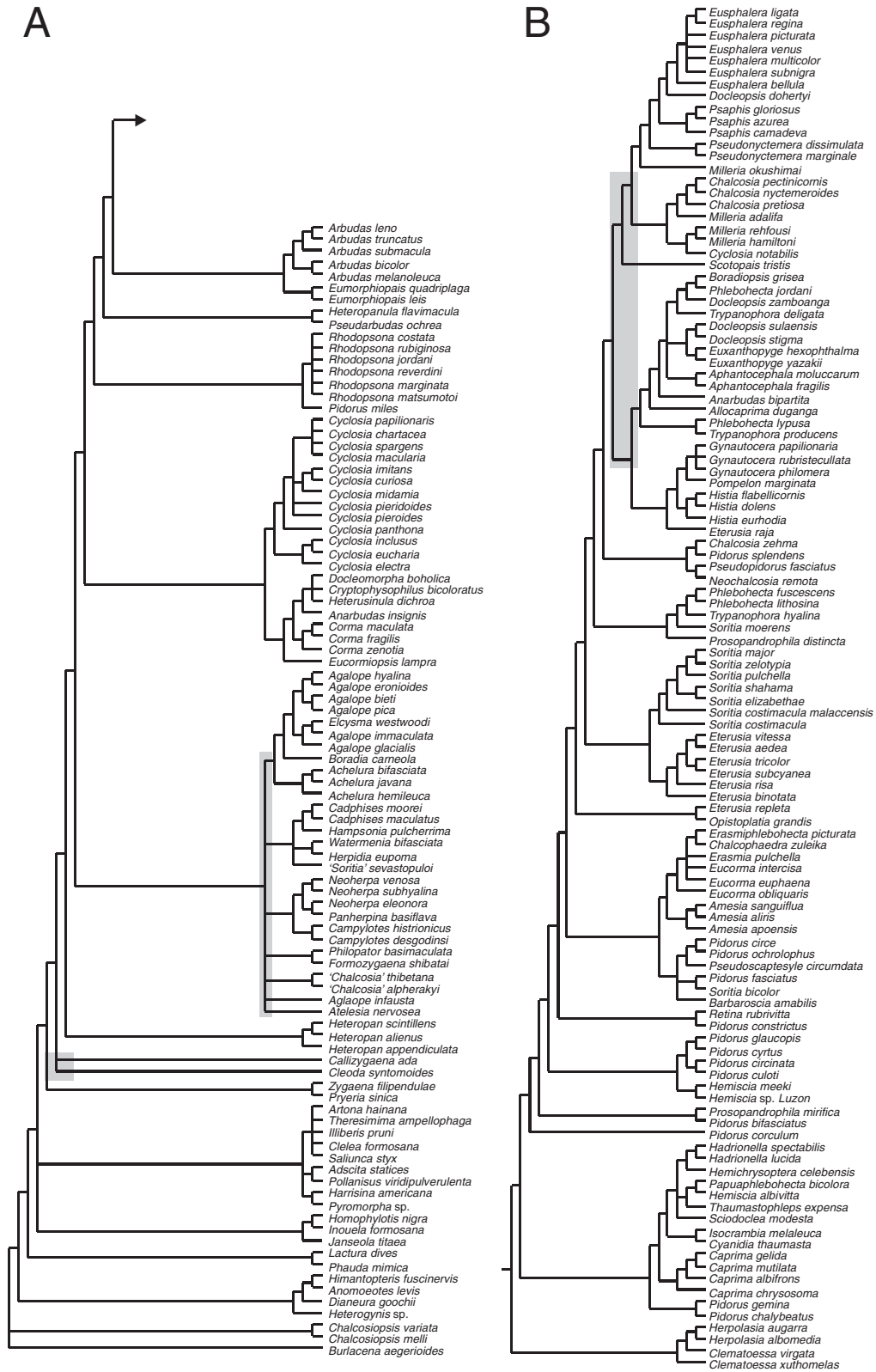


Figure 65. A, basal part of a strict consensus of 124 MPTs (tree length = 4664, CI = 0.244, RI = 0.746) with 'wing shape' characters inactivated. B, terminal part of a strict consensus of nine MPTs (tree length = 4586, CI = 0.243, RI = 0.743) with 'wing venation' characters inactivated. Tint boxes indicate the main topological differences from Fig. 57.

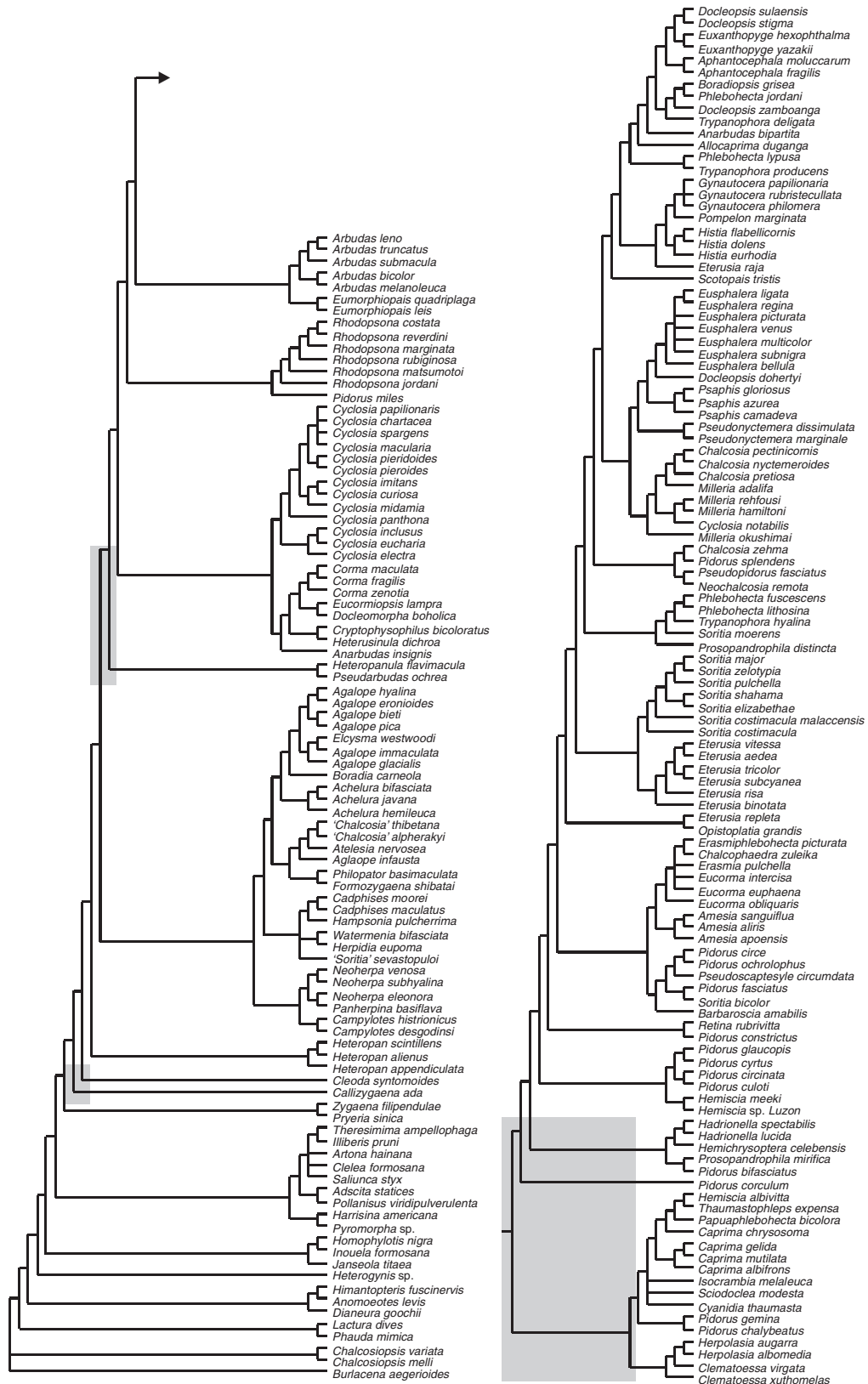


Figure 66. Strict consensus of five MPTs (tree length = 4552, CI = 0.232, RI = 0.739) based on the whole data set with ‘wing shape’ characters inactivated, under EW. Tinted boxes indicate the main topological differences from Fig. 57.

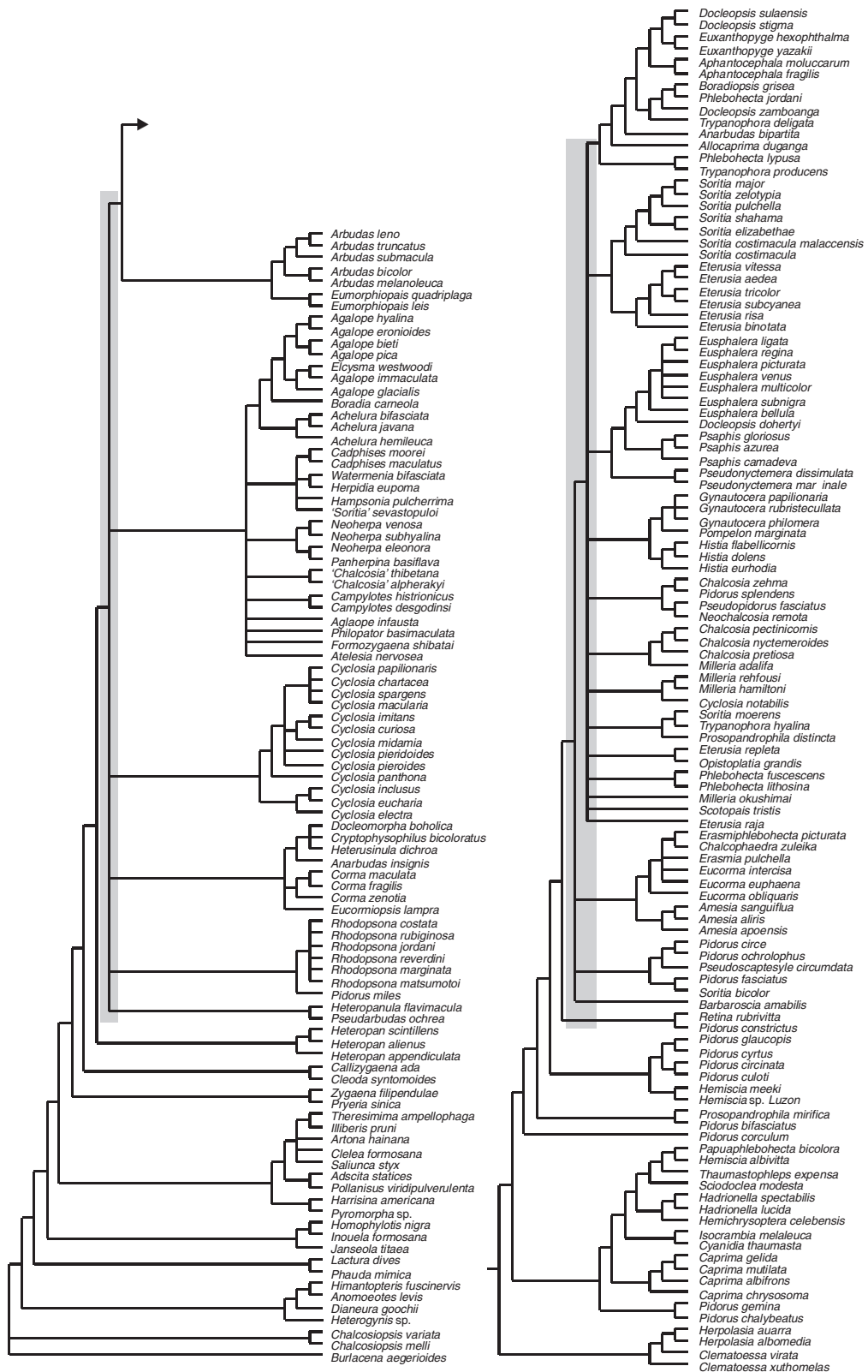


Figure 67. Strict consensus of 41 MPTs (tree length = 4550, CI = 0.235, RI = 0.736) based on the whole data set with 'male 8th abdominal segment' characters inactivated, under EW. Tinted boxes indicate the main topological differences from Fig. 57.

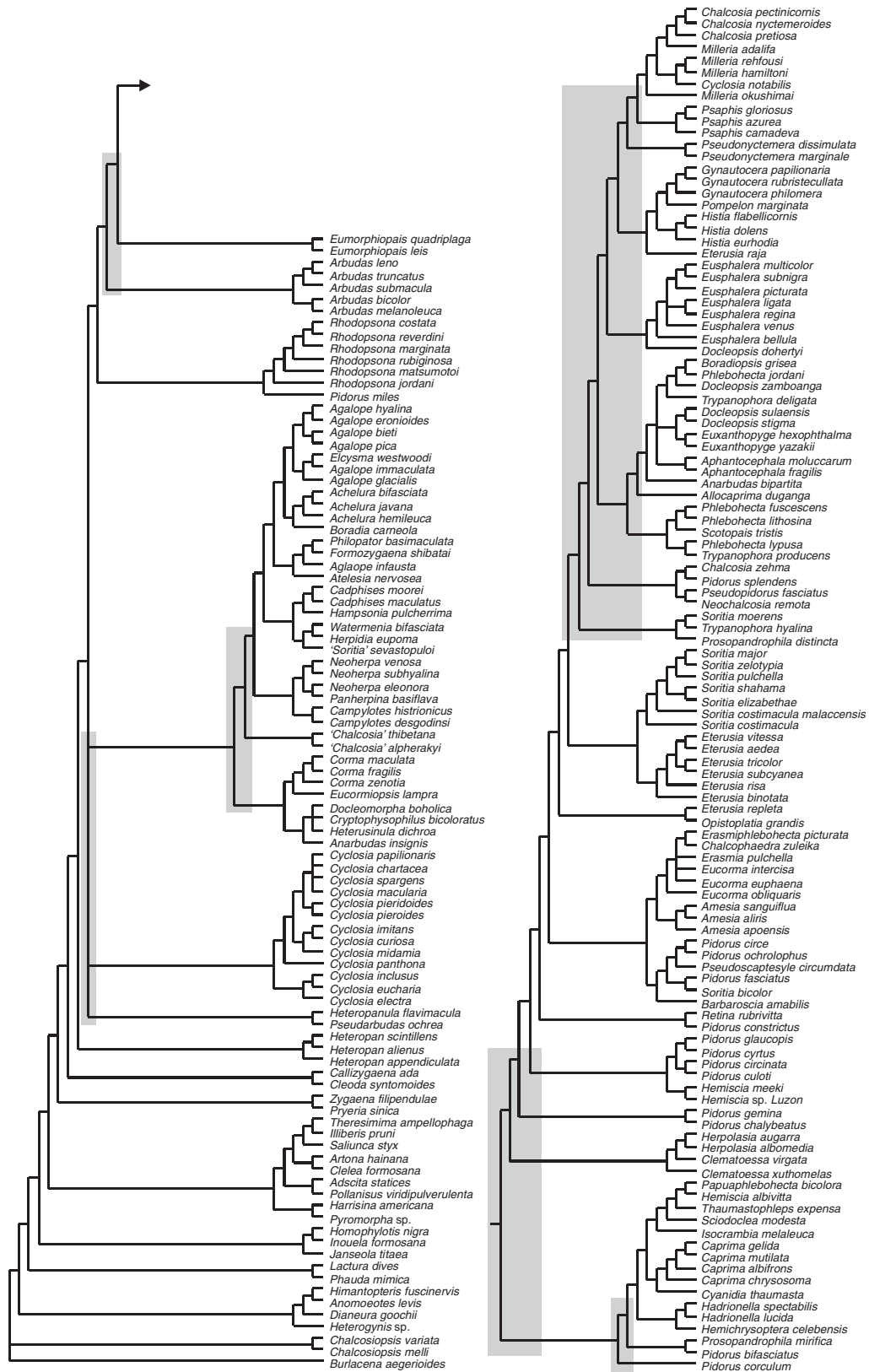


Figure 68. Strict consensus of ten MPTs (tree length = 4422, CI = 0.238, RI = 0.740) based on the whole data set, with 'female genitalia' characters inactivated, under EW. Tinted boxes indicate the main topological differences from Fig. 57.

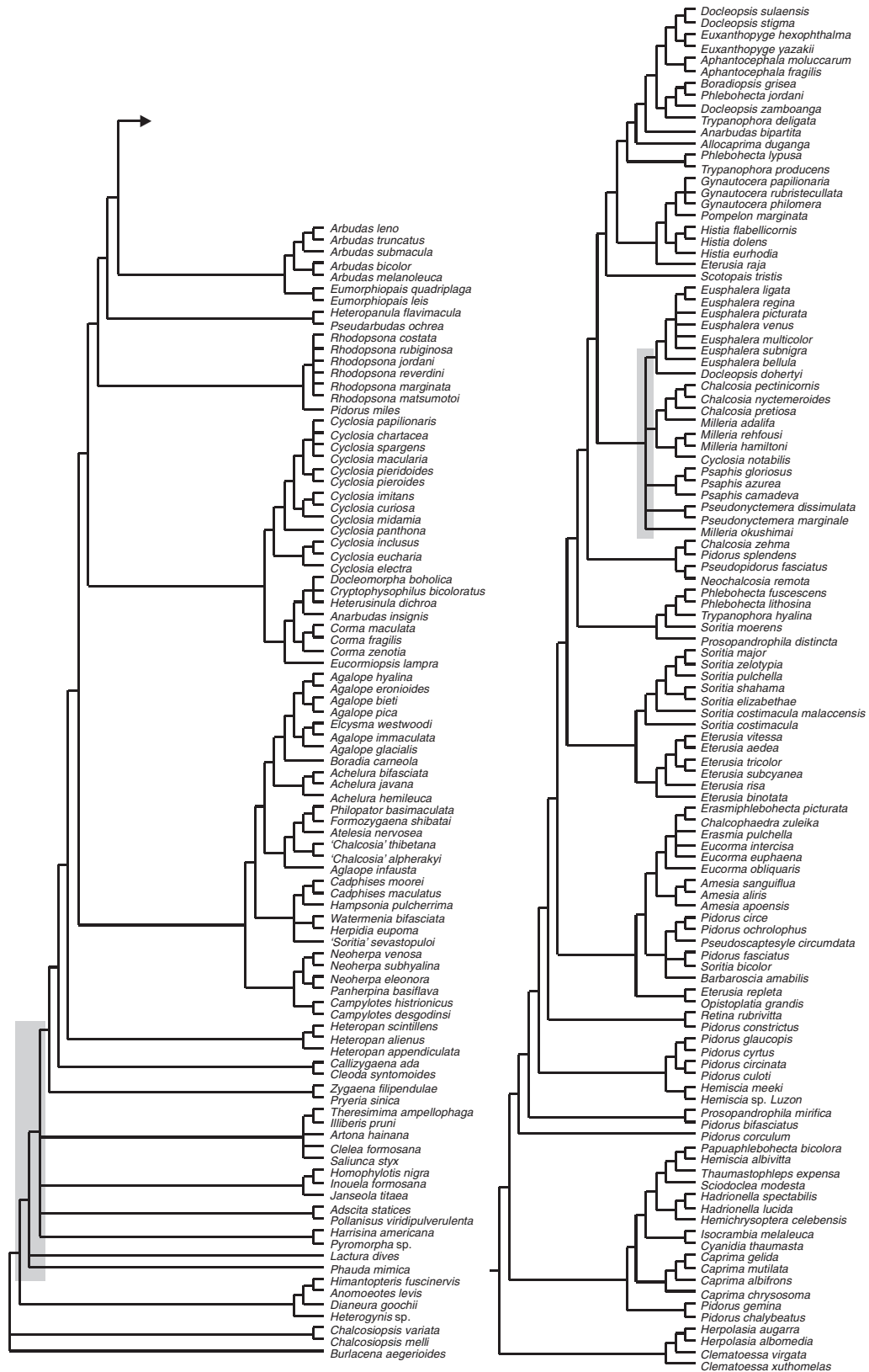


Figure 69. Strict consensus of 11 MPTs (tree length = 4671, CI = 0.242, RI = 0.735) based on the whole data set, with ‘scent organs’ characters inactivated, under EW. Tinted boxes indicate the main topological differences from Fig. 57.

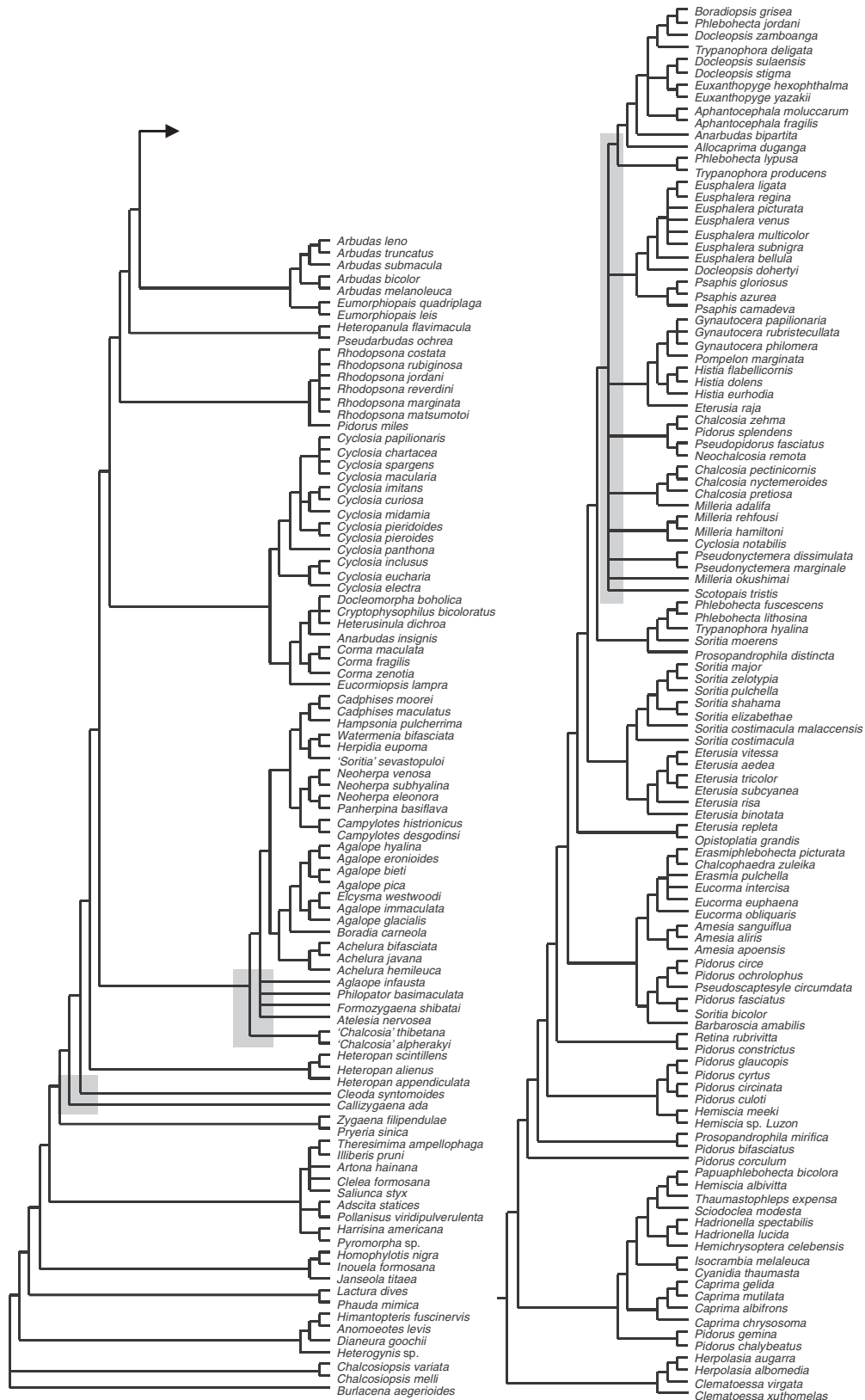


Figure 70. Strict consensus of 98 MPTs (tree length = 4767, CI = 0.240, RI = 0.741) based on the whole data set, with ‘chalcosemata’ characters inactivated, under EW. Tinted boxes indicate the main topological differences from Fig. 57.

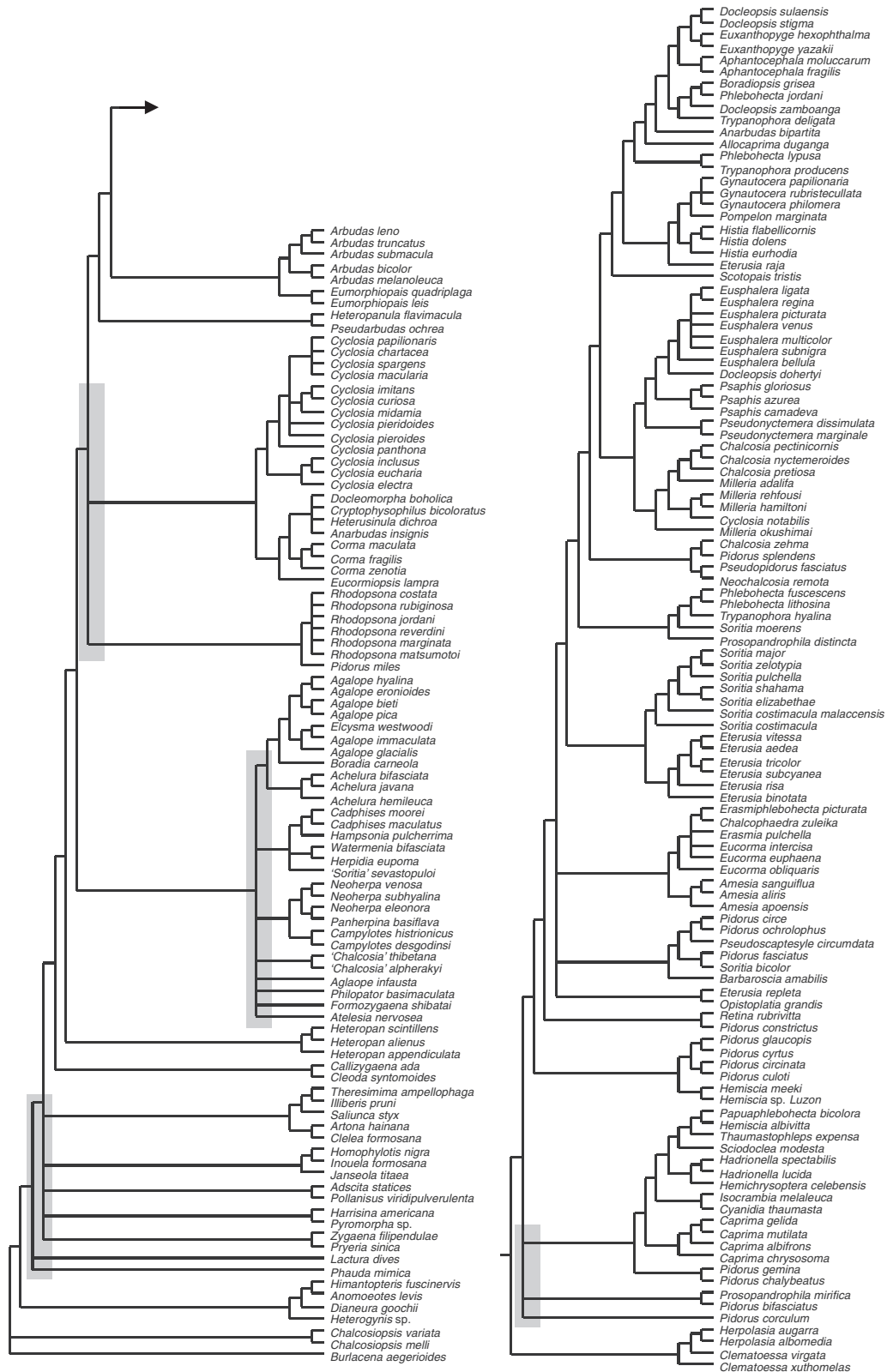


Figure 71. Strict consensus of 55 MPTs (tree length = 4773, CI = 0.239, RI = 0.739) based on the whole data set, with ‘chemical defence systems’ characters inactivated, under EW. Tinted boxes indicate the main topological differences from Fig. 57.

Table 5. Effects of inactivation of character subsets on phylogenetic structure of Chalcosiinae based on all 207 taxa. This table compares the tree scores of the MPTs from various treatments with character subsets inactivated, and also uses unpaired *t*-tests to examine if the symmetrical-difference distances (SDD) of these trees are significantly different from those of the trees based on the whole dataset. Only one MPT based on inactivated male characters was obtained so that the *t*-test was not conducted for this treatment. Templeton tests were also implied to examine significance of tree differences. Values significantly different at $P < 0.05$. All trees are under equal weighting (EW). Results of all the treatments in this table are ranked according to the means of SDD

Character subset inactivated	No. of characters inactivated	No. of trees	Tree length	CI	RI	Mean of SDD	Range of SDD	<i>P</i> -value (SDD)	<i>P</i> -values (Templeton test)
None	None	35	4829	0.241	0.741	–	–	–	–
Immature	56	19	4634	0.232	0.735	19	2–35	0.0194*	0.3020–1.0000*
Wing venation	24	9	4586	0.243	0.743	25	8–37	0.0095*	0.6776–1.0000*
Scent organs	17	11	4671	0.242	0.735	27	13–37	1×10^{-7} *	0.4990–0.7705*
Wing shape	11	124	4664	0.244	0.746	29	8–47	2×10^{-6} *	0.6885–1.0000*
Chemical defence systems	12	55	4773	0.239	0.739	31	7–50	7×10^{-17} *	0.4173–1.0000*
Chaetosemata	7	98	4767	0.240	0.741	35	16–56	2×10^{-22} *	0.5254–1.0000*
Male 8th abdominal segment	20	41	4550	0.235	0.736	57	24–81	2×10^{-20} *	0.1552–0.6990*
Wing scale	12	5	4552	0.232	0.739	59	47–70	0.2812	1.0000*
Female genitalia	58	10	4422	0.238	0.740	77	66–88	4×10^{-23} *	0.3245–0.4435*
Colours	54	45	3658	0.264	0.786	92	72–112	1.154×10^{-48} *	0.0334–0.4606*
All female	99	5	3275	0.273	0.771	130	109–155	3×10^{-5} *	0.0328–0.4564*
All male	110	1	3141	0.249	0.733	147	142–150	2×10^{-4} *	0.0192–0.0048*

ent from the whole data set cladogram in the terminal clades, where *Scotopais* forms the sister group of clade 17.

The systematic implications of the eighth abdominal segment in male chalcosiine moths have been emphasized by Owada (1989, 2001) and Owada & Horie (1999, 2002b). Yen (2003c, 2004a) suspected that the morphological diversification of this segment, in combination with the reduced and less variable genitalia, may have led to the high diversity of the terminal taxa. The results of excluding the eighth abdominal segment characters (Fig. 67) reveal that both basal and terminal inter-relationships of Chalcosiinae are collapsed to several polytomies, while the relationships among Chalcosiinae and the outgroups are not affected.

Deactivation only of 'female genitalia' characters produced a polytomy formed by clades 1, 2 and 4. In addition, the phylogeny (Fig. 68) resulting from this treatment is quite different from that produced by analysis of the whole data set in that the *Corma* genus-group is basal to clade 1; clade 5 becomes paraphyletic; clades 8 and 9 are placed to be the basal part of clade 7, while clade 7 is separated into three paraphyletic groups; clade 15 becomes paraphyletic; and the *Gynautocera-Histia-Pompelon* genus-group of clade 18 is inserted into clade 17.

The complex scent organs of Chalcosiinae are considered to be a potential synapomorphy of the subfamily (Tarmann, 1992c). When all the characters relevant to the scent/androconial systems were excluded, only the relationships among the zygaenid subfamilies plus the basal dichotomies of clade 17 were affected (Fig. 69).

We chose to investigate deactivation of chaetosemata characters (including the colours of the associated scales) because this organ has been considered to be a diagnostic character of the Zygaenidae (Tarmann, 1994; Epstein *et al.*, 1999). The consensus cladogram (Fig. 70) of this treatment reveals that only three places are markedly different from those in Figure 58: *Cleoda* and *Callizygaena* are paraphyletic; the *Aglaope* genus-group of clade 1 is paraphyletic; and the basal dichotomies of clades 16–18 are collapsed.

Exclusion of characters relating to chemical defence mechanisms (both adult and larval, morphological and biochemical) produced 55 MPTs, of which the consensus (Fig. 71) shows five main differences from the phylogenetic pattern of the total data set: monophyly of *Phauda* and *Lactura* is not supported; Procridae and Zygaeninae form an unsolved polytomy; internal relationships of clade 1 are collapsed; clades 2 and 3 are placed in a trichotomy with clades 4–18; and clades 8 and 9 form a trichotomy with clade 7.

In addition to using tree-to-tree distances to estimate the degree of incongruence among tree topologies, we also used the Templeton test to examine this issue. The results reveal that all the 'treatments' produce trees which are to a significant degree topologically incongruent from the original ones (Table 5). On the other hand, deactivating 'wing scale' characters does not produce significantly different trees according to the *t*-test results for SDD, while the results from the Templeton test suggests that it can. Compared to all previous analyses (Table 4), deactivation of the 'all male' or 'all female' characters results in much higher mean and range SDD values than all the other treatments, while exclusion of the characters relating to 'scent organs', 'wing venation' and 'immatures', respectively, results in much lower ones.

MONOPHYLETIC STATUS OF THE MAJOR TAXA

Results of the Templeton tests (Table 6) for the constrained taxa show that all the null hypotheses must be rejected except for those of 'Heterogynidae + Zygaenidae', '*Cleoda* + Chalcosiinae s.s.', 'Aglaopini *sensu* Tarmann' and '*Agalope* s.l.'. Therefore, the suspected sister-group relationship between Zygaeninae and Chalcosiinae (Naumann *et al.*, 1999), the current concept of Chalcosiinae, all the tribes defined by Alberti

(1954) and all the genera tested are not monophyletic. All of the major taxa should therefore be redefined based on the apomorphies found in all the previous analyses.

DISCUSSION

PHYLOGENETIC AFFINITIES OF THE NON-ZYGAENID GROUPS

Is Burlacena a member of the Zygaenidae?

Heppner (1982 [1981]) transferred *Burlacena* and *Cibdeloses* from Immidae (Immoidea) and Brachodidae (Sesioidea) to Zygaenidae without providing any reason. Subsequently, Tarmann (1996) stated that *Burlacena* is related to the zygaenoid family Lacturidae. However, none of the present analyses revealed any apomorphy which supports association of this genus with Zygaenidae or Zygaenoidea. In addition, searching the collections in the BMNH, two genera, *Anaphantis* Meyrick, 1907 (type species: *Anaphantis isochrysa* Meyrick, 1907) and *Balanopectica* Meyrick, 1903 (type species: *Cyme orbicularis* Felder & Roggenhofer, 1875), which had been placed in the Yponomeutidae for a long time, were found to be very similar to *Burlacena* in their external morphology (except for their clear wings) and genitalic structure,

Table 6. Tree lengths and number of the trees obtained from each constraint analysis with results of Templeton test that compares unconstrained trees with constrained ones. All values are significant at $P \leq 0.05$

Tree	Tree length (steps)	No. of trees	Test results <i>P</i>
Original MPTs (EW)	4839	35	—
Heterogynidae + Zygaenidae	4831	34	0.7237–0.7928
<i>Chalcosiopsis</i> + Chalcosiinae s.s.	4903	15	<0.0001*
<i>Inouela</i> + Chalcosiinae s.s.	4891	6	<0.0001*
<i>Inouela</i> + <i>Arbudas</i>	4916	13	<0.0001*
<i>Cleoda</i> + Chalcosiinae s.s.	4835	73	0.4047–0.7199
Zygaeninae + Chalcosiinae	4856	79	0.0016–0.0116*
Chalcosiinae s.l.	4905	74	<0.0001*
Heteropanini <i>sensu</i> Alberti	4897	54	<0.0001*
<i>Aglaope</i> + other chalcosiines	4848	46	0.0017*
<i>Aglaope</i> + Zygaeninae + Chalcosiinae	4856	72	0.0016–0.0116*
Aglaopini <i>sensu</i> Tarmann	4831	69	0.7928–0.8415
Agalopini <i>sensu</i> Alberti	4984	62	<0.0001*
Cyclosiini <i>sensu</i> Alberti	4867	26	0.0004–0.0013*
Chalcosiini <i>sensu</i> Alberti	5096	19	<0.0001*
<i>Agalope</i>	4836	212	0.1083–0.6007
<i>Pidorus</i>	5011	24	<0.0001*
<i>Eterusia</i>	4997	71	<0.0001*
<i>Soritia</i>	5024	25	<0.0001*
<i>Chalcosia</i>	4910	337	<0.0001*
<i>Trypanophora</i>	4875	21	0.0003–0.0011*
<i>Docleopsi</i>	4871	30	<0.0001*

and are probably closely related. The systematic position and taxonomic association of this group require further study.

Monophyly of Chalcosiopsis and where to accommodate it

Chalcosiopsis melli was grouped with *C. variata* because of shared wing venation characters (all radial veins arise from the radial cell and are separate at their bases) and female genitalia (long and spiralled ductus bursae; corpus bursae with paired signa) (Alberti, 1954). However, we are not convinced that these two species are congeneric, as other parts of their morphology are extremely distinct. Their association with both Zygaenidae and Zygaenoidea is also questionable. *Chalcosiopsis* was tentatively placed in Zygaenidae by Swinhoe (1894), and this placement was subsequently followed by Hampson (1896), Jordan (1908), Fletcher (1914) and Bryk (1936). Alberti (1954) discussed the systematic position of this genus based on *C. variata* in addition to describing a new species, *C. melli*, from S. China. He noted that many characters of this 'genus' were shared by other chalcosiine genera and that association of *melli* with *variata* was due principally to the resemblance of the corpus bursae, which has paired signa and spiral ductus bursae. He also tentatively associated this genus with his Heteropanini (comprising *Heteropan*, *Arbudas* and *Eumorphiopais*) based on their similar size and wing shapes.

Until recently, *melli* was known only from a unique female type, dissected by Alberti himself, in ZMHB. The immid *Alampla palaeodes* (Meyrick, 1914) (type locality: Kankau, Taiwan; = *Heliothela* [?] *Cretostrigalis* Caradja, 1925, type locality: Lienping, Kwangtung, China), appears to be identical to *Chalcosiopsis melli*, and therefore *melli* is a junior subjective synonym of *A. palaeodes*. However, this does not mean that *Chalcosiopsis variata* can be immediately transferred to the Immididae because the monophyly of the letter is still questionable and is not supported by any clearly defined synapomorphies (Dugdale *et al.*, 1999). Furthermore, the autapomorphic characters of this species – complex and developed type of chaetosemata, uncus with complex processes and a metathoracic androconial organ in male – have not been found in any species of Immididae *sensu* Heppner (1982). We therefore leave *Chalcosiopsis* unplaced in any family/superfamily, and its phylogenetic position will need to be investigated in future studies by comparing all the family groups of the non-obtectomeran Lepidoptera.

Are the Heterogynidae the sister group of the Zygaenidae?

The proposed monophyly of (*Heterogynis* + (*Dianeura* + (*Anomoeotes* + *Himantopterus*))) contradicts previ-

ous hypotheses that *Heterogynis* is either the sister group (Common, 1970; Minet, 1986, 1991; Fänger *et al.*, 1999) or part of the Zygaenidae (Fänger & Naumann, 2001). This clade is supported by 21 characters in the analyses presented here, but this number falls short of the total as they were only brought into the analyses in relation to the outgroups, so a large number of potentially informative characters were not coded because they are either absent or uninformative for the ingroup.

Interestingly, in all the previous analyses including EW/SAW, based on the whole data set (Figs 56–58) or EW based on the selected taxa (Fig. 63), characters of the chemical defence systems, which have always been expected to support the monophyly of Zygaenidae + Heterogynidae (Fänger *et al.*, 1999; Fänger & Naumann, 2001), do not clearly do so because a large proportion of the taxa was not scored for these characters (see Appendices 4 and 5). Furthermore, deactivation of 'chemical defence' characters has no effect on the relationships among *Heterogynis*, *Dianeura*, *Anomoeotes* and *Himantopterus* (Fig. 71). These results show that these systems, which include cyanoglucosides and the presence of cyanic fluid-storing cavities in the larvae, may have evolved independently in these two families. The adult morphological characters of *Heterogynis* are all unique and not comparable with those of other taxa, therefore any morphological link of this genus to Zygaenoidea must be provided by larval or pupal characters. However, the results from the Templeton test do not reject the hypothesis that Heterogynidae and Zygaenidae are potential sister groups (Table 6).

Are the Phaudinae a zygaenid subfamily?

The relationship of *Phauda* + *Lactura* uncovered in the present study provides a new hypothesis of the phylogenetic affinities of these two genera, which have had a peripatetic classificatory history, wandering around various families/superfamilies for a long time. *Phauda* was originally placed in Phaudinae by Kirby (1892), then in Zygaenidae by various authors (see Fig. 1) until Fänger *et al.* (1999) found several characters that provided evidence for exclusion of Phaudinae from Zygaenidae, and suggested an affinity between Phaudinae and the 'limacodid' families.

The genera associated with *Lactura* were originally placed in Yponomeutidae (Walker, 1854; Nye & Fletcher, 1982), associated with Zygaenidae (Common, 1990) or Phaudinae (Fletcher & Nye, 1982, citing J. Kyrki); they are currently placed in a separate family, Lacturidae (Heppner, 1995). Until recently, the phylogenetic affinity of Lacturidae within the superfamily was unclear. Comparison of immatures of several species of *Lactura s.l.* from the USA, Australia and Hong Kong and *Phauda* from Taiwan, China and Vietnam,

showed their immature as well as their adult characters. They are very similar in many aspects, and the two groups may need to be merged if these similarities turn out to be synapomorphies. However, the monophylies of Phaudinae (including *Phauda*, *Phaudopsis* and *Alophogaster*) and Lacturidae (including *Lactura*, *Anticrates*, *Lactura*, *Gymnogramma*, *Aictis* and *Thyridectis*) are still uncertain. Fänger *et al.* (1999) stated that the reduced larval 9th abdominal segment suggests an affinity of Phaudinae with the limacodid-group families, Himantopteridae and Somabrachyidae. However, we believe that this character does not bring *Phauda* within a monophyletic clade together with Himantopteridae, with the bulk of evidence suggesting that it has been derived independently at least twice during the evolution of the Zygaenoidea.

MONOPHYLY OF ZYGAENIDAE AND THEIR INTERNAL RELATIONSHIPS

Compared with earlier studies using incomplete taxon sampling and far fewer characters, the phylogenetic trees obtained during the present study are largely incongruent with previous hypotheses of zygaenid relationships. The new arrangements differ in the following aspects.

The Procridinae, either as a monophyletic group (EW) or as a paraphyletic one (SAW), are the most basal lineage of Zygaenidae. Inclusion of *Janseola* was first documented by Vári *et al.* (2002) who referred to an unpublished comment by Alberto Zilli. Although a clade that comprises *Janseola* and *Inouela* + *Homophylotis nigra* is recovered in the present study, the most closely related genus to *Janseola* is probably *Tascia* Walker, 1856 [type species: *T. chrysotelus* Walker, 1856, now called *T. finalis* (Walker, 1854)] from southern Africa. This relationship is based on the features of valval shape, articulated stick-like appendages derived from conjunction between valval bases and transtilla. The genus *Saliunca*, placed in 'Callizygaenini' by Alberti (1954), is placed in the Procridinae, and therefore the Callizygaenini *sensu* Alberti is paraphyletic.

Monophyly of the Zygaeninae is supported in the present study, but it is not suggested to be the sister group of Chalcosiinae because the clade comprising Callizygaeninae + *Cleoda* is more closely related to the clade which comprises *Heteropan* and Chalcosiinae.

Monophyly of the Callizygaeninae (presently comprising *Callizygaena* and *Procotes*) + *Cleoda* is strongly supported. However, the characters of '*Cleoda syntomoides*' are in fact based on a speculated 'marriage' between the 'male' and 'female' specimens. This species was described by Walker (as *Doclea syntomoides*) based on a male specimen with 'greenish forewing from Malakka'. However, the 'type specimen'

deposited in the Hope Entomological Collection of Oxford University Museum is in fact a female, which exhibits completely different body size and wing patterns (yellow wings, see Fig. 9) from the features described by Walker. This 'type specimen' was probably used for the figure of the '*Docleopsis sulaensis*' in Swinhoe (1892: t.2, f.10), but it is not conspecific with the true *Docleopsis sulaensis* Jordan, 1907 from Sula archipelago.

We were unable to locate the 'male type' of *Syntomoides* in Oxford University Museum, although two male specimens were found in the Natural History Museum in London. One of them may have been the model for the illustration of *Syntomoides* in Seitz's '*Gross-Schmetterlinge der Welt*' (Jordan, 1907: 16, t. 2e). The characters and collection locality ('Malakka') agree well with the description by Walker so we suspect that they are the 'real' *Syntomoides*. To examine whether the male and the suspected female were conspecific, we conducted a test analysis in which the male and female were treated as different terminal taxa. However, they still formed a monophyletic group, which clustered with *Callizygaena ada*. Therefore we tentatively associated the data sets of the male *Syntomoides* and the speculated female into one data set for all the analyses. *Cleoda* and *Callizygaena* are grouped with the characters of the multi-forked scales on the chaetosemata and wings. It is still uncertain whether *Cleoda* can be placed in Callizygaeninae because information on the immature stages is not available. The male androconial organ of *Cleoda* is homoplasious with those of *Harrisina* and *Pryeria*, and the extended female ovipositor is distinct from those of the species placed in *Callizygaena* and *Procotes*.

Heteropan and Chalcosiinae always form a sister-group relationship based on 27 synapomorphies (EW/SAW). Of these, seven characters are unique to this clade: patagia strongly sclerotized and sac-like (70: 4), patagia more developed than parapatagia (72: 2), T1 of larva with retractile cervical gland (354: 2), thoracic spiracles not concealed by 'spiracle access' (393: 1), terga 3–8 with multi-rowed spinulets (394: 3), spinulets occupying the whole terga of the pupa (395: 2), and A10 of pupa with an elevated transverse tuberculate band (396: 1). The three taxa of *Heteropan* are grouped by 27 apomorphies (EW/SAW), but of these only 56: 2 (lateral margin of flagellomeres ridged and undulated, 57: 2 (back-bone of flagellomere cristate or keeled along the whole antenna) are unique.

Monophyly of Chalcosiinae is supported by 24 (EW) or 23 (SAW) characters. Of these, only two characters, scales on patagia bending downwards (81: 1), subdorsal and lateral syndeses located posterior to front margin of tergum 2 (178: 3), are unique. Tarmann (1992c), Epstein *et al.* (1999) and Naumann *et al.* (1999) sus-

pected that the hindwing-abdominal androconial organ, developed ovipositor and absence of accessory glands in female genitalia provided the synapomorphies of Chalcosiinae. However, the present study shows that only two uncontradicted characters relevant to the scent organs – a bundle of long hair bristles inserting into the pleural pouch (337: 3) and presence of ‘normal type’ of pleural pouch (338: 4) – support the monophyly of Chalcosiinae. Presence of elongated ovipositor occurs inconsistently in the majority of the studied taxa, so this trait is not seen as a synapomorphy of the subfamily. In addition, 403: 5 (mandibular lobe long, with sclerotization from sub-basal to apical part), an uncontradicted character relevant to the chemical defence system, also supports the monophyly of Chalcosiinae.

THE INTERNAL RELATIONSHIPS OF CHALCOSIINAE

As shown in Table 6, none of the tribes recognized in previous studies is recovered as monophyletic. Except for those clades (see Fig. 57) which have received applicable names and taxonomic rank, all the clades in the following discussion are labelled according to their most basal and terminal taxa.

Clade 1 (*Agalopini*)

Alberti (1954) included nine genera (*Agalope*, *Boradia*, *Elcysma*, *Herpa*, *Philopator*, *Chalcophaedra*, *Campylotes*, *Corma* and *Rhodopsona*) in his *Agalopini*. This assemblage, however, is not monophyletic because *Chalcophaedra* is placed as sister to *Erasmiphlebohecta* (clade 12), *Corma* is grouped with the *Anarbudas–Docleomorpha* complex (clade 2), and *Rhodopsona* is placed as sister to ‘*Pidorus*’ *miles* (clade 3) (Fig. 59C, D).

The Atlanto-Mediterranean *Aglaope* was placed in its own tribe, *Aglaopini*, by Alberti, and regarded as the most basal lineage of the whole subfamily. Tarmann (1992b) added *Formozygaena* by referring to Inoue’s (1987a) observation. However, the monophyly of *Aglaopini sensu* Tarmann is not recovered in the present analysis. The Taiwanese endemic, *Formozygaena*, is grouped with the Indochinese-Himalayan *Philopator* by both EW and SAW. The isolated *Agalope* forms a monophyletic group with a clade comprising *Philopator*, *Formozygaena*, *Atelesia*, ‘*Chalcosia*’ *thibetana* and ‘*Chalcosia*’ *alpherakyi*. Since this group is completely ‘enclosed’ by the members of *Agalopini* (excluding *Chalcophaedra*, *Corma* and *Rhodopsona*), the validity of *Aglaopini* is questionable and a future synonymization is necessary. The *Agalope* genus-complex (see also Owada, 1992a) forms the most terminal lineage in clade 1. The current concept of the genus is apparently polyphyletic, because *A. immaculata* is sis-

ter to *Elcysma*, while *A. glacialis* is sister to the former two taxa. Owada (1992a) considered that *Elcysma* and *Achelura* are more closely related, while the present analysis does not recognize this affinity.

Clade 2 (*Cyclosia–Corma* group)

Alberti (1954) established *Cyclosiini* for *Cyclosia*, *Hampsonia* and *Cadphises*, based on their pointed uncus (212: 0) and associated setae (210: 1, 211: 0). These characters, however, are not unique to these three genera and do not support them as a monophyletic group. As *Hampsonia* and *Cadphises* are placed in clade 1, the composition of *Cyclosiini* therefore needs to be redefined. A monophyletic group which includes *Corma*, *Eucormiopsis*, *Docleomorpha*, *Heterusinula*, *Cryptophysophilus* and *Anarbudas* is recovered as the sister group of *Cyclosia*, and all the *Cyclosia* species-groups, which exhibit extremely diverse mimetic wing patterns, form a monophyletic clade. Interestingly, the *C. midama*, *C. curiosa* and *C. imitans* species-groups, which have mimetic relationships with *Euploea*, *Parantica*, *Ideopsis similis* and *Tirumala* danaine butterflies, are also monophyletic, while the *Idea*- and *Ideopsis gaura*-mimetic *C. pieridoides* is not placed in this group. This suggests that the ‘danaine butterfly mimicry’ in *Cyclosia* has evolved independently in different species-groups. Alberti considered that *Cyclosiini* was related to *Agalopini*, although clades 1 (*Agalopini*) and 2 (*Cyclosia–Corma* group) are not recovered as sister groups in the present study.

Clade 3 (*Rhodopsona* group)

Rhodopsona was placed in *Agalopini* by Alberti (1954) because he interpreted the deeply and sharply bifurcate uncus (212: 6) as being the same character state as the pointed uncus (212: 0). In the present study, this genus is recovered as monophyletic, while the internal relationships based on a strict consensus tree are unresolved (see Fig. 59I, J). The sexually dimorphic *R. matsumotoi* was tentatively placed in this genus by Owada & Horie (1999), and the SAW analysis (Fig. 59J) suggests that it is the most basal species in this genus. *Pidorus miles*, a north-east Indian species only known from the type material, is recovered as the sister group of *Rhodopsona*.

Clade 4 (*Heteropanula* + *Pseudarbudas* group)

Due to their strikingly similar wing pattern and size, these two genera were included within the *Arbudas*-complex by Tarmann (1992c). However, their morphological characters do not suggest placement with either *Arbudas* or *Eumorphiopais*. In the analysis in which the ‘colour pattern’ characters were inactivated

(Fig. 64), this clade was placed in an unresolved trichotomy with clades 2 and 3. On the other hand, the Bremer support values for the relationships of clades 3 and 4 are lower than those of other clades. The phylogenetic relationships of these two genera should therefore be reassessed when more information becomes available.

Clade 5 (*Arbudas* + *Eumorphiopais* group)

Arbudas and *Eumorphiopais* were associated with *Heteropanini* by Alberti (1954). Since *Heteropan* is not considered to be a member of Chalcosiinae, this tribe name is no longer applicable to these two genera. Efetov (1999) considered that *Inouela* was closely related to *Arbudas* through sharing the rounded valvae, valval processes, thorn-like aedeagus and rudimentary 'uncus'. However, as explained above, *Inouela* is associated with Procridinae and thus none of these phenetic similarities is homologous. Deactivation of colour pattern characters produces a change in the relationships of clade 5. With this treatment, *Eumorphiopais* is recovered as the sister group of clades 6–18, with *Arbudas* placed more basal than *Eumorphiopais*.

'Chalcosiini' (clades 6–18)

The Chalcosiini defined by Alberti (1954) comprise 22 genera, of which nine (including the type genus) appear not to form a monophyletic group with the rest, viz. *Trypanophora*, *Soritia*, *Prosopandrophila*, *Pidorus*, *Milleria*, *Eterusia*, *Docleopsis* and *Anarbudas*. The true *Anarbudas*, based on the type species *A. insignis*, is sister to (*Docleomorpha* + *Heterusinula* + *Cryptophysophilus*) in clade 2, while the remaining two *Anarbudas* species are placed in clade 18. By excluding the *Anarbudas insignis*, *Soritia sevastopuloi*, *Chalcosia tibetana* and *Chalcosia alpherakyi* species-groups, Alberti's concept of the Chalcosiini can be applied to the following 13 clades (see below).

Clade 6 (*Herpolasia* + *Clematoessa* group)

The phylogenetic affinity of these New Guinean genera is investigated for the first time in the present study. All the species included in this clade are extremely rare in museum collections, and no recent material is known. Hering's (1922) key to the genera of Chalcosiinae (see Fig. 2) placed *Herpolasia*, *Clematoessa*, *Pompelon* and *Panherpina* (as *Herpa basiflava*) as 'close' taxa, and the only character state to support this assemblage is '(R3 + R4) stalked with R5 in forewing'. However, this trait (ch. 101: 2) is not restricted to these taxa but is widely distributed among different lineages (e.g. *Dianeura*, *Philopator*, *Cyclosia* and *Campylotes*). In the analyses based on the entire data

set, *Herpolasia* + *Clematoessa* is placed as the most basal group of Chalcosiini; however, deactivation of colour pattern characters generates a topology in which these two genera are recovered within clade 7. *Clematoessa* is not monophyletic because *C. virgata* shares extremely similar genitalic structures with *Herpolasia augarra*. The phylogenetic position of *C. xuthomelas* requires sorting out because all of the known specimens are female.

Clades 7–9

The analyses based on the entire data set separate clades 7 (*Caprima*–*Papuaphlebohecta* group) 8 (*Pidorus corculum*) and 9 (*Pidorus bifasciatus* + *Prosopandrophila mirifica*). However, Bremer support values for the monophylies of clades 8 + 9–18 and 9 + 10–18 are relatively low. In contrast, analysis based on inactivation of colour pattern characters places clades 8 and 9 as the basal lineages of clade 7. As a result, these three clades are discussed together in this section. Four species-groups of *Pidorus* are distributed among these clades, but none of them is related to the type species-group of *Pidorus*, which comes out in clade 10.

Within the genus *Caprima*, the *C. chrysosoma* species-group always appears to be the most basal lineage of the genus; however, but because *C. chrysosoma* is only known from the unique female type specimen and has several character states distinct from those of other *Caprima* species-groups, its phylogenetic position requires further investigation. On the other hand, analyses based on the entire data set place *Caprima* as the basal lineage of clade 7 (Fig. 57), while it is switched to the most terminal lineage by deactivation of colour pattern characters (Fig. 64). In addition, *Hemiscia albivitta* is placed with *Papuaphlebohecta* as its sister group, but is apparently not monophyletic with the type species *Hemiscia meeki*, which is included in clade 10.

Clade 10 (*Pidorus*–*Hemiscia* group)

Under EW and SAW, *H. meeki*, an undescribed species from the Philippines, and four species-groups of *Pidorus* are placed in clade 10, which forms the sister group to clades 11–18. However, deactivation of colour pattern characters places clade 10, clades 7 + 8 + 9 and clades 11–18 (Fig. 64) in an unresolved trichotomy. The taxonomic history of *Pidorus* has been chaotic. In the present study, this heterogeneous genus is separated into 14 species-groups, which are distributed among six different clades. Owada & Horie (2002b) discussed the systematic positions of the *Eterusia culoti* and *Soritia circinata* species-groups and suggested placing them in *Pidorus*, a generic combi-

nation used here. This taxonomic treatment is supported by the present results, which associated both of them with *P. glaucopis*, the type species of the genus. Like most of the New Guinean chalcosiine taxa, *H. meeki* and its associated 'subspecies' are represented by very few specimens in museum collections. Bryk (1936) and Endo & Kishida (1999) recognized eight subspecies in this sexually dimorphic and mimetic species. However, examination of the male genitalia has revealed that there are at least three different allopatric species involved in this complex, and the subspecies from the Rossel archipelago, namely *Placiva* Jordan, 1930, is possibly not a member of this genus at all because the male has a very rudimentary proboscis and some other distinct characters from the nominotypical *H. meeki*.

Clade 11 (Retina + Pidorus constrictus group)

Based on EW/SAW applied to the entire data set and on the results of deactivation of various character subsets, this clade is always made the most basal lineage of a monophyletic group comprising clades 11–18. This clade exhibits two mimetic wing patterns typical of the Chalcosiinae. *Retina* is often considered to be related to the *Rhodopsona costata* species-group because both have a red arched stripe extending from outer margin across the forewing apex to the wing base along the costal margin as well as a 'red head'. In *Retina rubrivitta* and *R. vitripennis*, the 'red head' is formed by the red scales covering the vertex (ch. 26: 5, 27: 5), while the *Rhodopsona costata* species-group has additional red patagia (ch. 75: 5, 76: 5) and parapatagia (ch. 77: 6, 78: 6). In southern China and northern Vietnam, *Retina* and *Rhodopsona costata* are sympatric and thus possibly participate in the same mimicry complex. Interestingly, *Pidorus constrictus*, which has exactly the same wing pattern as the *P. glaucopis* species-group but a wing shape similar to that of *Retina*, becomes the sister group of *Retina*. Their genital and pregenital abdominal structures are almost the same, so a future combination of *P. constrictus* and *Retina* appears to be reasonable.

Clade 12 (Barbaroscia–Amesia group)

Two major subgroups are recognized within the clade: *Barbaroscia–Pidorus circe* and *Eucorma–Amesia*. *Barbaroscia amabilis* was originally (and ambiguously) placed in *Pidorus* by Jordan (1907) and then transferred to the present genus by Hering (1922). Hering considered that *Barbaroscia* shares several venational characters with *Hampsonia*, *Corma*, *Neoherpa*, *Rhodopsona*, *Agalope* and *Arbudas truncatus* (as *Pidorus truncatus*), but both EW and SAW suggest an affinity with the *Pseudoscaptesyale*, *Soritia bicolor*,

Pidorus fasciatus, *P. ochrolophus* and *P. circe* species-groups. Within the *Barbaroscia–P. circe* subgroup, the male of *P. ochrolophus* is not yet known, therefore its proposed sister-group relationship with the *P. circe* species-group is only based on female characters.

The relationships of the *Eucorma–Amesia* subgroup are not well resolved. Interestingly, SAW based on the full data set and deactivation of colour pattern characters recovered a monophyletic group comprising *Erasmia* + *Eucorma*, indicating that *Eucorma* is paraphyletic. *Erasmiphlebohecta* + *Chalcophaedra* are always recovered as sister groups but their phylogenetic position is not stable. EW makes them the most terminal group within the subgroup, but both SAW and deactivation of colour pattern character make them the most basal. The whole clade exhibits a specialized but uninvestigated copulatory mechanism; that is, the male genitalia are 'bound' by genitalic muscles, not movable and 'concealed' or 'enclosed' by the specialized eighth abdominal tergite and sternite. The aedeagus is usually very long, with a curved bulbus ejaculatorius (ch. 232: 2). Unlike the eighth sternite or tergite of the taxa in clades 14–18, these two sclerites are not articulated and are immovable. Their function may be to 'protect' the male genitalia, while the very reduced and membranous male genitalia cannot be 'exposed' to clasp/hold the female abdomen *in copula*. Because no specialized and 'matchable' structure has been found in the female abdomen, the copulatory mechanism of this clade requires further study.

Clade 13 (Eterusia repleta + Opisoplatia group)

Within clade assemblage 12–18, the Indochinese *Eterusia repleta* and Bornean *Opisoplatia grandis* are very characteristic in their large size and 'normal male copulatory mechanism', which has very sclerotized, well-developed and movable valvae and non-specialized eighth abdominal tergite and sternite. Inclusion of *E. repleta* in *Eterusia* generates significantly longer trees than the MPT under EW ($P < 0.005$, see Table 6), so this species is less likely to be a derived lineage within *Eterusia*.

Clade 14 (Eterusia + Soritia group)

These two genera have, historically, been confused, and most of their species have been switched between them over the years in various studies. Hering (1922) considered that the generic boundary between them was ambiguous, while Endo & Kishida (1999) considered that the two genera could be synonymized. Yen (2003a, b, 2004b) also doubted whether the similarities in the male genitalia between the *Eterusia subcyanea*, *E. tricolor*, *Soritia elizabethae* and *S. shahama*

species-group might be due to convergence. However, the individual monophyly and sister-group relationship of these two genera (excluding *S. sevastopuloi*, *S. bicolor*, *S. moerens*, *E. repleta*, *E. raja*) are strongly supported by all the analyses presented here. Kishida & Endo (1999) described a Philippine species *Yoshimotoi* in *Eterusia*. Subsequently, Yen (2003b) suggested transferring this species to *Prosopandrophila* because its morphological characters are extremely similar to those of the *P. distincta* species-group. The present analysis does not suggest any affinity between *Eterusia* and *Prosopandrophila*.

Clade 15 (*Prosopandrophila*–*Phlebohecta* group)

This well-supported clade comprises about 20 species currently placed in four polyphyletic genera, *Prosopandrophila*, *Soritia*, *Trypanophora* and *Phlebohecta*. Hering (1922) used the character 'm1 arising from r4 + r5' to diagnose *Prosopandrophila* and *Docleopsis*. However, this observation seems to be incorrect because the polyphyletic *Docleopsis* does not possess this character state. *Trypanophora* is apparently an assemblage of the species which have transparent wings or Syntominiæ/Lithosiinae-like wing patterns. Except for the *Trypanophora hyalina* species-group, which includes the type species, all the other species-groups are placed in clade 18. Hering also placed *Phlebohecta* closer to *Isocrambia*, an odd genus associated with *Cyanidia* in the present study based on the character 'r4 and r5 not stalked'. Although the males of all *Isocrambia* species are still unknown, analysis based only on female characters (Fig. 60) does not suggest any affinity between *Isocrambia* and *Phlebohecta*.

Clade 16 (*Neochalcosia*–*Chalcosia zehma* group)

Due to the presence of a white band in the forewing, the taxa included in this clade were either placed in *Chalcosia* or *Pidorus* by previous authors. Under EW and SAW, the characters involving the forewing band (141: 3 and 142: 3) do not provide any synapomorphy for this clade. Yen & Yang (1997) suspected that *Neochalcosia* + *Pseudopidorus* may form a sister group with *Chalcosia s.s.* + *Milleria*, and *Chalcosia zehma* is basal to the former genera; this hypothesis is apparently contradicted by the present analysis.

Clade 17 (*Chalcosia*–*Eusphalera* group)

Two major subgroups are recognized within the clade: *Milleria*–*Chalcosia* and *Pseudonyctemera*–*Eusphalera*. Within the former, the systematic position of *Milleria okushimai* is doubtful. When Owada & Horie (1999) described this unusual species, they noticed that the pregenital abdominal characters in the male

are distinct from those of *Chalcosia* and *Milleria*. This species is recovered as the sister group of *Chalcosia* + *Milleria* plus *Cyclosia notabilis* under EW, while it is grouped with *C. notabilis* + (*M. hamiltoni* + *M. rehfoysi* species-groups) under SAW. When colour pattern characters are inactivated, *M. okushimai* is recovered as the sister group of clades 17 + 18. However, no matter which hypothesis is accepted, *Okushimai* is never recovered as monophyletic with the *Milleria adalifa* species-group, which includes the type species of the genus.

The phylogenetic affinity of *Cyclosia notabilis* is intriguing as well. It was placed in *Cyclosia* by Kishida & Endo (1999) because its wing pattern resembles those of other *Parantica*-mimetic *Cyclosia* species, e.g. *C. imitans*, *C. parantica*, *C. pagenstecheri* (= *C. palawanica*) and *C. curiosa*. Nevertheless, examination of the copulatory structures and the constraint analysis (see Table 6) reveal that *notabilis* is not related to *Cyclosia* but is much closer the *M. hamiltoni* and *M. rehfoysi* species-groups. As to the 'true' *Chalcosia*, only three of the six defined species-groups are recovered as monophyletic with the type species, *C. pectinicornis*. *Pseudonyctemera*–*Eusphalera* comprises three monophyletic genera plus the New Guinean *Docleopsis dohertyi*. *Psaphis azurea* was originally placed in *Chalcosia* by Kishida & Endo (1999), and was subsequently transferred to *Psaphis* by Yen (2003c). This transfer is supported by the present study and also suggests that sexual dimorphism has evolved only once within the genus. The interrelationships of *Eusphalera* are not resolved by EW but are much better elucidated by SAW. Due to the complex mimetic wing patterns, several species were previously misplaced in other genera (see Yen, 2003a, b, c, 2004a), e.g. *Eusphalera bellula* in *Soritia* (Kishida & Endo, 1999), and *E. venus* and *E. subnigra* in *Eterusia* (Bryk, 1936).

Clade 18 (*Scotopais*–*Docleopsis* group)

Within the subfamily, this clade has the widest distribution, ranging throughout the Himalayas, eastern Asia, Indochina, the Malay peninsula, all the major South-East Asian islands, New Guinea, Fiji and Solomon islands. The EW and SAW trees show only minor topological differences (see Fig. 59U, V), while deactivating colour patterns generates an influence which switches *Scotopais tristis* from the most basal lineage of the whole clade to a derived position as the sister group of the *Trypanophora producens*–*Docleopsis sulaensis* subgroup. The relationship between *Histia*, *Gynautocera* and *Pompelon*, all having elongated forewings and metallic blue hindwings (not present in *H. dolens* and *H. eurhodia*), has been 'implied' by several authors (e.g. Hampson, 1892; Endo & Kishida,

1999). The present study corroborates that they belong to a monophyletic group and form a sister group with the north-east Indian *Eterusia raja*.

A RECLASSIFICATION OF CHALCOSIINAE?

As discussed above, the current classification of Chalcosiinae, from subfamily to species level, is not satisfactory and is probably highly misleading. We believe that a revised classification, assembled using the phylogenetic analysis presented here, would help fix the names and contents of each taxon. First of all, except for Zygaeninae, all the zygaenid subfamilies should be redefined. The synapomorphies of Procridinae still require investigation as the present taxon sampling is not sufficient to define this group. We suggest that *Chalcosiopsis*, *Arbudas* and *Eumorphiopais* be excluded from Heteropanini so that this tribe can be elevated to a rank equivalent to Chalcosiinae, while the tribal classification of Chalcosiinae itself should be rearranged. Agalopini (including Aglaopini) can be applied to clade 1, while clade 2 can be treated as a redefined and extended Cyclosiini. The name Chalcosiini should be allocated to clades 6–18. No further internal subgrouping is recommended because creating a plethora of infra-tribal names is not current systematic practice.

The phylogenetic analysis presented here also reveals that around a third of the current genera are not monophyletic. Much taxonomic work, including synonymy, new combinations and descriptions of new taxa, remains to be done to establish a stable nomenclature.

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APPENDIX 1

CHECKLIST OF SPECIES INCLUDED IN THE PHYLOGENETIC ANALYSIS

This appendix contains a checklist of the taxa examined and the species-groups defined for the phylogenetic analysis. Intraspecific taxon names are not listed. The genera are arranged according to their positions in the data matrix and phylogenetic affinities. The species of each group are listed alphabetically. Genus-level classification and nomenclature tentatively follow Yen (2003c). See notes concerning taxonomic treatment in the left column. The details of taxonomic treatments indicated in the right column are to be published in a separate paper.

Taxa	Locality	Proposed taxonomic changes
Outgroups		
Anomoerotidae		
<i>Anomoeris levis</i> Felder & Felder, 1874	South Africa (Natal)	
<i>Dianeura goochii</i> Butler, 1888	South Africa (Natal)	
Himantopteridae		
<i>Himantopterus fuscineris</i> Wesmael, 1836	Java	
Lacturidae		
<i>Lactura dives</i> Walker, 1854	Queensland	
Heterogynidae s.l.		
<i>Heterogynis</i> sp.	Italy	
<i>Janseola titaea</i> Druce, 1896	Transvaal	transferral to Procrinae sensu lato
Zygaenidae s.l.		
Subfamily uncertain		
<i>Burlacena aegerioides</i> Walker, [1865]1864	Papua New Guinea (Woodlark Island)	exclusion from Zygaenoidea exclusion from Zygaenidae
Phaudinae		
<i>Phauda mimica</i> Strand, 1915	Taiwan	
Procrinae s.l.		
<i>Artona hainana</i> (Butler, 1876) ¹	Taiwan	
<i>Theresimima ampellophaga</i> (Bayle-Barelle, 1808)	Austria	
<i>Adscita statices</i> (Linnaeus, 1758)	England	

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>Pollanisus viridipulverulenta</i> Guérin-Ménéville, 1839	Australia	
<i>Illiberis pruni</i> Dyar, 1905	Japan	
<i>Clelea formosana</i> Strand, 1915	Taiwan	
<i>Harrisina americana</i> Guérin-Ménéville, 1829	USA	
<i>Pyromorpha</i> sp.	Guatemala	
<i>Homophylotis nigra</i> (Hampson, 1892)	Myanmar	
Zygaeninae		
<i>Pryeria sinica</i> Moore, 1877	Taiwan	
<i>Zygaena filipendulae</i> (Linnaeus, 1758)	England	
Callizygaeninae		
<i>Saliunca styx</i> (Fabricius, 1775) ²	Cameroon	transferral to Procridinae <i>s.l.</i>
<i>Callizygaena ada</i> (Butler, 1892)	Borneo	
Ingroup		
Chalcosiinae <i>s.l.</i>		
<i>Inouela</i> Efetov, 1999		transferral to Procridinae <i>s.l.</i>
<i>exiguitata</i> Inoue, 1976	Japan	
<i>formosensis</i> Efetov, 1999	Taiwan	
sp. 1	Borneo	
sp. 2	Philippines (Mindanao)	
sp. 3	Malay Peninsula	
sp. 4	India	
<i>Chalcosiopsis</i> Swinhoe, 1894		exclusion from Zygaenoidea
<i>variata</i> -group		
<i>variata</i> Swinhoe, 1894	N. India (Shillong)	
<i>melli</i> -group		
<i>melli</i> Alberti, 1954	China	transferral to Immidae (Immioidea)
<i>Cleoda</i> Tremewan, 1973		transferral to Callizygaeninae <i>s.l.</i>
<i>syntomoides</i> Walker, [1865] ³	Malaysia (Malakka)	
<i>Heteropan</i> Walker, 1854		exclusion from Chalcosiinae
<i>scintillans</i> -group		
<i>albertii</i> Rothschild & Jordan, 1905	Papua New Guinea	
<i>albicosta</i> Semper, 1898	Philippines (Panaon)	
<i>albicruciatata</i> Hering, 1922	Malaysia (Malakka)	
<i>analisis</i> Jordan, 1907	Myanmar (Shipaw)	
<i>anisus</i> Jordan, 1907	Papua New Guinea	
<i>apicalis</i> Jordan, 1912	Papua New Guinea	
<i>argiolina</i> Oberthür, 1894	Sumatra	
<i>coeruleus</i> Jordan, 1907	Indonesia (Talaut)	
<i>cupreatus</i> Hampson, 1892	Sumatra	
<i>cyaneus</i> Jordan, 1907	Papua New Guinea	
<i>dolens</i> Druce, 1888	Fiji	
<i>ermophila</i> Hering, 1922	Malaysia (Malakka)	
<i>fuscescens</i> Dohrn, 1906	Sri Lanka	
<i>iscatus</i> Jordan, 1912	Papua New Guinea	
<i>lutulenta</i> West, 1932	Philippines (Lanao)	
<i>lycaenoides</i> (Walker, [1865])	Papua New Guinea	
<i>scintillans</i> Walker, 1854	Sri Lanka	
<i>truncata</i> (Oberthür, 1894)	Indonesia (Jobi Is.)	
<i>alienus</i> -group		
<i>alienus</i> (Jordan, 1912)	Papua New Guinea	
<i>appendiculata</i> -group		
<i>appendiculata</i> (Snellen, 1879)	Sulawesi (Ambarang, Saleyer)	
sp. 1	Sumatra	
<i>Cadphises</i> Moore, [1866]		
<i>maculate</i> -group		
<i>maculata</i> Moore, 1865	N.E. India (Darjeeling)	
sp. 1	Vietnam	
<i>moorei</i> -group		
<i>moorei</i> Butler, 1875	Sikkim	
sp. 2	China	
<i>Hampsonia</i> Swinhoe, 1894		
<i>pulcherrima</i> -group		
<i>pulcherrima</i> Swinhoe, 1894	N. India	
<i>ueharai</i> Owada & Horie, 2002	Vietnam	

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>Watermenia</i> Owada & Horie, 2002		
<i>bifasciata</i> Tremewan, 1959	N.E. India (Jaintia Hills)	
<i>Herpidia</i> Bryk, 1936		
<i>eupoma</i> (Swinhoe, 1897)	N.E. India (Jaintia Hills)	
sp. 1	Laos	
<i>Campylotes</i> Westwood, 1840		
<i>histrionicus</i> -group		
<i>altissima</i> Elwes, 1890 ³	N. India	
<i>atkinsoni</i> Moore, 1879	N. India	
<i>excelsa</i> Oberthür, 1896		
sp. & stat. rev. ⁴	N. India	
<i>histrionicus</i> Westwood, 1840	Nepal	
<i>kotzechi</i> Röber, 1926	N. India	
<i>wernickei</i> Röber, 1925	N. India	
<i>desgodinsi</i> -group		
<i>burmana</i> Hampson, 1919[1920]	Myanmar	
<i>desgodinsi</i> Oberthür, 1884	Tibet	
<i>maculosus</i> Wileman, 1910	Taiwan	
<i>minimus</i> Oberthür, 1894	W. China	
<i>pratti</i> Leech, 1898	W. China	
<i>romanovi</i> Leech, 1898	W. China	
<i>philomenus</i> Oberthür, 1923	W. China	
<i>sikkimensis</i> Elwes, 1898	N. India	
<i>splendida</i> Elwes, 1890 stat. nov. ⁵	N.E. India	
sp. 1	Thailand	
<i>Aglaope</i> Latreille, 1809		
<i>infausta</i> (Linnaeus, 1767)	S. Europe	
<i>labasi</i> Oberthür, 1922	N. Africa	
<i>Philopator</i> Moore, [1866]		
<i>basimaculata</i> Moore, [1866]	N.E. India (Darjeeling)	
<i>rotunda</i> Hampson, 1896	Sikkim	
<i>leucoptera</i> Yen & Xue, 2003	China	
<i>Formozygaena</i> Inoue, 1987		
<i>shibatai</i> Inoue, 1987	Taiwan	
sp. 1	Taiwan	
<i>Atelesia</i> Jordan, 1930		
<i>nivosa</i> Jordan, 1930	Papua New Guinea	
<i>Elcysma</i> Butler, 1881		
<i>delavayi</i> Oberthür, 1891	W. China	
<i>dohertyi</i> Elwes, 1890	Assam	
<i>westwoodii</i> (Snellen van Vollenhoven, 1863)	Japan	
<i>Agalope</i> Walker, 1854		
<i>hyalina</i> -group		
<i>butleri</i> Owada & Horie, 2000 ⁶	Nepal	
<i>formosana</i> Matsumura, 1927	Taiwan	
<i>glacialis</i> Butler, 1881 ⁶	N. India	
<i>grandis</i> Mell, 1922	China	
<i>harutai</i> Horie, 2000	Nepal	
<i>hyalina</i> (Kollar, 1844)	N. India	
<i>kishidaograndis</i> Owada & Horie, 2000	N. Vietnam	
<i>mineti</i> Owada, 2000	China	
<i>primularis</i> Butler, 1895	N. India	
<i>suzukikojii</i> Horie, 2000	Nepal	
<i>eronioides</i> -group		
<i>eronioides</i> (Moore, 1879)	Sikkim	
<i>livida</i> Moore, 1879 sp. rev. ⁷	China	
<i>bieti</i> -group		
<i>basiflava</i> (Moore, 1879)	Sikkim	
<i>bieti</i> (Oberthür, 1886)	W. China	
<i>dejeani</i> Oberthür, 1893	W. China	
sp. 1	Tibet	
<i>pica</i> -group		
<i>aurelia</i> Oberthür, 1923	W. China	

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>lucia</i> Oberthür, 1923	W. China	
<i>pica</i> Wileman, 1910	Taiwan	
<i>trimacula</i> Matsumura, 1927	Taiwan	
<i>wangi</i> Owada, 1992	Taiwan	
<i>glacialis</i> -group		transferral to a new genus
<i>ardjuna</i> Roepke, 1936	C. Java	
<i>glacialis</i> (Moore, 1872) ⁶	N. India	
<i>immaculata</i> -group		transferral to a new genus
<i>immaculata</i> Leech, 1898	W. China	
<i>Achelura</i> Kirby, 1892		
<i>bifasciata</i> -group		
<i>bani</i> Owada & Horie, 1999	Myanmar	
<i>bifasciata</i> (Hope, 1841)	N.E. India (Assam)	
<i>hai</i> Owada, 1996	N. Vietnam	
<i>maymyoana</i> Owada, 1999	Myanmar	
<i>sanguifasciata</i> Horie, 1994	Taiwan	
<i>yunnanensis</i> Horie & Xue, 1999	W. China	
<i>javana</i> -group		
<i>javana</i> Aurivillius, 1894	Java	
sp. 1	Indonesia (Bali)	
<i>hemileuca</i> -group		
<i>hemileuca</i> (Rothschild, 1904)	Papua New Guinea	
<i>simplex</i> Jordan, 1925	Papua New Guinea	
<i>Boradia</i> Moore, 1879		
<i>carneola</i> Moore, 1879	N. India	
<i>Neoherpa</i> Tremewan, 1973		
<i>venosa</i> -group		
<i>luteola</i> (Leech, 1898)	W. China	
<i>sinica</i> (Oberthür, 1891)		
stat. & sp. rev. ⁸		
<i>ochracea</i> (Leech, 1898)	W. China	
<i>venosa</i> (Walker, 1854)	N. E. India (Silhet)	
<i>eleonora</i> -group		
<i>eleonora</i> (Oberthür, 1923)	W. China	
<i>subhyalina</i> -group		
<i>primulina</i> (Elwes, 1890)	N. India	
<i>subhyalina</i> (Moore, 1879)	N. India	
<i>Panherpina</i> Bryk, 1936		
<i>basiflava</i> (Oberthür, 1891)	W. China	
<i>Eucormopsis</i> Jordan, 1907		
<i>lampra</i> Jordan, 1907	Java	
<i>Cryptophysophilus</i> Hering, 1922		
<i>bicoloratus</i> (Semper, 1898)	Mindanao	
sp. 1	Philippines (Luzon)	
sp. 2	Philippines (Luzon)	
sp. 3	Philippines (Mindoro)	
<i>Heterusinula</i> Bryk, 1936		
<i>dichroa</i> (Jordan, 1907)	N.E. India (Assam)	
<i>Docleomorpha</i> Hering, 1922		
<i>boholica</i> (Semper, 1898)	Philippines (Bohol)	
sp. 1	Philippines (Luzon)	
<i>Anarbudas</i> Jordan, 1907		
<i>insignis</i> -group		
<i>insignis</i> (Jordan, 1907)	China (Hainan)	
<i>bipartita</i> -group		transferral to a new genus
<i>aequalis</i> (Jordan, 1907)	Malaysia (Malakka)	
<i>bipartita</i> (Walker, 1864)	Borneo	
sp. 1	Borneo	
sp. 2	Sumatra	
<i>Corma</i> Walker, 1864		
<i>maculata</i> -group		
<i>maculata</i> Hampson, 1892	N.E. India (Assam)	
<i>laranda</i> Druce, 1896 stat. et sp. rev. ⁹	China	
sp. 1	Bangladesh	
<i>fragilis</i> -group		

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>fragilis</i> (Walker, 1862)	Borneo	
<i>zelica</i> (Doubleday, 1847)	N.E. India (Assam)	
<i>zenotia</i> -group		
<i>zenotia</i> (Doubleday, 1847)	N.E. India (Assam)	
<i>tamsi</i> Lemée, 1950	Vietnam	
<i>Rhodopsona</i> Jordan, [1907]		
<i>costata</i> -group		
<i>costata</i> (Walker, 1854)	E. China	
<i>bocki</i> (Swinhoe, 1905)	W. China	
<i>rubiginosa</i> -group		
<i>rubiginosa</i> (Leech, 1898)	W. China	
<i>jordani</i> -group		
<i>jordani</i> Oberthür, 1910	W. China	
<i>reverdini</i> -group		
<i>reverdini</i> Oberthür, 1910	W. China	
<i>marginata</i> -group		
<i>marginata</i> (Wileman, 1910)	Taiwan	
<i>rutila</i> Jordan, 1910	Taiwan	
<i>matsumotoi</i> -group		
<i>matsumotoi</i> Owada & Horie, 1999	S. China	
<i>Cyclosia</i> Hübner, [1820]		
<i>panthona</i> -group		
<i>panthona</i> (Stoll, [1780])	Hongkong	
<i>nivipetens</i> Walker, 1863	Sumatra	
<i>thecloides</i> Walker, 1862	Sarawak	
<i>unicolor</i> Hampson, 1919[1920]	Borneo	
<i>papilionaris</i> -group		
<i>papilionaris</i> (Drury, 1773)	S. China	
<i>latipennis</i> Hampson, 1891	S. India (Nilgiris)	
<i>chartacea</i> -group		
<i>chartacea</i> (Swinhoe, 1892)	Philippines (Luzon)	
<i>philippinensis</i> Draeseke, 1924	Philippines (Luzon)	
<i>spargens</i> -groups		
<i>pseudospargens</i> Hering, 1922	Philippines (Mindanao)	
<i>spargens</i> Walker, 1864	Sulawesi	
<i>tamara</i> Hering, 1922	Sulawesi	
<i>macularia</i> -group		
<i>macularia</i> (Guérin-Méneville, 1843)	Malaysia	
<i>perakensis</i> Hering, 1922	Malaysia (Malakka)	
<i>sordida</i> (Walker, 1862)	Borneo	
<i>imitans</i> -group		
<i>danaides</i> Walker, 1864	Sumatra	
<i>distanti</i> Druce, 1891	Malaysia (Malakka)	
<i>imitans</i> (Butler, 1881)	N. India	
<i>inornata</i> (Walker, 1864)	Borneo	
<i>curiosa</i> -group		
<i>curiosa</i> Swinhoe, 1900	Java	
<i>parantica</i> Holloway, 1982	Malaysia	
<i>pagenstecheri</i> (Grünberg, 1908)	Philippines (Palawan)	
<i>midama</i> -group		
<i>midama</i> (Herrich-Schäffer, 1853) ¹⁰	Thailand	
<i>pieridoides</i> -group		
<i>pieridoides</i> (Herrich-Schäffer, 1853)	Java	
<i>pieroides</i> -group		
<i>pieroides</i> Walker, 1862	Borneo	
<i>inclusus</i> -group		
<i>inclusus</i> Walker, 1864	Java	
<i>inclusoides</i> Hering, 1922	Sumatra	
<i>hecabe</i> Jordan, 1907	Malaysia (Penang)	
<i>eucharia</i> -group		
<i>eucharia</i> Jordan, 1907	Malaysia (Penang)	
<i>electra</i> -group		
<i>electra</i> (Swinhoe, 1905)	N. Borneo	
<i>notabilis</i> -group		transferral to a new genus
<i>notabilis</i> Kishida & Endo, 1999	China	

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>Arbudas</i> Moore, 1879		
<i>bicolor</i> -group		
<i>bicolor</i> Moore, 1879	N. India	
sp. 1	N. Vietnam	
<i>melanoleuca</i> -group		
<i>melanoleuca</i> Tarmann, 1992	Vietnam	
<i>submacula</i> -group		
<i>funerea</i> Jordan, 1907	China (Hainan)	
<i>rubricollum</i> (Alberti, 1954)	S. China	
<i>submacula</i> (Wileman, 1910)	Taiwan	
<i>tobaensis</i> (Tarmann, 1992)	Sumatra	
sp. 1	Taiwan	
sp. 2	India	
<i>leno</i> -group		
<i>leno</i> Swinhoe, 1900	Taiwan	
<i>truncatus</i> -group		
<i>truncatus</i> Jordan, 1907	Myanmar	
<i>Eumorphiopais</i> Hering, 1922		
<i>quadriplaga</i> -group		
<i>quadriplaga</i> Hering, 1922	Borneo	
<i>iris</i> Tarmann, 1992	Sumatra	
<i>leis</i> -group		
<i>leis</i> (Swinhoe, 1894)	N.E. India (Assam)	
<i>Heteropanula</i> Tarmann, 1992		
<i>flavimacula</i> (Hampson, 1892)	Myanmar	
<i>Pseudarbudas</i> Tarmann, 1992		
<i>ochrea</i> (Elwes, 1890)	N. India	
sp. 1	Vietnam	
<i>Hemiscia</i> Jordan, 1907		
<i>meekei</i> -group		
<i>meekei</i> (Rothschild, 1896)	Papua New Guinea	
<i>xenia</i> Hering, 1922 stat. nov. ¹¹	Halmaheira	
<i>parthenia</i> Jordan, 1930	Papua New Guinea	
<i>albivitta</i> -group		transferral to a new genus
<i>albivitta</i> (Rothschild, 1899)	Papua New Guinea	
'Luzon'-group		
sp. 1	Philippines (Luzon)	
<i>Pidorus</i> Walker, 1854		
<i>glaucopis</i> -group		
<i>atratus</i> Butler, 1877	Taiwan	
<i>glaucopis</i> (Drury, 1773)	N. India	
sp. 1	Malaysia	
<i>cyrtus</i> -group		
<i>cyrtus</i> Jordan, 1907	China (Hainan)	
sp. 1	Hongkong	
sp. 2	Tibet	
<i>circinata</i> -group		
<i>circinata</i> (Herrich-Schäffer, 1854)	N. India	
<i>yayoiiae</i> Owada & Horie, 2002	China	
<i>culoti</i> -group		
<i>culoti</i> Oberthür, 1910	W. China	
<i>dubernardi</i> Oberthür, 1910	W. China (Tse-ku)	
<i>corculum</i> -group		transferral to a new genus
<i>corculum</i> (Butler, 1879)	Java	
<i>miles</i> -group		transferral to a new genus
<i>miles</i> (Butler, 1881)	Sikkim	
<i>gemina</i> -group		transferral to a new genus
<i>gemina</i> (Walker, 1854)	S. China	
<i>bifasciatus</i> -group		transferral to a new genus
<i>bifasciatus</i> (Walker, 1862)	Borneo	
<i>latifasciatus</i> Talbot, 1929	Sumatra	
<i>chalybeatus</i> -group		transferral to a new genus
<i>chalybeatus</i> Joicy & Talbot, 1922	Papua New Guinea	
<i>splendens</i> -group		transferral to a new genus
<i>splendens</i> Jordan, 1907	Borneo	

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>hilaris</i> Jordan, 1907	Borneo	
<i>constrictus</i> -group		transferral to <i>Retina</i>
<i>constrictus</i> Walker, 1854	Thailand	
<i>circe</i> -group		
<i>circe</i> (Herrich-Schäffer, 1853)	N.E. India (Assam)	
<i>albifascia</i> (Moore, 1879)	N.E. India (Assam)	
sp. 1	N.E. India (Assam)	
<i>fasciatus</i> -group		transferral to a new genus
<i>fasciatus</i> Leech, 1898		
sp. & nom. rev. ¹²	W. China	
<i>ochrolophus</i> -group		transferral to a new genus
<i>ochrolophus</i> Mell, 1922	S. China	
<i>Caprima</i> Walker, [1865]		
<i>mutilata</i> -group		
<i>aurantiaca</i> Rothschild, 1899	Papua New Guinea (Lusiaden)	
<i>cincta</i> (Rothschild & Jordan, 1905)	Papua New Guinea	
<i>dohertyi</i> Rothschild, 1899	Papua New Guinea	
<i>mutilata</i> Walker, 1864	Papua New Guinea (Mysol)	
<i>necopina</i> Jordan, 1925	Papua New Guinea (New Hannover)	
<i>obliqua</i> Rothschild, 1899	Papua New Guinea	
<i>selenis</i> Jordan, 1925	Papua New Guinea	
<i>albifrons</i> -group		
<i>albifrons</i> Rothschild, 1899	Papua New Guinea (Bismarck Is.)	
<i>gelida</i> -group		
<i>cleora</i> Jordan, 1925	Papua New Guinea	
<i>gelida</i> Walker, 1864	Papua New Guinea	
<i>plagiata</i> Jordan, 1912	Papua New Guinea	
<i>chrysosoma</i> -group		transferral to a new genus
<i>chrysosoma</i> Prout, 1918	Indonesia (Aru Island)	
<i>Herpolasia</i> Rothschild & Jordan, 1905		
<i>augarra</i> -group		
<i>augarra</i> Rothschild & Jordan, 1905	Papua New Guinea	
<i>albomedia</i> -group		
<i>albomedia</i> (Rothschild, 1897)	Papua New Guinea	
<i>Clematoessa</i> Jordan, 1915		
<i>xuthomelas</i> -group		
<i>ledouxi</i> Hering, 1922	Papua New Guinea (Etappenberg)	
<i>xuthomelas</i> Jordan, 1915	Irian Jaya	
<i>virgata</i> -group		
<i>virgata</i> Joicy & Talbot, 1922	Papua New Guinea	
<i>Hemichrysoptera</i> Roepke, 1943		
<i>celebensis</i> Roepke, 1943	Sulawesi	
sp. 1	Sulawesi	
<i>Sciodoclea</i> Jordan, 1907		
<i>modesta</i> Jordan, 1907	Moluccas	
<i>Papuaphlebohecta</i> Yen, gen. nov.		
<i>bicolora</i> sp. nov. ¹³	Papua New Guinea	
<i>Hadrionella</i> Jordan, 1925		
<i>spectabilis</i> -group		
<i>spectabilis</i> (Rothschild, 1899)	Papua New Guinea	
<i>ludia</i> -group		
<i>ludia</i> Jordan, 1926	Papua New Guinea (New Ireland)	
<i>Thaumastophleps</i> Jordan, 1907		
<i>expansa</i> (Walker, [1865])	Irian Jaya	
<i>Cyanidia</i> Jordan, 1925		
<i>thaumasta</i> (Jordan, 1907)	Irian Jaya	
<i>Isocrambia</i> Jordan, 1907		
<i>melaleuca</i> (Rothschild & Jordan, 1905)	Papua New Guinea	
<i>apicalis</i> Jordan, 1907	Papua New Guinea	
<i>lutea</i> Jordan, 1907	Papua New Guinea	
<i>tricolor</i> (Rothschild & Jordan, 1905)	Papua New Guinea	
<i>Phlebohecta</i> Hampson, [1893]		
<i>fuscescens</i> -group		
<i>fuscescens</i> (Moore, 1879)	Sikkim	
<i>lithosina</i> -group		

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>lithosina</i> (Felder & Felder, 1874)	Borneo	
<i>jordani</i> -group		
<i>jordani</i> (West, 1932)	Philippines (Lanao)	
<i>lypusa</i> -group		transferral to a new genus
<i>lypusa</i> Jordan, 1907	Borneo	
<i>viduata</i> Jordan, 1912	Indonesia (Sintang)	
<i>Prosopandrophila</i> Hering, 1922		
<i>distincta</i> -group		
<i>distincta</i> (Guérin-Méneville, 1843)	Malaysia (Malakka)	
<i>oenone</i> (Butler, 1883) ¹⁴	Indonesia (Nias Island)	<i>Prosopandrophila distincta oenone</i> (Butler, 1883) comb. nov.
<i>xanthina</i> (Jordan, 1907) stat. nov. ¹⁴	Cambodia	
<i>yoshimotoi</i> (Kishida & Endo, 1999)	Philippines (Palawan)	
<i>mirifica</i> -group		transferral to a new genus
<i>mirifica</i> (Swinhoe, 1903)	Thailand	
<i>Trypanophora</i> Kollar		
<i>semihyalina</i> -group		
<i>anchora</i> Druce, 1891	Sumatra	
<i>australis</i> Jordan, 1907	S. India	
<i>elliptica</i> Jordan, 1907	Malaysia (Alor)	
<i>flavalis</i> Hampson, 1892	Myanmar	
<i>hosemanni</i> Hering, 1922	N.E. India (Darjeeling)	
<i>javanica</i> Snellen, 1902	Java	
<i>semihyalina</i> Kollar, [1844]	N.W. India (Kashmir)	
<i>trapobange</i> Walker, 1854	Sri Lanka	
<i>deligata</i> -group		
<i>deligata</i> Jordan, 1907	Philippines (Mindoro)	
<i>producens</i> -group		transferral to a new genus
<i>producens</i> (Walker, 1862)	Sumatra	
<i>dissimilis</i> -group ¹⁵		
<i>dissimilis</i> Snellen, [1902]1903	Java	
<i>Amesia</i> Duncan [& Westwood], 1841		
<i>sanguiflua</i> -group		
<i>sanguiflua</i> (Drury, 1773)	N. India	
<i>aliris</i> -group		
<i>aliris</i> (Doubleday, 1847)	N. India	
<i>namouna</i> (Doubleday, 1847)	N. India	
<i>apoensis</i> -group		
<i>apoensis</i> Kishida & Horie, 1989	Philippines (Mindanao)	
<i>Pseudoscaptosyle</i> Hering		
<i>circumdata</i> Walker, [1865]	N. India	
<i>Barbaroscia</i> Hering, 1922		
<i>amabilis</i> Jordan, 1907	N. Vietnam	
<i>Erasmiphlebohecta</i> Strand, 1916		
<i>picturata</i> (Wileman, 1910)	Taiwan	
<i>Chalcophaedra</i> Jordan, 1907		
<i>zuleika</i> (Doubleday, 1847)	N.E. India (Silhet)	
sp. 1	S. Vietnam	
<i>Erasmia</i> Hope, 1841		
<i>pulchella</i> Hope, 1841	N.E. India (Assam)	
<i>Eucorma</i> Jordan, 1907		
<i>euphaena</i> Jordan, 1907	Sulawesi	
<i>intercisa</i> (Walker, 1854)	Java	
<i>obliquaria</i> (Fabricius, 1787)	Thailand	
<i>Opisoplatia</i> Jordan, 1907		
<i>grandis</i> Jordan, 1907	N. Borneo	
<i>Eterusia</i> Hope, 1841		
<i>aedea</i> -group		
<i>aedea</i> (Linnaeus, 1763)	N. India	
<i>vitessa</i> -group		
<i>vitessa</i> Yen, 2003b	Philippines (Mindanao)	
<i>binotata</i> -group		
<i>binotata</i> Mell, 1922	S. China	
<i>tricolor</i> -group		
<i>nobuoi</i> Owada, 1996	Vietnam	

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>sublutea</i> Walker, 1852	N. India	
<i>taiwana</i> Wileman, 1911	Taiwan	
<i>tricolor</i> Hope, 1841	N.E. India (Assam)	
<i>watanabei</i> Inoue, 1982	Japan	
<i>subcyanea</i> -group		
<i>feminata</i> Kishida & Endo, 1999	Philippines (Mindanao)	
<i>joiceyi</i> Talbot, 1929	Sumatra	
<i>subcyanea</i> Walker, 1854	Borneo	
<i>risa</i> -group		
<i>angustipennis</i> (Röber, 1897)	Java	
<i>risa</i> (Doubleday, 1844)	Borneo	
sp. 1	Philippines (Palawan)	
<i>raja</i> -group		transferral to a new genus
<i>raja</i> Moore, 1859	Sikkim	
<i>repleta</i> -group		transferral to a new genus
<i>repleta</i> Walker, 1864	Thailand	
<i>Soritia</i> Walker, 1854		
<i>pulchella</i> -group		
<i>proprimarginata</i> (Prout, 1918)	E. China	
<i>pulchella</i> (Kollar, 1844) (s.l.)	N. India	
<i>strandi</i> Kishida, 1995	Taiwan	
<i>major</i> -group		
<i>major</i> (Jordan, 1907)	Vietnam	
<i>zelotypia</i> Hering, 1922	Malaysia	
<i>terioides</i> (Mell, 1922) ¹⁶	W. China	
<i>elizabetha</i> -group		
<i>azurea</i> Yen, 2003c	S. Taiwan	
<i>choui</i> Yen & Yang, 1998	S. Taiwan	
<i>elizabetha</i> (Walker, 1854)	E. China	
' <i>proprimarginata</i> ' <i>sensu</i> Endo & Kishida, 1999	Vietnam	
<i>shahama</i> -group		
<i>lacreuzei</i> (Oberthür, 1910) ¹⁷	W. China	
<i>lydia</i> Oberthür, 1923	W. China	
<i>shahama</i> (Moore, 1865)	N. India	
<i>costimacula</i> -group		
<i>costimacula</i> Aurivillius, 1894	Java	
<i>semiflava</i> (Talbot & Joicy, 1922) ¹⁸	W. Sumatra	
<i>malaccensis</i> -group		
' <i>costimacula</i> ' <i>malaccensis</i> (Jordan, 1907)	Malaysia (Perak)	
<i>bicolor</i> -group		transferral to a new genus
<i>bicolor</i> (Moore, 1884) ¹⁹	N. India	
<i>lata</i> (Jordan, 1907) stat. nov. ²⁰	Vietnam	
<i>moerens</i> -group		transferral to a new genus
<i>moerens</i> (Oberthür, 1910)	China (Sichuan)	
<i>sevastopuloi</i> -group		transferral to a new genus
<i>sevastopuloi</i> Tremewan, 1959	N. India	
<i>Chalcosia</i> Hübner, [1819]		
<i>pectinicornis</i> -group ²¹		
<i>affinis</i> (Guérin-Méneville, 1843)	S. India	
<i>diana</i> Butler, 1877	Taiwan	
<i>idaeoides</i> Herrich-Schäffer, 1853	N. India	
<i>nympha</i> Moore, 1878	China (Hainan)	
<i>pectinicornis</i> (Linnaeus, 1758)	China (Guangdong)	
<i>phalaenaria</i> (Guérin-Méneville, 1843)	Java	
<i>pretiosa</i> -group		
<i>pretiosa</i> Walker, 1864	Sri Lanka	
<i>venosa</i> Walker, 1854	Sri Lanka	
<i>nyctemeroides</i> -group		
<i>flavicollis</i> Jordan, 1907	Indonesia (Flores Islands)	
<i>nyctemeroides</i> Semper, 1898	Philippines (Luzon)	
<i>zehma</i> -group		transferral to a new genus
<i>zehma</i> (Herrich-Schäffer, 1853)	W. Malaysia	
sp. 1	Philippines (Palawan)	
<i>tibetana</i> -group		transferral to a new genus
<i>syfanica</i> (Oberthür, 1894)	China (Sichuan)	

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>tibetana</i> (Oberthür, 1894)	Tibet	
<i>alpherakyi</i> -group		transferral to a new genus
<i>alpherakyi</i> (Leech, 1898)	Tibet	
sp. 1	China (Sichuan)	
<i>Milleria</i> Herrich-Schäffer, 1853		
<i>adalifa</i> -group		
<i>adalifa</i> (Doubleday, 1847)	N. India	
<i>formosana</i> Matsumura, 1911	Japan (Iriomote Island)	
<i>litana</i> (Druce, 1896)	China (Hubei)	
<i>reticularis</i> Leech, 1898	China (Jiangxi)	
<i>hamiltoni</i> -group		transferral to a new genus
<i>dualis</i> Hering, 1941	N. India	
<i>hamiltoni</i> Swinhoe, 1891	N. India	
<i>rehfousi</i> -group		transferral to a new genus
<i>rehfousi</i> Oberthür, 1910	China (Sichuan)	
<i>okushimai</i> -group		transferral to a new genus
<i>okushimai</i> Owada & Horie, 1999	N. Vietnam	
<i>Eusphalera</i> Jordan, 1907		
<i>ligata</i> -group		
<i>aurantidiscus</i> Joicy & Talbot, 1922	Papua New Guinea	
<i>bicolora</i> Bethune-Baker, 1908	Papua New Guinea	
<i>buergesi</i> Hering, 1922	Papua New Guinea	
<i>cadmium</i> Joicey & Talbot, 1922	Papua New Guinea	
<i>casta</i> Jordan, 1915	Papua New Guinea	
<i>janthina</i> Joicy & Talbot, 1922	Indonesia (Seram Island)	
<i>jordani</i> Joicy & Talbot, 1922	Papua New Guinea	
<i>ligata</i> (Rothschild, 1903)	Papua New Guinea	
<i>lutescens</i> Bethune-Baker, 1908	Papua New Guinea	
<i>satisbonensis</i> Jordan, 1915	Papua New Guinea	
<i>semiflava</i> Rothschild, 1904	Papua New Guinea	
<i>splendens</i> Bethune-Baker, 1908	Papua New Guinea	
<i>bellula</i> -group		
<i>bellula</i> Kishida & Endo, 1999	Philippines (Mindanao)	
<i>picturata</i> -group		
<i>permitens</i> Jordan, 1925	Papua New Guinea	
<i>picturata</i> (Talbot & Joicey, 1922)	Papua New Guinea	
<i>venus</i> -group		
<i>nigrovata</i> Bethune-Baker, 1908	Papua New Guinea	
<i>uniens</i> Hulstaert, 1924	Papua New Guinea	
<i>venus</i> (Rothschild, 1915)	Papua New Guinea	
<i>regina</i> -group		
<i>hampsoni</i> (Holland, 1900)	Indonesia (Buru Island)	
<i>regina</i> (Rothschild, 1903)	Papua New Guinea	
<i>millionioides</i> Joicey & Talbot, 1922	Papua New Guinea	
<i>pratti</i> Bethune-Baker, 1908	Papua New Guinea	
sp. 1	Philippines (Luzon)	
<i>multicolor</i> -group		
<i>multicolor</i> Jordan, 1925	Papua New Guinea (New Ireland)	
<i>subnigra</i> -group		
<i>flavifrons</i> Jordan, 1912	Papua New Guinea	
<i>subnigra</i> (Bethune-Baker, 1911)	Papua New Guinea	
<i>Psaphis</i> Walker, 1854		
<i>camadeva</i> -group		
<i>camadeva</i> (Doubleday, 1847)	Borneo	
<i>euschemoides</i> (Moore, [1865])	N. India	
<i>scotais</i> Jordan, 1907	Borneo	
<i>gloriosus</i> -group		
<i>albivitta</i> (Rothschild, 1907)	Java	
<i>gloriosus</i> Rothschild, 1900	Sumatra	
<i>rothschildi</i> Joicey & Talbot, 1922	Sumatra	
<i>azurea</i> -group		
<i>azurea</i> Kishida & Endo, 1999	Philippines (Mindanao)	
<i>Pseudonyctemera</i> Piepers & Snellen, 1903		
<i>marginale</i> -group		
<i>marginale</i> (Snellen van Vollenhoven, 1863)	Java	
<i>dissimulata</i> -group		

APPENDIX 1 *Continued*

Taxa	Locality	Proposed taxonomic changes
<i>adalifoides</i> Schultz, 1925	Philippines (Palawan)	
<i>decipiens</i> Snellen, 1903	Java	
<i>dissimulata</i> (Walker, 1862)	Borneo	
<i>invaria</i> (Walker, 1864)	Sumatra	
<i>Pseudopidorus</i> Yen & Yang, 1997		
<i>fasciatus</i> (Felder & Felder, 1862)	W. China	
<i>Scotopais</i> Hering, 1922		
<i>tristis</i> (Mell, 1922)	W. China	
<i>Neochalcusia</i> Yen & Yang, 1997		
<i>remota</i> (Walker, 1862)	China (Sichuan)	
<i>Retina</i> Walker, 1854		
<i>rubrivitta</i> Walker, 1854	N. India	
<i>viripennis</i> (de Joannis, 1903)	Cambodia	
sp. 1	Sumatra	
<i>Gynautocera</i> Guérin-Méneville, 1831		
<i>papilionaris</i> -group		
<i>papilionaris</i> Guérin-Méneville, 1831	Bangladesh	
<i>fraterna</i> Moore, 1883	S. India	
<i>philomela</i> -group		
<i>philomela</i> Herrich-Schäffer, 1853	Java	
<i>rubriscutellata</i> -group		
<i>rubriscutellata</i> Hering, 1922	Taiwan	
<i>zera</i> Swinhoe, 1891	Vietnam	
<i>Histia</i> Hübner, [1820]		
<i>flabellicornis</i> -group		
<i>flabellicornis</i> (Fabricius, 1775)	N. India	
<i>libelluloides</i> (Herrich-Schäffer, 1853)	Java	
<i>dolens</i> -group		
<i>dolens</i> Druce, 1888	Sulawesi	
<i>nigridorsalis</i> Röber, 1925	Java	
<i>porphyropyga</i> (Hering, 1925)	Sulawesi	
<i>eurhodia</i> -group		
<i>eurhodia</i> Jordan, 1907	Philippines (Luzon)	
<i>Pompelon</i> Walker, 1854		
<i>marginata</i> (Guérin-Méneville, 1843)	Malaysia	
<i>Boradiopsis</i> Hering, 1922		
<i>grisea</i> (Semper, 1898)	Philippines (Luzon)	
<i>Aphantocephala</i> Felder, 1861		
<i>moluccarum</i> -group		
<i>moluccarum</i> Felder, 1861	Indonesia (Ambon Island)	
<i>centralis</i> Rothschild, 1898	Papua New Guinea	
<i>collaris</i> Jordan, 1926	New Hannover	
<i>solitaria</i> Jordan, 1907	Papua New Guinea	
<i>vicina</i> Jordan, 1925	Papua New Guinea	
<i>fragilis</i> -group		
<i>fragilis</i> Rothschild, 1899	Papua New Guinea	
<i>Docleopsis</i> Jordan, 1907		
<i>sulaensis</i> -group		
<i>sulaensis</i> Jordan, 1907	Indonesia (Sula Island)	
<i>fumigata</i> (Rothschild, 1899)	Sulawesi	
<i>stigma</i> -group		
<i>stigma</i> (Rothschild, 1899)	Sulawesi	
<i>dohertyi</i> -group		transferral to a new genus
<i>dohertyi</i> (Rothschild, 1899)	Sulawesi	
<i>zamboanga</i> -group		
<i>boradioides</i> (Semper, 1898)	Philippines (Luzon)	
<i>zamboanga</i> (Semper, 1898)	Philippines (Mindanao)	
<i>Allocaprima</i> Hering, 1922		
<i>duganga</i> (Semper, 1898) comb. nov. ²²	Philippines (Mindanao)	
<i>Euxanthopyge</i> Hering, 1922		
<i>hexophthalma</i> -group		
<i>hexophthalma</i> Hering, 1922	Sulawesi	
<i>toxopeii</i> Roepke, 1943	Sulawesi	
<i>yazakii</i> -group		
<i>yazakii</i> (Kishida & Endo, 1999)	Sulawesi	

NOTES

¹This species has been referred to as *Artona hainana* Butler, 1876 by various authors (e.g. Tarmann, 1992b, Wang, 1999), while Tarmann, 1994 indicated that the Taiwanese population may represent an undescribed taxon.

²*Saliunca* is tentatively listed in Callizygaeninae when it was considered for the sampling of taxa. It was placed in Callizygaenini by Alberti (1954) but its systematic status was not discussed by Tarmann (1994) when he elevated Callizygaenini to subfamily status. Recently, Vári *et al.* (2002) listed the genus in Procridinae, without providing reasons.

³The 'type specimen' of *Doclea syntomoides* Walker (now *Cleoda syntomoides*), which is deposited in OXUM, does not agree with the description given by Walker. Walker stated that the specimen his description was based on was male, had a 'greenish forewing' and 'hair tufts on abdomen'. However, the 'type specimen' in OXUM is female, with an orange forewing and yellow head. Swinhoe (1892) illustrated a 'female' of this species, but his illustration was in fact based on a misidentification of a female *Docleopsis sulaensis* Jordan, 1907, which shares very similar wing patterns. Jordan (1907) provided the illustration of the 'male' and linked it to the 'female' of *C. syntomoides*. The drawing of the female is apparently based on the 'type specimen' in OXUM, while the male specimen, which was also collected from Malacca, is still preserved in BMNH. The characters of the male illustrated by Jordan seem to agree with Walker's description. However, we cannot be sure if the male specimen used by Jordan is just the 'true type' of *C. syntomoides* because Walker stated the specimen was derived from 'Saunders' collection'. No evidence attached to the male specimen in BMNH has shown that it was derived from that collection. Therefore, in the present study, we tentatively adopt Jordan's opinion, 'marrying' the two specimens and calling the species *Cleoda syntomoides*.

⁴The taxonomic histories of these two species are confusing. Originally, *C. altissima* Elwes, 1890 was described as a 'variety' of *Campylotes histrionicus* Westwood, 1840. Then it was regarded as a 'form' of *Histrionicus* by various authors, e.g. Hampson (1892), Jordan (1907), Hering (1922), and Bryk (1936). However, based on a mistaken identification of the type specimens, *Excelsa* Oberthür, 1896 was treated as a junior subjective synonym of *Altissima* by Yen (1996). Subsequently Wang (1999) brought *Altissima* back into *Histrionicus*; he appears not to have noticed the remarkable differences between them. In the present study we revive *Excelsa* as a valid species, distinct from *altissima* and *histrionicus* due to the differences in genital and abdominal structures.

⁵*Campylotes splendida* Elwes, 1890 (*Proc. Zool. Soc. London* 1890: 384, t.33, f.3, syntypes in BMNH, examined) was originally proposed as a 'variety' of *C. desgodinsi* (Oberthür, 1884) (*Etudes d'Entomologie* 9: 18, t.2, f.10, type in BMNH, examined). Having compared their genitalia, it is obvious that these two taxa are distinct species. *C. splendida* is probably more closely related to *C. burmanus* Hampson, 1919 because they both have bright red stripes and longer valvae.

⁶Owada & Horie (1999) proposed a new name, *Agalope butleri*, to replace *Agalope glacialis* Butler, which was thought to be homonymous with *Agalope glacialis* Moore. However, the present cladistic results do not support the opinion that these taxa are congeneric. Therefore *Agalope glacialis* Butler is retained.

⁷*Agalope livida* Moore, 1879 (*Proc. Zool. Soc. London*: 391, type in ZMHB, examined) was regarded as a 'form' of *Hyalina* (Kollar, 1844) since Kirby (1892: 57); this treatment was followed by Hering (1922) and Bryk (1936). The type material, however, reveals that *Livida* is not related to *Hyalina* but is conspecific with *Davidi* (Oberthür, 1884) (*Etudes d'Entomologie* 9: 19, t.1, f.2, originally placed in *Chalcosia*, type in BMNH, examined). Since *Livida* is senior, the well-known *Davidi* has to be treated as a new junior synonym.

⁸*Neoherpa sinica* (Oberthür, 1891) was originally described as a species, then Jordan (1907) and Hering (1922) treated it as a subspecies of *Neoherpa venosa* (Walker, 1854). The senior author examined numerous specimens, including the type, and found that *sinica* is smaller, and the colour of the wing is whiter than that of *venosa*. There are also differences in the genitalia; therefore we revalidate the status of *sinica*.

⁹*Corma laranda* Druce, 1896 (*Ann. & Mag. Nat. Hist.* (6) 18: 235, syntypes in BMNH, examined) is here revalidated and re-elevated to species level from a subspecies of *Corma maculata* Hampson, 1892 (*Fauna Brit. Ind., Moths* 1: 268, nr. 573, type not found in BMNH). The females of these two species are almost identical in wing pattern and genitalia, but the male genital characters reveal that they are distinct species with allopatric distribution. *C. laranda* is mainly distributed from central to south-western China, while *C. maculata* tends to be distributed from northern India to Tibet. It is still unknown whether they share a sympatric zone in northern Vietnam, Laos and Myanmar.

¹⁰The current taxonomic concept of *Cyclosia midama* (Herrich-Schäffer, 1853) (*Samml. Aussereurop. Schmett.* 1: wrapper, pl. 1, figs 5, 6, pl. 2, figs 7–10, originally placed in *Epyrgis*) contains 5–7 'subspecies' found in an area ranging from India through the Indochinese peninsula to the Sunda islands (Bryk, 1936; Endo & Kishida, 1999). These subspecies, however, may represent more than one species due to remarkable differences in wing shape, size and genital structure. The year and spelling of the nominotypical subspecies were often misquoted as '*Midamia* (Herrich-Schäffer, 1853)' (see Hering, 1922; Bryk 1836; Endo & Kishida, 1999). According to Fletcher & Nye (1982), both the names *Epyrgis* and *E. midama* were first published on the wrapper of plates 1–4. The corresponding text was published later, and on pages 7 and 57 the names were cited as '*Epyrgis* bd. *Midamia* bd.'. On page 78 the names were cited as fig. 7. Subsequently, both spellings of the specific name have been used. Thus the original spelling *Midama* has been retained.

¹¹Hering (1922) treated *Xenia*, originating from Halmaheira, as a subspecies of *Meeki* (Rothschild, 1897) from the Woodlark Islands of Papua New Guinea. Having compared the female genitalia, we believe that *Xenia* is a valid species, although the male has not been discovered. The infraspecific taxonomy of *Meeki* needs to be revised as there is no solid evidence to prove that all the subspecies are conspecific and congeneric.

¹²*Pidorus leechi* Jordan, 1907 (in Seitz, *Gross-schmett. Erde* 2: 11, t.2d) was proposed to replace *Pidorus fasciatus* Leech, 1898 (*Trans. Ent. Soc. London*: 339, types in BMNH, examined), which was considered to be a homonym of *Pidorus fasciatus* (Felder, 1862) (*Wien, Ent. Mon.* 6: 32, n. 38, originally placed in *Aglaope*, type in BMNH, examined). However, since Felder's *fasciatus* has been transferred to *Pseudopidorus* by Yen & Yang (1997), Jordan's replacement name *leechi* is no longer necessary. In the present study, Leech's *fasciatus* is revalidated with *leechi* as a new junior subjective synonym.

¹³During examination of the material in the 'pest Lepidoptera collection' in BMNH, the senior author found a pair of chalcosiine specimens representing a previously unknown taxon. The adults were reared from *Nothofagus grandis* Steen. (Nothofagaceae) from Papua New Guinea. As far as we know, this species does not belong to any of the presently known genera, so we have decided to erect a new genus to accommodate it (see Appendix 8). The species was included in the phylogenetic analysis to elucidate its phylogenetic affinities.

¹⁴*Eterusia xanthia* Jordan, 1907 was transferred to *Prosopandrophila* and treated as a subspecies of *distincta* (Guérin-Méneville, 1843) by Hering (1922), Bryk (1936) and Endo & Kishida (1999). The type material of *xanthia*, however, reveals clear morphological differences from all the other subspecies of *distincta*; we therefore re-elevate *xanthia* to specific rank in this study. We believe that *Oenone* (Butler, 1883) (*Chalcosia*), regarded as a valid species by Bryk (1936) and Endo & Kishida (1999), is very likely a subspecies of *distincta*.

¹⁵According to the original drawing made by Snellen, this species does not seem to belong to *Trypanophora*. However, we failed to locate the type specimen in Leiden and have not found any specimen which agrees with the original drawing and description. Therefore, this species was not brought into the phylogenetic analysis.

¹⁶Yen (2003a) stated that the type of *Mimascaptesyle terioides* Mell, 1922 (*Deutsch. Ent. Zeitschr.* 127, originally placed in *Eterusia*) 'is probably missing' because the specimen associated with the label of '*terioides*' appeared to be missing, and no record was found in the card index of ZMHB. When we re-examined the type material of Chalcosiinae in ZMHB, we found a 'type' specimen, which has a hand-written label by Mell. It reads '*Eterusia citronella* sp. N., 17–9. 14, Kua Ho'. Apparently the name has never been published, although the morphology, date and locality of the specimen agree with the original description by Mell. A small label in Hering's blurred handwriting, reads '*Mimascaptesyle* n.g.', also corroborating that this specimen is the type of *terioides*. This species resembles *Soritia major* (Jordan, 1907) but is smaller in size. The relationship between them requires further study.

¹⁷*Eterusia lacruzei* Oberthür, 1910 was recently placed in *Soritia* by Yen (2003a) since the male genitalia reveals a close affinity with the *Soritia elizabethae* species-complex (also see Yen, 2003c).

¹⁸*Eterusia semiflava* Talbot & Joicey 1922, originates from Sumatra. It was ignored by Bryk (1936) and Endo & Kishida (1999). The morphology of wing patterns and genitalia of this species suggests an affinity with the *Soritia costimacula* species-complex (Yen, 2003a).

¹⁹Having examined the type material of both *Soritia viridibasalis* (Dudgeon, 1906) (*J. Bombay Nat. Hist. Soc.*: 339, type in BMNH) and *Soritia nigribasalis* Hampson, 1892 (*Fauna Brit. Ind., Moths* 1: 253, nr. 528, type in BMNH), we have come to the conclusion that they are synonymous and are the male of *Soritia bicolor* (Moore, 1884). In addition, in Bryk (1936: 203), the year of original description of *viridibasalis* was misquoted as 1905, and the original generic placement of this species was also mis-cited as *Eterusia*.

²⁰The genitalia of the type material and recent collection of *Soritia bicolor* (Moore, 1884) (*Trans. Ent. Soc. London*: 955, type in BMNH, examined) does not confirm that *S. b. lata* (Jordan, 1907) (in Seitz, *Gross-schmett. Erde* 10: 32, t.6b, type in BMNH) from northern Vietnam is its subspecies. We have treated them as distinct species because of their prominent genitalic differences and sympatric distribution.

²¹The species concepts in this complex are provisional. At present it is difficult to determine how many distinct species can be recognized based on adult morphological characters. Endo & Kishida (1999), following the viewpoint of Hering (1922), considered that *auxo* (Linnaeus, 1767) (*Sphinx*) is valid, with two subspecies *albata* Moore, 1879 and *campa* Jordan, 1907 from Nepal and Vietnam, respectively. Since Honey & Scoble (2001) have stated that *auxo* is a junior synonym of *pectinicornis* (Linnaeus, 1758) (*Sphinx*), we have not included this species in the present checklist. As to the taxonomic status of *albata* and *campa*, the question can only be resolved by a complete cladistic study of all members of the taxa concerned.

²²Based on the specimens currently obtained from the Philippines and examined in the Meyrick Collection, BMNH, *Allocastrima tricoloratus* (Semper, 1898) (*Schmett. Philipp.-Ins., Heteroc.* 2: 431, n. 115, originally placed in *Pidorus*, holotype in SNG, examined) has proven to be the female and a new synonym of *Docleopsis duganga* (Semper, 1898) (*Schmett. Philipp.-Ins., Heteroc.* 2: 430, t.53, f.8, originally in *Doclea*, holotype in SNG, examined). *Allocastrima* is considered to be the valid generic name of this species as *duganga* is not monophyletic with other species of *Docleopsis*. The page number of the original description of *duganga* precedes that of *tricoloratus* so *duganga* deserves nomenclatural priority.

APPENDIX 2

CHARACTERS USED IN THE CLADISTIC ANALYSIS

ADULT HEAD

General features of cranium (Figs 7, 11–13)

1. *Scales covering frontoclypeus (male)*: smooth (0); short hair-like (1); long hair-like (2).
2. *Scales covering frontoclypeus (female)*: smooth (0); short hair-like (1); long hair-like (1).
3. *Height/width of frontoclypeus (frontal view) (male)*: <1 (0); = 1 (1); 1.5 (2); = 2 (3); 2.5 (4).
4. *Height/width of frontoclypeus (frontal view) (female)*: <1 (0); = 1 (1); 1.5 (2); = 2 (3); 2.5 (4).
5. *Upper portion of frontoclypeus (frontal view) (male)*: truncate (0); convex (1); elevated (2); triangular (3); projected (4).
6. *Upper portion of frontoclypeus (frontal view) (female)*: truncate (0); convex (1); elevated (2); triangular (3); projected (4).
7. *Lateral margin of frontoclypeus in male*: parallel (0); attenuated towards bottom (1); attenuated towards top (2).
8. *Lateral margin of frontoclypeus in female*: parallel (0); attenuated towards bottom (1); attenuated towards top (2).
9. *Lower margin of frontoclypeus (frontal view) in male*: convex (0); truncate (1); emarginated (2); projected (3).
10. *Lower margin of frontoclypeus (frontal view) in female*: convex (0); truncate (1); emarginated (2).
11. *Lower margin of frontoclypeus in male*: above subgena (0); the same as subgena (1); lower than subgena (2).
12. *Lower margin of frontoclypeus in female*: above subgena (0); the same as subgena (1); lower than subgena (2).
13. *Anterior margin of frons (dorsal view) in male*: convex (0); truncate (1); campanulate (2); emarginated (3).
14. *Anterior margin of frons (dorsal view) in female*: convex (0); truncate (1); campanulate (2); emarginated (3).
15. *Frons (dorsal view) in male*: caudad to frontal margin of eyes (0); at the same plain as frontal margin of eyes (1); slightly exceeding eyes (2); exceeding, W : L=3 : 1 (3); W : L=2 : 1 (4); W : L=1.5 : 1 (5); W : L=1 : 1 (6).
16. *Frons (dorsal view) in female*: at the same plane as frontal margin of eyes (0); slightly exceeding eyes (1); exceeding, W : L=3 : 1 (2); W : L=2 : 1 (3); W : L=1.5 : 1 (4); W : L=1 : 1 (5).
17. *w/d.f. ratio of upper portion of frontoclypeus (lateral view) in male*: >5 (0); about 5 (1); 4 (2); 3 (3); 2.5 (4); 2 (5); 1.5 (6); 1 (7).
18. *w/d.f. ratio of upper portion of frontoclypeus (lateral view) in female*: >5 (0); about 5 (1); 4 (2); 3 (3); 2.5 (4); 2 (5); 1.5 (6); 1 (7).
19. *de /d.f. in male*: 5/1 (0); 3/1 (1); 2.5/1 (2); 2/1 (3); 1.5/1 (4); 1/1 (5); 1/1.5 (6).
20. *de /d.f. in female*: 5/1 (0); 3/1 (1); 2.5/1 (2); 2/1 (3); 1.5/1 (4); 1/1 (5); 1/1.5 (6); 1/2 (7).
21. *Anterodorsally elevated portion of frontoclypeus*: without lateral depressions (0); with prominent lateral depressions (1).
22. *Frontoclypeus*: compressed cephalocaudally (0); emarginated anteriorly (1).
23. *Vertex*: flattened, without verrucae-like projection (0); with a verruca-like projection medially (1); with conic projection medially (2).
24. *Vertex*: 'smooth-scaled' (0); hairy (1).
25. *Scales covering vertex*: flattened, arising from lateral sides towards anteromedial part (0); curved, arising from medioposterior margin towards anteromedial part (1).
26. *Scales covering vertex (male)*: black (0); blue (1); green (2); white (3); yellow (4); red (5).
27. *Scales covering vertex (female)*: black (0); blue (1); green (2); white (3); yellow (4); red (5).
28. *Subgena in male*: not prominent (0); prominent, lower than lower margin of eyes (1); higher than lower margin of eyes (2).
29. *Subgena in female*: not prominent (0); prominent, lower than lower margin of eyes (1); higher than lower margin of eyes (2).
30. *Length of postoccipt/diameter of compound eye (male)*: 1/5 (0); 1/4 (1); 1/3 (2); 1/2 (3); 1 (4).
31. *Length of postoccipt/diameter of compound eye (female)*: 1/5 (0); 1/4 (1); 1/3 (2); 1/2 (3); 1 (4).

Mouthparts and associated appendages (Fig. 13)

32. *Galeae*: fused (0); separate (1).
33. *Proboscis in male*: developed, length >> 4 × height of frontoclypeus (0); about 2.5 × height of frontoclypeus (1); about 1–1.5 × height of frontoclypeus (2); extremely short, concealed by labial palpus (3); reduced, only basal lobes visible (4); totally absent (5).
34. *Proboscis in female*: developed, length >> 4 × height of frontoclypeus (0); about 2.5 × height of frontoclypeus (1); about 1–1.5 × height of frontoclypeus (2); extremely short, concealed by labial palpus (3); reduced, only basal lobes visible (4); totally absent (5).
35. *Sensillae styloconica at distal region of proboscis*: sparse (0); long and developed (1).
36. *Maxillary palpus*: present, 2-segmented (0); only the basal segment remains (1).
37. *Labial palpus*: 3-segmented (0); 2-segmented (1); absent (2).
38. *Basal segment of labial palpus*: straight (0); arcuate (1); helmet-like (2); reniform (3).
39. *Basal segment of labial palpus*: compressed laterally (0); swelled laterally (1).
40. *Second segment of labial palpus*: equal to basal segment in length (0); about 1/2 of basal segment in length (1); less than 1/3 of basal segment in length (2).
41. *Second segment*: oblong (0); oblanceolate (1); oval (2).
42. *Terminal segment of labial palpus*: up-curved (0); straight (1); slightly curved along eye (2); downwards (3).
43. *Terminal segment of labial palpus*: acicular (0); oblanceolate (1); oval (2).
44. *Terminal segment of labial palpus*: longer than the 2nd segment (0); as long as the 2nd segment (1); shorter than 2nd segment (2).
45. *Terminal segment of labial palpus*: behind lower margin of frontoclypeus (0); slightly exceeding margin (1); extending beyond the margin (2).

46. *Pilifer*: present, long, with a lobe (0); present, short, without a lobe (1); rudimentary (2).

Sensory organs (Figs 14–16)

47. *Antennal bases*: located posteriorly on vertex (0); medially (1); anteriorly (2).
48. *Male flagellomeres*: inpectinate (0); biserrate (1); short-bipectinate (2); long-pectinate (3); quadripectinate (4).
49. *Female flagellomeres*: inpectinate (0); biserrate (1); short-bipectinate (2); long-bipectinate (3).
50. *Scaling on flagellomeres*: dense (0); sparse (1).
51. *Sensillae trichodea*: distributed mainly on rami (0); distributed mainly on flagellomeres (1).
52. *Sensillae trichodea on rami (male)*: longer than length of each flagellomere (0); extremely short (1).
53. *Rami of flagellomeres (male)*: fusiform (0); stilliform (1); plate-like (2).
54. *Rami of terminal segments (male)*: absent (0); present, much shorter than medial ones (1); as long as other segments (2); longer (3); longer and expended (4).
55. *Rami of terminal segments (female)*: absent (0); present, much shorter than medial ones (1); as long as other segments (2); longer (3); longer and expended (4).
56. *Lateral margin of flagellomeres*: not produced (0); ridged and slightly undulate at margin (1).
57. *Back bone of flagellomeres*: smooth (0); keeled near apex (1); cristate or keeled along the whole antennae (2).
58. *Female antennae*: without white patch near apex (0); with white patch near apex (1).
59. *Upper margin of compound eyes (lateral view)*: emarginated (0); depressed (1).
60. *Ocelli*: absent (0); present (1).
61. *Chaetosemata*: absent (0); simple, without clearly defined area posterodorsal to compound eye (1); located on a spherical area posterodorsal to antennal base (2); upper margin extending near to midline of vertex (3); upper margin extending to midline of vertex, lateroventral margin extending near to lower margin of compound eyes (4).
62. *Shape of chaetosemata*: oblong (0); orbicular (1); triangular (2); reniform (3); narrow oblique-reniform (4); broad oblique-reniform (5).
63. *Sensillae of chaetosemata*: loosely arranged (0); densely arranged (1).
64. *Chaetosemata*: without scales (0); with scales (1).
65. *Apex of scales on chaetosemata*: emarginated (0); deeply forked (1); rounded (2); acute (3).
66. *Outline of scales on chaetosemata*: ovate (0); oblong (1); linear (2); filiform (3).
67. *Scales on chaetosemata*: black (0); red (1); yellow (2); white (3).
70. *Patagia*: membranous (0); sclerotized, with a simple sclerite (1); blade-like (2); sclerotized, simple (3); strongly sclerotized, sac-like (4).
71. *Parapatagia*: membranous (0); simple, not sac-like (1); weakly sclerotized, sac-like (2); strongly sclerotized, sac-like (3).
72. *Patagia*: less developed than parapatagia (0); as developed as parapatagia (1); more developed than parapatagia (2).
73. *Parapatagia*: straight down to episternum (0); curved backward (1).
74. *Parapatagia*: without middle protuberance (0); protruded at middle (1); greatly swelling (2).
75. *Scales on patagia (male)*: black (0); blue (1); green (2); yellow (3); orange (4); red (5).
76. *Scales on patagia (female)*: black (0); blue (1); green (2); yellow (3); orange (4); red (5).
77. *Scales on parapatagia (male)*: black (0); blue (1); green (2); white (3); yellow (4); orange (5); red (6).
78. *Scales on parapatagia (female)*: black (0); blue (1); green (2); white (3); yellow (4); orange (5); red (6).
79. *Parapatagia, male*: without lateral dots (0); with lateral white dots (1).
80. *Parapatagia, female*: without lateral dots (0); with lateral white dots (2).
81. *Scales on patagia*: flattened (0); curved and bending down posteroventrally (1).
82. *Scales on parapatagia*: flattened (0); curved and bending down posteroventrally (1).
83. *Tegula*: extending to 1/2 of mesothorax (0); beyond mesothorax (1).
84. *Subtegula*: small (0); developed, arm-like (1).
85. *Tegula*: without apical spot (0); with apical spot (1).
86. *Anterior margin of mesoscutum*: truncate (0); concave (1).
87. *Mesoscutellum*: oblong (0); trapezoid or 'hamlet-like' (1); hexagonal (2).
88. *Metascutellum*: without bilateral spots (0); with two bilateral red spots (1).
89. *Euphragmata, fully developed*: absent (0); present (1).
90. *Epiphysis on foretibia*: present (0); absent (1).
91. *Foreleg*: length normal (0); reduced in length and tibial segments (1).
92. *Tibial spurs formula*: 0-2-4 (0); 0-2-2 (1); 0-0-0 (2).
93. *Sensillae trichodea beneath the 5th tarsomere of female*: absent (0); present (1).

Wing coupling device

94. *Female frenulum number*: none (0); one (1); two (2); three (3); four (4); five (5); six (6).

Wing venation (Figs 18–21)

95. *Veins (male)*: smooth or sparsely hairy (0); underside of tornus hairy (1).
96. *Cross veins of FW between C and Sc*: absent (0); present (1).
97. *FW: Sc separate from R1* (0); Sc connected to R1 at distal end (1); Sc connected to R1 before 1/3 of R1 (2).
98. *FW: R1 arising near base of cell* (0); R1 arising near middle of cell (1); R1 arising near posterior angle (2).

ADULT THORAX (EXCLUDING SCENT ORGAN)

Thoracic sclerites and appendages (Fig. 17)

68. *Crested scales in front of patagia*: black (0); blue (1); green (2); white (3); yellow (4); orange (5); red (6).
69. *Dorsonotal plate*: weakly sclerotized (0); strongly sclerotized (1).

99. *FW*: R1 and R2 separated (0); fused as R1 + 2 (1).
 100. *FW*: R2 and R3–R5 separated (0); R2 stalked with R3 + R4 (1).
 101. *FW*: R3, R4 and R5 separated (0); R3 + R4 close to R5 at base (1); R3 + R4 stalked with R5 (2); R3 + R4 fused and stalked with R5 (3).
 102. *FW*: R3, R4 and R5 separated (0); R3 separated from R4 + R5 (1); R3 stalked with R4 + R5 (2); R4 + R5 stalked near apex (3).
 103. *FW*: R veins separated from M1 (0); M1 close to R veins at base (1); M1 stalked with R3(4)–5 (2); M1 absent (3).
 104. *FW*: M2 and M3 separated (0); close at base (1); stalked (2); M2 + 3 stalked with CuA1 (3).
 105. *FW discal cell*: with medial stem sclerotized (0); with medial stem unsclerotized (1); with trace of medial stem visible (2).
 106. *FW cell*: without chorda (0); chorda present, forming by medial fork connecting to middle of ldc (1); fork connecting to M3 (2); fork present, but unsclerotized (3).
 107. *FW*: subcell 1 and 2 equal in length (0); subcell 1 longer than subcell 2 (1); subcell 1 shorter than subcell 2 (2).
 108. *FW, cross vein between CuP and 1A + 2A*: absent (0); present (1).
 109. *FW*: with developed 1A + 2A (0); medioposterior part of 1A + 2A reduced, basal stem connected to cell and 3A by cross veinlets (1).
 110. *FW 1A + 2A*: with basal fork (0); without basal fork (1).
 111. *HW*: Sc + R1 arising near posterior angle of cell (0); Sc + R1 free from Rs (1); Sc + R1 arising from base and connected to M1 near posterior angle of cell (2); Sc + R1 connected to M with a short cross veinlet (3).
 112. *HW, Rs and M1*: separated (0); stalked (1).
 113. *HW, M2 and M3*: separate (0); stalked (1).
 114. *HW, M1*: present (0); absent (1).
 115. *HW*: M3 present (0); M2 and M3 fused (1).
 116. *HW, medial stem of cell*: incomplete (0); complete (1).
 117. *HW*: subcell 1 and 2 equally long (0); subcell 1 longer than subcell 2 (1); subcell 1 shorter than subcell 2 (2).
 118. *HW, 1A + 2A*: present (0); absent (1).

Wing shape (Fig. 22)

119. *Wing shape*: not sexually dimorphic (0); sexually dimorphic (1).
 120. *Wing size*: not sexually dimorphic (0); sexually dimorphic (1).
 121. *FW base*: without modification (0); the area between C and Sc broadened (2).
 122. *FW apex*: rounded (0); acute (1).
 123. *FW termen*: not incised (0); slightly incised (1).
 124. *FW (male)*: type I (0); type II (1); type III (2); type IV (3); type V (4); type VI (5); type VII (6); type VIII (7); type IX (8).
 125. *FW (female)*: type I (0); type II (1); type III (2); type IV (3); type V (4); type VI (5); type VII (6); type VIII (7); type IX (8).
 126. *HW termen*: rounded (0); truncate between Sc + R1 to CuA1 (1).
 127. *HW*: without tail (0); Rs, M1–M3 forming a tail (1).
 128. *HW*: without elongation (0); Sc + R1, M1, M2 and M3 forming a short tail (2).
129. *HW, inner margin*: straight (0); with a protruded lobe between 1A + 2A and 3A (1).

Wing patterns (Figs 8, 22)

130. *Wing pattern*: not sexually dimorphic (0); sexually dimorphic (1).
 131. *FW, maculation*: upperside the same as undersides (0); upperside different from underside (1).
 132. *FW base (zone a)*: without colour patch (0); a white dot present on interradial plate (1).
 133. *FW base (zone a)*: without colour patch (0); a spotted colour patch present between C and Sc (1); colour patch between C and Sc more slender (2); colour patch broad (3).
 134. *FW base (zone a)*: without colour patch on 1a + 2a (0); colour patch between C and Sc extending to the base of 1a + 2a (1).
 135. *FW*: without transverse stripe on 1a + 2a (0); transverse stripe present from zone a to zone d (1); transverse stripe extending to zone h (2); transverse stripe extending to tornus (3).
 136. *FW*: without clearly defined zone b (0); zone b with one spot present on 1a + 2a (1); two spots present on c-sc and 1a + 2a (2); three small spots present on c-sc, discal and 1a + 2a (3); c-sc and 1a + 2a spots much larger than the discal one (4); zone b forming a continuous band (5); zone b forming a disjunctive band (6).
 137. *FW (male)*: without clearly defined zone b–d (0); outer margin of zone d defined, zone b–d not differentiated (1); zone b–d with radiate stripes on each cell (2); zone b–d with two defined longitudinal stripes (3); zone b–d with three defined longitudinal stripes (4); zone b–d with scattered spots (5).
 138. *FW (female)*: without clearly defined zone b–d (0); outer margin of zone d defined, zone b–d not differentiated (1); zone b–d with radiate stripes on each cell (2); zone b–d with two defined longitudinal stripes (3); zone b–d with three defined longitudinal stripes (4); zone b–d with scattered spots (5).
 139. *FW (male)*: without zone e–g differentiated (0); outer margin of zone e–g clearly defined (1); discal, cua2 and 1a + 2a patches present (2); five patches present on cu, discal, cua2, 1a + 2a and 3a cells (3); five patches forming a band (4); e–g zone separated into three oblique stripes (5).
 140. *FW (female)*: without zone e–g differentiated (0); outer margin of zone e–g clearly defined (1); discal, cua2 and 1a + 2a patches present (2); five patches present on cu, discal, cua2, 1a + 2a and 3a cells (3); five patches forming a band (4); e–g zone separated into three oblique stripes (5).
 141. *FW (male)*: without defined zone h (0); zone h narrow, arched at base of m3 (1); zone h broad, with five patches on sc, discal, cua1, cua2 and 1a + 2a cells (2); all patches on zone h forming a broad continuous band (3).
 142. *FW (female)*: without defined zone h (0); zone h narrow, arched at base of m3 (1); zone h broad, with five patches on sc, discal, cua1, cua2 and 1a + 2a cells (2); all patches on zone h forming a broad continuous band (3).

143. *FW (male)*: without defined zone i (0); zone i clearly defined, inner margin dentate (1); inner margin of zone i smooth (2).
144. *FW (female)*: without defined zone i (0); zone i clearly defined, inner margin dentate (1); inner margin of zone i smooth (2).
145. *FW*: without zone i band (0); zone i band present (1).
146. *FW (male)*: without r-m patches along zone j (0); r2-3 patches present (1); patches present on r2-3 and M3 (2); patches present on r2-m3 and m2-m3 (3); r2-m3 patches forming a continuous band (4); cua1, cua2 and 1a + 2a patches present (5).
147. *FW (female)*: without r-m patches along zone j (0); r2-3 patches present (1); patches present on r2-3 and m3 (2); patches present on r2-m3 and m2-m3 (3); r2-m3 patches forming a continuous band (4); cua1, cua2 and 1a + 2a patches present (5).
148. *FW zone j*: without lunar stripe (0); lunar stripe present on underside (1); lunar stripe present both on under and upper sides (2).
149. *FW zone i-j*: without oblique patch (0); with orange patch (1); with brownish red patch (2).
150. *FW*: without spot on discal end (0); spot on discal end present (1).
151. *FW*: underside without metallic blue crescentic patch (0); metallic blue crescentic patch present in zone i (1).
152. *HW*: without costal patch (0); costal patch present at middle of cell, obscure (1); costal patch present at middle of cell (2).
153. *HW (male)*: without clearly defined zone n (0); zone n confined near apex only (1); zone n ended at cua2 (2); zone n ended at 1a + 2a (3); zone n extended to zone m (4); zone n extended to inner margin (5); zone n extended to inner margin and occupying about 1/2 of HW area (6).
154. *HW (female)*: without clearly defined zone n (0); zone n confined near apex only (1); zone n ended at cua2 (2); zone n ended at 1a + 2a (3); zone n extended to zone m (4); zone n extended to inner margin (5); zone n extended to inner margin and occupying about 1/2 of HW area (6).
155. *Male costal area*: without transverse stripe (0); stripe present from wing base to apex (1); medial part of stripe extended to discal cell (2).
156. *HW (male)*: without clearly defined zone k (0); zone k confined to wing base (1); zone k extended from wing base to 1/2 of subcostal margin (2); zone k extended to inner margin (3); zone k broad, parallel to outer margin, about 1/3 of HW area (4); zone k broad, extended to tornus (5).
157. *HW (female)*: without clearly defined zone k (0); zone k confined to wing base (1); zone k extended from wing base to 1/2 of subcostal margin (2); zone k extended to inner margin (3); zone k broad, parallel to outer margin, about 1/3 of HW area (4); zone k broad, extended to tornus (5).
158. *HW (male)*: without large yellow area from zone k to m (0); a large yellow area ranging from zone k to m (1); zone n border extending to tornus (2); zone n border extending along inner margin to wing base (3).
159. *HW (female)*: without large yellow area from zone k to m (0); a large yellow area ranging from zone k to m (1); zone n border extending to tornus (2); zone n border extending along inner margin to wing base (3).
160. *HW (male)*: with 1a + 2a to inner margin concolorous with other part (0); yellow area present on underside only (1); yellow area present both on upper- and underside (2); green on upperside (3); blue on upperside (4).
161. *HW (female)*: with 1a + 2a to inner margin concolorous with other part (0); yellow area present on underside only (1); yellow area present both on upper and under sides (2).
162. *HW*: underside without metallic blue crescentic patch (0); metallic blue crescentic patch present on zone n (1).

Wing scales (excluding androconial scales) (Figs 23, 24)

163. *Surface*: without windows (0); with windows and internal reticulate lamellae (1); with windows but without reticulate lamellae (2).
164. *Sockets of scales*: repressed (0); semi-erect (1); erect (2).
165. *Scales*: arranged in multiple overlapping rows (0); not overlapping with each other (1).
166. *Scales on cells*: lamellar (0); spindle-like (1); piliform (2).
167. *Type I scale on FW*: distributed on the whole range (0); confined to zone f-I (1); only on veins (2); absent or indistinguishable from Type II (3).
168. *Type I scale on HW*: distributed on the whole range (0); confined to costal region (1); absent or indistinguishable from Type II (2).
169. *Apex of type I scales on FW*: deep 5-toothed backing (0); deep 4-toothed backing (1); deeply bifurcate (2); slightly concave (3); undulate, asymmetrical or truncate (4); rounded (5); convex (6); pointed (7).
170. *Apex of type II scales on FW*: deep 5-toothed backing (0); deep 4-toothed backing (1); slightly trifurcate (2); slightly concave (3); undulate, asymmetrical or truncate (4); rounded (5); convex (6); pointed (7).
171. *General outline of type I scales on FW*: filiform (0); oblong-lanceolate (1); oblong (2); orbicular (3); triangular (4).
172. *General outline of type II scales on FW*: filiform (0); oblong-lanceolate (1); oblong (2); tubinate (3); cordate-pyriform (4); triangular (5).
173. *Apex of type I scales on HW*: deep 5-toothed backing (0); deep 4-toothed backing (1); deeply trifurcate (2); slightly concave (3); rounded (4); convex (5); pointed (6).
174. *Apex of type II scales on HW*: deep 5-toothed backing (0); deep 4-toothed backing (1); deeply trifurcate (2); slightly concave (3); rounded (4); convex (5); pointed (6).

ADULT ABDOMEN

Pregenital abdominal segments 1-7 (Figs 25, 26)

175. *Abdomen*: without spinules on tergites (0); multi-rowed spinules present (1).
176. *Sternal apodeme of sternum A2*: rather short (0); slender (1); spatulate near apex (2); broad and compressed (3).
177. *Anterolateral process (= anterosternal syndesial process) of sternum A2*: absent (0); present, cornate (1); slender and narrow (2); sickle-like (3); short-auriculate (4); fin-like (5); long-auriculate (6).

178. *Anterotergal syndeses*: absent (0); a pair of subdorsal anterotergal syndeses present along front margin of tergum A2 (1); subdorsal and lateral syndeses present along front margin of tergum 2 (2); subdorsal and lateral syndeses located posterior to front margin of tergum A2 (3); subdorsal and lateral syndeses fused (4); syndeses on tergum A2 more sclerotized and protruded (5).
179. *Male abdominal tergites*: unicoloured along the whole abdomen (0); tergal area differentiated into anteromedial part and posterior annular wing (1); tergal area interrupted by a 'T' pattern (2); tergal area separated into two patches (3).
180. *Female abdominal tergites*: unicoloured along the whole abdomen (0); tergal area differentiated into anteromedial part and posterior annular wing (1); tergal area interrupted by a 'T' pattern (2); tergal area separated into two patches (3).
181. *Male abdominal tergites*: unicoloured along the whole abdomen (0); T1–T2 with distinct colour from the remaining segments (1).
182. *Female abdominal tergites*: unicoloured along the whole abdomen (0); T1–T2 with distinct colour from the remaining segments (1).
183. *Male abdomen*: without annular rings (0); annular rings on tergal area only (1); annular rings from tergal to pleural area (2); annular rings extending to sternal area (3); annular rings from pleural to sternal area (4); annular rings on sternal area only (5).
184. *Female abdomen*: without annular rings (0); annular rings on tergal area only (1); annular rings from tergal to pleural area (2); annular rings extending to sternal area (3); annular rings from pleural to sternal area (4); annular rings on sternal area only (5).
185. *Male abdomen*: without pleural dots (0); pleural dots present on A1–A7 (1).
186. *Female abdomen*: without pleural dots (0); pleural dots present on A1–A7 (1).
187. *Male abdomen*: without sternal dots (0); sternal dots present on A1–A7 (1).
188. *Female abdomen*: without sternal dots (0); sternal dots present on A1–A7 (1).
- The eighth abdominal segment* (Figs 27, 28)
189. *Valva*: exposed from sternite of eighth segment (0); partly exposed from eighth segment (1); concealed by 'normal' eighth segment (2); concealed by 'specialized' eighth segment (3).
190. *Tergite and sternite*: almost equal in length (excluding posterior projections) (0); sternite about 2/3 of tergite in length (1); sternite about 1/2 of tergite in length (2); sternite about 1/3 tergite shorter than sternite (3); tergite about 2/3 of sternite in length (4); tergite about 1/3 of sternite in length (5).
191. *Medial part of hind margin*: truncate (0); obtuse (1); retuse (2); concave (3); emarginated (4); V-shaped (5); U-shaped (6); single projection (7); two projections (8); multiple projections (9).
192. *Tergite*: without a complete elongated extension (0); with a complete, strongly sclerotized elongated portion extending posteriorly (1).
193. *Tergite*: without lateroposterior projections (0); a pair of short caudolateral projections present and extending ventroposteriorly (1); projections extending downwards along the pleural membrane, apical part bending anteriorly (2); projections extending posteriorly with apex bending downwards (3); projections arising from hind margin then immediately bending downwards (4); projections bending downwards and folding anteriorly into and beneath the tergite (5); *Chalcosia zehma*-type (6); *Chalcosia*-type (7); *Milleria okushimai*-type (8); *Pseudonyctemera*-type (9).
194. *Tergite*: without bilobed projections (0); a paired short bilobed projections present near middle of hind margin (1); bilobed projections as long as 1/6 of length of tergum (2); about 1/5 of length of tergum (3); about 1/4 of length of tergum (4); about 1/3 of length of tergum (5); about 2/3 of length of tergum (6).
195. *Tergal shape*: attenuated towards caudal end with truncate hind margin (0); dorsum of tergite rectangular without prominent incision (1); lateral margins incised near caudal end with a retuse hind margin (2); dorsum attenuated towards caudal end with a prominent incision at middle of hind margin (3); a paired auriculate process present besides middle projection of hind margin (4); lateral margin slightly incised near caudal end, hind margin truncate (5); hind margin emarginated, lateral margins incised near anterior margin (6); lateral margins with strong incision near middle and immediately attenuated towards a narrow caudal end (7).
196. *Hind margin of sternite*: obtuse (0); truncate (1); retuse (2); U-shaped (3); V-shaped (4); notched (5); W-shaped (6); deep W-shaped (7).
197. *Hind margin of sternite*: without sclerotized modification (0); with sclerotized bilateral short projections (1); bilateral projections folded interiorly (2); with developed bilateral arms (3).
198. *Hind margin of sternum*: without middle process (0); medial short process present (1); erect, horn-like medial process at middle (2); digital process (3); with two short processes (4); two short processes widely separated (5).
199. *Hind margin of sternite*: smooth (0); with single-rowed spinules at middle (1); with multi-rowed spinules at middle (2).
200. *Hind margin of sternal arms*: entire (0); toothed (1); short, serrate (2); larger and shorter serration mixed (3); densely serrate (4).
201. *Sternite*: complete without posterior extensions (0); lateral view of ventral part rectangular with lateral part rounded and swollen (1); ventral part narrowly rectangular with lateral part rounded and swollen (2); ventral part rectangular, lateral part not swollen (3); ventral part triangular, inner ridge present (4); ventral part triangular, separated from lateral arm (5); ventral part narrow and slender, separated from lateral arm (6); ventral part triangular, inner ridge present, forming a rectangular combination (7); ventral part rectangular, upper margin of inner ridge somewhat parallel with lower margin of lateral part (8); ventral part narrowly rectangular, inner ridge developed, lateral arms not separated from ventral part (9).

202. *Sternal arms*: short, narrow and cornate (0); short, broad and cornate (1); long, narrow, without modification along lateral margins (2); arm-like, caudal end pointed, medio-ventral portion separated with lateral arms (3); lateral arms slender from base till caudal end, pointed at caudal end (4); lateral arms slender, serrate at margin, medio-ventral portion not separated; (5) lateral arm digital (6); oblique-oval (7); broad, 'helmet'-like (8); lateral arms arched to be 'U'-shaped (9).
203. *Medial process of sternal arm*: absent (0); cornate, short (1); long, extending posteriorly (2); long, extending downwards (3).
204. *Sternite*: without subdivision (0); subdivided at base (1); subdivided into posteromedial and anterodorsal plates (2).
205. *Sternite*: without inner ridge (0); inner ridges present, sloping downwards (1); sloping nearly horizontally (2); sloping upwards (3); straight longitudinally (4).
206. *Surface of the 8th tergite*: scaled (0); smooth (1).
207. *Surface of the 8th sternite*: scaled (0); smooth (1).
208. *Hind margin of sternal arms*: smooth (0); sparsely setose (1); densely setose (2); densely spiny (3).

MALE GENITALIA (FIGS 29–39)

Uncus and subscaphium

209. *Uncus*: articulated with tegumen (0); fused medially (1); completely fused (2).
210. *Uncus*: without dorsal setae (0); with dense dorsal setae (1).
211. *Uncus*: with sensory setae along lateral margin (0); without sensory setae (1).
212. *Apex of uncus*: pointed (0); obtuse (1); emarginated (2); retuse (3); concave (4); bifurcate (5); sharply and deeply bifurcate (6).
213. *Apex of uncus-tegumen complex*: obtuse (0); slightly triangular with a rounded tip (1); rectangular with a rounded tip (2); rectangular with a emarginated tip (3); wide dorsally, with two cornate projections widely separated (4); similar to the former type but with longer uncus-tegumen complex and shallower emargination (5); bi-auriculate (6); uncus-tegumen very narrow, with an emarginated apex (7); similar to the preceding state, but with very shallow emargination (8); bilobed (9).
214. *Apex of uncus*: without sculptured structure (0); with a complex sculptured structure (1).
215. *Base of uncus*: not concealed by tegumen (0); concealed by dorsoposterior margin of tegumen (1).
216. *Uncus*: well sclerotized dorsoventrally (0); sclerotized dorsally (1); lateral margins sclerotized only (2); completely membranous (3).
217. *Socii*: absent (0); present (1).
218. *Subscaphium*: absent (0); single and oblong at middle (1); single, U-shaped (2); single, orbicular (3); double, at both sides (4).

Tegumen, its apodemes and derived sclerites

219. *Dorsum of tegumen*: connected (0); weakly connected by a slender sclerite (1); connected by a membrane (2); widely separated (3).
220. *Dorsoposterior margin of tegumen (dorsal view)*: truncate (0); U-shaped (1); forming a ring-like structure by fusing with uncus (2).
221. *Dorsum of tegumen*: developed, roof-like (0); slender and reduced (1); extremely slim (2).
222. *Hind margin of tegumen (dorsal view)*: emarginated (0); truncate (1); rounded (2); protruded (3).
223. *Posterodorsal surface of tegumen*: smooth (0); sparsely setose (1); setose area concealed by a lateral fold (2); setose area extended to medial process formed by teguminal extension (3).
224. *Tegumen*: simple, without specialized protuberance (0); paired, weakly sclerotized protuberances arising from interior fold of tegumen (1); paired protuberances arising near base of tegumen, separated (2); bilateral protuberances connected by a medial plate (3); bilateral protuberance completely fused with medial plate plus a bifurcate posterior projection (4); medial plate and posterior projection forming a gnathos-like structure with an inner ventral ridge (5); gnathos-like structure without an inner ventral ridge (6).
225. *Tegumen*: without posterior bilateral projections (0); with developed bilateral posterior projections near dorsum of tegumen (1); paired projections arising near base of tegumen (2); projections connected by a medial sclerotized band (3); projections nearly fused by a medial plate near apex (4); projections completely fused to a gnathos-like structure (5).
226. *Tegumen*: without posterior projections (0); apices of posterior bilateral projections stout (1); truncate (2); sharp (3).
227. *Tegumen*: without prominent apodemes to serve as attachment for M2 and M4 muscles (0); a pair of short apodemes situated at inner margins of tegumen (1); apodemes more prominent, spiculate (2); apodemes digital and extended anteriorly (3); elongate, situated between lower margin of tegumen and valval bases (4); apodemes situated at a pair of anteriorly extended sclerites from tegumen (5).
228. *Apodemes*: separated (0); connected by a posteromedial transverse bridge (1); connected by an transverse sclerite with an anterior projection (2); apices connected by a thin sclerite (3); apices connected by an undulate and broad sclerite (4); separated, teguminal extensions without connection in the middle (5); forming a cap-like structure (6) connected by a basal sclerite, apices swollen and large (7); very close or partly fused near apices (8); apodemes and teguminal extension forming a bridge-like structure (9).
229. *Teguminal arms*: without posterior projections (0); paired posterior projections present (1).
230. *Transtilla*: absent (0); band-like (1); rather short and heavily sclerotized (2).

Aedeagus and supporting apparatus

231. *Aedeagus*: slender (0); medium (1); thick (2).
232. *Aedeagus*: without prominent bulbus ejaculatorius (0); bulbus ejaculatorius prominent, cap-like (1); bulbus ejaculatorius long and curved (2).
233. *Bulbus ejaculatorius arising from phallobase*: caudodorsally (0); posteriorly (1); caudoventrally (2).

234. *Basal part of aedeagus*: straight (0); *Retina*-type (1); *Erasmia*-type (2); *Chalcosia*-type (3).
235. *Medial part of aedeagus*: straight (0); *Caprima*-type (1); *Erasmia*-type (2); *Eterusia*-type (3); *Chalcosia zehma*-type (4); *Retina*-type (5); *Chalcosia*-type (6); *Alloca-prima*-type (7).
236. *Apical part of aedeagus*: stout (0); truncate (1); pointed (2); beaked (3).
237. *Medioventral part of aedeagus*: without paired protuberances (0); paired protuberances present (1).
238. *Aedeagus*: without medioventral protuberance (0); slightly swelling ventrally (1); sac-like (2); coniform (3); digital (4); deltoid (5); long-conical (6).
239. *Medioventral protuberance*: absent (0); present near apex (1); present at middle (2); present near base (3).
240. *Cornuti*: absent (0); present, thickly spined (1); multiple rows of thick spines (2); short spines at apex (3); slender and thread-like spines (4); single short spine (5); multiple short spines (6); single long spine (7).
241. *Phallobase*: present (0); absent (1).
242. *Fultura inferior*: membranous (0); a slightly sclerotized, ridged and scobinate folded structure present (1).
243. *Surface of fultura inferior*: smooth (0); granulate (1); setose (2).
244. *Independent' juxta*: absent (0); ellipsoid (1); rectangular (2); bifurcate (3).
245. *Derived' juxta*: absent (0); truncate at apex (1); concave at apex (2); emarginated (3); bifurcate, concavity U-shaped (4); bifurcate, concavity V-shaped (5); deeply bifurcate, concavity U-shaped (6); deeply bifurcate, concavity V-shaped (7).
246. *Tegumenal apodeme*: without anteroventral extension (0); a pair of band-like sclerites arising from the junction between valval bases and posterior projections (1); outer margins of band-like sclerites fused with tegumen, inner margins slightly swelling (2); ventral sclerites roof-like (3); *Pidorus*-type (4); *Herpolasia*-type (5); *Caprima*-type (6); *Chalcosia*-type (7).
247. *Bases of interior extension of tegumen*: separated (0); slightly fused (1); fused (2); grooved medially (3); grooved part with a spatulate process (4); grooved part with a posterior projection (5); derived sclerite from base bifurcate at apex (6); sclerotized anellus and medial fused part of ventral sclerites forming a loop-like structure (7).
- Valva*
248. *Cucullus*: without specialized scaling (0); scale tufts present along cucullus (1).
249. *Valvula*: without scale tuft (0); scale tufts present (1).
250. *Cucullus*: sclerotized (0); membranous (1).
251. *Costal margin of cucullus*: entire (0); projected (1); cleft (2).
252. *Distal margin of cucullus*: entire (0); cleft (1).
253. *Costal margin of valvula*: entire (0); *Illiberis*-type (1); *Heteropan*-type (2); *Agalope*-type (3); *Cyclosia*-type (4); *Corma*-type (5); *Chalcosia*-type (6).
254. *Cucullus*: general (0); *Arbudas*-type (1); *Pidorus*-type (2); *Eterusia*-type (3); *Soritia*-type (4); *Chalcosia*-type (5); *Phlebohecta lypusa*-type (6); *Gynautocera*-type (7); *Boradiopsis*-type (8); *Histia*-type (9).
255. *Sacculus*: without apical spur (0); apical spur upcurved, hairy (1); apical spur smooth (2); docleomorpha (3).
256. *Mediobasal process of sacculus*: absent (0); *Rhodopsona*-type (1); *Corma maculata*-type (2); *Arbudas*-type (3); *Pidorus*-type (4); *Caprima*-type (5); *Chalcosia*-type (6); *Eterusia*-type (7); *Erasmia*-type (8); *Soritia*-type (9).
257. *Sacculus*: general (0); *Arbudas*-type (1); *Pidorus*-type (2); *Pidorus corculum*-type (3); *Retina*-type (4); *Chalcosia*-type (5); *Boradiopsis*-type (6); *Erasmia*-type (7); *Eterusia*-type (8); *Soritia*-type (9).
258. *Surface of sacculus*: without ridges (0); uni-ridged (1); obliquely ridged (2); loosely ridged (3); with dense transverse ridges (4); with spiky transverse ridges (5); with multiple rows of ridges (6).
259. *Ventral conjunction between valvae*: flexible (0); immovable (1).
260. *Base of valva*: without specialized process (0); with weakly sclerotized process (1); short, triangular sclerite (2); digitate process (3); beak-like (4).
- Vinculum and saccus*
261. *Position of articulation between tegumen and vinculum*: type 1 (0); type 2 (1); type 3 (2); type 4 (3); type 5 (4); type 6 (5).
262. *Apexes of vinculum*: arms not prominent (0); arms prominent beyond articulation between vinculum and tegumen (1).
263. *Anterodorsal view of vinculum*: U-shaped (0); V-shaped (1); pentagonal (2); cordate (3); oblong, attenuated ventrally (4) rhomboid (5); hexagonal (6); narrower hexagonal (7).
264. *Saccus*: absent (0); present (1).
265. *Saccus*: extending anteriorly (0); anterodorsally (1); downwards (2); posteriorly (3).
266. *Posteroventral view of saccus*: elongated; apex shape rounded (0); auriculate (1); triangular (2); compressed triangular (3); convex (4); rectangular with rounded edges (5); rectangular with sharper edges (6); bifurcate with deeper medial concave (7); bifurcate with shallower medial concave (8).
- Genitalic musculature*
267. *g1 (= m1)*: present, from dorsal cavity of tegumen to ventral base of uncus (0); reduced, only with a small bundle of fibre (1).
268. *g2*: absent (0); present, attached on tegumenal apodemes (1).
269. *g3 (= m2)*: from valval base to posterior part of tegumen (0); reduced (1).
270. *g4*: from vinculum to valval base (0); from vinculum to transtilla (1); from vinculum to tegumenal apodeme (2).
271. *g5 (= m7)*: present (0); absent (1).

FEMALE GENITALIA (FIGS 40–42)

Ovipositor, eighth tergite and sternite

272. *Ratio of ovipositor / A7 tergite*: <1 (0); 1 (1); 1.5 (2); 2 (3); 2.5 (4); 3 (5); 3.5 (6); 4 (7).
273. *Papillae anales*: bilobed (0); weakly bilobed (1).

274. *Papillae anales*: membranous (0); sclerotized (1).
 275. *Papillae anales*: flattened and short (0); compressed laterally (1).
 276. *Papillae anales*: disc-like (0); reduced (1).
 277. *Sensory setae of papillae anales*: dense and short (0); sparse and longer (1).
 278. *Anterior apophysis*: short (0); as long as length of tergite A7 (1).
 279. *Tergite A8*: present, broad, about 1/2 of A7 in length (0); shorter than 1/2 of A7 (1); about 1/3 of A7 (2); about 1/4 of A7, narrow (3); very narrow (4); almost reduced (5).
 280. *Tergite A8*: independent (0); fused with lamella postavagilis (1).
 281. *Tergite A8*: without lateral extension (0); extended lateroventrally (1); extended sclerite slightly separated from tergite (2); with a pair of slender extensions (3).
 282. *Sternite A8*: absent (0); present only in form of band-like sclerite (1); present in form of a complete sternite (2).

Antrum and surrounding region

283. *Antrum*: located behind the 7th sternite (0); located at hind margin of sternite (1); enclosed by posterior margin of sternum (2); deeply located in incised posterior margin of sternum (3); surrounded by sternum (4).
 284. *Middle part of hind margin of sternite A7*: obtuse (0); truncate (1); emarginated (2); incised (3); emarginated into a large rounded incision (4); caudate, uni-horned (5); caudate, with truncate apex; (6); caudate, apex slightly bifurcate (7); tri-caudate (8).
 285. *Ostium bursae*: membranous (0); sclerotized near opening (1); forming a cylindrical tube and sclerotized posteriorly (2); sclerotized till ductus bursae (3).
 286. *Antrum*: not surrounded by an annular sclerite (0); surrounded by an annular sclerite (1).
 287. *Antrum*: not surrounded by a rounded sclerite (0); ostium surrounded by a disk-like sclerite enclosed by posterior margin of sternite A7 (1).
 288. *Lamella antevaginalis*: absent (0); separated from antrum (1); fused with antrum (2).
 289. *Lamella postvaginalis*: absent (0); separated from antrum (1); fused with antrum (2).
 290. *Non-specialized structure (not lamella antevaginalis)*: posterior to antrum (0); intersegmental membrane posterior to antrum slightly sclerotized and wrinkled (1); strongly sclerotized and separated from antrum (2).
 291. *Antrum*: no paired sclerite posterior to it (0); posterior paired sclerites present (1).

Intersegmental membrane

292. *Intersegmental membrane between A7 and A8*: without a ring of scales (0); a ring of hair-like scales present (1).
 293. *Base of ovipositor*: smooth (0); setose ventrally (1).
 294. *Intersegmental membrane between sternites A6 and A7*: loosely linked (0); tightly linked (1).
 295. *Intersegmental membrane between A6 and A7*: without dense scales (0); dense scales tufts present on intersegmental membrane between A6 and A7 (1).
 296. *Pleural folds*: absent (0); present (1).

A6–A7

297. *Sternite A6*: scaled (0); smooth (1).
 298. *Sternite A7*: scaled (0); smooth (1).
 299. *Tergal lateroventral extension in A7*: absent (0); present and reaching to spiracle (1).
 300. *Tergum A7 shape (lateral view)*: type 1 (0); type 2 (1); type 3 (2); type 4 (3); type 5 (4); type 6 (5); type 7 (6); type 8 (7).
 301. *Upper margin of sternum A7 (lateral view)*: type 1 (0); type 2 (1); type 3 (2); type 4 (3); type 5 (4); type 6 (5); type 7 (6); type 8 (7), type 9 (8).
 302. *Posteroventral invagination on tergite A7*: absent (0); present (1).
 303. *Middle notch at upper margin of sternite A7*: absent (0); present (1).
 304. *Anterior notch at upper margin of sternite A7*: absent (0); present (1).
 305. *Posterior notch at upper margin of sternite A7*: absent (0); present (1).
 306. *Lateral invagination on sternite A7*: absent (0); present (1).
 307. *Scaling of pleural membrane of A7*: normal (0); with densely scaled area (1).
 308. *Sternite A7*: normal (0); much shorter than the tergite (1); extended dorsoposteriorly, lobed (2); crescentic (3).
 309. *Ventral part of sternite A7*: complete (0); split ventromedially (1).
 310. *Sternite A7*: complete (0); separated into three parts with cleft running posterodorsally (1).
 311. *Sternite A7*: without additional sclerites (0); split into ventral and lateral parts, cleft running lateroventrally (1).
 312. *Sternite A7*: narrower than tergite A7 (0); much narrower than tergite (1).

Internal ducts and glands

313. *Ductus seminalis*: arising from distal part of ductus bursae (0); arising from proximal part of ductus bursae (1); arising near base of corpus bursae (2); arising from corpus bursae (3).
 314. *Pseudobursa*: absent (0); present (1).
 315. *Accessory glands*: absent (0); present (1); 'Peterson's glands' present (2).
 316. *Surface of ductus bursae*: smooth (0); crenulate (1).
 317. *Ductus bursae*: membranous (0); sclerotized posteriorly (1); sclerotized until corpus bursae (2).
 318. *Ductus bursae*: straight (0); spiral at middle (1).
 319. *Ductus bursae*: straight (0); folded (1).
 320. *Corpus bursae*: anterior end almost reaches A1 (0); between A4 and A5 (1); at around A6 (2); partly concealed by A7 (3); covered by A7 (4).
 321. *Surface of corpus bursae*: smooth (0); granulate (1).
 322. *Surface of corpus bursae*: smooth (0); sclerotized pleats laterally (1); sclerotized area uni-band-like (2).
 323. *Pea-like signa*: absent (0); single (1); paired (2).
 324. *Crescentic signa*: absent (0); present and paired (1).
 325. *Comb-like signa*: absent (0); present (1).
 326. *Horn-like signa*: absent (0); present (1).
 327. *Band-like signa*: absent (0); present (1).
 328. *Asteroid signa*: absent (0); present (1).

329. *Appendix bursae*: absent (0); present at proximal part (1); present at middle part (2); present at distal part (3); derived from anterior end of corpus bursae (4).

SCENT ORGANS

Eversible coremata between A8 and A9 in males (Fig. 44C–G)

330. *Coremata between A8 and A9*: absent (0); paired, eversible and short (1); paired and short with long tufts (2); paired and long (3); paired and long, attached to sclerotized platelets on intersegmental membrane (4).

Coremata in male genitalia

331. *Coremata*: absent (0); attached between valval base and vinculum (1).

332. *Coremata*: absent (0); long, seta-like, attached to vinculum (1).

333. *Coremata*: absent (0); eversible, on valva (1).

Androconial scales in males (Fig. 44B, J, K)

334. *Androconial scales*: absent on wings (0); present on cup (1).

335. *Androconial scales*: present on tergum (0); present on tergites of A5–A7, two paired pouches formed by intersegmental membrane between tergites of A5/6 and A6/7 (1).

Metathoracic scent organ in males (Figs 43A, 44H, I)

336. *Metathoracic androconial organ*: absent (0); paired organ present (1).

Hindwing-abdominal scent organ (Figs 43B–T, 45, 46)

337. *HW base (male)*: androconial hair bristle absent (0); bundle of short filiform scales arising from anal plate (1); bundle of oblong scales arising from anal plate (2); bundle of long hair bristles inserting into a pleural pouch (3).

338. *Pleural membrane of A1–A2*: without glandular cells (0); a patch formed by several glandular cells behind A1 spiracle (1); glandular cells enclosed within a concave region (2); a simple pouch present (3); double-folding type (4); elongated-type (5); complicated-type (6).

339. *Male pouch*: not sclerotized (0); upper pleural sclerite sclerotized (1).

340. *Male pouch*: not sclerotized (0); lower pleural part sclerotized (1); lower pleural part strongly sclerotized (2).

341. *HW base (female)*: androconial hair bristle absent (0); bundle of hair-like scales arising from anal plate (1); bundle of short spatulate scales present at anal plate (2); spatulate scales as long as the first abdominal tergum (3); spatulate scales longer than the first abdominal tergum (4).

342. *Female*: without abdominal pouch (0); pleural pouch present between A1–A2 (1).

343. *Female*: without derived sclerites between tergum and sternum of A1 (0); tergal sclerite present (1); complete sclerite present (2).

344. *Female*: without derived sclerites between tergum and sternum of A1 (0); lower sclerite present (1); lower sclerite more sclerotized (2).

Eversible gland between female A8–A9

345. *Pheromone gland in the 8th/9th intersegmental fold*: absent (0); present (1).

Tergal gland of female

346. *Pheromone gland on tergum*: absent (0); present (1).

IMMATURE STAGES

General shape and coloration of larva (Figs 47, 48)

347. *Body*: cylindrical (0); flattened (1).

348. *Body*: stout (0); attenuated at both ends (1).

349. *Dorsal light-coloured patches*: absent (0); present until last instar (1).

350. *Dorsal colour pattern*: uniform throughout the whole abdomen (0); A4–A5 with narrow light colour pattern in earlier instars (1); A4–A5 with rectangular light colour pattern in earlier instars (2).

351. *D and SD verrucae*: without basal colour circles (0); with basal colour circles (1).

352. *A8 and A9*: developed (0); reduced (1).

Internal structure of larva

353. *Larva*: without cross-muscle (0); with cross-muscle around mid-gut (1).

Larval chaetotaxy and other cuticular structures (Figs 29, 51A–I)

354. *Paired cervical gland*: absent (0); present (1); retractile into T1 (2).

355. *Thoracic shield*: undeveloped (0); developed (1).

356. *Dorsum*: without transverse groove between D verrucae (0); transverse grooves between D verrucae present on all segments (1).

357. *Mentum*: sclerotized (0); weakly sclerotized (1).

358. *Mature instar*: with primary setae only (0); with secondary setae (1).

359. *Tonofibrillary platelet*: absent (0); present on SD verrucae (1).

360. *D verrucae*: not developed (0); developed, cone-shaped (1); tubercle-like (2).

361. *L verrucae*: not developed (0); developed, cone-shaped (1); tubercle-like (2).

362. *D, SD and L1 verrucae on T2*: not developed (0); SD and L1 verrucae developed (1); D, SD and L1 verrucae developed (2); D verrucae closer to SD and L1 verrucae (3).

363. *L1 verrucae*: not significantly longer than L2 + L3 verrucae (0); much longer than L2 + L3 verrucae (1).

364. *D verrucae from T1 to A8*: similar to other verrucae (0); with dense microspinules which make them distinct from the surrounding cuticle (1); microspinules reduced on T1, A4 and A5 (2).

365. *Mesothoracic SD1 and SD2*: both white (0); SD1 black, SD2 white (1); both black (2).
366. *Mesothoracic L1 setae*: both white (0); one black, one white (1); both black (2).
367. *D setae*: rather short (0); long (1).
368. *SD setae*: short (0); long (1).
369. *L setae*: shorter than 1/2 of body width at final instar (0); longer than 1/2 of body width at final instar (1).
370. *SD verrucae on A4–A5*: similar to those on other segments (0); strongly sclerotized (1).
371. *SD area*: without scar-like structure (0); with strongly sclerotized scar (1).
372. *L verrucae on A4–A5*: similar to those on other segments (0); with dense microspinules (1).
373. *D1 and D2, situated*: above/below each other (0); before/behind each other (1).
374. *L group on T1*: bisetose (0); trisetose (1).
375. *SD1 and SD2 of T2*: unisetose (0); bisetose (1).
376. *SD2 of T3*: unisetose (0); bisetose (1).
377. *SV of T2–T3 group*: bisetose (0); unisetose (1).
378. *SD2 of A3–A6*: present (0); absent (1).
379. *SV2 of A3–A6*: present (0); absent (1).
380. *SD setae*: smooth (0); plumose (1).
381. *L and SV setae*: smooth (0); densely plumose (1); sparsely plumose (2).
382. *Anal plate*: developed (0); reduced (1).

Structures relevant to locomotion (Fig. 51J–L)

383. *Thoracic legs*: without spatulate seta (0); with one spatulate seta (1); with paired spatulate setae (2).
384. *Crochets of abdominal segments*: uniserial (0); biserial (1).
385. *Crochets of abdominal segments*: uniordinal (0); biordinal (1).
386. *Crochets of abdominal segments*: lateral penellipse (0); mesoserries (1); bipartite mesoserries (2).
387. *Prolegs*: developed (0); reduced (1).

Pupa (Fig. 50)

388. *Cross-section of pupa*: spherical (0); dorsoventrally compressed (1).
389. *Eyepiece*: simple (0); small flange present (1); large flange present (2).
390. *Maxilla*: prominent (0); reduced (1).
391. *Proboscis case*: present (0); reduced (1).
392. *Anterior rim*: intersegmental furrow between the pro- and mesothoracic segments without sculptured anterior rim (0); anterior rim of the intersegmental opening bearing outgrowths (1).
393. *Thoracic spiracle*: concealed by 'spiracle access' (0); not concealed by 'spiracle access' (1).
394. *Tergites A3–A8*: without spined field (0); with single row of spinules (1); with 2–3 rows (2); with multiple rows (3).

395. *Spinules*: spined field confined to anterior half (0); some spinules loosely arranged behind the band (1); spinules occupy the whole terga (2).
396. *Tuberculate band on segment A10*: absent (0); present (1).
397. *Frons*: without seta (0); paired C1 and C2 setae present (1).

Cocoon (Fig. 52)

398. *Inner and outer layers of cocoon*: combined (0); separated (1).
399. *Outer layer of cocoon*: without crystallites (0); with densely packed crystallites (1).
400. *Cocoon*: enclosed within leaf litter (0); loosely attached to leaves (1); bottom firmly attached to leaves (2).
401. *Cocoon shape*: bluntly fusiform (0); ovoid (1); spindle-like (2); flattened and compressed dorsoventrally (3); *Chalcosia*-type (4); *Cyclosia*-type (5).
402. *Cocoon*: soft (0); rather hard (1).

CHEMICAL DEFENCE SYSTEM (FIGS 53, 54)

403. *Mandibular lobe*: absent (0); membranous, without prominent process (1); membranous, short (2); short, sclerotized at apex (3); conical, sclerotized near apex (4); long, sclerotized from sub-basal part to apex (5); short, a sclerotized ring present at middle (6); conical, sclerotized only at margin (7); conical, sclerotized laterally near apex (8); long, lateral margins sclerotized from apex to base (9).
404. *Adult head*: without chemical defence system (0); cyanic fluids released below compound eyes (1).
405. *Opening for cyanid foam between parapetium and prescutum*: absent (0); present (1).
406. *Cyanoglucoside-A, in adult*: absent (0); present (1).
407. *Larval cuticular cavities for storing cyanic fluids*: absent (0); present (1).
408. *Larval cuticular cavities*: without opening mechanism (0); with opening pores (1).
409. *Mature larvae*: without opening pore (0); SD with one pore on each verruca (1); SD with two pores on each verruca (2).
410. *Opening mechanism on larval cuticle*: absent (0); formed by a single pore (1); formed by fusion of two or more pores (2).
411. *Larvae*: without chemical defence system (0); with cyanogenetic defence system (1).
412. *Larval defensive secretion*: without linamarin (0); with linamarin (1).
413. *Larval defensive secretion*: without lotaustralin (0); with lotaustralin as minor component (1); with lotaustralin as major component (2).
414. *Larval defensive secretion*: without sarmentosin (0); with sarmentosin (1).

APPENDIX 3
DATA MATRIX

Matrix of 414 characters utilized in the phylogenetic analysis of Chalcosinae and the group taxa. Missing data (including inapplicable character states) coded as ?. Symbols for polymorphic characters: A. 0/1. B. 0/2. C. 0/3. D. 0/4. E. 0/6. F. 1/2. G. 2/3. H. 2/4. I. 3/4. J. 3/5. K. 3/6. L. 4/5. M. 5/6

Characters	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	111-120	121-130	131-140
<i>Burlacota aegertoides</i>	0000000000	0000100000	?000000000	0000000000	0000000000	0000000000	1000?00000	0??0000000	0000000010	0070000000	0000000000	0000000000	0000000000	0000000000
<i>Himantopteris fuscinervis</i>	2211110000	0000210000	?001000000	0033012???	?????20330	0001100000	0001100000	2110?0400	0??0000001	0210000210	1?00101000	0000000000	0008800000	0000000000
<i>Anomoeetes levis</i>	2211110000	0000210000	0001000000	0?55?12???	?????20330	0001100000	2101012400	0??0332200	?000000001	0270000210	1?00101000	0000011000	0006600000	0000000000
<i>Dianaura gochii</i>	2211110000	0000210000	0001000000	0?55?12???	?????20330	0001100000	2100?00000	0??0000000	?000000001	0270010210	2?00101000	0000011000	0000660000	0000000000
<i>Lactura dives</i>	0011110000	0000323344	0000033220	0022000000	0002001000	1000000000	1000?05030	31?0000000	?000010001	0012000200	0000100000	0000000000	0001100000	0000000000
<i>Phaouda mimica</i>	2211110000	0000213344	0000044000	0044000002	2000012210	0001100000	2100?06030	31?5566000	?00010001	0212000200	0000100000	3000000000	0000000000	0000000000
<i>Heterogynis</i> sp.	2?1?1?1?3?	0?0?0?0?0?	000100?0?0	??5?12???	????224?0	0001?00?00	2100?0?011	1??0?0?0?	?000000000	000?000020	0000200001	00000000??	0003?0000?	0000000?0?
<i>Artona hainana</i>	0000111122	2211324444	0000100223	3011010000	1002002010	0011100101	2211000013	3000000000	0000010000	0003000200	0000100000	2000000000	0003300000	0000000000
<i>Theresimima ampelophaga</i>	0000110000	2211322222	0000100221	1011010001	1300200210	0011100001	2111000013	3000000000	0000010000	0103000200	0000200000	0000000000	0001100000	0000000000
<i>Adscita statives</i>	00001?1100	1100323344	0000122222	2011000002	1200200210	0010100001	2111000213	3000222200	0000010000	0104000200	0000200000	2000000000	0001100000	0000000000
<i>Pollanisus viridipulverulenta</i>	0000110000	1100323344	0000122222	2011000002	1100200210	0010100001	2211000213	3000222200	0000010000	01?2000200	0000200000	2000000000	0003300000	0000000000
<i>Ilitharis pruni</i>	0022110000	2211322222	0000100221	1011000002	1200001210	0011100001	2311000013	3000000000	0000010000	0102000200	0000000000	2000000000	0001100000	0000000000
<i>Clelea formosana</i>	0000110022	2211324444	0000111221	1011010001	1200200210	0011100001	2111000013	3000000000	0000010000	0104000200	0000200000	2000000000	0003300000	0000000000
<i>Harrisina americana</i>	0011110000	0000104444	0000100222	2011010001	1200100210	0011100001	2111000013	3000000000	0000010000	0104000200	0000200001	0000000000	0000000000	0000000000
<i>Pyromorpha</i> sp.	0011110000	0000104444	0000100222	2011000001	1200100210	0011100001	2111000013	3000000000	0000010000	0104000200	0000200001	0000000000	0005500000	0000000000
<i>Salicinea styx</i>	0000110000	2211322222	0000100221	1011000001	1200100210	0010000001	2211000013	3000000000	0000010000	01?4000200	0000200000	3000000000	0000000000	0000000000
<i>Janssola bitaea</i>	00111?1?3?	00002100??	0001000000	?44?12???	?????01210	0001?00001	2111220013	3000000000	0000010000	01?1000200	0000200000	0000000000	0003300000	0000000000
<i>Homophylotis nigra</i>	?03?1?0?2?	1?0?2?1?4?	00001001?4	?055?12???	?????1210	0001?00001	2112000013	3000000000	0000010000	01?1000100	0000100000	3000000000	0003200000	0000000000
<i>Zygaena filipendulae</i>	2211110011	2200102233	0001000233	0001000010	1000201000	1?01100001	3410?0?013	3100000000	0001010000	0106000200	1?00100000	2000000000	0002200000	0000000011
<i>Pryeria sinica</i>	2211110011	2200102233	0001000022	2055012???	?????02210	0101100001	3410?0?013	2100334400	0000010001	0200010201	?00000100	2000000010	0007700000	0000000000
<i>Calizygaena ada</i>	0022100111	2200212211	0001144222	2011010111	1202012210	0111101101	4511111613	2100556600	0000010001	0103000200	0000200001	3000000000	0000000000	0000500011
<i>Chalcopsopsis variata</i>	0011001111	1111210000	0000100311	1022100000	1012210001	1?00000000	2111000012	0??0000000	0001002010	10?3000000	?110130001	1100000000	0114400000	0000000000
<i>Chalcopsopsis melli</i>	0011001111	1111210000	0000100111	1022100000	1012210001	1?00000000	0??0000000	0??0000000	0000002010	10?3000000	0010100001	1100000000	0114400000	0000000000
<i>Inouela formosana</i>	003?1?0?2?	1?0?2?1?4?	00001001?4	?055?12???	?????1210	0001?00001	4511110413	2100334400	0000010001	01?4000200	3?00000001	2000010010	0000000000	0000000000
<i>Cleoda syntomoides</i>	0021210020	2020415353	0000123210	1042011012	222?012310	0122300001	4511110413	2100334400	0000010001	01?4000200	3?00000001	2000010010	0000000000	0000000000
<i>Heteropan scintillans</i>	0022400000	0022436655	0100100113	3000011011	1110221210	0112212001	4511000014	3200000000	0001011001	01?2000200	?200100001	2000010000	0004400000	0000000000
<i>Heteropan alienus</i>	0022400000	0022326655	0000100113	3000011011	1110221210	0112212001	4511000014	3200000000	0001011001	01?2000200	?200100001	2000010000	0004400000	0000000000
<i>Heteropan appendiculata</i>	0022400000	0022326655	0000100113	3000011011	1110221210	0112212001	4511000014	3200000000	0001011001	01?2100100	?200002001	0000110100	0004400010	0000000000
<i>Cadphises moorei</i>	1021210110	2133425544	0000100213	3011011212	22211112210	0122200011	4511000014	3200000000	1001011001	0104000201	2?02001001	2000012000	0006600000	0000000000
<i>Cadphises maculatus</i>	1021210110	2133425544	0000100213	3011011212	22211112210	0122200011	4511000014	3200000000	1001011001	01?4000201	?202001001	2000012000	0006600000	0000000000
<i>Hampsonia pulcherrima</i>	2000110000	2222436644	0100100113	3011011212	22211112210	0122200011	4511000014	3200000000	1001011001	01?2000200	?212000001	3010010000	0003300000	0000040022
<i>Watermentia bifasciata</i>	1022211100	1122435555	0100100113	3011011212	22211112320	0122200011	4511000014	3200000000	1001011001	01?3000200	?212000001	2000010001	0003300001	0000050000
<i>Herpidea eupoma</i>	1011111000	1133325555	0000100113	3011011212	22211112320	0122200011	4511000014	3200000000	1001011001	?01?3000200	?202000001	2000010001	0003300001	0000050000
<i>Aglaope infusta</i>	1100010001	1202336274	0011000013	2140111212	2221112210	0122200001	4511120014	3200000000	0001011001	0102000000	?202100000	200000?000	0003300000	0000000000
<i>Phyllopor basimaculata</i>	0011131111	1233426655	0000133013	2011011212	2221112210	0122120001	4511012414	3200334400	1001011001	01?4000200	?202002001	2000010010	0002300001	0010020024
<i>Formozygmeta sibirata</i>	0022220000	2222426655	0000100103	2011011212	22211112320	0121200001	4511010014	3200000000	1001011001	0104000200	1?02001001	2000010000	0005500000	0000000000
<i>Alelesia nerossea</i>	0?2?2?1?1?	?0?0?3?4?6?	000010?1?4	?01?011212	222111122?0	0122?00?01	45111010014	32000?0?0?	1001011001	01?0000200	3?00001001	3000010000	0003?0000?	0000000?0?
<i>Elycisma westwoodi</i>	0033120001	12?0433333	0022100212	1011011212	22211112320	0122300001	4511330014	3200000000	1001011001	0104000200	?202001001	3010012000	0006601000	0000050000
<i>Achelura bifasciata</i>	0022110000	1111326655	0012100113	2012011212	22211112320	0121300001	4511330014	3200000000	1001011001	0105000200	?202001001	3000011000	1003300000	0000050044

<i>Achelura javana</i>	0022110000	1111326655	0012100013	20120111212	22211112320	0121330001	45111330014	3200000000	1001011001	01050000200	2702001001	3000011000	1003300001	0000550044
<i>Achelura hemileuca</i>	0022110000	1111326655	0012100113	20120111212	22211112320	0121330001	45111330014	3200000000	1001011001	01750000200	2702001001	3000010000	0003300000	0000000000
<i>Boradida carneola</i>	0011101100	2100214433	0010100313	20230101212	22211112320	0122330001	45111330014	3200000000	1001011001	01750000210	1712000001	3000010000	0005500000	0000000000
<i>Agalope glacialis</i>	0011110001	1011324433	0022100214	3011011212	2221112320	0122330001	45111330014	3200000000	1001011001	01030000200	2702001001	3000010000	0006600000	0000050000
<i>Agalope immaculata</i>	0032120101	2121423333	0012100202	4031011212	22211112310	0121330001	45111330014	3200000000	1001011001	01040000200	2702001001	2000010000	0005500000	0000000000
<i>Agalope hyalina</i>	0011110000	1011324444	0010100004	4011011212	22211112210	0122330001	45111330014	3200000000	1001011001	01050000200	2702001001	3000010000	0005500000	0000050000
<i>Agalope eronioides</i>	0011110000	1011324444	0010100004	4011011212	22211112210	0122330001	45111330014	3200000000	1001011001	01050000200	2702001001	3000010000	0005500000	0000050000
<i>Agalope beti</i>	0022111111	2111325544	0010100314	4011011212	2221112310	0121330001	45111330014	3200000000	1001011001	01050000200	2702001001	3000010000	0003300000	0000050000
<i>Agalope pica</i>	0022111111	2111325544	0010100314	4011011212	2221112310	0121330001	45111330014	3200000000	1001011001	01050000200	2702001001	3000010000	0003300000	0000050000
<i>Campylotes</i>	2210110000	0103234565	0010100003	3011010212	22211112210	0122200001	45111000014	3200000000	1001011001	01050000200	2203000001	30100012000	1005500000	0000250011
<i>Campylotes</i>	2210110000	0103234565	0010100003	3011010212	22211112210	0122200001	45111000014	3200000000	1001011001	01050000201	2202000001	30100012000	1005500000	0000250011
<i>Neoharpa venosa</i>	0022221111	2122435456	0000100013	4022010212	22211112320	0121200001	45111000414	3210334400	1001011001	01740000200	220A001001	2000011000	0005500000	0000000000
<i>Neoharpa subhyalina</i>	0033220010	1122436556	0100100012	1033010212	2221112320	0121200001	45111002414	3210334400	1001011001	0173000F200	2202001001	3000011000	0003300000	0000000000
<i>Neoharpa eleonora</i>	2222220011	1122435456	0000100014	3022010212	2221112320	0121200001	45111000414	3210334400	1001011001	01740000200	220B002001	3000011000	0005500000	0000050000
<i>Pantherpina basiflava</i>	2222220011	1122435456	0000100014	3022010212	2221112320	0121200001	45111000414	3210334400	1001011001	01740000200	220B002001	3000011000	0005500000	0000050000
<i>Cyclosia panthona</i>	0033220000	2222547766	1100100013	3000010012	2222112220	0121100001	45111000014	3210000000	1101011001	01030112100	?210022001	3000012001	0005500000	0000000000
<i>Cyclosia panthona</i>	0033220001	2222547766	1100100013	3000010012	2222112220	0121100001	45111000014	3210000000	1101011001	01030112100	?210022001	3000012001	0005500000	0000000000
<i>Cyclosia papilionaris</i>	0033220011	2222656633	1100101111	1000010012	2222112220	0121100001	45111003014	3210000000	1101011001	01040121100	2720012001	3000012011	0002500001	0110F00001
<i>Cyclosia chartacea</i>	0033220011	2222656633	1100101111	1000010012	2222112220	0121100001	45111003014	3210000000	1101011001	01040121100	2720012001	3000012011	0002500001	0110F00001
<i>Cyclosia spargens</i>	0033220011	2222656633	1100101111	1000010012	2222112220	0121100001	45111003014	3210000000	1101011001	01040121100	2720012001	3000012011	0002500001	0110F00001
<i>Cyclosia macularia</i>	0033220011	2222656633	1100101111	1000010012	2222112220	0121100001	45111003014	3210000000	1101011001	01040121100	2720012001	3000012011	0002500001	0110F00001
<i>Cyclosia imitans</i>	0044222211	2222657733	1100100011	1000010012	2222112220	0121100001	45111003014	3210000011	1101011001	01750112100	222002001	3000012001	0003300001	0110200000
<i>Cyclosia curiosa</i>	0044222211	2222657733	1100100011	1000010012	2222112220	0121100001	45111003014	3210000011	1101011001	01750112100	222002001	3000012001	0003300001	0110200000
<i>Cyclosia midamia</i>	0044222211	2222657733	1100101111	1000010012	2222112220	0121100001	45111000014	3210001100	1101011001	01750112100	2720012101	3000012001	0003300001	0100100000
<i>Cyclosia pieroides</i>	0033220011	2222657733	1100100112	2000010012	2222112220	0121100001	45111003014	3210001300	1101011001	01730112100	?220002001	3000012011	0005500001	0100200000
<i>Cyclosia pieroides</i>	0022220011	2222547733	1100100112	2000010012	2222112220	0121100001	45111000014	3210000000	1101011001	01740112100	?220002001	3000012011	0005500001	1100200000
<i>Cyclosia inclusus</i>	0021111101	2022335544	0000101012	3000010012	2222112220	0121100001	45111000014	3210111100	1101011001	01040112100	2710012001	3000012011	0002500001	0000000000
<i>Cyclosia eucharita</i>	0033221111	2022435555	0000122012	3000010012	2222112220	0121100001	45111000014	3210000200	1101011001	01730112100	2720012001	3000012011	0002500001	0000000000
<i>Cyclosia electra</i>	0022220011	2022435555	0000111013	3000010012	2222112220	0121100001	45111000014	3210000000	1101011001	01730112100	2710000201	3000012001	0003500000	0000000000
<i>Cyclosia notabilis</i>	0022221111	2122436655	0000111113	4011010312	2222112220	0122200001	45111001614	3211111100	1101011001	01730000200	2712001001	2000011000	0003300000	0102000000
<i>Rhodopsoma costata</i>	0011331111	1122325544	0000155113	2011010312	2222112320	0121330001	45111000014	3210556600	1101011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312	2222112320	0121330001	45111000014	3210445500	1001011001	01040000200	1700000201	2000010000	0003300000	0000000000
<i>Rhodopsoma</i>	0011331111	1122325544	0000100313	2011010312										

APPENDIX 3 Continued

Taxa	Characters													
	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	111-120	121-130	131-140
<i>Arbutus submaculata</i>	0022321011	2122425544	0000100021	2022010012	2222112320	0121300001	4511001614	3211000000	1001011001	0104002200	?2A0000001	6000010000	0003300000	0000000000
<i>Arbutus leno</i>	0021220110	2111325544	0000100203	4022010012	2222112320	0121300001	4511001614	3211000000	1001011001	0103002200	2700000001	3000010000	0003300000	0000000000
<i>Arbutus truncatus</i>	0033230000	2122653344	0000100213	4022010012	2222112320	0121300001	4511001614	3211000000	1001011001	0122000200	?200000001	3000010000	0003300000	0000000000
<i>Eumorphiopais quadripilosa</i>	0021330110	2022425544	0000100104	4022010012	2222112310	0122200001	4511000014	3211222200	1001011001	0124000200	2200002001	3000010000	0003300000	0000000000
<i>Eumorphiopais levis</i>	0021330110	2022425544	0000100104	4022010012	2222112310	0122200001	4511000014	3211222200	1001011001	0124000200	2200002001	3000010000	0003300000	0000000000
<i>Pidorus glaucopsis</i>	0022330011	1122434444	0100155113	4011010312	2222112320	0121200001	4511001614	3211000000	1010110001	0104000200	2700000001	3000010000	0003300000	0000000000
<i>Pidorus cyrtus</i>	0022330011	1122434444	0100155113	4011010312	2222112320	0121200001	4511001614	3211000000	1010110001	0104000200	2700000001	3000010000	0003300000	0000000000
<i>Pidorus circinata</i>	0011440011	1122444444	1100100113	3011010312	2222112320	0121200001	4511000014	3211000000	1101011001	0104000200	2710000001	3000010000	0003300000	0000000011
<i>Pidorus caloti</i>	002747071?	072757774?	11001111?3	?01?010312	2222112370	0121200011	4511000014	3211111100	1101011001	0124000200	27100002001	3000010000	0003300000	0012050000
<i>Pidorus corulum</i>	0022200111	1122324444	0000100113	4011010312	2222112320	0121200001	4511001014	3211000000	1001011001	0124000200	2702002001	3000010000	0003300000	0000000000
<i>Pidorus gemina</i>	0021331000	1002335555	0000100101	3045010312	2222112320	0121100001	4511001614	3211000000	1001011001	0104000200	2700000001	2000010000	0003300000	0000000000
<i>Pidorus bifasciatus</i>	072727071?	172737474?	00001071?3	?03?010312	2222112370	0121200011	4511001614	32110707?0	1001011001	0124000200	2702002001	30000100??	0003300000	00000007?0
<i>Pidorus chalybeatus</i>	074271?0?	273747372?	00001022?2	?03?010312	2222112370	0121200011	4511000614	32110707?0	1001011001	0124000200	2700001001	30000100??	0003300000	00000007?0
<i>Pidorus constrictus</i>	0021100111	1122435566	0000100002	3022010312	2222112320	0121100001	4511001614	3211000000	1101011001	0124000200	2702000001	2000010000	0003300000	0000000000
<i>Pidorus fasciatus</i>	0022331111	2122435555	1000100113	4011010312	2222112210	0122200001	4511000014	3212000000	1101011001	0124000200	2721000001	3000010000	0003300000	0000000444
<i>Pidorus circe</i>	0022220011	2111325555	0000100113	4011010312	2222112220	0122200001	4511000014	3212000000	1101011001	0124000200	2701000001	3000010000	0005500000	0000000000
<i>Pidorus ochrophus</i>	0071?371?1	?1?2?2?575	00001?0?1?	?07?010312	2222112720	07??200001	4511000014	3212?0?070	1101011001	0124000200	2701000000	30000100??	0007300000	00000007?0
<i>Pidorus splendens</i>	0011220011	2122435555	0000155113	3000010312	2222112320	0121200001	4511001614	3211000000	1101011001	0124000200	271F001001	3000010001	0003300000	0000000011
<i>Pidorus miles</i>	0011001111	1122325544	0000100113	2022010312	2222112210	0121300001	4511000014	3210334400	1001011001	0124000200	?210000001	3000010000	0003300000	0000000000
<i>Hemisita meeki</i>	0022221011	1211434655	0000111111	2022010312	2222112320	0121200001	4511001014	3211000100	1001011001	0124000200	?210000001	3000010001	0003300000	0000000010
<i>Hemisita sp. Luzon</i>	0022221011	1211434655	0000111111	2022010312	2222112320	0121200001	4511000014	3211222200	1001011001	0124000200	?210000001	3000010000	0003300000	0000000000
<i>Hemisita albivitta</i>	0011111000	0011324433	0000100003	4022010312	2222112210	0121100001	4511002414	3211334400	0001011001	0124000200	2732000001	3000010000	0001100000	0000000000
<i>Isocrambia melaleuca</i>	?0?1?1?0?1	?1?0?1?7?5	00001?4?0?	?0?2?11?312	2222112720	07??100001	4511000414	3211?0?070	0001011001	0124000200	2731000001	30000100??	000740000?	00000007?0
<i>Herpodesia augarra</i>	0032010111	0122545555	0000113011	2054011312	2222112320	0121100000	4511003414	3211000000	0001011001	0124000200	27100002001	3000012011	0003300001	0000000000
<i>Herpodesia albomedia</i>	?0?2?1?0?1	?1?2?4?5?5	00001?3?1?	?0?7?011312	2222112720	07??100001	4511003014	3211?3?470	0001011001	0124?02200	27100002001	30000120??	0007300001	00000007?0
<i>Clematessa virgata</i>	0021121011	0022535565	0000101011	2044011312	2222112320	0121100001	4511000014	32110707?0	0001011001	0124000200	27100002001	3000012011	0003300001	0000000000
<i>Clematessa xuthomela</i>	?0?1?2?0?1	?0?2?2?3?5?5	00001?1?1?	?0?7?011312	2222112720	07??100001	4511000014	3211?0?070	1001011001	0124?00200	?2100002001	300001120??	000730000?	00000007?0
<i>Hemichrysoptera celbensis</i>	0021221111	2111323333	0000122221	2022010312	2222112220	0121100001	4511000014	3211222200	1001011001	0124000200	27000002001	3000010000	0003300000	0000001100
<i>Sciotoecia modesta</i>	072727071?	173737474?	00001070?2	?02?010312	2222112270	0121200011	4511000014	32110707?0	0001011001	0124000200	3732000001	30000100??	000330000?	00000007?0
<i>Papuaphlebohecta bicolora</i>	0011111000	0011324433	0000100003	4022010312	2222112210	0121100001	4511002414	3211334400	0001011001	0124000200	2732000001	0000010000	0001100000	0000000000
<i>Caprima albifrons</i>	0011220011	1000215555	0000100003	4022010312	2222112320	0121100001	4511000014	3211000000	0001011001	0124000200	2710000001	2000010000	0003300000	0000000000
<i>Caprima gelida</i>	0011220011	1000215555	0000100003	4022010312	2222112320	0121100001	4511000014	3211000000	0001011001	0124000200	2710000001	2000010000	0003300000	0000000011
<i>Caprima mutilata</i>	0011220011	1000215555	0000100003	4022010312	2222112320	0121100001	4511000014	3211000000	0001011001	0124000200	2710000001	2000010000	0003300000	0000000011
<i>Caprima chryssoma</i>	?0?1?2?0?1	?0?0?1?5?5	00001?0?0?	?0?2?010312	2222112720	07??100001	4511002414	3211?3?470	0001011001	0124000200	2710000001	20000100??	000330000?	00000007?0
<i>Cyanidia thaumasta</i>	?0?3?2?0?1	?0?0?2?5?5	00001?0?0?	?0?7?011312	2322112720	07??100001	4511000014	3211?0?070	0001011001	0124000200	2700000001	20000100??	000750000?	00000007?0
<i>Hadronella spectabilis</i>	0032220011	1111324444	0000100002	3053010312	2222112320	0121100001	4511000014	3211000000	1001011001	0124000200	2702000001	3000010001	0001300000	0000000000
<i>Hadronella lucida</i>	0032220011	1111324444	0000133002	3053010312	2222112320	0121100001	4511000014	3211330400	1001011001	0124000200	2702000001	3000010001	0003300000	0000000011
<i>Thaumastophleps expensa</i>	0011111000	0011324433	0000100003	4022010312	2222112320	0121100001	4511002414	3211334400	0001011001	0124000200	2732000001	0000010000	0001100000	0000000000
<i>Retina rubrivitta</i>	0000221002	1221435566	0000100112	3022010312	2222112320	0121100001	4511001614	3211112200	1101011001	0103000200	2702000001	2000010010	0001200000	0000000000
<i>Barbarosa amabilis</i>	0022220011	2122434444	0000100113	4011010312	2222112320	0122200001	4511000014	3212004400	1101011001	0124000200	2702000001	3000010000	0005500000	0010020000
<i>Pseudoscaptelys circumdata</i>	0011321111	2111325555	0000100112	3011010312	2222112210	0122200001	4511000014	3212000000	1101011001	0124000200	2701100001	3000010000	0003500000	0000000000
<i>Erasmiphlebohecta picturata</i>	0011331111	2122546667	1100111113	4000010312	2222112220	0122400001	4511000114	3212111100	1101011001	0104000200	2702001001	2000010000	1001100000	0020063344
<i>Chalophaedra zuluika</i>	0022330011	2122437767	1100122112	3000010312	2222112220	0122400001	4511000214	3212222200	1101011001	0124000200	?2222000001	2000010000	0003300000	0000063344

<i>Erasmia pulchella</i>	1100111112	3000010312	2222112220	0122400001	4511000014	3212111100	1101011100	0105000200	2702001001	2000010000	1003300000	0020164455
<i>Eucrema obliquaris</i>	1100100312	3000010312	2222112220	0122400001	4511000014	3212000000	1101011100	0175000200	2702001001	2000010000	0003300000	0000000044
<i>Eucrema intericia</i>	1100111112	3000010312	2222112220	0122400001	4511000014	3212111100	1101011100	0175000200	2702001001	2000010000	0003300000	0000000044
<i>Eucrema euphaena</i>	1100111112	3000010312	2222112220	0122400001	4511000014	3212111100	1101011100	0175000200	2702001001	2000010000	0003300000	0000000044
<i>Amesia sanguiflua</i>	1100100312	3000010312	2222112220	0122400001	4511000014	3212000000	1101011100	0105000200	2712000001	2000010000	0003300000	0020035500
<i>Amesia alaris</i>	1100100312	3000010312	2222112220	0122400001	4511000014	3212000000	1101011100	0105000200	2712000001	2000010000	0003300000	0010035500
<i>Amesia apensis</i>	1100100312	3000010312	2222112220	0122400001	4511000014	3212000000	1101011100	0174000200	2712000001	2000010000	0004400000	0000000000
<i>Opisthoplatia grandis</i>	1100100312	3000010312	2222112220	0122400001	4511000014	3212000000	1101011100	0174000200	2702000001	2000010011	0005500000	0000000000
<i>Phlebohecta</i>	0000100111	1011325544	0000100111	0122211220	0122400001	4511000014	3212000000	0173000200	2712000001	3000010001	0001100000	0000000000
<i>fuscescens</i>	0000100111	1011325544	0000100111	0122211220	0122400001	4511000014	3212000000	0173000200	2712000001	3000010001	0001100000	0000000000
<i>Phlebohecta lithosina</i>	0010001111	1011325544	0000100112	2222112220	0122400001	4511000014	3210334400	0001011100	0173000200	2712000001	0001100000	0000000000
<i>Phlebohecta jordani</i>	0030210011	2133325554	0000100201	2022010312	2222112220	0122200001	4511000014	0172000200	3732000001	3000010001	1003300000	0000000000
<i>Phlebohecta typusa</i>	0021120011	2111325555	0000100212	2022010312	2222112220	0122300101	4511000014	0173000200	2700000001	0000010001	0001100000	0000000000
<i>Eterusia risa</i>	0012331111	1122435646	1100100312	3000010312	2222112320	0121400001	4511001614	0103000200	2722000001	2000010011	0002300001	0000011144
<i>Eterusia vitessa</i>	071737121?	172747594?	110014712?	3007010312	2222112320	0121400001	4511000014	0177000200	2722000001	2000010000	0003300000	001100012?
<i>Eterusia aedea</i>	0032432110	2122647755	1100100212	3000010312	2222112320	0121400001	4511000014	0103000200	2722000001	3000010000	0003300000	0011001133
<i>Eterusia binotata</i>	0012341111	2022446556	1100100312	3000010312	2222112320	0121400001	4511000614	0103000200	2722000001	3000010011	0003300001	0000000001
<i>Eterusia tricolor</i>	0022330011	1022435545	1100100312	3000010312	2222112320	0121400001	4511000014	0104000200	2722000001	3000010000	0002200000	0031001122
<i>Eterusia subcyanea</i>	0022330011	1022435545	1100100312	3000010312	2222112320	0121400001	4511000014	0104000200	2722000001	3000010001	0002200001	0031001133
<i>Eterusia replata</i>	0022221111	1122446556	0100111112	3000010312	2222112220	0124400001	4511000014	0173000200	2722000001	3000010000	0003300000	0000000011
<i>Eterusia raja</i>	0012331111	2122547744	0100122113	4011010312	2222112220	0124300001	4511000014	01730001200	2712000001	2000010000	0003300000	0000000000
<i>Soritia pulchella</i>	0022330011	2122536556	1100105112	3000010312	2222112320	0121400001	4511001614	0103000200	2712000001	2000010011	0001300001	0000000022
<i>Soritia major</i>	0022330011	2122536556	1100105112	3000010312	2222112320	0121400001	4511001614	0103000200	2712000001	2000010011	0001300001	0000000010
<i>Soritia zelandica</i>	072737071?	272757676?	110010712?	3007010312	2222112370	0121400001	4511001614	0177000200	2712000001	2000010011	0001700001	000000071?
<i>Soritia costimacula</i>	0022330011	1222536556	1100100312	3000010312	2222112320	0121400001	4511001614	0103000200	2712000001	2000010011	0003300001	0000000001
<i>Soritia costimacula malaccensis</i>	?072737071?	272757676?	110017571?	3007010312	2222112320	0777400001	4511001614	0173000200	2712000001	2000010011	0003300001	0000000071
<i>Soritia shahama</i>	0022330011	1222537776	1100111112	3000010312	2222112320	0121400001	4511002414	0173000200	2712000001	2000010000	0003300000	0000000022
<i>Soritia elizabethae</i>	0022330011	1222537776	1100104112	3000010312	2222112320	0121400001	4511002414	0102000200	2712000001	2000010011	0003300000	0000000020
<i>Soritia bicolor</i>	0022331111	2122435555	1100100312	3000010312	2222112220	0122200001	4511000014	0103000200	2721000001	3000010000	0003300001	0000000044
<i>'Soritia' sevastopuloi</i>	1000111100	1122325555	0000100313	3011011212	2222112320	0122200001	4511000014	0173000200	?2020000001	2000010000	0003300000	0000000000
<i>Soritia moerens</i>	1100000011	1122324455	0000100003	3033010312	2222112320	0122200001	4511001614	01730001100	2712000001	2000010000	0001100000	0000000000
<i>Chalcosia</i>	0011220011	2111326555	0000155113	4011010312	2222112220	0122200001	4511001614	0103000200	2711000001	3000010000	0005500000	000A02222
<i>pectinicornis</i>												
<i>Chalcosia pretiosa</i>	0011220011	2111326555	0000122113	4011010312	2222112220	0122200001	4511001214	0173000200	2711000001	3000010000	0005500000	0000000044
<i>Chalcosia</i>	0011220071	2111326555	0000144113	4011010312	2222112220	0122200001	4511002414	0173000200	2721000001	3000010000	0005500000	000002211
<i>rycemeroides</i>												
<i>'Chalcosia' thibetana</i>	0011221111	2022325555	0000100114	3022011212	2222112210	0122200001	4511000014	0174000200	?300001001	2000010000	0005500000	0000000000
<i>'Chalcosia' alpherakyi</i>	0011221111	2022325555	0000142214	3022011212	2222112210	0122200001	4511000214	0174000200	?300001001	2000010000	0005500000	0000000000
<i>Chalcosia zehma</i>	0011220011	2122435555	0000155113	3000010312	2222112320	0121200001	4511001614	0174000200	2712001001	3000010001	0002300001	0000000111
<i>Millieria adalifa</i>	0011220011	2111326555	0000111113	4011010312	2222112220	0122200001	4511001614	0103000200	2712001001	3000011010	0002300001	00020A0A11
<i>Millieria rehfousi</i>	0022221111	2122437755	0000111113	4011010312	2222112220	0122200001	4511001614	0173000200	2712000001	3000011000	0003300000	0010000000
<i>Millieria hamiltoni</i>	0022221111	2122437755	0000111113	4011010312	2222112220	0122200001	4511001614	0173000200	2712000001	3000011000	0003300000	0003022200
<i>Millieria okushimai</i>	0022330011	2122436666	0100111113	3011010312	2222112220	0122200001	4511003014	0173000200	2712001001	3000011000	0003300000	0010110000
<i>Eusphadera ligata</i>	0031230110	2131425544	0100111211	4022010312	2222112320	0122200001	4511000014	0173000200	2711001001	3000010000	0003300000	0000000000
<i>Eusphadera bellula</i>	0031230110	2131425544	0100111211	4022010312	2222112320	0122200001	4511000014	0173000200	2711001001	3000010000	0003300000	0000000000
<i>Eusphadera picturata</i>	0031230110	2131425544	0100111211	4022010312	2222112320	0122200001	4511000014	0173000200	2711001001	3000010000	0003300000	0000000000
<i>Eusphadera venus</i>	0031230110	2131425544	0100111211	4022010312	2222112320	0122200001	4511000014	0173000200	2711001001	3000010000	0003300000	0000000000
<i>Eusphadera regina</i>	0031230110	2131425544	0100111211	4022010312	2222112320	0122200001	4511000014	0173000200	2711001001	3000010000	0003300000	0000000000
<i>Eusphadera</i>	0031230110	2131425544	0100111211	4022010312	2222112320	0122200001	4511000014	0173000200	2711001001	3000010000	0003300001	0000000011
<i>multicolor</i>												
<i>Eusphadera subnigra</i>	073727071?	27374754?	0100117271	?027010312	2222112370	0122200001	4511000014	0177000200	2711001001	300001007?	000370000?	000000070?
<i>Psaphis camadeia</i>	0011230000	2111324444	0000144113	4011010312	2222112220	0122200001	4511002014	0174000200	2222001001	3000010000	0007710000	0010023322
<i>Psaphis gloriosus</i>	0011230000	2111324444	0000100113	4011010312	2222112220	0122200001	4511003014	0174000200	2222001001	3000010011	0007510001	0010021013
<i>Psaphis azurea</i>	0011230000	2111324444	0000100113	4011010312	2222112220	0122200001	4511003014	0174000200	2222001001	3000010011	0007510001	0010022013
<i>Pseudonycetema dissimulata</i>	0011220011	2111326555	0000100113	4011010312	2222112220	0122200001	4511003314	0173000200	3700001001	3000012001	0005500001	1000300000
<i>Pseudonycetema marginale</i>	0011220011	2111326555	0000133113	4011010312	2222112220	0122200001	4511003314	0173000200	3700001001	3000012001	0005500000	0000300000

APPENDIX 3 Continued

Taxa	Characters													
	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	111-120	121-130	131-140
<i>Pseudopidorus fuscatus</i>	0023230011	2102335646	0100155113	2033011312	2222112220	0122200001	4511001614	3211000000	1101011001	0103000200	2700000001	3000010000	0003300000	0000000000
<i>Neochalcocisia remota</i>	0033220011	2122335645	0100155213	3043010312	2222112320	0122200001	4511001614	3211000000	1101011001	0104000200	2711000001	3000010000	0003300000	0000000000
<i>Proseanorophila distincta</i>	0011221100	1122326655	0100104113	3000010312	2222112320	0121400001	4511002114	3212010100	1001011001	0103000200	2732000001	2000010011	0007300001	0000002224
<i>Proseanorophila mirifica</i>	0032110000	2111224444	0000155201	2033010312	2222112320	0121100001	4511001614	3211000000	1001011001	01730001200	?202002001	3000010001	0003300000	0000000000
<i>Trypanophora hyalina</i>	0000130111	1011333646	0000141113	3000010312	2222112320	0122400101	4511000014	3212304000	1101011001	0103000200	27F0100001	2001000011	0002100000	0000000000
<i>Trypanophora deligata</i>	0021110011	?223325555	0000100002	3022010312	2222112320	0122200001	4511000014	3211000000	0001011001	0172000200	0132000001	3000010001	1001300000	0000000000
<i>Trypanophora produens</i>	0011121111	2111325645	0000100112	2022010312	2222112200	0122300101	4511000014	3211334400	1101011001	0173000200	2700000001	0000010001	0001100000	0000000000
<i>Scotopais tristis</i>	0011110011	1100325555	0000145002	2011010312	2222112210	0122200001	4511001514	3211445500	1101011001	0173000200	2702002001	3000010000	0001100000	0000000000
<i>Hisia flabelliformis</i>	0000331111	2111326655	0100155112	3011010312	2222112320	0122200001	4511000614	3211000000	1101011001	0104012200	2700001001	3000012000	0008800100	0000000000
<i>Hisia dolens</i>	0000331111	2111326655	0100155112	3011010312	2222112320	0122200001	4511000614	3211000000	1101011001	0104012200	2700001001	3000012000	0006600000	0000200000
<i>Hisia eurhadia</i>	?070?3?1?1	?1?1?2?6?4	01001?5?1?1	?0?1?010312	2222112?20	07?7?200001	4511000614	3211?0?0?0	1101011001	01?4?1?2200	2700001001	3000012000	000?30000?0	00000?0?0
<i>Gynautocera papilionaria</i>	0011331111	2122326666	0100155112	3011010312	2222112320	0122200001	4511000614	3211000000	1101011A01	0104010200	2701001001	3000010000	0002200000	0000000000
<i>Gynautocera rubristictulata</i>	0011331111	2122326666	0100155112	3011010312	2222112320	0122200001	4511000614	3211000000	1101011101	0104010200	2701001001	3000010000	0002200000	0000000000
<i>Gynautocera philomera</i>	0011331111	2133326666	0100155112	3011010312	2222112320	0122200001	4511000614	3211000000	1101011001	01?4010200	2701001001	3000010000	0002200000	0000000000
<i>Pompelon marginata</i>	0011331111	2133436655	0000111112	3011010312	2222112320	0122200001	4511000614	3211000000	1101011001	0104012200	2700001001	3000010000	0003300000	0000000000
<i>Boradiopsis grisea</i>	0030210011	2133325554	0000100201	2033010312	2222112210	0122200001	4511000414	3211000000	0001011001	01?2000200	3732000001	3000010000	1003300000	0000000000
<i>Aphantacephala moluccarum</i>	0011000011	1100217766	0000100003	4022010312	2222112210	0122?00001	4511000014	3211000000	0001011001	01?4000200	3732000001	3000010000	0003300000	0000000000
<i>Aphantacephala fragilis</i>	?0?1?0?0?1	?1?0?1?7?6	00001?0?0?1	40?2?010312	2222112?10	07??200001	4511000014	3211?0?0?0	00010111001	01?4?00200	3732000001	3000010000	0003300000	00000?0?0
<i>Allocaprina duganga</i>	0012120001	2111324444	0000103103	3013011312	2222112220	0122100001	4511000014	3211334400	1001011001	01?2000200	2702000001	30000100??	000030000?0	0000000041
<i>Doceleopsis dohertyi</i>	?0?3?2?0?1?	?2?3?4?5?4?	010010?2?1	?0?2?011312	22221123?0	0122?0?0?01	4511000014	32110?0?0?	1101011001	01?7000200	2711001001	30000100??	0003?00000?	0000000?0?
<i>Doceleopsis zambonga</i>	0030210011	2133325554	0000100201	2022010312	2222112210	0122200001	4511000014	3211000000	0001011001	01?2000200	3732000001	3000010001	1003300000	0000000000
<i>Doceleopsis sulcaensis</i>	0?2?1?0?1?	?2?2?4?5?4?	000010?2?2	?0?3?010312	22221122?0	0122?0?0?1	4511001014	32115?5?0?	1001011001	01?7000200	3732000001	30000100??	0003?0000?	0000000?0?
<i>Doceleopsis stigma</i>	0032220111	2122425544	0000101202	2032010312	22221122?0	0122?00001	4511001014	3211555500	1001011001	01?7000200	3732000001	30000100??	0003300000?	0000000?0?
<i>Euxanthopyge hexophthalma</i>	?0?2?2?1?1	?1?2?2?5?4	00001?0?0?	?0?2?010312	2222112?10	07??200001	4511001614	3211?5?5?0	0001011001	01?2?01200	3732000001	30000100??	000?30000?0	000000?0?0
<i>Euxanthopyge yazakii</i>	?0?2?2?2?1?	?1?2?2?2?5?4	00001?1?0?	?0?2?010312	2222112?10	07??200001	4511001614	3211?5?6?0	0001011001	01?2?01200	3732000001	30000100??	000?200000?	0000000?0?
141-150	151-160	161-170	171-180	181-190	191-200	201-210	211-220	221-230	231-240	241-250	251-260	261-270	271-280	
<i>Burlacena aegerioides</i>	0000000000	0011000000	0000000000	0000111000	0000000000	0000000000	0?0?0000?0	0?00020000	2200000?00	0000000000	0003000000	0000000000	3001050000	0000000001
<i>Himantopteris fuscinervis</i>	0000000000	0044000000	0001023277	0066100000	0000000020	0000000000	0?0?0000?0	0?0?0000?00	0200000?00	0000000000	0000000000	0000000000	3011000000	0000000000
<i>Anomoeotes levis</i>	0000000000	0000000000	0001023277	0066100000	0000000020	0000000000	0?0?0000?00	0?0?0000?00	0100000?00	0000000000	0000000000	0000000000	3001000000	0000000000
<i>Dianeura goochii</i>	0000000000	0000000000	0001023277	0066100000	0000000020	0000000000	0?0?0000?00	0?0?0000?00	0100000?00	0000000000	0000000000	0000000000	3011000000	0000000000
<i>Lactura dives</i>	0000000000	0066000000	0000000000	0000000033	2234010000	0000000000	0?0?0000?00	0?0?0000?00	0200000?00	0000000000	0000000000	0000000000	3001000000	0000000000
<i>Phauda mimica</i>	0000000000	0011000000	0000000000	0000000010	0000000000	0000000000	0?0?0000?00	0?0?0000?00	0200000?00	0000000000	0000000000	0000000000	3001000000	0001000000
<i>Heterogynis sp.</i>	?0?0?0?000	000?00?000	?000023277	0066002000	0000000000	0000000000	0?0?0000?00	0?0?0000?00	01?0000000	0000000000	0000000000	0000000000	30000?0000	1000000000
<i>Artonea hainana</i>	0000000000	0055000220	0010000033	2334011010	0035000021	000001000?0	0?0?0000?00	0?0?0000?00	0000000001	2000000000	0000000000	0010000000	1000?0001	0001100000
<i>Theresimima ampellophaga</i>	0000000000	0000000000	0010000033	2334011000	0000000020	0000000000	0?0?0000?00	0?0?0000?00	0000000001	2000000001	0000000000	0010000000	3010?0001	0001100000
<i>Adscita stitices</i>	0000000000	0000000000	0010000033	2334011000	0000000020	0000000000	0?0?0000?00	0?0?0000?00	0000000000	2000000001	0001000000	0010000000	3010?0000	0000100000
<i>Pollanisus viridipulverulenta</i>	0000000000	0000000000	0010000033	2334012100	0000000020	000001000?0	0?0?0000?00	0?0?0000?00	0000000000	2000000001	0001000000	0010000000	1000?0000	0000100000

<i>Ilitiberis pruni</i>	0000000000	0055000000	0010000033	2334011100	0000000020	000001000?	0?P0000?00	0?P00000000	0000000001	0001000000	0010000000	0010000000	3010?P0001	1001100000
<i>Clelea formosana</i>	0000000000	0000000000	0010000033	2334011100	0000000020	000001000?	0?P0000?00	0?P00000000	0000000001	0000000000	0010000000	0010000000	3000?P0000	0000100000
<i>Harrisina americana</i>	0000000000	0000000000	0010000033	2334011100	0000000020	000000000?	0?P0000?00	0?P00000000	0000000001	0000000000	0010000000	0010000000	3000?P0000	0000100000
<i>Pyromorpha sp.</i>	0000000000	0055000000	0010000033	2334011100	0000000020	000000000?	0?P0000?00	0?P00000000	0000000001	0000000000	0010000000	0010000000	3000?P0000	0000100000
<i>Saliunca styx</i>	0000000000	0000000000	0010000033	2334011100	0000000011	200001000?	0?P0000?00	0?P00000000	0000000001	0000000000	0010000000	0010000000	3000?P0000	0000100000
<i>Jansoula titaea</i>	0000000000	0000000000	0010000055	2334011100	0000000020	000001000?	0?P0000?00	0?P00000000	0000000000	0000000000	0000000000	0000000000	3010?P0000	0001100000
<i>Hemophylotus nigra</i>	0000000000	0000000000	0010000055	2344011000	0000000020	000001000?	0?P0000?20	0450010000	0000000001	0000000000	0010000000	0010000000	2010?P0001	0301100110
<i>Zogaena filipendulae</i>	0000000000	0000000000	0010000033	2333023300	0000000020	100001000?	0?P0000?00	0?P00000000	0000000002	0002000000	0000000000	0000000000	3001150000	1001100000
<i>Pnyrtia sinica</i>	0000000000	0000000000	0010200777	0666011000	0000000010	000001000?	0?P0000?00	01P0000000	0000000000	0000000000	0000000000	0000000000	3031120010	1001100000
<i>Callizogaena ada</i>	0000000000	0000000000	0022A0032FF	2622010000	0000000021	100001000?	0?P0000?00	01P0000000	0000000000	1001000000	0000000000	0000000000	1000?P0?70	1110111120
<i>Chalcosiopsis variata</i>	0000000000	0064010000	0000003200	2200013011	0022000020	000000000?	0?P0000?00	0000000000	0000000000	0000000000	0000000000	0000000000	300?P00000	0001000000
<i>Chalcosiopsis melli</i>	0000000000	0000000000	0000003200	2200013000	0000000020	000000000?	0?P0000?01	0?P0001000	0000000000	0000000000	0000000000	0000000000	300?P00000	0000000000
<i>Inoueta formosana</i>	0000000000	0000000000	0010000055	2344010100	0000000020	000001000?	0?P0000?20	0450010000	0000000001	0000000000	0010000000	0010000000	2010?P0001	0301000110
<i>Cleoda syntomoides</i>	0000000000	0005000000	002100326G	2322020200	0000000022	100001000?	0?P0000?00	05P0000000	0000010000	0000000000	0000000000	0000000000	2000?P0?70	1410111140
<i>Heteropan scintillens</i>	0000000000	0000000000	0020000033	2334013200	0000000001	100000000?	0?P0000?00	02P0000000	0000000001	1000000000	0000000000	0000000000	2011000001	1210111130
<i>Heteropan athenus</i>	0000000000	0055000000	0020000033	2334013200	0000000001	100000000?	0?P0000?00	04P0000000	0000000001	1000000000	0000000000	0020000000	3011000001	1210111130
<i>Heteropan appendiculata</i>	0000000000	0000000000	0020000033	2334013200	0000000001	100000000?	0?P0000?00	01P0000000	0000000000	1000000000	0000000000	0000000000	3011000000	1210111130
<i>Cadphises moorei</i>	0000000000	0000000000	0021103266	3355015300	0000000002	100012000?	0?P0011?00	0?P00000100	0011003000	0120000000	0030100000	0030100000	1101040112	1101011120
<i>Cadphises maculatus</i>	0000000000	0000000002	0021103266	3355015300	0000000002	100012000?	0?P0011?00	0?P0000100	0011003000	0120000000	0030100000	0030100000	1101040112	1101011120
<i>Hampsonia pulcherrima</i>	0000000000	0055000002	0021103266	3355016300	0000000002	100012000?	0?P0000?00	0?P00000100	0012003000	0120000000	0030100000	0030100000	1101040112	1101011120
<i>Watermania bifasciata</i>	0020000000	0000200000	0021103266	3355014300	0000000002	100012000?	0?P0000?00	0?P00000100	0012003000	0120000000	0030100000	0030100000	1101040112	1101011120
<i>Herpida eupoma</i>	0000000000	0002200000	0021103266	3355016300	0000000002	100012000?	0?P0000?00	0?P00000100	0012003000	0120000000	0030100000	0030100000	1101040112	1101011120
<i>Aglaope infausta</i>	0000000000	0055000000	0021103233	1133014300	0000000002	300001000?	0?P0000?00	04P0000330	0023003100	0010000000	0020010001	0030200000	1101040112	1310111120
<i>Philopator basimaculata</i>	0000000000	0060011000	0021103266	3355014311	0044111102	200001000?	0?P0000?00	03P00000100	0023003100	0010000000	1000010001	0030200000	1101030112	1210111120
<i>Formozogaena shibatai</i>	0000000000	0055200000	0021103266	3355014300	0000000002	200001000?	0?P0000?00	03P0000330	0023003100	0010000000	1000010001	0030200000	1101030112	1210111120
<i>Atlesia nervosa</i>	0P0P0P0P00	005P00P0?0	0021103266	335501530?P	0P0P0P0P02	100001000?	0?P0000?00	04P0000430	0033003100	0010000000	1000610001	0130100000	1101030112	????????
<i>Elysima westwoodi</i>	0000000000	0000000000	00221113277	0666016300	0000000002	000024000?	0?P0001?00	01P0000130	0135003100	0010000000	1000510001	0030100000	1101040112	1210111130
<i>Achelura bifasciata</i>	0000000000	0000000000	00221113277	0666031300	0000000000	000011000?	0?P0011?00	05P0000130	0134003100	0010000000	1000310001	0030200000	1101040112	1310111130
<i>Achelura javana</i>	0000000000	0000000000	00221113277	0666031300	0000000000	000011000?	0?P0011?00	05P0001300	0134003100	0010000000	1000310001	0030200000	1101040112	1310111130
<i>Achelura hemileuca</i>	0000000000	0000000000	00221113277	0666014300	0000000000	001012000?	0?P0011?00	05P0000130	0134003100	0010000000	1000010001	0030200000	1101040112	1210111130
<i>Boradia carneola</i>	0000000000	0000000000	00221113277	0666014300	0000000002	000002000?	0?P0011?00	02P0000130	0134003100	0010000000	1000710001	0000000000	3101040112	1101011130
<i>Agalope glacialis</i>	0000000000	0000000000	00221113277	0666013300	0000000003	100001000?	0?P2200?00	01P0000230	0135003100	0010000000	1000210001	0030100000	11010350112	1101011130
<i>Agalope immaculata</i>	0000000000	0000000000	00221113277	0666016300	0000000002	100001000?	0?P0000?00	01P0000120	0135003100	0010000000	1000710001	0030000000	1101040112	1101011130
<i>Agalope hyalina</i>	0000110000	0000000000	00221113277	0666010300	0000000002	600413000?	0?P0000?00	01P0000120	0136003100	0010000000	1000410001	0030100000	3101040112	1101011130
<i>Agalope eronioides</i>	0000000000	0000000000	00221113277	0666010300	0000000002	600013000?	0?P0000?00	01P0000120	0136003100	0010000000	1000410001	0030100000	1101040112	1101011130
<i>Agalope bieti</i>	0000033000	0000000000	00221113277	0666013300	0000000003	600512000?	0?P22000?00	01P0000130	0133003100	0010000000	1000FI0001	0030100000	1101040112	1101011130
<i>Agalope pica</i>	0000033000	0000000000	00221113277	0666013300	0000000003	600012000?	0?P22000?00	01P0000130	0133003100	0010000000	1000110001	0030100000	1101040112	1101011130
<i>Campylotes histronicus</i>	0000055000	0000000000	0021103266	3355014300	0040000003	210012000?	0?P0000?00	02P0100121	0000122000	0010000000	1000010001	0030100000	3101030112	1101011120
<i>Campylotes desgandini</i>	0000055000	0060000000	0021103266	3355016300	0040000003	210012000?	0?P0000?00	02P0100121	0000122000	0010000000	1000010001	0030100000	3101030112	1101011120
<i>Neotherpa venosa</i>	0000000000	0000000000	002110326G	3133014311	0011000003	410012000?	0?P0000?00	03P0100121	0000122000	2010000007	1000010001	0030000000	3001240112	1210111120
<i>Neotherpa subhyalina</i>	0000000000	0000000000	00211032KK	1144014311	0011000003	410012000?	0?P0000?00	03P0100121	0000122000	2010000007	1000010001	0030000000	3001250112	1210111120
<i>Neotherpa eleonora</i>	0000000000	0000000000	002110326G	3433014300	0011000003	410002000?	0?P0000?00	03P0100121	0000122000	2010000007	1001010001	0030000000	3101040112	1210111120
<i>Pantherpina basiflava</i>	0000000000	0000000000	002110326G	3433014300	0011000003	410002000?	0?P0000?00	03P0100121	0000122000	2010000007	1001010001	0030000000	3101040112	1210111120
<i>Cyclosia panthona</i>	00001L0000	0000000000	0020001034	2333014300	0000000021	100000000?	0?P0000?00	0?P0000100	0100233000	0010000004	1000020001	0040000000	3011020112	1210111130
<i>Cyclosia papilionaris</i>	0001035000	0004000000	0020001034	2333014301	00B3000021	100000000?	0?P0000?00	0?P0000100	0100233000	0010000004	1000020001	0040000000	3011020112	1310111100
<i>Cyclosia chartacea</i>	0001035000	0004000000	0020001034	2333014302	0002000001	100000000?	0?P0000?00	0?P0000100	0100233000	0010000004	1000020001	0040000000	3011020112	1310111100
<i>Cyclosia spargens</i>	0001035000	0004000000	0020001034	2333014300	0004000021	100000000?	0?P0000?00	0?P0000100	0100233000	0010000004	1000020001	0040000000	3011020112	1310111100
<i>Cyclosia maculata</i>	0001035000	000D000000	0020001034	2333014301	000I000001	100000000?	0?P0000?00	0?P0000100	0100233000	0010000004	1000020001	0040000000	3011020112	1310111100
<i>Cyclosia imitans</i>	0000055000	0000000000	0020001034	23330143AA	0004000021	100000000?	0?P0000?00	0?P0000100	0100233000	0010000004	1000020001	0040000000	3011020112	1410111150
<i>Cyclosia curiosa</i>	0000055000	0000000000	0020001034	2333014300	0000000021	100000000?	0?P0000?00	0?P0000100	0100233000	0010000004	1000020001	0040000000	3011020112	1410111150

APPENDIX 3 Continued

Taxa	141-150	151-160	161-170	171-180	181-190	191-200	201-210	211-220	221-230	231-240	241-250	251-260	261-270	271-280
<i>Cyclostia inclusis</i>	0021100000	0002000010	0020001034	2333014310	0010000021	1000000002	0?0000000?	0?0000000?	0100233000	0010000004	1000020001	0040000000	3011020012	1510111150
<i>Cyclostia eucharta</i>	0021045000	0002000010	0020001034	2334014301	0051000021	1000000002	0?0000000?	0?0000000?	0100233000	0010000004	1000020001	0040000000	3011020112	1510111150
<i>Cyclostia electra</i>	0000000000	0033000000	0020001234	2333014310	0010000021	1000000002	0?0000000?	0?0000000?	0100233000	0010000004	1000020001	0040000000	3011020112	1410111150
<i>Cyclostia notabilis</i>	0000055000	0066000000	0020002233	2344026300	0000110032	2070643004	8600200020	0?60010002	1?00005500	1123640520	1000072?21	0065065510	5071081112	1210111130
<i>Rhodopsona costata</i>	0000002000	0000000000	0020001033	2333L016300	0000000022	1000650002	0?0000000?	0?0000000?	0100000000	0010000000	1000030011	0050100000	3011020000	1101011130
<i>Rhodopsona rubiginosa</i>	0000000000	0000000000	0020001033	2333L016300	0000000022	1000620002	0?0000000?	0?0000000?	0100000000	0010000000	1000030011	00500010000	3011020000	1210111130
<i>Rhodopsona jordani</i>	0?000?0200	00?00?0?0?0?	0020001033	2333L0163?0	0?00000?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0100000000	0010000000	1000030011	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?
<i>Rhodopsona reverdini</i>	0?000?0200	00?00?0?0?0?	0020001033	2333L0163?0	0?00000?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0100000000	0010000000	1000030011	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?
<i>Rhodopsona marginata</i>	0000000000	0055000000	0020001033	2333L016300	0000000022	1000620002	0?0000000?	0?0000000?	0100000000	0010000000	1000030011	00500010000	3011020000	1210111130
<i>Rhodopsona matsumotoi</i>	0000000100	0000100000	0020001033	2333L016300	0000000022	1000620002	0?0000000?	0?0000000?	0100000000	0010000000	1000030011	00500010000	3011020000	1210111130
<i>Heteropanula flavimaculata</i>	0000011000	0000000000	0020001034	1344013300	0000000021	1000020002	0?0?0000000?	0?0?0000000?	0100004000	2100000005	1000030001	00500000000	4011000010	1110111130
<i>Pseudarbutus ochrea</i>	0000000000	0000000000	002000103L	2344014300	00000000?1	100002000?	0?00000?0?	0?00000?0?	0?00004000	2010000005	1001000001	00500000000	1011061110	1110111120
<i>Corma maculata</i>	0211022000	0002000000	0020001233	2344014331	0022111113	200002000?	0?00000?0?	0?00000?0?	0000213200	0010000000	1000020011	0050020000	0101030112	1410111150
<i>Corma fragilis</i>	3322022000	0022000000	0020001233	2344014310	0010100012	200002000?	0?00000?0?	0?00000?0?	0000213200	0010000006	1000020011	0050310000	1101030112	1310111150
<i>Corma zenobia</i>	3311063000	00C3000000	0020001233	2333014300	0000110021	200002000?	0?00000?0?	0?00000?0?	0000213200	0010000006	1000020011	0050300000	1101040112	1210111130
<i>Eucomriopsis lampra</i>	0000000000	0000000000	0020001233	2333014300	0002000021	100002000?	0?00000?0?	0?00000?0?	0000533200	0010000000	1000020011	00503000000	2101040112	1210111130
<i>Dodecomorpha boholica</i>	0?0?0?0?00	000?00?0?0?	0?020001255	234401431?	0?2?0?0?21	100002000?	0?00000?0?	0?00000?0?	0000313200	0010000000	1000020011	00503000000	3101040112	1?0?0?0?0?0?
<i>Cryptophysophilus bicoloratus</i>	0?0?0?3000	10?2?0?0?0?	01200001255	23440143?0	0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?
<i>Heterustinula dichroa</i>	0?0?0?3000	10?2?0?0?0?	01200001255	23440143?0	0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?
<i>Anarbutus insignis</i>	1122000000	0000000000	0020000255	2344013300	0000000021	100002000?	0?00000?0?	0?00000?0?	0000213200	0010000000	1000000111	00503000000	4111000012	1410111130
<i>Anarbutus bipartita</i>	1111044000	0033000000	0021000023	2334010300	0000110032	2000633000	0?0?03000?	0?0?03000?	1?00005500	1123640310	1000072001	0069005010	5001011112	1310111150
<i>Arbutus bicolor</i>	0000000000	0033000000	0020001033	2345014300	0000000021	100002000?	0?00000?0?	0?00000?0?	0?00004000	0010000003	1000030001	0061031000	3011030012	1110111120
<i>Arbutus melanoleuca</i>	0?0?0?0?00	003?00?0?0?	0?020001033	2345014300	0?0?0?0?21	100002000?	0?00000?0?	0?00000?0?	0?00004400	0010000003	1000030001	0061031000	3011030012	1?0?0?0?0?0?
<i>Arbutus submaculata</i>	0002000000	0003000000	0020001033	2345014300	0000000021	100002000?	0?00000?0?	0?00000?0?	0?00004400	0010000003	1000030001	0061031000	3011030012	1110111120
<i>Arbutus leno</i>	0022100000	0011000000	0020001033	2345014300	0000000021	100002000?	0?00000?0?	0?00000?0?	0?00004400	0010000003	1000030001	0061031000	3011030012	1110111120
<i>Arbutus truncatus</i>	0022100000	0000000000	0020001033	2345014300	0000000021	100002000?	0?00000?0?	0?00000?0?	0?00004400	0010000003	1000030001	0061031000	3011030012	1110111120
<i>Euromorphiopsis quadripaga</i>	0000000000	0000000000	0020001233	1244014300	0000000021	100001000?	0?00000?0?	0?00000?0?	0?00005500	0000000003	1000040001	0061031000	3021031112	1110111120
<i>Euromorphiopsis leis</i>	0000000000	0056000030	0020001233	1244014300	0000000021	100001000?	0?00000?0?	0?00000?0?	0?00005500	0000000003	1000040001	0061031000	3021031112	1110111120
<i>Pidorus glaucopsis</i>	0022100000	0000000000	0020001036	2334025400	0000000031	501024100?	0?00000?0?	0?00000?0?	0?00005500	0000000000	1000040001	0062042000	4041021112	1110111130
<i>Pidorus cyrtus</i>	0022100000	0000000000	0020001036	2334025400	0000000031	501024100?	0?00000?0?	0?00000?0?	0?00005500	0000000000	1000040001	0062042000	4041021112	1210111130
<i>Pidorus cretinata</i>	0022000000	0033000000	002002046	3334024400	0000000031	901024100?	0?00000?0?	0?00000?0?	0?00005500	0000000000	1000040001	0062042001	4041031112	1210111130
<i>Pidorus culoti</i>	0000000000	0055022000	0020002046	3334024400	0000000031	501034108?	0?00000?0?	0?00000?0?	0?00005500	0000000000	1000040001	0062042001	4041061112	1210111130
<i>Pidorus corculum</i>	0022100000	0000000000	0020001033	2334014300	0000000021	100006000?	0?00000?0?	0?00000?0?	0?00005600	0010000000	1000060001	0062053000	5041051112	1110111130
<i>Pidorus gemina</i>	0022100000	1000000000	0120000031	2330143000	0000000021	100006000?	0?00000?0?	0?00000?0?	0?00005600	0110000000	1000060001	0062043304	5041001112	1410111140
<i>Pidorus bifasciatus</i>	3?1?0?0?00	000?00?0?0?	0020001036	233401630?	0?0?0?0?21	100006000?	0?00000?0?	0?00000?0?	0?00005600	0110000000	1000060001	0062042002	5011021112	1?0?0?0?0?0?
<i>Pidorus chalybeatus</i>	3?2?0?0?00	000?00?0?0?	00200000?3	193401630?	0?0?0?0?25	6010233000	3220000220	0?30010002	2?00005600	0110000000	1000060001	0062052004	5041011112	1?0?0?0?0?0?
<i>Pidorus constrictus</i>	0022100000	1000000000	012000103M	2644024300	0000000031	002034146?	0?00000?0?	0?00000?0?	0?00005510	1222241000	1000070001	0065094000	5051121112	1310111130
<i>Pidorus fasciatus</i>	0022000000	0033024000	0020001034	2344024300	0000000030	603467210?	0?00000?0?	0?00000?0?	0?00005800	1222233000	1000070001	0065077010	4011031112	1110111130
<i>Pidorus circe</i>	0022100000	1100000000	0120001034	2344025300	0000000030	400467210?	0?00000?0?	0?00000?0?	0?00005700	1222230000	1000070001	0065077010	3001041112	1210111130
<i>Pidorus ochrophonus</i>	0?0?0?0?00	11?0?0?0?0?	0120001034	23340253?0	0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?
<i>Pidorus splendens</i>	0022000000	0033000000	002000123K	2333026300	000000003?	0?06233004	7500300020	0?10030002	1?00005500	0113400000	1000072001	0065065110	5071031112	1210111130
<i>Pidorus miles</i>	0000000000	0000200000	0020001031	2334016300	0000000022	000004000?	0?00000?0?	0?00000?0?	0000004001	0010000000	1000030011	00500000000	4011000010	1210111120
<i>Hemiselia meeki</i>	0022033000	0044011000	0020001033	2343024400	0000000031	501001000?	0?00000?0?	0?00000?0?	0?00005500	0000000000	1000040001	0062042000	4011021112	1410111150
<i>Hemiselia sp. Luzon</i>	0011033000	0044000000	0120001033	2343024400	0000000031	501001000?	0?00000?0?	0?00000?0?	0?00005500	0000000000	1000040001	0062042000	4011021112	1410111150
<i>Hemiselia albivitta</i>	0000000000	0055000000	0020000303	1343014300	0000000021	100006100?	0?00000?0?	0?00000?0?	0?00005600	0110100000	1000060111	0062052004	4041011112	1210111140
<i>Isocambica melaleuca</i>	0?0?0?0?00	000?0?0?0?	0020000303	22340143?0	0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?	0?0?0?0?0?0?
<i>Herpotosia augarra</i>	0000011000	0055000000	002000103K	2343011301	0003000023	000001000?	0?00000?0?	0?00000?0?	0?00005500	0010000000	1000050111	00620000000	5001041112	1110111140

APPENDIX 3 Continued

Taxa	141-150	151-160	161-170	171-180	181-190	191-200	201-210	211-220	221-230	231-240	241-250	251-260	261-270	271-280
<i>Chalostia nycetemeroides</i>	2211033000	0065000000	0020000113J	2343026311	00111110030	2070643002	8600200020	0750010002	1700005500	1123640520	1000072001	0065065510	5061061112	1210111130
<i>'Chalostia' thibetana</i>	1111100000	0033000000	0021103233	2344016311	0022111102	1000030002	0721000700	0570000030	0133000310	0010000000	1000010001	0030200000	3101040112	1210111120
<i>'Chalostia' alpherakyi</i>	1111000000	0033000000	0021103233	2344016300	0000000002	1000030002	0721000700	0570000030	0133000310	0010000000	1000010001	0030200000	3101040112	1210111120
<i>Chalostia zehna</i>	0012000000	1033004000	012000123K	2333026300	0040000030	20602233004	7500030020	0710010002	1700005500	1113400000	1000072001	0065005110	5071031112	1610111130
<i>Milleria adalifa</i>	2211055000	000200000F	020000123J	2344026300	0040000020	2070643004	8600200020	0750010002	1700005500	1123640520	1000072001	0065065510	5061061112	1210111130
<i>Milleria rehousi</i>	0000055000	0000000002	202000323J	2344026300	0040000022	2070643004	8600200020	0750010002	1700005500	1123640520	1000072001	0065065510	5041081112	1210111130
<i>Milleria hamiltoni</i>	2211055000	0000000002	202000323J	2344026300	0040000032	2070643004	8600200020	0750010002	1700005500	1123640520	1000072001	0065065510	5061081112	1210111130
<i>Milleria okushimai</i>	0000033001	0000022002	020000123J	2334026300	0040000034	0080643000	8730100020	0780010002	1700005500	1123640130	1000072001	0065065510	5071261112	1210111130
<i>Eusphalera ligata</i>	0022000000	0033000220	0020001233	2344026300	0000000032	2070643000	8610100120	0700010002	1700005500	1123640520	1000072001	0065065510	5071061112	1510111130
<i>Eusphalera bellula</i>	0027033000	1022000000	0120001233	2344026300	0000000032	2070643000	8610100120	0700010002	1700005500	1123640520	1000072001	0065065510	5071061112	1510111130
<i>Eusphalera picturata</i>	0022000000	1033055000	0120001233	2344026300	0000000032	2070643000	8610100120	0700010002	1700005500	1123640520	1000072001	0065065510	5071061112	1510111130
<i>Eusphalera venus</i>	0022000000	0033000000	0020001233	2344026300	0000000032	2070643000	8610100120	0700010002	1700005500	1123640520	1000072001	0065065510	5071061112	1510111130
<i>Eusphalera regina</i>	3322000000	0033000220	0020001233	2344026300	0000000032	2070643000	8610100120	0700010002	1700005500	1123640520	1000072001	0065065510	5071061112	1510111130
<i>Eusphalera</i>	3322000000	0000004000	0020001233	2344026300	0000000032	2070643000	8610100120	0700010002	1700005500	1123640520	1000072001	0065065510	5071061112	1510111130
<i>multicolor</i>														
<i>Eusphalera subnigra</i>	3727070000	0007007070	7020001233	2344026300	0707070732	2070643000	8610100120	0700010002	1700005500	1123640520	1000072001	0065065510	5071067777	7777777777
<i>Psaphis canadana</i>	000033001	0000000000	00200012L3	2344026311	0022000032	2070643000	8720100120	0760010002	1700005500	1123640520	1000072001	0065065510	5041061112	1510111130
<i>Psaphis gloriosus</i>	0001033001	0022000000	00200012L3	2344026301	0042000032	2070643000	8720100120	0760010002	1700005500	1123640520	1000072001	0065065510	5041061112	1510111130
<i>Psaphis azurea</i>	2201033001	0002000000	00200012L3	2344026301	0023110132	2070643000	8720100120	0760010002	1700005500	1123640520	1000072001	0065065510	5041061112	1510111130
<i>Pseudonyctemera dissimulata</i>	00AA050000	0004000000	1020001033	2334026300	0000110031	2090143000	8900300020	0760010002	1700005500	1123640520	1000072001	0065065510	5071061112	1210111130
<i>Pseudonyctemera marginale</i>	0022055000	0033000000	0020001033	2334026300	0000110031	2090143000	8900300020	0760010002	1700005500	1123640520	1000072001	0065065510	5071061112	1210111130
<i>Pseudopidorus fasciatus</i>	3322000000	0066000000	0021001033	2333026300	0000000033	2010233000	7500030020	0710010002	1700005500	1123640120	1000072001	0062095210	4041041112	1310111130
<i>Neochalcosia remota</i>	3322000000	0066000000	002000103J	2333026300	0000000032	2010233001	6400200020	0750010002	1700005500	1123640520	1000072001	0065068010	5071051112	1210111130
<i>Prospanandrophila distincta</i>	2211044000	0034022000	0020000123I	2344026310	0125000032	1000633003	6400200020	0700010102	1700005500	1123340420	1000073001	0065098010	5071021112	1310111150
<i>Prospanandrophila mirifica</i>	3311000000	0000000000	0020000033	2344014300	0000000022	1000060002	0720000720	0700010002	2700005600	0110000000	1000060001	0062042002	5011021112	1310111140
<i>Trypanophora hyalina</i>	0000000000	0055000000	002B0032II	4533026311	0033000033	8084433000	6400200020	0750010002	1700005500	1123340220	1000075001	0065008010	5071321112	1210111130
<i>Trypanophora deligata</i>	0000000000	0033000000	0020003033	2343016311	0033000034	0000143004	5300100020	0780010002	1700005500	1123640330	1000072001	0066062010	5071011112	1310111140
<i>Trypanophora proluens</i>	0000000000	0000000000	0021000223	2344026300	0000000034	2070633004	6400100020	0770010002	1700005500	1123640620	1000072001	0065065510	5071261112	1210111130
<i>Scotopais tristis</i>	0000000000	00CC000000	0020003244	3355025311	0033111133	2070633000	2100300220	0760010002	1700005500	1123640310	1000072001	0069095410	5071331112	1210111130
<i>Hisia flabelliformis</i>	0011005000	00CC000000	0020003244	3355025311	0033111133	2070633000	2100300220	0760010002	1700005500	1123640310	1000072001	0069095410	5071331112	1210111130
<i>Hisia dolens</i>	7072070000	0073770707	0020003244	3355025330	0705111173	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777
<i>Hisia eurhodia</i>	0000000000	0000000000	0020003244	3355025500	0055000032	3001233001	5300100020	0760010002	1700005500	1123640310	1000072001	0067005410	5061231112	1210111130
<i>Gynatocera papilionaria</i>	0000000000	0000000000	0020003244	3355025500	0055000032	3001233001	5300100020	0760010002	1700005500	1123640310	1000072001	0067005410	5061231112	1210111130
<i>Gynatocera rubriscuellata</i>	0000000000	00CC000000	0020003244	3355025500	0055000032	3001233001	5300100020	0760010002	1700005500	1123640310	1000072001	0067005410	5061231112	1210111130
<i>Gynatocera philomera</i>	0000000000	0022000000	0020003244	3355025500	0044110032	0000533004	5300100020	0760010002	1700005500	1123640100	1000072001	0065005010	5071241112	1210111130
<i>Pompelops marginata</i>	0000000000	0055000000	0021000023	1334010300	0000000034	3000120000	0720000720	0750010002	1700005500	1123640620	1000072000	0068046310	5071031112	1410111140
<i>Boradopsis grisea</i>	0000000000	0000000000	0021000023	134I010300	0000000034	4005361010	0720000720	0750010002	1700005900	1123640520	1000072001	0067065310	4041011112	1410111140
<i>Aphantocphala molucarum</i>	7070070000	0075770777	0021000023	134I010370	7070707070	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777
<i>Aphantocphala fragilis</i>	0300100010	0043000000	0020000223	2344016300	0000000030	6006321000	0720000720	0770010002	1700005900	1123740130	1000072001	0067065410	0031061112	1110111140
<i>Allocaprima duganga</i>	0707070000	0057007070	7020001233	2344026307	0707070732	2070643000	8200400020	0750010002	1700005500	1123640520	1000072001	0065065510	5071061112	1777777777
<i>Docleopsis dohertyi</i>														

<i>Doceopsis zambaanga</i>	0000000000	0055000000	0020000000	2334010300	0000000034	3000120000	0750000020	0750000020	0750010002	1000005500	1123640620	1000072000	0068046310	5071031112	1410111140
<i>Doceopsis sulauensis</i>	0707010000	0007007220	7021000023	1331010307	0707070731	3001233004	4300100020	0750010020	0750010020	1000005500	1123640620	1000072001	0067065310	4031061112	1777777777
<i>Doceopsis stigma</i>	0707010000	0000000000	0021000023	1331010300	0000000030	3001233004	4300100020	0750010020	0750010020	1000005500	1123640620	1000072001	0067065310	5031061112	1410111140
<i>Euxanthopyge hexophthalma</i>	7270070000	002477D70?	0021003223	1344026370	7070707070?	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777
<i>Euxanthopyge yazakii</i>	7070070000	0076777070?	0021003223	1344026370	7070707070?	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777	7777777777

Characters

Taxa	281-290	291-300	301-310	311-320	321-330	331-340	341-350	351-360	361-370	371-380	381-390	391-400	401-410	411-414
<i>Buriceana aegerioides</i>	0000100000	0000000000	0000000000	0000000000	0000000001	0000010000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Himantopteris fuscineris</i>	0001000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0100101100	0000000000	1010000000	0000000000
<i>Anomoeates levis</i>	0001000000	0000000000	0000000000	0000000000	0000000002	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Dianura goochii</i>	0001000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Lactura dives</i>	0001000000	0000000000	0000000000	0000000000	0000000100	0000000044	0000000000	0100000000	0000000000	0000000000	0111121001	0001000000	0001000000	0000000000
<i>Phaeta mimica</i>	0001000000	0000000000	0000000000	0000000000	0000000100	0000000044	0000000000	0100000000	0000000000	0000000000	0111121001	0002000000	0000000000	0000000000
<i>Heterogynis sp.</i>	0007000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Artona hainana</i>	0001300000	0000000000	0000000000	0030202003	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0021110110	0001000000	3041001000	000111
<i>Theresimima ampellophaga</i>	0001300010	0000000000	0000000000	0030002000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0021110010	0001000000	2011001000	000111
<i>Adscita statices</i>	0001300010	0000000000	0000000000	0030202000	0000000020	0000000000	0000000000	0000000000	0000000000	0000000000	0021110010	0001000000	2031001000	000111
<i>Polianisia viridipulverulenta</i>	0001000020	0000000000	0000000000	0030202004	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Ililiberis pruini</i>	0001300210	0000000000	0000000000	0030202002	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0021110010	0011000000	2021001000	000111
<i>Clelea formosana</i>	0001000210	0000000000	0000000000	0030000003	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0021110110	0011000000	2031001000	000111
<i>Harrisia americana</i>	0001000000	0000000000	0000000000	0030000000	0000000003	0000000000	0000000000	0000000000	0000000000	0000000000	0021110010	0001000000	2031001000	000111
<i>Pyromorpha sp.</i>	0001000000	0000000000	0000000000	0030000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0021110010	0001000000	2031001000	000111
<i>Saluana styx</i>	0001000000	0000000000	0000000000	0030000003	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Jansola titaea</i>	0001000000	0000100002	0000000000	0020000004	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Zomophylotus nigra</i>	0000000000	0000100012	0000000000	0020000004	0000000000	0100000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Zomygna filipendulae</i>	0001100110	0000000002	0000000000	0000100002	0000000000	0000000001	0000000000	0000000000	0000000000	0000000000	0021110010	0001000000	2041001111	1111
<i>Pyretia sinica</i>	0001100220	0000000000	0000000000	0000100002	0000000000	0000000002	0000000000	0000000000	0000000000	0000000000	0021110010	1001000000	3010000111	1111
<i>Callizygna ada</i>	0001300000	0000000002	0000000000	0011001002	0000000000	1000000000	0000000000	0000000000	0000000000	0000000000	0021110021	0002101012	4141071111	1777
<i>Chalcosiopsis variata</i>	0000010000	0000000001	0000000000	0000000100	0000000000	0000010000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Chalcosiopsis melli</i>	0000010002	0000000001	0000000000	0000000100	0000010000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Inouela formosana</i>	0000000000	0000100012	0000000000	0020000004	0000000000	0100000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Cleoda syntomoides</i>	0021000000	0000000003	0000000000	0020000004	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Heteropan scintillans</i>	0021000000	0000000000	0000000000	0000000002	0000010000	0000010000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Heteropan alienus</i>	0003100000	0000000000	0000000000	0000000000	0000000001	0000010000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Heteropan appendiculata</i>	0003100000	0000000000	0000000000	0000000000	0000000002	0000010000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
<i>Cadphises moorei</i>	0201000000	0011001100	0000010000	0021000003	0001000000	0000001200	1020000000	0000000000	0000001200	0011111111	0021110101	00013211012	4161000111	1111
<i>Cadphises maculatus</i>	0201000000	0011001100	0000010000	0021000003	0001000000	0000001200	1020000000	0000000000	0000001200	0011111111	0021110101	00013211012	4161000111	1111
<i>Hampsonia pulcherrima</i>	0201000000	0011000000	0000010000	0021000003	0001000000	0000003600	1110000000	0000003600	0000003600	0011111111	1021110101	0013211011	4161001000	0121
<i>Watermania bifasciata</i>	0201000000	0011000000	0000010000	0021000003	0001000000	0000003600	1010000000	0000003600	0000003600	0011111111	0021110101	00013211012	4161001000	0121
<i>Herpidia eupoma</i>	0201000000	0011000000	0000010000	0021000003	0001000000	0000003600	1010000000	0000003600	0000003600	0011111111	0021110101	00013211012	4161001000	0121
<i>Aglaepe infauista</i>	0001000000	0010000000	0000010000	0021000003	0001000000	0000003300	1010000000	0000003300	0000003300	0011111111	1021110101	0013211011	4161001000	0121
<i>Philopator basimaculata</i>	0001000000	0020000000	0000000000	0021000003	0001000000	0000003400	1010000000	0000003400	0000003400	0011111111	0021110101	00013211012	4161001000	0121
<i>Formozygna shibatai</i>	0001000000	0010000000	0000000000	0021000003	1001000000	0000003400	1010000000	0000003400	0000003400	0011111111	0021110101	00013211012	4161001000	0121
<i>Atelesia nerosea</i>	7777777777	7777777777	0777777777	7777777777	7777777777	0000003400	0000003400	0000003400	0000003400	0000003400	0000003400	0000003400	0000003400	0000003400
<i>Elcysma westwoodi</i>	3001000000	0010000000	0010000000	0121000003	0001000000	0000003400	1010000000	0000003400	0000003400	0011111111	1021110101	00013211012	4161001000	0121
<i>Achelura bifasciata</i>	1001000000	0010000100	3000000000	0121000003	0001000000	0000003400	1010000000	0000003400	0000003400	0011111111	1021110101	00013211012	4161001000	0121
<i>Achelura javana</i>	1001000000	0010000100	3000000000	0121000003	0001000000	0000003400	1010000000	0000003400	0000003400	0011111111	1021110101	00013211012	4161001000	0121
<i>Achelura hemileuca</i>	1001000000	0010000100	3000000000	0121000003	0001000000	0000003400	1010000000	0000003400	0000003400	0011111111	1021110101	00013211012	4161001000	0121

APPENDIX 3 Continued

Taxa	281-290	291-300	301-310	311-320	321-330	331-340	341-350	351-360	361-370	371-380	381-390	391-400	401-410	411-414
<i>Boradia carnea</i>	1001000000	0010000100	0000000000	0021000003	0001000000	0000000340	1010002????	???	???	???	???	???	???	???
<i>Agalope glacialis</i>	3001000000	0010000100	0000000000	0421000003	0001000000	0000000340	1010000000	0042101010	0100210010	0011111111	1021101010	0013211012	4161011111	1121
<i>Agalope immaculata</i>	3001000000	0010000100	3000000000	0421000003	0001000000	0000002200	1010000000	0042102010	1100100010	0011111111	1021101010	0013211012	4161011111	1121
<i>Agalope hyalina</i>	2001000000	0010000100	0000000000	0021000003	0001000000	0000000340	1010000000	0042101010	0100100010	0011111111	1021101010	0013211012	4161011111	1121
<i>Agalope eronioides</i>	2001000000	0010000100	0000000000	0021000003	0001000000	0000003400	1010000000	0042101010	0100100010	0011111111	1021101010	0013211012	4161011111	1121
<i>Agalope bieti</i>	2001000000	0010000100	3010000101	0021000003	0001000000	0000002000	1010000000	0042101010	2100100010	0011111111	1021101010	0013211012	4161011111	1121
<i>Agalope pita</i>	2001000000	0010000100	0000000000	0021000003	0001000000	0000000200	1010000000	0042101010	2100100010	0011111111	1021101010	0013211012	4161011111	1121
<i>Campylotes histrionicus</i>	0001300000	0000000004	2000110000	0021000002	0000000000	0000001100	1010000000	0042101010	0100100010	0011111110	1021101010	0013211012	4161001111	1111
<i>Campylotes desgodinsi</i>	0101100000	0000000004	2000110000	0021000003	0000000000	0000001100	1010000000	0042101010	0100100010	0011111110	1021101010	0013211012	4161001111	1111
<i>Neotherpa venosa</i>	0001100000	0000000000	0000010000	0021000003	0000000000	0000002100	1010002????	???	???	???	???	???	???	???
<i>Neotherpa subhyalina</i>	0001100000	0000000000	0000000000	0021000003	0000000000	0000002100	1010002????	???	???	???	???	???	???	???
<i>Neotherpa eleonora</i>	0001100000	0000000000	0000000000	0021000002	0000000000	0000001100	1010002????	???	???	???	???	???	???	???
<i>Pantherpina basiflava</i>	0001100000	0000000000	0000000000	0021000002	0000000000	0000001100	1010002????	???	???	???	???	???	???	???
<i>Cyclosia panthona</i>	0013100000	0100000003	0000000000	0021000003	0000000000	0000003500	0000000000	1042101010	1200220000	0011111110	0021101010	0013211012	5171001111	1111
<i>Cyclosia papilionaris</i>	0011100000	0100000003	0000000000	0021000003	0000000000	0000003500	0000000000	1042101011	1200220000	0011111110	0021101010	0013211012	5171001111	1111
<i>Cyclosia chartacea</i>	0011100000	0100000003	0000000000	0021000003	0000000000	0000003500	0000000000	1042101011	1200220000	0011111110	0021101010	0013211012	5171001111	1111
<i>Cyclosia spargens</i>	0011100000	0100000003	0000000000	0021000003	0000000000	0000003500	0000000000	1042101011	1200220000	0011111110	0021101010	0013211012	5171001111	1111
<i>Cyclosia macularia</i>	0011100000	0100000003	0000000000	0021000003	0000000000	0000003500	0000000000	1042101011	1200220000	0011111110	0021101010	0013211012	5171001111	1111
<i>Cyclosia imitans</i>	0011300000	0100000003	4000000000	0021020111	0000000000	0000003500	0000002????	???	???	???	???	???	???	???
<i>Cyclosia curiosa</i>	0011300000	0100000003	4000000000	0021020111	0000000000	0000003500	0000002????	???	???	???	???	???	???	???
<i>Cyclosia midamia</i>	0011100000	0100000003	0000000000	0021000002	0000000000	0000003500	0000002????	???	???	???	???	???	???	???
<i>Cyclosia pteroides</i>	0011100000	0100000003	0000000000	0021000002	0000000000	0000003500	0000002????	???	???	???	???	???	???	???
<i>Cyclosia inclusus</i>	0011100000	0100000005	1000000000	0021000002	0020000000	0000003500	0000000000	1042101011	1200220000	0011111110	0021101020	0013211012	5171001111	1111
<i>Cyclosia euchartha</i>	0011100000	0100000005	0000000000	0021000002	0000000000	0000003500	0000002????	???	???	???	???	???	???	???
<i>Cyclosia electra</i>	0011100000	0100000003	0000000000	0021000002	0000000000	0000003500	0000002????	???	???	???	???	???	???	???
<i>Cyclosia notabilis</i>	0023100000	0100000000	7001000000	0021000002	000000002?	???	2121002????	???	???	???	???	???	???	???
<i>Rhodopsona costata</i>	0000100000	0100000000	0000000000	0021000001	0000000000	0010000330	3000000000	0042101010	0000101100	0011111110	0021100001	0013211012	4151001111	1111
<i>Rhodopsona rubiginosa</i>	0000100000	0100000000	0000000000	0021000002	0000000000	0000000340	3000000000	0042101010	0000101100	0011111110	0021100001	0013211012	4151001111	1111
<i>Rhodopsona jordani</i>	0000100000	0100000000	0000000000	0021000002	000000000?	???	3000002????	???	???	???	???	???	???	???
<i>Rhodopsona reverdini</i>	0000100000	0100000000	0000000000	0021000002	000000000?	???	3000002????	???	???	???	???	???	???	???
<i>Rhodopsona marginata</i>	0000100000	0100000000	0000000000	0021000002	0000000000	0010000330	2000000000	0042101010	0000101100	0011111110	0021100001	0013211012	4151001111	1111
<i>Rhodopsona matsumotoi</i>	0000200000	0100000000	0000000000	0021001003	0000000000	0000000330	3000000000	???	???	???	???	???	???	???
<i>Heteropanula flavimacula</i>	0023200000	0100000000	0000000000	0021001002	0000000000	0000000000	1000002????	???	???	???	???	???	???	???
<i>Pseudarbutus ochrea</i>	0034200000	0100000002	0000000000	0031002002	0000000000	0000000340	1000002????	???	???	???	???	???	???	???
<i>Corma maculata</i>	0023000000	0100000003	0000000000	0021000002	0000000000	0000001500	1120002????	???	???	???	???	???	???	???
<i>Corma fragilis</i>	0011100000	0100000003	0000000000	0021000002	0000000000	0000001200	2120002????	???	???	???	???	???	???	???
<i>Corma zenobia</i>	0013000000	0100000000	2000000000	0021000002	0000000000	0000003500	2112000011	0042101010	1200100010	0011111110	0021100001	0013211012	4121001111	1111
<i>Eucommiopsis lampra</i>	0012000000	0100000000	0000000000	0021000002	0000000000	0000000350	0122002????	???	???	???	???	???	???	???
<i>Doelcomorpha bohatica</i>	???	???	???	???	???	0000003500	???	???	???	???	???	???	???	???
<i>Cryptophysophilus bicoloratus</i>	0023000000	0100000001	0000000000	0021000002	000000000?	???	3000002????	???	???	???	???	???	???	???
<i>Heterusinula dichroa</i>	0023000000	0100000001	0000000000	0021000002	000000000?	???	3000002????	???	???	???	???	???	???	???
<i>Anarbutus insignis</i>	0013000000	0100000003	0000000100	0021000001	0020000000	0000003400	2000002????	???	???	???	???	???	???	???
<i>Anarbutus bipartita</i>	0023100000	0100000003	0000000000	0021000002	0000000000	0000003411	0021002????	???	???	???	???	???	???	???
<i>Arbutus bicolor</i>	0013100000	0100000000	0000000000	0021000002	0000001000	0000003400	0000001100	0042101010	0000000000	0011111110	0021101010	0103211012	4110011111	1111

APPENDIX 3 Continued

Taxa	281-290	291-300	301-310	311-320	321-330	331-340	341-350	351-360	361-370	371-380	381-390	391-400	401-410	411-414
<i>Amesia aliris</i>	0034100000	0100000000	4000000000	0021000001	0100000040	0000002211	2122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4181101111	1111
<i>Amesia apoensis</i>	0034100000	0100000000	4000000000	0021000001	0100000040	0000002211	2122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4181101111	1111
<i>Opisthoplatia grandis</i>	0034101000	0100000000	3000000000	0021000002	0000000040	0000002211	3122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4181101111	1111
<i>Phlebohecta</i>	0012100000	0100000000	0000000000	0021000002	0000000000	0000003412	1121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4181101111	1111
<i>fuscascens</i>														
<i>Phlebohecta lithosina</i>	0012100000	0100000000	0000000000	0021000002	0000000000	0000003412	1121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4181101111	1111
<i>Phlebohecta jordani</i>	0013100000	0100000000	0000000000	0021000004	0000000000	0000000200	1120000012	0012101011	1301110000	0011111110	2021110001	0103211012	4181101111	1111
<i>Phlebohecta lyrusa</i>	0010200000	0100000000	4000000000	0021001002	0100000000	0000003411	1122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4181101111	1111
<i>Eterusia risa</i>	0023100000	0100000006	0000000000	0021000002	0000000030	0000002211	1122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Eterusia vitessa</i>	??????????	??????????	??????????	??????????	??????????	0000002211	??????????	??????????	??????????	??????????	??????????	??????????	??????????	????
<i>Eterusia aedea</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	1122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Eterusia binotata</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	1122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Eterusia tricolor</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	1122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Eterusia subcyanea</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	2122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Eterusia replata</i>	0034101000	0100000000	3001000000	0021000002	0000000040	0000002211	1122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Eterusia raja</i>	0023100000	0100000000	0000000000	0021000002	0000000020	0000003411	2121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Soritia pulchella</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	2122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Soritia major</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	2122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Soritia zelotypia</i>	??????????	??????????	??????????	??????????	??????????	0000002211	??????????	??????????	??????????	??????????	??????????	??????????	??????????	????
<i>Soritia costimacula</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	2122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Soritia costimacula malaccensis</i>	0023100000	0100000000	0000000000	0021000002	0000000030	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	????
<i>Soritia shahama</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	2122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Soritia elizabethae</i>	0023100000	0100000000	0000000000	0021000002	0000000030	0000002211	2122000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Soritia bicolor</i>	0025100000	0100000005	1000000000	0021000003	0000000040	0000003411	2121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4181101111	1111
'Soritia' sevastopuloi	0201000000	0011000000	0000000000	0021000003	0001000000	0000003600	1010000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Soritia moerens</i>	0015100000	0100000000	0100000000	0021000002	0000000000	0000002211	1121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Chalostia</i>	0023100000	0100000000	0000000000	0021000002	0000000020	0000003411	2122000012	0012101011	1300220000	0111111110	0021110001	0103211012	4191101111	1111
<i>pectinicornis</i>														
<i>Chalostia pretiosa</i>	0023100000	0100000000	0000000000	0021000002	0000000020	0000003411	2121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Chalostia</i>	0023100000	0100000000	0000000000	0021000002	0000000020	0000003411	2121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>nyctemeroides</i>														
'Chalostia' thibetana	0001000000	1010000000	1000000210	0021000003	0001000000	0000003400	1010000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
'Chalostia' alpherakyi	0001000000	0010000000	0000000200	0021000003	0001000000	0000003400	1010000012	0012101011	1301110000	0011111110	2021110001	0103211012	4121101112	1111
<i>Chalostia zehma</i>	0023100000	0100000000	4000000000	0021000002	0000000000	0000003411	0121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Milleria adalifa</i>	0023100000	0100000000	0000000000	0021000002	0000000020	0000003411	2121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Milleria rehfousi</i>	0023100000	0100000000	7001000000	0021000002	0000000020	0000003411	2121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Milleria hamiltoni</i>	0023100000	0100000000	7001000000	0021000002	0000000020	0000003411	2121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Milleria okushimai</i>	0023100000	0100000000	0000000000	0021000002	0100000000	0000003411	2121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Eusphalera ligata</i>	0023100000	0100000000	7000001000	0021000002	0200000000	0000003411	0121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Eusphalera bellula</i>	0023100000	0100000000	7000001000	0021000002	0200000000	0000003411	0121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Eusphalera picturata</i>	0023100000	0100000000	7000001000	0021000002	0200000000	0000003411	0121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Eusphalera venus</i>	0023100000	0100000000	7000001000	0021000002	0200000000	0000003411	0121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Eusphalera regina</i>	0023100000	0100000000	7000001000	0021000002	0200000000	0000003411	0121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111
<i>Eusphalera multicolor</i>	0023100000	0100000000	7000001000	0021000002	0200000000	0000003411	0121000012	0012101011	1301110000	0011111110	2021110001	0103211012	4191101111	1111

APPENDIX 4

Character change lists of the strict consensus cladogram from EW analysis based on the whole data set. Node numbers correspond to those in Figure 55; each is followed by a list of character numbers and unambiguous state changes. Changes are listed for the main clades.

node_394 → node_208 (<i>Chalcosiopsis</i>)	node_394 → node_393 (<i>Zygaenoidea</i>)	264	1 → 0	357	0 → 1	
7	5	266	0 → 2	403	0 → 1	
8	6	275	0 → 1	408	0 → 1	
9	33	313	0 → 2	409	0 → 1	
10	34	353	0 → 1	410	0 → 1	
11	36	386	2 → 1	411	0 → 1	
12	48	389	0 → 1	412	0 → 1	
13	49	399	0 → 1	413	0 → 1	
14	54	400	0 → 2	node_390 → node_220 (<i>Zygaeninae</i>)		
25	55	401	0 → 2	1	0 → 2	
28	89	404	0 → 1	2	0 → 2	
29	98	407	0 → 1	10	0 → 1	
30	124	414	0 → 1	12	0 → 2	
31	169	node_219 → node_218 (<i>Inouela + Homophylotis</i>)		15	2 → 1	
33	170	3	1 → 3	16	1 → 0	
34	173	11	0 → 1	24	0 → 1	
35	174	17	0 → 1	38	0 → 1	
41	280	28	0 → 1	42	2 → 0	
43	284	30	0 → 4	64	1 → 0	
44	286	98	2 → 1	94	4 → 0	
46	node_392 → node_212 (<i>Phauda + Lactura</i>)		105	2 → 1	101	0 → 1
50	17	111	0 → 3	124	3 → 2	
51	18	119	0 → 1	125	3 → 2	
63	26	125	3 → 2	174	4 → 3	
64	26	173	3 → 4	244	0 → 2	
87	27	177	1 → 0	265	0 → 1	
91	33	178	0 → 1	285	0 → 1	
94	34	209	0 → 2	288	0 → 1	
103	36	212	0 → 4	289	0 → 1	
110	68	216	0 → 1	313	2 → 0	
111	72	221	0 → 1	315	0 → 1	
112	90	230	1 → 2	330	0 → 1	
122	93	240	0 → 1	345	0 → 1	
123	124	250	0 → 1	node_390 → node_389 (<i>Callizygaeninae-Chalcosiinae</i>)		
124	153	253	0 → 1	3	1 → 2	
125	154	261	3 → 2	13	0 → 2	
167	222	270	0 → 1	17	2 → 5	
168	318	272	0 → 3	19	3 → 5	
171	330	278	0 → 1	29	0 → 1	
172	352	279	0 → 1	33	5 → 1	
177	382	284	1 → 0	34	5 → 1	
189	383	299	0 → 1	37	0 → 1	
210	387	332	0 → 1	39	0 → 1	
300	node_392 → node_391 (<i>Zygaenidae</i>)		node_391 → node_390 (<i>Zygaenidae</i> excluding <i>Procridinae</i>)		43	0 → 2
318	25	9	0 → 1	44	0 → 2	
node_208 → <i>Chalcosiopsis variata</i>		11	0 → 2	46	0 → 1	
69	30	17	0 → 2	53	0 → 1	
70	31	18	0 → 2	54	1 → 2	
83	40	19	4 → 3	61	3 → 4	
102	41	20	4 → 3	62	4 → 5	
106	42	47	0 → 2	110	0 → 1	
130	60	52	0 → 1	116	0 → 1	
153	63	61	2 → 3	163	1 → 2	
154	64	62	1 → 4	167	0 → 3	
156	69	72	0 → 1	178	0 → 2	
179	92	90	0 → 1	190	0 → 1	
180	94	105	2 → 0	231	2 → 0	
183	105	177	1 → 3	241	0 → 1	
184	125	189	2 → 0	272	0 → 1	
214	163	191	0 → 1	273	0 → 1	
222	172	212	0 → 1	274	1 → 0	
264	177	264	0 → 1	276	0 → 1	
274	189	271	0 → 1	277	0 → 1	
325	196	320	0 → 2	278	0 → 1	
336	231					

APPENDIX 4 *Continued*

279	0 → 2	94	4 → 3	node_388 → node_223	263	1 → 0
314	0 → 1	105	0 → 2	(<i>Heteropan</i>)	266	2 → 4
355	0 → 1	111	2 → 3	4	320	2 → 3
359	0 → 1	116	1 → 0	5	341	0 → 1
365	0 → 1	136	0 → 5	6	343	0 → 1
373	0 → 1	139	0 → 1	11	362	0 → 1
374	0 → 1	140	0 → 1	17	369	0 → 1
375	0 → 1	178	2 → 0	18	388	0 → 1
376	0 → 1	244	0 → 1	33	403	5 → 6
377	0 → 1	285	0 → 3	34	node_250 → node_244	
378	0 → 1	313	2 → 1	42	37	0 → 1
379	0 → 1	317	0 → 1	43	111	3 → 2
389	1 → 0	331	0 → 1	44	223	0 → 1
394	1 → 2	403	1 → 4	46	224	0 → 2
395	0 → 1			47	261	3 → 1
397	0 → 1	node_221 →		56	293	0 → 1
401	2 → 4	<i>Cleoda syntomoides</i>		57	324	0 → 1
402	0 → 1	5	1 → 2	94	380	0 → 1
		9	1 → 2	124	node_244 → node_227	
		15	2 → 4	125	(<i>Cadphises-Herpidia</i>)	
node_389 → node_221		18	2 → 3	167	1	0 → 1
(<i>Callizygaeninae</i>)		30	2 → 0	240	7	0 → 1
26	0 → 2	31	2 → 1	266	8	0 → 1
27	0 → 3	33	1 → 4	279	59	0 → 1
45	2 → 0	34	1 → 2	284	94	4 → 3
65	0 → 1	40	1 → 2	285	169	3 → 6
66	0 → 1	41	1 → 2	313	170	3 → 6
68	0 → 4	48	2 → 3	314	212	2 → 0
71	3 → 2	53	1 → 2	326	232	0 → 1
75	0 → 3	55	1 → 3		233	1 → 2
76	0 → 3	101	0 → 3	node_388 → node_387	242	0 → 1
77	0 → 4	119	0 → 1	(<i>Chalcosiinae</i>)	243	0 → 1
78	0 → 4	130	0 → 1	12	272	2 → 1
124	3 → 0	154	0 → 5	7	282	0 → 2
125	3 → 0	176	1 → 2	0	294	0 → 1
164	0 → 1	190	1 → 2	1	306	0 → 1
168	0 → 2	212	1 → 5	5	338	4 → 6
169	3 → 2	261	1 → 2	8	356	0 → 1
170	3 → 2	272	1 → 4	9	360	0 → 2
173	3 → 2	279	2 → 4	3	361	0 → 2
174	4 → 2	283	0 → 2	1	362	1 → 3
177	3 → 0	300	2 → 3	11	365	1 → 2
189	0 → 2	330	0 → 3	77	node_227 → node_225	
227	0 → 1			78	7	1 → 0
261	3 → 1	node_389 → node_388		96	11	1 → 2
264	1 → 0	(<i>Heteropan-Chalcosiinae</i>)		18	15	3 → 4
300	0 → 2	9	1 → 0	27	19	5 → 4
361	0 → 2	14	0 → 2	46	20	5 → 4
389	0 → 2	15	2 → 3	50	48	3 → 2
		16	1 → 2	53	49	2 → 1
node_221 →		18	2 → 5	68	94	3 → 2
<i>Callizygaena ada</i>		20	3 → 5	69	160	0 → 2
4	1 → 2	28	2 → 1	70	161	0 → 2
0	0 → 1	30	2 → 3	37	177	4 → 5
2	0 → 2	31	2 → 3	38	node_225 → node_224	
3	2 → 0	55	1 → 2	03	(<i>Cadphises</i>)	
7	5 → 2	70	3 → 4		5	1 → 2
9	5 → 1	72	1 → 2	node_387 → node_250	9	0 → 1
0	3 → 1	84	0 → 1	(clade 1)	13	2 → 3
4	0 → 1	87	0 → 1	11	14	2 → 3
6	2 → 4	101	0 → 2	38	28	1 → 2
7	3 → 4	102	0 → 2	44	94	2 → 4
9	1 → 2	196	1 → 0	104	100	0 → 1
3	2 → 0	212	1 → 2	164	107	0 → 1
4	2 → 1	233	0 → 1	165	117	0 → 2
57	0 → 1	253	0 → 2	168	124	3 → 6
58	0 → 1	263	0 → 1	171	125	3 → 6
67	0 → 1	272	1 → 2	173	206	0 → 1
68	4 → 6	354	0 → 2	174	207	0 → 1
75	3 → 5	393	0 → 1	190	224	2 → 1
76	3 → 5	394	2 → 3	195	297	0 → 1
77	4 → 6	395	1 → 2	255		
78	4 → 6	396	0 → 1	262		

APPENDIX 4 *Continued*

298	0 ⇒ 1	48	3 ⇒ 2	169	3 ⇒ 6	177	4 ⇒ 5
337	3 ⇒ 1	49	2 ⇒ 1	170	3 ⇒ 6	218	3 ⇒ 4
338	6 ⇒ 2	153	0 ⇒ 5	266	4 ⇒ 3	245	0 ⇒ 6
343	1 ⇒ 2	154	0 ⇒ 5			252	0 ⇒ 1
node_225 →		195	1 ⇒ 0	node_229 → node_228		255	2 ⇒ 1
<i>Hampsonia pulchella</i>		196	2 ⇒ 1	15	3 ⇒ 4	node_231 → node_230	
1	1 ⇒ 2	212	2 ⇒ 4	30	4 ⇒ 3	3	2 ⇒ 1
3	2 ⇒ 0	218	1 ⇒ 3	48	2 ⇒ 3	12	2 ⇒ 0
4	1 ⇒ 0			54	2 ⇒ 1	17	6 ⇒ 5
8	1 ⇒ 0	node_232 → <i>Aglaope infausta</i>		104	0 ⇒ 2	31	2 ⇒ 3
12	1 ⇒ 2	1	0 ⇒ 1	191	1 ⇒ 2	33	1 ⇒ 2
16	2 ⇒ 3	2	0 ⇒ 1	212	4 ⇒ 3	34	1 ⇒ 2
17	5 ⇒ 6	3	2 ⇒ 0	223	3 ⇒ 2	44	1 ⇒ 2
18	5 ⇒ 6	4	1 ⇒ 0	node_228 →		141	0 ⇒ 1
22	0 ⇒ 1	13	2 ⇒ 0	<i>Philopator basimaculata</i>		142	0 ⇒ 1
103	0 ⇒ 1	16	2 ⇒ 3	3	2 ⇒ 1	143	0 ⇒ 1
111	2 ⇒ 3	18	6 ⇒ 2	5	2 ⇒ 3	144	0 ⇒ 1
113	0 ⇒ 1	19	5 ⇒ 7	6	2 ⇒ 3	153	5 ⇒ 3
136	0 ⇒ 4	20	5 ⇒ 4	11	2 ⇒ 1	154	5 ⇒ 3
139	0 ⇒ 2	24	0 ⇒ 1	13	2 ⇒ 3	171	3 ⇒ 2
140	0 ⇒ 2	28	1 ⇒ 0	14	2 ⇒ 3	173	5 ⇒ 4
153	0 ⇒ 5	32	0 ⇒ 1	17	6 ⇒ 3	174	5 ⇒ 4
154	0 ⇒ 5	33	1 ⇒ 4	18	6 ⇒ 2	177	4 ⇒ 6
177	5 ⇒ 6	34	1 ⇒ 4	26	0 ⇒ 3	196	1 ⇒ 3
342	0 ⇒ 1	66	0 ⇒ 2	27	0 ⇒ 3	204	0 ⇒ 1
node_227 → node_226		81	1 ⇒ 0	28	1 ⇒ 0	212	4 ⇒ 5
120	0 ⇒ 1	94	4 ⇒ 2	67	0 ⇒ 2	218	3 ⇒ 0
130	0 ⇒ 1	105	0 ⇒ 1	68	0 ⇒ 4	222	0 ⇒ 1
136	0 ⇒ 5	107	1 ⇒ 0	75	0 ⇒ 3	261	1 ⇒ 3
155	0 ⇒ 2	116	1 ⇒ 0	76	0 ⇒ 3	308	0 ⇒ 2
node_226 →		171	3 ⇒ 1	77	0 ⇒ 4	node_243 → node_242	
<i>Watermenia bifasciata</i>		172	3 ⇒ 1	78	0 ⇒ 4	13	2 ⇒ 1
4	1 ⇒ 2	173	5 ⇒ 3	107	1 ⇒ 2	14	2 ⇒ 1
5	1 ⇒ 2	174	5 ⇒ 3	119	0 ⇒ 1	55	2 ⇒ 3
15	3 ⇒ 4	191	1 ⇒ 3	124	5 ⇒ 2	65	0 ⇒ 3
16	2 ⇒ 3	223	3 ⇒ 2	125	5 ⇒ 3	66	0 ⇒ 3
22	0 ⇒ 1	243	0 ⇒ 2	130	0 ⇒ 1	94	4 ⇒ 5
103	0 ⇒ 1	272	2 ⇒ 3	133	0 ⇒ 1	111	2 ⇒ 3
143	0 ⇒ 2	306	0 ⇒ 1	136	0 ⇒ 2	164	1 ⇒ 2
node_226 → <i>Herpidia eupoma</i>		338	4 ⇒ 3	139	0 ⇒ 2	166	0 ⇒ 1
3	2 ⇒ 1	358	0 ⇒ 1	140	0 ⇒ 4	169	3 ⇒ 7
13	2 ⇒ 3	362	1 ⇒ 0	153	5 ⇒ 6	170	3 ⇒ 7
14	2 ⇒ 3	366	0 ⇒ 2	154	5 ⇒ 0	171	3 ⇒ 0
154	0 ⇒ 2	369	1 ⇒ 0	156	0 ⇒ 1	172	3 ⇒ 0
177	4 ⇒ 6	391	0 ⇒ 1	157	0 ⇒ 1	173	5 ⇒ 6
node_227 →		400	2 ⇒ 1	179	0 ⇒ 1	174	5 ⇒ 6
<i>'Soritia' sevastopuloi</i>		408	1 ⇒ 0	180	0 ⇒ 1	191	1 ⇒ 0
3	2 ⇒ 0	409	1 ⇒ 0	183	0 ⇒ 4	206	0 ⇒ 1
4	1 ⇒ 0	410	1 ⇒ 0	184	0 ⇒ 4	207	0 ⇒ 1
153	0 ⇒ 3	411	1 ⇒ 0	185	0 ⇒ 1	222	0 ⇒ 1
154	0 ⇒ 3	node_232 → node_231		186	0 ⇒ 1	224	3 ⇒ 4
255	1 ⇒ 0	5	0 ⇒ 2	187	0 ⇒ 1	279	2 ⇒ 3
306	1 ⇒ 0	6	1 ⇒ 2	188	0 ⇒ 1	281	0 ⇒ 1
node_244 → node_243		7	0 ⇒ 1	218	3 ⇒ 1	298	0 ⇒ 1
17	5 ⇒ 6	8	0 ⇒ 1	node_228 → <i>Formozygaena shibatai</i>		406	0 ⇒ 1
18	5 ⇒ 6	9	0 ⇒ 1	4	1 ⇒ 2	node_242 → node_239	
23	0 ⇒ 1	11	1 ⇒ 2	7	1 ⇒ 0	3	2 ⇒ 1
31	3 ⇒ 2	23	1 ⇒ 0	8	1 ⇒ 0	17	6 ⇒ 4
107	0 ⇒ 1	30	3 ⇒ 4	9	1 ⇒ 0	18	6 ⇒ 4
219	0 ⇒ 3	102	2 ⇒ 3	10	1 ⇒ 0	19	5 ⇒ 3
223	1 ⇒ 3	104	2 ⇒ 0	19	6 ⇒ 5	20	5 ⇒ 3
224	2 ⇒ 3	124	3 ⇒ 5	29	1 ⇒ 0	29	1 ⇒ 0
228	0 ⇒ 1	125	3 ⇒ 5	101	2 ⇒ 1	124	3 ⇒ 5
255	1 ⇒ 2	361	0 ⇒ 1	155	0 ⇒ 2	125	3 ⇒ 5
381	0 ⇒ 1	380	1 ⇒ 0	321	0 ⇒ 1	245	0 ⇒ 7
413	1 ⇒ 2	381	1 ⇒ 0	node_229 → <i>Atelesia nervose</i>		255	2 ⇒ 0
node_243 → node_232		node_231 → node_229		13	2 ⇒ 0	272	2 ⇒ 1
5	1 ⇒ 0	19	5 ⇒ 6	17	6 ⇒ 4	node_239 → node_238	
10	0 ⇒ 1	49	1 ⇒ 2	101	2 ⇒ 3	10	0 ⇒ 1
12	1 ⇒ 2	66	0 ⇒ 1	111	2 ⇒ 3	30	3 ⇒ 4
				124	5 ⇒ 3		

APPENDIX 4 *Continued*

31	2 → 4	337	3 → 2	215	0 → 1	31	3 → 1
94	5 → 3	338	4 → 2	219	0 → 2	136	5 → 0
136	0 → 5	361	0 → 1	220	0 → 1	179	0 → 1
177	4 → 3	365	2 → 1	225	0 → 1	180	0 → 1
191	0 → 1	366	1 → 0	226	0 → 2	262	1 → 0
206	1 → 0	node_234 → <i>Agalope gliacialis</i>		227	3 → 2	265	0 → 2
207	1 → 0	12	1 → 0	337	3 → 1	337	1 → 2
212	2 → 1	31	4 → 3	338	4 → 1	node_248 → node_247	
224	4 → 3	190	2 → 3	node_249 → node_245		30	3 → 4
255	0 → 1	204	0 → 2	(<i>Campylotes</i>)		107	1 → 2
281	1 → 2	218	1 → 2	3	2 → 1	195	1 → 0
node_238 → node_234		245	7 → 2	11	1 → 0	244	0 → 1
23	1 → 2	265	0 → 3	13	2 → 0	320	3 → 2
24	0 → 2	266	4 → 5	14	2 → 3	node_387 → node_386	
28	1 → 2	node_238 → node_237		17	5 → 4	5	1 → 2
29	0 → 1	(<i>Agalope</i>)		19	5 → 6	6	1 → 2
124	5 → 6	19	3 → 4	23	0 → 1	7	0 → 1
125	5 → 6	20	3 → 4	29	1 → 0	8	0 → 1
196	2 → 1	49	2 → 1	48	3 → 2	9	0 → 1
224	3 → 5	59	0 → 1	49	2 → 1	10	0 → 1
281	2 → 3	146	0 → 1	59	0 → 1	54	2 → 1
312	0 → 1	147	0 → 1	94	4 → 5	55	2 → 3
365	1 → 2	191	1 → 6	113	0 → 1	73	0 → 1
366	0 → 1	245	7 → 1	117	1 → 2	107	0 → 2
node_234 → node_233		node_239 →		121	0 → 1	167	3 → 1
3	1 → 3	<i>Boradia carneola</i>		35	0 → 2	189	0 → 2
4	1 → 2	6	1 → 0	39	0 → 1	246	1 → 2
6	1 → 2	7	0 → 1	40	0 → 1	253	3 → 5
13	1 → 2	8	0 → 1	46	0 → 5	292	0 → 1
15	3 → 4	11	1 → 2	47	0 → 5	node_386 → node_267	
17	4 → 3	13	1 → 0	69	3 → 6	(clade 2)	
18	4 → 3	14	1 → 0	70	3 → 6	12	1 → 2
30	4 → 2	15	3 → 2	83	1 → 4	94	4 → 3
94	3 → 4	16	2 → 1	84	1 → 4	96	0 → 1
177	3 → 6	33	1 → 2	66	4 → 3	174	4 → 3
195	1 → 0	34	1 → 3	72	2 → 1	225	0 → 2
node_233 →		99	0 → 1	85	0 → 1	226	0 → 3
<i>Elcysma westwoodi</i>		101	2 → 1	00	0 → 4	279	2 → 3
4	2 → 3	103	0 → 1	01	0 → 2	283	0 → 1
12	1 → 2	107	1 → 0	05	0 → 1	300	0 → 3
16	2 → 3	195	1 → 0	06	0 → 1	338	4 → 5
31	4 → 1	253	3 → 0	node_249 → node_248		361	0 → 1
113	0 → 1	261	1 → 3	4	0 → 2	362	0 → 2
117	0 → 2	node_242 → node_241		5	1 → 2	node_267 → node_260	
127	0 → 1	(<i>Achelura</i>)		6	1 → 2	(<i>Cyclosia</i>)	
191	1 → 0	4	1 → 2	9	0 → 1	4	1 → 3
195	0 → 2	24	0 → 2	10	0 → 1	15	3 → 4
196	1 → 4	34	1 → 2	15	2 → 4	16	2 → 3
207	0 → 1	54	2 → 1	18	5 → 4	33	1 → 0
245	7 → 5	190	2 → 0	20	5 → 6	34	1 → 0
272	1 → 2	212	2 → 5	33	1 → 2	48	3 → 2
303	0 → 1	301	0 → 3	34	1 → 2	55	3 → 1
node_233 →		312	0 → 1	54	2 → 1	82	0 → 1
<i>Agalope immaculata</i>		409	1 → 2	68	0 → 4	97	0 → 2
8	0 → 1	node_250 → node_249		73	0 → 1	98	2 → 1
11	1 → 2	1	0 → 2	75	0 → 3	103	0 → 1
23	2 → 1	2	0 → 2	76	0 → 3	117	0 → 2
29	1 → 0	4	1 → 0	77	0 → 4	120	0 → 1
33	1 → 3	15	3 → 2	78	0 → 4	125	3 → 5
49	2 → 1	16	2 → 3	107	0 → 1	170	3 → 4
54	2 → 1	28	1 → 0	172	3 → 4	196	2 → 0
103	0 → 1	117	0 → 1	173	5 → 3	212	2 → 0
104	2 → 0	124	3 → 5	174	5 → 3	222	0 → 1
111	3 → 2	125	3 → 5	191	2 → 4	240	0 → 4
124	6 → 5	136	0 → 5	212	2 → 3	253	5 → 4
125	6 → 5	183	0 → 1	231	0 → 2	272	2 → 4
136	5 → 0	184	0 → 1	240	0 → 7	279	3 → 5
219	3 → 2	190	2 → 3	255	1 → 0	351	0 → 1
251	0 → 1	191	1 → 2	node_248 → node_246		360	0 → 1
255	1 → 0	192	0 → 1	(<i>Neoherpa</i>)		365	1 → 2
301	0 → 3			1	2 → 0	366	0 → 2
				2	2 → 0		

APPENDIX 4 *Continued*

388	0 → 1	37	0 → 1	<i>node_263</i> →	76	0 → 3	
401	4 → 5	94	2 → 4	<i>Heterusinula dichroa</i>	77	0 → 4	
403	5 → 7	111	3 → 2	16	2 → 1	78	0 → 4
<i>node_267</i> → <i>node_266</i>		130	0 → 1	24	1 → 0	101	2 → 1
17	5 → 4	179	0 → 1	94	2 → 3	177	4 → 6
29	1 → 0	183	0 → 1	115	1 → 0	190	1 → 2
30	3 → 2	189	2 → 1	<i>node_264</i> →		212	2 → 0
54	1 → 2	190	1 → 2	<i>Anarbudas insignis</i>		249	0 → 1
104	0 → 1	218	0 → 1	11	2 → 1	338	4 → 3
107	2 → 1	256	0 → 1	12	2 → 0	367	0 → 1
168	0 → 2	266	4 → 3	15	3 → 4	368	0 → 1
218	1 → 0	272	2 → 3	18	5 → 6		
228	0 → 2	279	3 → 5	48	3 → 2	<i>node_269</i> → <i>node_268</i>	
249	0 → 1	<i>node_262</i> → <i>Corma zenotia</i>		49	2 → 1	(<i>Rhodopsona</i>)	
255	0 → 3	9	1 → 0	103	0 → 3	5	0 → 3
262	0 → 1	17	4 → 6	104	2 → 0	6	0 → 3
263	1 → 0	18	5 → 6	111	3 → 2	75	3 → 5
266	2 → 4	124	5 → 3	141	0 → 1	76	3 → 5
284	1 → 2	139	1 → 2	142	0 → 1	77	4 → 6
342	0 → 1	140	1 → 2	143	0 → 2	78	4 → 6
343	0 → 2	154	2 → 3	154	2 → 0	111	3 → 2
349	0 → 1	173	4 → 3	167	1 → 0	148	0 → 2
350	0 → 1	174	4 → 3	177	4 → 3	195	0 → 6
369	0 → 1	300	3 → 0	246	2 → 0	211	0 → 1
<i>node_266</i> → <i>node_265</i>		343	2 → 1	248	0 → 1	212	0 → 6
10	1 → 0	344	0 → 2	261	3 → 4	219	0 → 1
28	1 → 0	<i>node_265</i> → <i>node_264</i>		263	0 → 1	228	0 → 3
94	3 → 2	5	2 → 3	266	4 → 0	256	0 → 1
96	1 → 0	33	1 → 2	272	2 → 4	268	1 → 0
104	1 → 2	34	1 → 2	279	3 → 5	269	1 → 0
124	3 → 5	125	3 → 5	308	0 → 1	279	2 → 3
144	0 → 1	144	1 → 2	320	2 → 1	284	1 → 0
154	0 → 2	169	3 → 5	323	0 → 2	<i>node_269</i> → <i>Pidorus miles</i>	
173	3 → 4	170	3 → 5	338	5 → 4	33	1 → 3
174	3 → 4	212	2 → 3	<i>node_266</i> →		34	1 → 3
226	3 → 1	219	0 → 1	<i>Eucormiopsis lampra</i>		48	3 → 2
284	2 → 3	342	1 → 0	3	2 → 1	49	2 → 1
341	0 → 2	343	2 → 0	4	1 → 0	103	0 → 1
<i>node_265</i> → <i>node_262</i>		<i>node_264</i> → <i>node_263</i>		5	2 → 1	107	2 → 0
4	1 → 2	3	2 → 1	6	2 → 1	155	0 → 2
8	1 → 0	6	2 → 3	9	1 → 2	191	1 → 0
12	2 → 1	9	1 → 2	18	5 → 4	196	2 → 4
13	2 → 3	10	0 → 2	19	5 → 4	218	1 → 3
14	2 → 3	17	4 → 6	20	5 → 4	230	0 → 1
31	3 → 2	24	0 → 1	68	0 → 6	261	3 → 4
38	0 → 3	33	2 → 3	119	0 → 1	266	2 → 0
54	2 → 1	107	1 → 0	131	0 → 1	285	1 → 2
55	3 → 2	115	0 → 1	180	0 → 1	300	0 → 1
113	0 → 1	147	0 → 3	184	0 → 2	317	0 → 1
137	0 → 1	151	0 → 1	219	0 → 3	<i>node_385</i> → <i>node_384</i>	
138	0 → 1	162	0 → 1	225	2 → 5	15	3 → 4
139	0 → 1	179	0 → 1	261	3 → 2	30	3 → 2
140	0 → 1	183	0 → 2	300	3 → 0	33	1 → 2
141	0 → 3	225	2 → 3	344	0 → 2	34	1 → 2
142	0 → 3	283	1 → 2	<i>node_386</i> → <i>node_385</i>		173	3 → 4
143	0 → 1	300	3 → 1	38	0 → 3	209	0 → 2
146	0 → 2	341	2 → 3	227	3 → 4	216	0 → 1
147	0 → 2	403	5 → 4	246	2 → 3	218	1 → 0
185	0 → 1	<i>node_263</i> →		270	2 → 0	220	0 → 2
186	0 → 1	<i>Docleomorpha boholica</i>		285	0 → 1	222	0 → 1
191	1 → 2	22	0 → 1	341	0 → 3	267	0 → 1
240	0 → 6	104	2 → 1	<i>node_385</i> → <i>node_269</i>		272	2 → 1
261	3 → 1	105	0 → 1	(<i>clade 3</i>)		283	0 → 2
403	5 → 2	124	5 → 3	3	2 → 1	284	1 → 3
<i>node_262</i> → <i>node_261</i>		151	1 → 0	5	2 → 0	365	1 → 0
(<i>Corma</i>)		162	1 → 0	6	2 → 0	392	0 → 1
7	1 → 0	<i>node_263</i> →		11	2 → 1	393	1 → 0
10	0 → 1	<i>Cryptophysophilus bicoloratus</i>		19	5 → 4	403	5 → 1
15	3 → 4	125	5 → 3	20	5 → 4	<i>node_384</i> → <i>node_270</i>	
19	5 → 3			31	3 → 2	(<i>clade 4</i>)	
20	5 → 4			75	0 → 3	9	1 → 0

APPENDIX 4 *Continued*

10	1 → 0	node_383 → node_276	11	0 → 1	6	2 → 3
17	5 → 6	(clade 5)	143	0 → 2	18	6 → 4
18	5 → 6	5	144	0 → 2	19	5 → 4
28	1 → 2	19	196	1 → 6	22	0 → 1
29	1 → 0	20	221	1 → 2	33	2 → 1
37	0 → 1	38	228	5 → 6	34	2 → 1
94	4 → 3	209	246	5 → 6	94	3 → 4
124	3 → 5	213	256	0 → 5	173	4 → 3
125	3 → 5	216	257	0 → 2	195	0 → 2
170	3 → 4	240	263	0 → 4	196	1 → 4
231	0 → 2	256	342	0 → 1	263	1 → 4
240	0 → 5	257	343	0 → 2	329	0 → 4
261	3 → 1	266	node_378 → node_363			
266	2 → 0	347	4	1 → 2	node_281 → node_280	
285	1 → 2	348	12	0 → 1	(<i>Hemiscia</i>)	
317	0 → 1	358	17	5 → 4	7	0 → 1
341	3 → 1	388	18	5 → 4	8	0 → 1
			19	5 → 4	9	1 → 0
node_270 →		node_276 → node_274	20	5 → 4	12	1 → 2
<i>Heteropanula flavimacula</i>		28	20	5 → 4	13	2 → 1
6	2 → 3	94	30	2 → 3	14	2 → 1
107	2 → 1	97	67	0 → 1	20	4 → 5
111	3 → 0	107	104	0 → 2	30	3 → 1
146	0 → 1	174	279	4 → 3	31	3 → 2
147	0 → 1	196	338	0 → 4	78	0 → 1
171	2 → 1	218	365	0 → 1	82	1 → 0
177	4 → 3	221	node_363 → node_362		130	0 → 1
209	2 → 0	227	31	4 → 2	146	0 → 3
220	2 → 0	228	94	4 → 3	147	0 → 3
232	0 → 1	267	170	3 → 6	153	0 → 4
233	1 → 0	283	256	5 → 4	154	0 → 4
261	1 → 4	327	263	4 → 1	170	6 → 3
267	1 → 0	341	272	1 → 2	174	4 → 3
279	2 → 3	node_276 → node_275	340	0 → 1	197	1 → 0
337	3 → 0	(<i>Eumorphiopais</i>)	341	3 → 2	272	2 → 4
338	4 → 0	6	403	1 → 4	279	3 → 5
node_270 →		7	node_362 → node_360		284	3 → 2
<i>Pseudarbutas ochrea</i>		10	15	3 → 4	301	0 → 1
3	2 → 3	29	6	2 → 3	308	0 → 2
4	1 → 2	30	8	4 → 6	323	0 → 2
15	4 → 6	49	9	4 → 5	338	4 → 3
16	2 → 3	54	1	2 → 3	node_360 → node_359	
18	6 → 7	55	2	0 → 1	17	4 → 5
19	5 → 6	75	07	2 → 0	20	4 → 6
20	5 → 7	76	76	1 → 2	30	3 → 2
21	0 → 1	77	89	2 → 3	195	0 → 1
33	2 → 3	78	91	1 → 0	231	0 → 1
38	3 → 0	168	96	6 → 1	232	0 → 2
75	0 → 3	171	97	0 → 1	233	0 → 2
76	0 → 3	172	21	2 → 1	234	0 → 2
77	0 → 4	213	28	6 → 5	235	0 → 2
78	0 → 4	233	33	1 → 0	236	0 → 3
216	1 → 3	246	46	6 → 4	246	4 → 7
219	0 → 2	263	44	0 → 1	254	2 → 5
244	0 → 1	284	node_360 → node_281		256	4 → 9
246	3 → 0	328	(clade 10)		257	2 → 0
266	0 → 6	node_383 → node_382	26	0 → 1	344	1 → 2
283	2 → 3	8	27	0 → 1	349	0 → 1
284	3 → 4	11	55	1 → 2	350	0 → 2
300	0 → 2	15	103	0 → 1	364	0 → 1
313	2 → 3	55	104	2 → 0	403	4 → 8
317	1 → 2	246	178	3 → 4	405	0 → 1
node_384 → node_383		254	191	0 → 5	node_359 → node_282	
12	1 → 0	261	193	0 → 1	(clade 11)	
31	3 → 4	263	213	0 → 1	18	6 → 5
74	0 → 1	279	216	1 → 0	19	5 → 6
196	2 → 1	338	261	5 → 4	68	0 → 6
221	0 → 1	339	283	2 → 3	111	3 → 2
227	4 → 5	360	360	1 → 0	124	3 → 1
228	0 → 5	361	361	1 → 0	125	3 → 1
253	5 → 6	362	node_281 → node_279		193	0 → 2
254	0 → 1	node_382 → node_378	(<i>Pidorus</i>)		195	1 → 3
270	0 → 2	7	5	2 → 3	196	1 → 4

APPENDIX 4 Continued

198	0 → 4	228	7 → 8	node_284 →	node_290 → node_289		
199	0 → 2	284	1 → 5	<i>Pidorus ochrolophus</i>	26	0 → 1	
229	0 → 1	300	3 → 5	6	2 → 3	27	0 → 1
236	3 → 4	320	1 → 2	14	1 → 2	75	0 → 1
237	0 → 1	344	2 → 1	101	2 → 1	76	0 → 1
257	0 → 4			125	5 → 3	77	0 → 1
263	1 → 5	node_286 → node_283		148	0 → 2	78	0 → 1
265	0 → 1	(<i>Pidoromorpha</i>)		173	4 → 3		
272	2 → 3	6	2 → 3	405	1 → 0	node_289 → node_288	
341	2 → 0	21	0 → 1			(<i>Erasmiphleboecta</i> +	
365	1 → 0	103	0 → 2	node_287 →		<i>Chalcophaedra</i>)	
369	0 → 1	125	5 → 3	<i>Barbaroscia amabilis</i>		3	3 → 1
node_359 → node_358		130	0 → 1	5	3 → 2	4	3 → 1
5	2 → 3	139	0 → 4	19	5 → 4	20	6 → 7
17	5 → 6	140	0 → 4	68	0 → 4	68	0 → 1
22	0 → 1	156	0 → 2	77	0 → 4	94	5 → 4
33	2 → 0	157	0 → 4	78	0 → 4	136	0 → 6
34	2 → 0	177	5 → 4	97	0 → 1	137	0 → 3
54	1 → 2	191	6 → 4	124	3 → 5	138	0 → 3
55	1 → 4	261	3 → 4	133	0 → 1	173	4 → 3
67	1 → 0	272	2 → 1	136	0 → 2	174	4 → 3
74	1 → 2	301	0 → 1	143	2 → 1	190	0 → 3
153	0 → 3	320	2 → 3	144	2 → 1	195	3 → 6
154	0 → 3	node_286 → node_285		146	0 → 2	196	7 → 1
168	0 → 2	4	2 → 1	147	0 → 2	198	3 → 5
170	6 → 4	13	2 → 1	153	3 → 2	213	8 → 0
190	1 → 0	14	2 → 1	154	3 → 2	236	3 → 2
191	0 → 6	15	4 → 3	179	0 → 1	250	0 → 1
259	0 → 1	16	3 → 2	180	0 → 1	263	1 → 0
266	2 → 3	263	1 → 0	183	0 → 3	265	0 → 1
284	3 → 4	266	3 → 4	184	0 → 3	266	3 → 4
329	0 → 4	322	0 → 1	190	0 → 1	272	5 → 4
node_358 → node_294		329	4 → 0	236	3 → 2	279	3 → 5
(clade 12)		337	3 → 2	283	2 → 1	300	0 → 7
11	1 → 2	338	4 → 2	308	0 → 1	301	4 → 8
48	3 → 2	node_285 →		323	0 → 2	320	1 → 2
193	0 → 3	<i>Pseudoscaptesyale circumdata</i>		339	1 → 0	349	1 → 0
194	0 → 1	3	2 → 1	340	1 → 0	350	2 → 0
196	1 → 7	30	3 → 2	node_294 → node_293		360	1 → 0
197	1 → 2	31	4 → 3	(<i>Erasmia-Chalcophaedra</i>)		361	1 → 0
198	0 → 1	105	0 → 1	6	2 → 3	365	1 → 0
228	5 → 7	143	2 → 1	19	5 → 6	366	1 → 0
256	9 → 7	144	2 → 1	1	0 → 1	369	1 → 0
257	0 → 7	158	0 → 1	4	3 → 5	381	2 → 0
261	5 → 3	159	0 → 1	11	3 → 2	node_288 →	
320	2 → 1	191	6 → 5	52	0 → 1	<i>Erasmiphleboecta picturata</i>	
366	0 → 1	256	7 → 0	67	1 → 2	7	0 → 1
node_294 → node_287		266	4 → 5	69	3 → 4	8	0 → 1
17	6 → 4	322	1 → 2	93	3 → 4	15	4 → 5
18	6 → 4	node_285 → node_284		94	1 → 2	16	3 → 4
20	6 → 5	5	3 → 2	98	1 → 2	30	2 → 3
22	1 → 0	7	1 → 0	13	0 → 8	31	3 → 4
30	2 → 3	49	1 → 2	50	1 → 0	121	0 → 1
31	3 → 4	124	3 → 5	01	0 → 4	124	3 → 1
33	0 → 1	151	0 → 1	22	0 → 1	125	3 → 1
34	0 → 1	152	0 → 1	81	0 → 2	133	0 → 2
55	4 → 2	153	3 → 0	node_293 → node_290		143	2 → 1
125	3 → 5	154	3 → 0	3	2 → 3	144	2 → 1
168	2 → 0	193	3 → 4	4	2 → 3	150	0 → 1
177	4 → 5	194	1 → 0	107	0 → 1	156	0 → 1
195	1 → 6	213	0 → 3	139	0 → 4	157	0 → 1
284	4 → 1	228	8 → 7	140	0 → 4	177	4 → 5
300	0 → 3	283	2 → 1	141	0 → 3	179	0 → 1
node_287 → node_286		300	5 → 6	142	0 → 3	180	0 → 1
7	0 → 1	node_284 → <i>Pidorus circe</i>		153	3 → 4	183	0 → 2
8	0 → 1	4	1 → 2	154	3 → 4	184	0 → 3
17	4 → 5	8	1 → 0	195	1 → 3	node_288 →	
18	4 → 5	145	0 → 1	198	2 → 3	<i>Chalcophaedra zuleika</i>	
49	2 → 1	301	0 → 8	272	2 → 5	3	1 → 2
104	2 → 1	341	2 → 3	284	4 → 7	4	1 → 2
162	0 → 1			369	0 → 1	17	6 → 7
						18	6 → 7

APPENDIX 4 *Continued*

26	1 → 2	77	0 → 1	16	3 → 2	78	0 → 4
27	1 → 2	78	0 → 1	17	6 → 5	81	1 → 0
68	1 → 2	103	0 → 2	20	6 → 5	111	2 → 3
75	1 → 2	139	0 → 1	22	1 → 0	153	5 → 0
76	1 → 2	140	0 → 1	30	2 → 3	154	5 → 0
77	1 → 2	141	0 → 3	170	4 → 3	168	2 → 0
78	1 → 2	142	0 → 3	201	1 → 6	173	3 → 4
103	0 → 2	143	0 → 2	202	2 → 4	190	3 → 5
107	1 → 0	144	0 → 2	208	2 → 0	193	8 → 0
152	1 → 0	156	0 → 4	263	1 → 7	201	6 → 4
153	4 → 2	157	0 → 4	341	1 → 0	231	1 → 0
154	4 → 2	170	4 → 2	344	2 → 1	234	3 → 0
185	0 → 1	172	3 → 4	349	1 → 0	235	3 → 0
186	0 → 1	173	4 → 3	365	1 → 2	236	4 → 0
265	1 → 3	190	0 → 5	node_343 → node_299		238	2 → 0
node_293 → node_292		205	0 → 1	(clade 15)		239	2 → 0
(Amesia)		213	6 → 8	82	1 → 0	247	5 → 1
15	4 → 5	216	1 → 2	111	3 → 2	250	1 → 0
16	3 → 4	235	0 → 6	120	0 → 1	253	6 → 0
103	0 → 1	236	3 → 0	124	3 → 1	257	8 → 0
143	2 → 0	247	2 → 0	154	3 → 4	265	3 → 0
144	2 → 0	251	0 → 1	247	2 → 3	266	2 → 3
146	0 → 5	254	5 → 6	266	3 → 2	340	1 → 2
147	0 → 5	266	3 → 1	283	2 → 1	node_297 →	
177	4 → 1	304	0 → 1	284	3 → 5	<i>Trypanophora hyalina</i>	
261	3 → 4	node_295 →		302	0 → 1	5	0 → 1
263	1 → 5	<i>Opisthoptatia grandis</i>		363	0 → 1	6	0 → 3
266	3 → 4	4	2 → 1	366	0 → 1	16	2 → 3
283	2 → 3	6	2 → 3	node_299 → node_298		17	5 → 3
337	3 → 2	19	5 → 6	3	1 → 0	20	4 → 6
338	4 → 2	31	3 → 2	4	1 → 0	26	0 → 4
node_358 → node_357		94	3 → 4	5	2 → 0	27	0 → 1
3	2 → 1	111	3 → 0	6	2 → 0	48	2 → 3
8	0 → 1	119	0 → 1	48	3 → 2	49	1 → 2
143	2 → 0	120	0 → 1	49	2 → 1	58	0 → 1
144	2 → 0	124	3 → 5	125	3 → 1	67	1 → 0
174	4 → 3	125	3 → 5	153	3 → 5	82	0 → 1
177	4 → 6	153	3 → 0	154	4 → 5	104	2 → 0
213	0 → 6	154	3 → 2	173	4 → 3	105	0 → 1
232	2 → 1	160	0 → 4	193	0 → 8	114	0 → 1
235	2 → 0	167	1 → 3	195	6 → 3	116	1 → 0
247	0 → 2	168	2 → 1	247	3 → 5	119	0 → 1
337	3 → 2	169	3 → 4	265	0 → 3	124	1 → 2
338	4 → 2	171	2 → 3	341	0 → 1	167	1 → 3
341	2 → 1	234	2 → 0	node_298 → node_297		171	2 → 4
403	8 → 9	250	1 → 0	12	1 → 0	179	0 → 1
node_357 → node_295		253	6 → 0	13	2 → 1	180	0 → 1
(clade 13)		263	1 → 0	14	2 → 1	183	0 → 3
7	0 → 1	341	1 → 3	19	5 → 4	184	0 → 3
151	0 → 1	node_357 → node_356		20	5 → 4	191	6 → 8
162	0 → 1	67	0 → 1	68	6 → 0	195	3 → 4
189	3 → 0	68	0 → 6	75	0 → 3	213	6 → 5
191	6 → 0	103	0 → 1	77	0 → 4	272	3 → 2
218	0 → 4	190	0 → 2	170	3 → 4	283	1 → 2
231	1 → 2	195	1 → 6	172	3 → 5	301	0 → 4
240	0 → 2	196	1 → 3	190	2 → 3	320	2 → 3
256	9 → 0	197	1 → 3	194	0 → 4	341	1 → 2
259	1 → 0	201	0 → 1	256	9 → 0	node_298 →	
283	2 → 3	205	0 → 2	284	5 → 2	<i>Soritia moerens</i>	
287	0 → 1	234	2 → 3	302	1 → 0	1	0 → 1
301	0 → 3	235	0 → 3	337	2 → 3	2	0 → 1
node_295 → <i>Eterusia repleta</i>		236	3 → 4	338	2 → 4	8	1 → 0
3	1 → 2	238	0 → 2	node_297 → node_296		17	5 → 4
5	3 → 2	239	0 → 2	3	0 → 1	18	6 → 4
16	3 → 4	257	0 → 8	7	0 → 1	28	1 → 0
26	0 → 1	272	2 → 3	18	6 → 5	29	1 → 0
27	0 → 1	284	4 → 3	30	3 → 2	33	0 → 3
48	3 → 2	329	4 → 0	33	0 → 1	34	0 → 3
54	2 → 4	node_356 → node_343		34	0 → 1	97	0 → 1
75	0 → 1	4	2 → 1	68	0 → 4	98	2 → 1
76	0 → 1	5	3 → 2	74	2 → 0	191	6 → 7
		15	4 → 3	76	0 → 3	200	0 → 4

APPENDIX 4 Continued

201	6 ⇒ 5	201	6 → 7	257	5 ⇒ 8	node_305 → node_304	
202	4 ⇒ 5	202	4 → 5	266	4 → 5	26	1 → 2
205	2 ⇒ 1	205	1 → 3	node_342 → node_341		27	1 → 2
213	6 ⇒ 1	213	6 ⇒ 1	33	0 ⇒ 1	75	1 → 2
node_299 →		350	2 → 0	34	0 ⇒ 1	76	1 → 2
<i>Prosopandrophila distincta</i>		360	1 → 0	48	3 ⇒ 2	77	1 → 2
7	0 ⇒ 1	365	2 → 0	68	6 → 0	78	1 → 2
9	1 ⇒ 0	node_302 → node_300		153	3 → 0	104	2 ⇒ 1
10	1 ⇒ 0	15	3 ⇒ 4	174	3 → 4	107	1 ⇒ 0
17	5 → 6	18	6 ⇒ 5	193	1 → 7	117	1 ⇒ 0
22	0 → 1	54	2 ⇒ 1	258	0 → 5	124	2 → 5
27	0 ⇒ 4	107	0 ⇒ 1	266	3 ⇒ 6	125	3 ⇒ 5
54	2 ⇒ 1	120	0 ⇒ 1	341	0 → 2	146	5 → 1
67	1 ⇒ 2	130	0 ⇒ 1	366	0 ⇒ 2	147	5 → 2
68	6 ⇒ 1	139	0 ⇒ 1	node_341 → node_319		160	2 → 0
76	0 ⇒ 1	140	0 ⇒ 1	(clade 17)		161	2 → 0
78	0 ⇒ 1	190	2 → 0	17	5 → 6	183	4 → 0
103	1 ⇒ 3	193	1 → 6	26	5 → 0	185	0 ⇒ 1
119	0 ⇒ 1	200	0 ⇒ 4	27	5 → 0	186	0 ⇒ 1
124	1 → 7	233	2 ⇒ 1	31	3 → 4	200	4 ⇒ 2
130	0 ⇒ 1	235	6 ⇒ 4	67	1 → 3	361	0 → 1
137	0 ⇒ 2	236	4 ⇒ 0	107	0 ⇒ 1	372	0 → 1
138	0 ⇒ 2	238	5 ⇒ 0	147	0 ⇒ 3	node_305 → <i>Milleria adalifa</i>	
139	0 ⇒ 2	239	2 ⇒ 0	196	3 ⇒ 4	119	0 ⇒ 1
140	0 ⇒ 4	251	0 ⇒ 2	201	6 ⇒ 8	130	0 ⇒ 1
141	0 ⇒ 2	258	0 ⇒ 1	202	4 ⇒ 6	135	0 ⇒ 2
142	0 ⇒ 2	301	0 → 4	node_319 → node_309		189	3 ⇒ 2
143	0 ⇒ 1	node_302 → node_301		3	1 → 2	349	0 ⇒ 1
144	0 ⇒ 1	3	1 → 2	4	1 → 2	363	0 ⇒ 1
146	0 ⇒ 4	4	1 ⇒ 3	15	3 → 4	node_308 → node_307	
147	0 ⇒ 4	19	5 ⇒ 4	16	2 → 3	7	0 ⇒ 1
156	0 ⇒ 2	22	0 → 1	26	0 → 1	8	0 ⇒ 1
157	0 ⇒ 2	33	0 → 3	27	0 → 1	167	1 ⇒ 3
174	3 → 4	34	0 ⇒ 3	117	0 ⇒ 1	266	6 ⇒ 8
179	0 ⇒ 1	104	2 → 0	133	0 → 1	301	0 ⇒ 7
182	0 ⇒ 1	141	0 ⇒ 3	146	0 → 3	304	0 ⇒ 1
183	0 ⇒ 2	142	0 ⇒ 3	154	3 ⇒ 0	node_309 →	
184	0 ⇒ 5	153	3 ⇒ 6	160	0 → 2	<i>Milleria okushimai</i>	
191	6 → 1	154	3 ⇒ 6	161	0 → 2	5	2 ⇒ 3
200	0 ⇒ 3	168	2 ⇒ 0	183	0 → 4	6	2 ⇒ 3
213	6 ⇒ 0	266	3 → 4	node_309 → node_308		19	5 ⇒ 6
218	0 ⇒ 1	node_301 →		67	3 → 1	20	5 ⇒ 6
279	3 ⇒ 5	<i>Pseudopidorus fasciatus</i>		68	0 ⇒ 6	22	0 ⇒ 1
300	0 ⇒ 6	6	2 ⇒ 3	75	0 ⇒ 1	31	4 → 3
301	0 ⇒ 6	13	2 ⇒ 0	76	0 ⇒ 1	135	0 ⇒ 1
node_343 → node_342		20	5 ⇒ 6	77	0 ⇒ 1	136	0 ⇒ 1
8	1 → 0	31	3 ⇒ 2	78	0 ⇒ 1	150	0 ⇒ 1
11	1 ⇒ 2	37	0 ⇒ 1	146	3 → 5	156	0 ⇒ 2
26	0 → 5	48	3 ⇒ 2	147	3 → 5	157	0 ⇒ 2
27	0 → 5	94	4 → 3	200	0 ⇒ 4	173	4 ⇒ 3
55	4 ⇒ 2	103	1 ⇒ 0	205	1 ⇒ 2	184	0 ⇒ 4
74	2 ⇒ 1	164	0 ⇒ 1	263	7 → 6	190	2 ⇒ 4
191	6 → 2	190	2 ⇒ 3	329	0 ⇒ 2	191	2 ⇒ 0
193	0 → 1	238	5 ⇒ 1	node_308 → node_305		193	7 ⇒ 8
205	2 → 1	254	5 ⇒ 2	3	2 → 1	202	6 → 7
235	3 → 6	256	6 ⇒ 9	4	2 → 1	203	0 ⇒ 3
238	2 ⇒ 5	258	0 ⇒ 2	13	2 ⇒ 1	213	6 ⇒ 8
256	9 ⇒ 6	261	5 ⇒ 4	14	2 ⇒ 1	238	5 ⇒ 1
257	8 ⇒ 5	263	7 ⇒ 4	15	4 → 3	239	2 ⇒ 3
272	3 → 2	272	2 ⇒ 3	16	3 → 2	265	0 ⇒ 2
337	2 ⇒ 3	323	0 ⇒ 2	124	3 → 2	322	0 ⇒ 1
338	2 ⇒ 4	node_301 →		133	1 → 0	node_319 → node_318	
361	1 → 0	<i>Neochalcosia remota</i>		139	0 ⇒ 1	13	2 ⇒ 1
364	1 ⇒ 0	3	2 → 3	140	0 ⇒ 1	14	2 ⇒ 1
node_342 → node_302		28	1 ⇒ 2	141	0 ⇒ 2	78	0 → 3
(clade 16)		33	3 → 4	142	0 ⇒ 2	125	3 → 5
16	2 → 3	104	0 → 1	143	0 ⇒ 1	301	0 ⇒ 7
94	3 → 4	200	0 ⇒ 1	144	0 ⇒ 1	307	0 ⇒ 1
143	0 ⇒ 2	201	7 → 6	153	0 → 2	341	2 → 0
144	0 ⇒ 2	202	5 → 4	154	0 → 2	node_318 → node_316	
173	4 ⇒ 3	205	3 → 2	190	2 ⇒ 0	6	2 ⇒ 3
195	6 ⇒ 2	213	1 ⇒ 5	213	6 ⇒ 5		

APPENDIX 4 *Continued*

10	1 ⇒ 0	117	0 ⇒ 2	8	0 ⇒ 1	14	2 ⇒ 1
17	6 → 4	120	0 ⇒ 1	17	5 → 6	117	0 ⇒ 2
18	6 → 4	124	3 ⇒ 5	22	0 ⇒ 1	124	3 → 6
19	5 ⇒ 4	135	0 ⇒ 3	97	0 → 1	179	0 → 1
20	5 ⇒ 4	147	3 → 5	170	3 ⇒ 4	183	5 → 3
154	3 → 2	168	2 ⇒ 0	183	0 ⇒ 5	187	0 ⇒ 1
208	0 → 1	173	4 ⇒ 3	184	0 ⇒ 5	188	0 ⇒ 1
272	2 ⇒ 5	185	0 ⇒ 1	190	4 → 2	190	2 → 3
322	0 ⇒ 2	186	0 ⇒ 1	213	7 → 1	200	4 → 0
node_316 → node_313		190	2 ⇒ 1	256	6 ⇒ 9	201	5 → 2
3	1 ⇒ 3	193	7 ⇒ 9	258	0 → 4	202	3 → 1
8	0 → 1	195	6 ⇒ 1	329	0 → 2	205	1 → 3
13	1 ⇒ 3	202	6 ⇒ 9	node_325 → <i>Eterusia raja</i>		208	0 → 2
15	3 ⇒ 4	205	1 ⇒ 3	4	1 ⇒ 2	254	7 → 9
17	4 → 5	284	3 ⇒ 5	15	3 ⇒ 5	265	2 → 3
18	4 → 5	296	0 ⇒ 1	16	2 ⇒ 4	284	0 → 8
22	0 ⇒ 1	node_341 → node_340		17	6 → 7	300	3 → 6
28	1 ⇒ 2	(clade 18)		18	6 ⇒ 7	322	0 ⇒ 1
30	3 ⇒ 1	5	2 ⇒ 1	20	5 ⇒ 4	329	2 → 0
33	1 ⇒ 2	30	3 ⇒ 2	26	5 → 2	node_324 → node_323	
34	1 → 2	102	2 → 1	27	5 → 2	154	3 → 0
48	2 ⇒ 3	103	1 ⇒ 0	30	2 ⇒ 3	178	3 ⇒ 5
67	3 ⇒ 0	190	2 → 4	31	3 ⇒ 4	191	2 → 0
76	0 → 1	200	0 ⇒ 4	54	2 ⇒ 4	193	7 ⇒ 0
78	3 → 1	213	6 → 7	55	2 ⇒ 3	195	6 → 2
104	2 ⇒ 1	238	5 → 3	75	0 ⇒ 2	256	9 ⇒ 0
125	5 → 3	356	0 → 1	76	0 ⇒ 2	301	0 ⇒ 4
144	0 → 2	360	1 → 2	77	0 ⇒ 2	337	3 ⇒ 0
153	0 → 2	361	0 → 2	78	0 ⇒ 2	338	4 ⇒ 1
213	6 → 0	node_340 →		103	0 ⇒ 1	351	0 ⇒ 1
node_313 →		<i>Scotopais tristis</i>		111	3 ⇒ 2	363	0 ⇒ 1
<i>Docleopsis dohertyi</i>		6	2 ⇒ 1	141	0 ⇒ 2	364	0 → 1
37	0 ⇒ 1	11	2 ⇒ 1	142	0 ⇒ 2	370	0 ⇒ 1
153	2 → 5	13	2 ⇒ 0	143	0 ⇒ 1	node_323 → node_322	
202	6 → 2	14	2 ⇒ 0	144	0 ⇒ 1	(<i>Gynautocera</i>)	
205	1 ⇒ 4	18	6 ⇒ 5	160	0 ⇒ 3	19	5 ⇒ 6
208	1 → 0	28	1 ⇒ 0	161	0 ⇒ 3	20	5 ⇒ 6
213	0 → 5	29	1 ⇒ 0	201	5 ⇒ 9	97	2 → 0
node_313 → node_312		31	3 ⇒ 2	202	3 ⇒ 5	104	0 ⇒ 1
(<i>Eusphalera</i>)		49	2 ⇒ 1	238	3 ⇒ 4	124	3 ⇒ 2
75	0 ⇒ 1	68	0 ⇒ 5	247	2 ⇒ 6	125	3 ⇒ 2
77	0 ⇒ 1	75	0 ⇒ 4	344	2 → 1	185	1 → 0
143	0 ⇒ 2	76	0 ⇒ 4	node_325 → node_324		186	1 → 0
203	0 ⇒ 1	77	0 ⇒ 5	19	4 → 5	191	0 → 3
node_316 → node_315		78	0 ⇒ 5	48	2 ⇒ 3	194	0 ⇒ 1
(<i>Psaphis</i>)		107	0 ⇒ 2	68	0 ⇒ 6	200	4 ⇒ 1
9	1 ⇒ 0	124	3 ⇒ 1	94	3 ⇒ 4	263	7 ⇒ 6
94	3 ⇒ 4	125	3 ⇒ 1	96	0 ⇒ 1	283	2 ⇒ 4
103	1 ⇒ 2	154	3 ⇒ 0	97	1 → 2	287	0 ⇒ 1
124	3 ⇒ 7	164	0 ⇒ 1	104	2 ⇒ 0	329	2 → 4
126	0 ⇒ 1	167	1 ⇒ 0	107	0 ⇒ 1	341	2 ⇒ 1
133	0 ⇒ 1	169	3 ⇒ 2	153	3 → 0	364	1 → 2
136	0 ⇒ 2	238	3 → 6	167	1 ⇒ 3	node_323 →	
138	0 → 1	265	0 ⇒ 2	169	3 ⇒ 4	<i>Pompon marginata</i>	
140	0 → 2	301	0 ⇒ 6	171	2 ⇒ 3	13	2 ⇒ 3
146	0 ⇒ 3	304	0 ⇒ 1	173	4 ⇒ 5	14	2 ⇒ 3
150	0 ⇒ 1	322	0 ⇒ 1	174	4 ⇒ 5	15	3 ⇒ 4
169	3 ⇒ 4	341	2 → 1	177	6 ⇒ 5	16	2 ⇒ 3
180	0 ⇒ 1	node_340 → node_339		185	0 → 1	22	1 ⇒ 0
183	0 ⇒ 2	19	5 → 4	186	0 → 1	26	5 ⇒ 1
184	0 ⇒ 2	67	1 ⇒ 0	213	1 → 6	27	5 ⇒ 1
202	6 → 7	153	0 → 3	239	2 ⇒ 1	153	0 → 2
203	0 ⇒ 2	201	6 ⇒ 5	265	0 → 2	154	0 → 2
263	7 ⇒ 4	202	4 ⇒ 3	266	6 ⇒ 3	183	5 ⇒ 4
node_318 → node_317		254	5 ⇒ 7	284	3 → 0	184	5 ⇒ 4
(<i>Pseudonycytemera</i>)		258	5 → 0	300	0 → 3	195	2 → 5
68	0 ⇒ 3	344	1 → 2	node_324 → node_321		238	3 ⇒ 1
77	0 ⇒ 3	node_339 → node_325		(<i>Histia</i>)		239	1 ⇒ 0
101	2 ⇒ 3	5	1 ⇒ 3	3	1 → 0	254	7 ⇒ 5
103	1 ⇒ 0	6	2 ⇒ 3	4	1 ⇒ 0	258	4 ⇒ 0
104	2 ⇒ 0	7	0 ⇒ 1	13	2 → 1	266	3 ⇒ 4
						356	1 → 0

APPENDIX 4 *Continued*

360	2 → 1	147	0 → 4	20	4 → 6	30	2 → 3
361	2 → 1	185	0 → 1	30	2 → 3	33	2 → 1
node_339 → node_338		186	0 → 1	31	2 → 4	34	2 → 3
13	2 → 1	190	4 → 2	94	2 → 4	55	2 → 1
14	2 → 1	195	3 → 6	191	3 → 4	75	0 → 3
26	5 → 0	205	0 → 3	194	1 → 5	76	0 → 3
27	5 → 0	254	7 → 9	196	3 → 6	77	0 → 4
33	1 → 2	256	6 → 0	197	3 → 1	78	0 → 4
34	1 → 2	263	3 → 0	199	0 → 1	124	3 → 0
120	0 → 1	279	4 → 5	228	5 → 9	139	0 → 4
168	2 → 0	300	0 → 3	238	6 → 2	140	0 → 1
176	2 → 1	341	2 → 0	263	3 → 4	142	0 → 3
193	7 → 0	344	0 → 1	301	0 → 4	145	0 → 1
195	6 → 1	node_335 → node_334		311	0 → 1	149	0 → 1
239	2 → 3	13	1 → 2	341	2 → 0	153	3 → 4
266	6 → 1	18	4 → 5	403	2 → 1	168	0 → 2
272	2 → 3	31	3 → 2	node_333 → node_332		190	4 → 0
279	3 → 4	37	1 → 0	4	1 → 2	191	2 → 6
node_338 → node_336		81	1 → 0	6	0 → 2	194	0 → 6
18	6 → 4	101	2 → 3	8	0 → 1	196	3 → 2
20	5 → 4	153	3 → 0	14	0 → 2	197	3 → 1
29	1 → 0	154	3 → 0	15	2 → 4	228	5 → 9
37	0 → 1	191	2 → 3	27	0 → 1	235	6 → 7
82	1 → 0	213	4 → 5	28	0 → 2	238	3 → 1
94	3 → 2	238	3 → 6	33	2 → 3	258	0 → 4
167	1 → 0	239	1 → 2	67	0 → 1	261	5 → 0
169	3 → 2	258	0 → 3	75	0 → 5	266	1 → 6
195	1 → 3	272	3 → 4	76	0 → 5	272	3 → 1
200	4 → 0	337	3 → 0	77	0 → 5	283	2 → 3
201	5 → 0	338	4 → 0	78	0 → 5	284	3 → 2
205	1 → 0	node_334 → node_328		146	0 → 1	290	0 → 2
263	7 → 3	(<i>Boradiopsis</i>)		190	4 → 0	301	0 → 2
344	2 → 0	6	0 → 1	195	3 → 2	308	0 → 3
403	9 → 2	14	0 → 3	200	0 → 4	341	2 → 3
node_336 → node_335		19	4 → 5	201	0 → 4	343	2 → 0
3	1 → 2	121	0 → 1	205	0 → 1	405	1 → 0
5	1 → 2	153	0 → 5	218	0 → 1	node_338 → node_337	
6	2 → 0	154	0 → 5	266	1 → 6	(<i>Syntomochalcosia</i>)	
14	1 → 0	164	1 → 0	300	0 → 3	31	3 → 2
28	1 → 0	195	3 → 1	339	1 → 0	49	2 → 0
49	2 → 1	196	3 → 2	340	1 → 0	55	2 → 3
103	0 → 3	197	3 → 0	node_332 → node_330		58	0 → 1
164	0 → 1	250	1 → 0	(<i>Docleopsis</i>)		104	2 → 0
173	4 → 3	254	7 → 8	81	0 → 1	111	3 → 0
177	6 → 0	256	6 → 4	94	2 → 1	124	3 → 1
213	7 → 4	257	5 → 6	173	4 → 3	125	3 → 1
239	3 → 1	263	3 → 7	284	3 → 2	174	4 → 3
342	1 → 0	266	1 → 3	301	0 → 3	179	0 → 1
node_335 →		283	2 → 1	308	0 → 1	180	0 → 1
<i>Anarbudas bipartite</i>		320	2 → 4	320	2 → 3	183	0 → 3
16	2 → 1	338	0 → 1	342	0 → 1	184	0 → 3
17	5 → 3	342	0 → 1	343	0 → 1	191	2 → 0
19	4 → 3	403	2 → 9	344	0 → 1	196	3 → 4
26	0 → 4	node_334 → node_333		node_332 → node_331		213	7 → 8
27	0 → 4	15	3 → 2	(<i>Euxanthopyge</i>)		254	7 → 6
30	2 → 1	120	1 → 0	68	0 → 6	257	5 → 2
67	0 → 2	171	2 → 1	97	0 → 1	283	2 → 1
68	0 → 4	173	3 → 4	154	0 → 4	301	0 → 4
75	0 → 2	194	0 → 1	167	0 → 3	323	0 → 1
76	0 → 2	261	5 → 4	168	0 → 2	341	2 → 1
77	0 → 2	343	2 → 0	176	1 → 2	node_356 → node_355	
78	0 → 2	node_333 → node_329		177	0 → 6	(clade 14)	
97	0 → 1	(<i>Aphantcephala</i>)		272	4 → 3	6	2 → 3
111	3 → 2	3	2 → 1	279	4 → 5	21	0 → 1
137	0 → 2	5	2 → 0	322	0 → 1	54	2 → 1
138	0 → 2	11	2 → 1	node_336 →		119	0 → 1
141	0 → 1	13	2 → 0	<i>Allocaprina duganga</i>		130	0 → 1
142	0 → 1	16	2 → 1	4	1 → 2	140	0 → 1
143	0 → 1	17	5 → 7	9	1 → 0	153	3 → 6
144	0 → 1	18	5 → 7	17	5 → 4	159	0 → 1
146	0 → 4	19	4 → 6	27	0 → 3	191	6 → 3

APPENDIX 4 *Continued*

193	0 → 5	node_361 →	node_371 → node_364	338	2 → 0	
213	6 → 2	<i>Prosopandrophila mirifica</i>	37	0 → 1	343	0 → 2
247	2 → 1	3	125	3 → 4	node_366 →	
254	5 → 3	5	167	1 → 3	<i>Hemichrysoptera celebensis</i>	
261	5 → 4	9	172	3 → 2	7	0 → 1
329	0 → 3	11	284	3 → 1	11	1 → 2
403	9 → 2	13	285	1 → 3	17	4 → 3
410	1 → 2	15	317	0 → 2	18	4 → 3
node_355 → node_348		26	319	0 → 1	26	0 → 2
(<i>Eterusia</i>)		28	node_364 →		27	0 → 2
7	0 → 1	30	<i>Isocrambia melaleuca</i>		28	0 → 2
67	1 → 0	167	6	2 → 1	29	0 → 2
103	1 → 2	170	12	0 → 1	30	2 → 1
156	0 → 1	190	16	2 → 1	75	0 → 2
157	0 → 1	node_361 →	18	5 → 7	76	3 → 2
174	3 → 4	<i>Pidorus bifasciatus</i>	27	0 → 4	77	0 → 2
190	2 → 4	173	49	2 → 1	78	4 → 2
196	3 → 4	177	68	0 → 4	97	0 → 2
205	2 → 3	node_363 →	103	0 → 3	104	2 → 0
208	2 → 1	<i>Pidorus corculum</i> (clade 8)	104	0 → 1	107	0 → 2
213	2 → 5	33	164	1 → 0	137	0 → 1
239	2 → 1	34	173	4 → 3	138	0 → 1
247	1 → 7	145	283	1 → 0	153	5 → 2
256	9 → 7	173	node_364 →		154	5 → 2
node_355 → node_354		213	<i>Cyanidia thaumasta</i>		155	0 → 1
(<i>Soritia</i>)		257	4	1 → 3	169	3 → 2
3	1 → 2	266	20	5 → 6	183	0 → 5
8	1 → 0	285	31	4 → 3	184	0 → 5
12	1 → 2	319	34	2 → 4	191	1 → 2
15	4 → 5	342	42	2 → 3	235	0 → 1
19	5 → 6	node_378 → node_377	101	2 → 0	256	0 → 9
76	0 → 3	(clade 7)	111	3 → 2	263	5 → 1
78	0 → 4	13	125	4 → 5	266	1 → 3
111	3 → 2	29	144	0 → 2	272	2 → 7
120	0 → 1	102	168	0 → 2	279	3 → 5
146	0 → 1	107	169	3 → 5	300	0 → 3
150	0 → 1	141	170	3 → 5	305	0 → 1
158	0 → 3	203	177	4 → 6	337	0 → 3
173	4 → 3	232	272	2 → 1	338	0 → 4
180	0 → 1	260	279	4 → 2	339	0 → 1
184	0 → 3	266	296	0 → 1	340	0 → 1
195	6 → 0	272	320	2 → 1	341	3 → 1
201	1 → 3	283	341	3 → 2	403	4 → 2
227	5 → 2	337	342	1 → 0	node_366 → node_365	
228	5 → 0	351	403	4 → 2	3	2 → 3
254	3 → 4	node_377 → node_375	node_371 → node_370		4	1 → 2
257	8 → 9	14	8	0 → 1	8	1 → 0
258	0 → 6	28	14	0 → 1	19	3 → 4
263	1 → 5	81	18	5 → 4	20	3 → 4
266	3 → 7	94	20	5 → 3	31	2 → 3
341	1 → 2	143	76	0 → 3	33	2 → 5
node_362 → node_361		144	78	0 → 4	34	2 → 3
(clade 9)		153	104	0 → 2	48	2 → 3
6	2 → 1	213	154	0 → 5	94	3 → 2
10	1 → 0	248	174	4 → 3	120	0 → 1
14	2 → 1	249	279	4 → 3	145	0 → 1
27	0 → 5	261	node_370 → node_366		164	1 → 0
29	1 → 0	338	12	0 → 1	167	1 → 3
33	2 → 3	339	31	4 → 2	168	0 → 2
34	2 → 3	343	81	0 → 1	173	4 → 3
68	0 → 6	403	142	0 → 3	189	2 → 0
97	0 → 1	node_375 → node_371	158	0 → 3	197	0 → 1
120	0 → 1	13	159	0 → 2	213	7 → 8
141	0 → 3	17	213	5 → 7	216	1 → 2
142	0 → 3	19	254	2 → 0	260	2 → 3
143	2 → 1	48	256	5 → 0	284	3 → 0
144	2 → 1	153	257	2 → 0	308	0 → 1
232	0 → 1	164	260	4 → 2	344	0 → 2
260	0 → 2	263	261	4 → 3	node_370 → node_369	
272	2 → 3	272	301	0 → 4	6	2 → 1
279	3 → 4	node_375 → node_371	320	2 → 3	10	1 → 0
341	2 → 4	13			49	2 → 1

APPENDIX 4 *Continued*

94	3 → 1	node_368 →	node_377 → node_376	190	1 ⇒ 5	
103	0 ⇒ 3	<i>Thaumastophleps expansa</i>	6	2 → 3	191	1 ⇒ 6
125	3 → 1	97	7	0 → 1	193	0 ⇒ 1
141	3 → 0	109	8	0 → 1	195	0 ⇒ 2
171	2 ⇒ 1	166	9	1 ⇒ 0	196	6 ⇒ 3
node_369 →		169	10	1 → 0	197	0 ⇒ 3
<i>Sciodoeclea modesta</i>		172	16	2 → 3	201	0 ⇒ 3
13	1 ⇒ 3	177	31	4 → 3	213	0 ⇒ 3
19	3 → 4	189	33	2 → 3	node_382 → node_381	
101	2 ⇒ 3	213	34	2 → 5	5	2 → 0
153	5 → 0	216	68	0 ⇒ 6	15	3 → 5
167	1 ⇒ 0	254	167	1 ⇒ 0	16	2 → 3
256	5 ⇒ 7	260	173	4 ⇒ 3	27	0 → 1
263	5 ⇒ 0	261	284	3 → 6	28	1 → 0
266	1 ⇒ 0	283	301	0 → 8	30	2 → 1
node_369 → node_368		341	326	0 → 1	31	4 → 2
3	2 ⇒ 1	342	341	3 → 1	33	2 → 4
5	2 ⇒ 1	403	344	0 → 1	37	0 → 1
7	0 → 1	node_375 → node_374	node_376 →	103	0 → 1	
9	1 ⇒ 0	3	2 → 1	117	0 → 2	
11	1 ⇒ 0	15	3 → 2	119	0 → 1	
30	2 → 3	16	2 ⇒ 1	120	0 → 1	
67	0 ⇒ 2	30	2 → 3	130	0 → 1	
68	0 ⇒ 4	103	0 ⇒ 1	146	0 → 1	
75	0 ⇒ 3	111	3 ⇒ 2	153	0 → 1	
77	0 ⇒ 4	168	0 ⇒ 2	174	4 → 3	
111	3 ⇒ 0	190	1 → 3	190	1 → 3	
124	3 ⇒ 1	197	0 → 1	191	1 → 0	
node_368 → node_367		235	0 → 1	248	0 → 1	
164	1 → 0	279	4 ⇒ 5	249	0 → 1	
197	0 ⇒ 1	283	1 → 2	266	2 → 4	
235	0 ⇒ 1	284	3 → 0	283	2 → 4	
263	5 → 4	341	3 → 0	284	3 → 4	
node_367 →		node_374 → node_373	(<i>Caprima</i>)	308	0 → 1	
<i>Papuaphlebohecta bicolora</i>		142	0 ⇒ 3	320	2 → 1	
183	0 ⇒ 5	154	0 ⇒ 4	337	3 → 1	
272	2 ⇒ 1	284	0 → 7	341	3 → 0	
284	3 ⇒ 1	301	0 ⇒ 7	node_381 → node_380		
290	0 ⇒ 1	341	0 → 2	(<i>Herpolasia</i>)		
301	0 ⇒ 3	342	1 ⇒ 0	34	2 ⇒ 4	
308	0 ⇒ 1	node_374 →	3	2 ⇒ 4	81	1 ⇒ 0
341	3 → 2	<i>Caprima chrysosoma</i>	11	1 ⇒ 2	97	0 ⇒ 2
node_367 →		67	13	0 ⇒ 3	147	0 → 1
<i>Hemiscia albivitta</i>		68	15	3 ⇒ 4	154	0 → 1
279	3 ⇒ 4	76	17	5 ⇒ 3	177	4 → 1
283	1 ⇒ 3	78	19	5 ⇒ 2	341	0 → 1
300	0 ⇒ 4	272	28	1 ⇒ 2	node_381 →	
343	0 ⇒ 2	296	107	0 ⇒ 1	<i>Clematoessa xuthomelas</i>	
344	0 ⇒ 1	300	171	2 ⇒ 1	272	1 ⇒ 2
		343	177	4 ⇒ 6		

APPENDIX 5

Character change lists of the strict consensus tree obtained from SAW analysis based on the whole data set. Node numbers correspond to those in Figure 56; each is followed by a list of character numbers and unambiguous state changes. Changes are listed only for the main clades which have topologies different from those in the EW analysis.

node_408 → node_407	358	0 → 1	26	0 → 3	330	0 → 1	
(Zygaenoidea)	390	1 → 0	27	0 → 3	345	0 → 1	
5	0 → 1	398	0 → 1	33	5 → 2	node_404 → node_403	
6	0 → 1			34	5 → 2	(Callizygaeninae–Chalcosiinae)	
33	0 → 5	node_223 → node_220	36	1 → 0	3	1 → 2	
34	0 → 5	15	2 → 1	68	0 → 5	13	0 → 2
36	0 → 1	16	1 → 0	93	0 → 1	17	2 → 5
48	0 → 2	17	0 → 4	124	3 → 0	19	3 → 5
49	0 → 1	18	0 → 4	153	0 → 1	29	0 → 1
54	0 → 1	29	0 → 2	154	0 → 1	33	5 → 1
55	0 → 1	33	5 → 1	222	0 → 2	34	5 → 1
89	1 → 0	34	5 → 1	318	0 → 1	37	0 → 1
90	0 → 1	53	0 → 1	330	0 → 4	39	0 → 1
98	0 → 2	274	1 → 0	352	0 → 1	43	0 → 2
124	0 → 3	313	2 → 3	382	0 → 1	44	0 → 2
169	0 → 3	403	0 → 3	383	2 → 1	46	0 → 1
170	0 → 3	node_223 → node_222	387	0 → 1	53	0 → 1	
173	0 → 3	9	0 → 2	node_405 → node_404	54	1 → 2	
174	0 → 4	28	2 → 0	(Zygaenidae excluding Procridinae)	61	3 → 4	
280	1 → 0	30	2 → 0	9	0 → 1	62	4 → 5
284	0 → 1	32	0 → 1	11	0 → 2	110	0 → 1
286	1 → 0	37	0 → 2	17	0 → 2	116	0 → 1
node_406 → node_405	47	0 → 1	18	0 → 2	163	1 → 2	
(Zygaenidae)	65	0 → 2	19	4 → 3	167	0 → 3	
25	0 → 1	94	4 → 1	20	4 → 3	178	0 → 2
30	0 → 2	169	3 → 5	47	0 → 2	190	0 → 1
31	0 → 2	170	3 → 5	52	0 → 1	231	2 → 0
40	0 → 1	230	0 → 1	61	2 → 3	241	0 → 1
41	0 → 1	263	0 → 1	62	1 → 4	272	0 → 1
42	0 → 2	295	0 → 1	177	1 → 3	273	0 → 1
60	0 → 1	300	0 → 2	191	0 → 1	274	1 → 0
63	0 → 1	320	0 → 4	212	0 → 1	276	0 → 1
64	0 → 1	404	1 → 0	271	0 → 1	277	0 → 1
69	0 → 1	node_222 → node_221	320	0 → 2	278	0 → 1	
92	0 → 1	(<i>Inouela</i> + <i>Homophylotis</i>)	357	0 → 1	279	0 → 2	
94	2 → 4	3	1 → 3	403	0 → 1	314	0 → 1
105	1 → 0	11	0 → 1	408	0 → 1	355	0 → 1
125	0 → 3	17	0 → 1	409	0 → 1	359	0 → 1
163	0 → 1	28	0 → 1	410	0 → 1	365	0 → 1
172	2 → 3	30	0 → 4	411	0 → 1	373	0 → 1
177	0 → 1	98	2 → 1	412	0 → 1	374	0 → 1
196	0 → 1	105	2 → 1	413	0 → 1	375	0 → 1
231	0 → 2	111	0 → 3	node_404 → node_224	376	0 → 1	
266	0 → 2	119	0 → 1	(Zygaeninae)	377	0 → 1	
275	0 → 1	125	3 → 2	1	0 → 2	378	0 → 1
313	0 → 2	173	3 → 4	2	0 → 2	379	0 → 1
353	0 → 1	177	1 → 0	10	0 → 1	389	1 → 0
386	2 → 1	178	0 → 1	12	0 → 2	394	1 → 2
389	0 → 1	209	0 → 2	15	2 → 1	395	0 → 1
399	0 → 1	212	0 → 4	16	1 → 0	397	0 → 1
400	0 → 2	216	0 → 1	24	0 → 1	401	2 → 4
401	0 → 2	221	0 → 1	38	0 → 1	402	0 → 1
404	0 → 1	230	1 → 2	42	2 → 0	node_403 → node_225	
407	0 → 1	250	0 → 1	64	1 → 0	(Callizygaeninae)	
414	0 → 1	261	3 → 2	94	4 → 0	26	0 → 2
node_405 → node_223	270	0 → 1	101	0 → 1	27	0 → 3	
(Procridinae)	272	0 → 3	124	3 → 2	45	2 → 0	
72	1 → 0	278	0 → 1	125	3 → 2	65	0 → 1
90	1 → 0	279	0 → 1	174	4 → 3	66	0 → 1
105	0 → 2	284	1 → 0	244	0 → 2	68	0 → 4
111	2 → 0	299	0 → 1	265	0 → 1	71	3 → 2
189	0 → 2	332	0 → 1	285	0 → 1	75	0 → 3
213	0 → 5	node_406 → node_212	288	0 → 1	76	0 → 3	
240	0 → 1	(<i>Phauda</i> + <i>Lectura</i>)	289	0 → 1	77	0 → 4	
253	0 → 1	17	0 → 3	313	2 → 0	78	0 → 4
264	1 → 0	18	0 → 3	315	0 → 1	124	3 → 0

APPENDIX 5 *Continued*

125	3 → 0	38	0 ⇒ 2	117	0 ⇒ 2	240	0 ⇒ 5
164	0 → 1	44	2 → 1	120	0 ⇒ 1	261	3 → 1
168	0 ⇒ 2	104	0 ⇒ 2	125	3 ⇒ 5	266	2 → 0
169	3 → 2	164	0 ⇒ 1	170	3 ⇒ 4	341	3 ⇒ 1
170	3 → 2	165	0 ⇒ 1	179	0 → 1	node_397 → node_286	
173	3 ⇒ 2	168	0 ⇒ 2	196	2 ⇒ 0	(clade 5)	
174	4 ⇒ 2	171	2 ⇒ 3	212	2 ⇒ 0	5	2 ⇒ 3
177	3 → 0	173	3 → 5	218	0 ⇒ 1	19	5 ⇒ 4
189	0 ⇒ 2	174	4 ⇒ 5	222	0 ⇒ 1	20	5 ⇒ 4
227	0 ⇒ 1	190	1 → 2	240	0 ⇒ 4	38	3 → 0
261	3 → 1	195	0 ⇒ 1	253	5 ⇒ 4	209	2 → 1
264	1 ⇒ 0	218	0 ⇒ 1	272	2 → 4	213	0 → 4
300	0 → 2	262	0 ⇒ 1	279	3 → 5	216	1 → 0
361	0 → 2	263	1 → 0	351	0 ⇒ 1	240	0 ⇒ 3
389	0 → 2	266	2 → 4	360	0 → 1	256	0 ⇒ 3
node_403 → node_402		320	2 → 3	365	1 ⇒ 2	257	0 ⇒ 1
(<i>Heteropan-Chalcosiinae</i>)		341	0 ⇒ 1	366	0 ⇒ 2	266	2 → 3
9	1 → 0	343	0 ⇒ 1	388	0 → 1	347	0 → 1
14	0 ⇒ 2	362	0 ⇒ 1	401	4 → 5	348	0 → 1
15	2 ⇒ 3	369	0 ⇒ 1	403	5 → 7	358	0 → 1
16	1 ⇒ 2	388	0 ⇒ 1	node_399 → node_279		388	0 → 1
18	2 → 5	403	5 → 6	(clade 3)		node_374 → node_291	
20	3 ⇒ 5	node_249 → node_232		3	2 ⇒ 1	(clade 10)	
28	2 → 1	(<i>Cadphises-Herpida</i>)		5	2 → 0	26	0 → 1
30	2 → 3	1	0 ⇒ 1	6	2 → 0	27	0 → 1
31	2 ⇒ 3	7	0 → 1	11	2 ⇒ 1	55	1 ⇒ 2
55	1 ⇒ 2	8	0 ⇒ 1	19	5 ⇒ 4	103	0 → 1
70	3 ⇒ 4	59	0 ⇒ 1	20	5 ⇒ 4	104	2 ⇒ 0
72	1 ⇒ 2	94	4 → 3	30	2 → 3	178	3 ⇒ 4
84	0 ⇒ 1	169	3 ⇒ 6	31	3 ⇒ 2	191	0 → 5
87	0 ⇒ 1	170	3 ⇒ 6	75	0 → 3	193	0 ⇒ 1
101	0 → 2	212	2 ⇒ 0	76	0 → 3	213	0 ⇒ 1
102	0 ⇒ 2	232	0 ⇒ 1	77	0 → 4	216	1 ⇒ 0
196	1 → 0	233	1 ⇒ 2	78	0 → 4	261	5 ⇒ 4
212	1 → 2	242	0 ⇒ 1	101	2 → 1	283	2 → 3
233	0 ⇒ 1	243	0 ⇒ 1	103	0 → 1	360	1 → 0
253	0 → 2	272	2 ⇒ 1	177	4 ⇒ 6	361	1 → 0
263	0 → 1	282	0 ⇒ 2	190	1 ⇒ 2	node_373 → node_292	
272	1 → 2	294	0 ⇒ 1	249	0 ⇒ 1	(clade 11)	
354	0 → 2	338	4 → 6	338	4 ⇒ 3	18	6 → 5
393	0 → 1	356	0 → 1	367	0 → 1	19	5 → 6
394	2 → 3	360	0 → 2	368	0 → 1	68	0 ⇒ 6
395	1 → 2	361	0 → 2	node_279 → node_278		111	3 ⇒ 2
396	0 → 1	362	1 → 3	(<i>Rhodopsona</i>)		124	3 ⇒ 1
node_402 → node_401		365	1 → 2	5	0 → 3	125	3 → 1
(<i>Chalcosiinae</i>)		node_400 → node_274		6	0 → 3	193	0 ⇒ 2
12	0 ⇒ 1	(clade 2)		75	3 → 5	196	1 → 4
37	1 → 0	12	1 ⇒ 2	76	3 → 5	198	0 ⇒ 4
40	1 ⇒ 2	94	4 ⇒ 3	77	4 → 6	199	0 ⇒ 2
41	1 ⇒ 2	96	0 → 1	78	4 → 6	229	0 ⇒ 1
45	2 ⇒ 1	174	4 → 3	111	3 → 2	236	3 → 4
48	2 ⇒ 3	225	0 ⇒ 2	195	0 → 6	237	0 ⇒ 1
49	1 ⇒ 2	226	0 ⇒ 3	228	0 → 3	257	0 → 4
53	1 → 2	279	2 → 3	256	0 → 1	263	1 ⇒ 5
81	0 ⇒ 1	283	0 ⇒ 1	268	1 → 0	265	0 ⇒ 1
111	2 → 3	300	0 → 3	269	1 → 0	272	2 → 3
177	3 → 4	338	4 ⇒ 5	279	2 → 3	341	2 → 0
178	2 → 3	361	0 ⇒ 1	284	1 → 0	365	1 → 0
196	0 → 2	362	0 ⇒ 2	node_398 → node_280		369	0 → 1
227	0 ⇒ 3	node_274 → node_266		(clade 4)		node_372 → node_305	
246	0 → 1	(<i>Cyclosia</i>)		9	1 ⇒ 0	(clade 12)	
250	0 ⇒ 1	4	1 → 3	10	1 ⇒ 0	11	1 ⇒ 2
253	2 → 3	15	3 → 4	17	5 ⇒ 6	48	3 ⇒ 2
268	0 ⇒ 1	16	2 → 3	18	5 → 6	193	0 → 3
269	0 ⇒ 1	33	1 ⇒ 0	28	1 ⇒ 2	194	0 → 1
270	0 → 2	34	1 ⇒ 0	29	1 ⇒ 0	196	1 → 7
337	0 ⇒ 3	48	3 ⇒ 2	37	0 ⇒ 1	197	1 ⇒ 2
338	0 → 4	55	3 ⇒ 1	94	4 ⇒ 3	198	0 → 1
403	1 → 5	82	0 ⇒ 1	124	3 ⇒ 5	228	5 ⇒ 7
node_401 → node_255		97	0 ⇒ 2	125	3 ⇒ 5	256	9 ⇒ 7
(clade 1)		98	2 ⇒ 1	170	3 ⇒ 4	257	0 → 7
11	2 ⇒ 1	103	0 ⇒ 1	231	0 ⇒ 2	261	5 ⇒ 3

APPENDIX 5 *Continued*

284	3 → 1	240	0 → 2	18	6 → 7	97	0 → 1
366	0 → 1	256	9 → 0	19	5 → 4	120	0 → 1
node_305 → node_304		259	1 → 0	21	0 → 1	141	0 → 3
(<i>Erasmia-Chalcophaedra</i>)		283	2 → 3	54	2 → 1	142	0 → 3
6	2 → 3	284	3 → 4	139	0 → 2	143	2 → 1
17	5 → 6	287	0 → 1	146	0 → 3	144	2 → 1
19	5 → 6	301	0 → 3	147	0 → 3	232	0 → 1
21	0 → 1	341	2 → 1	150	0 → 1	260	0 → 2
94	3 → 4	node_357 → node_310		184	0 → 3	272	2 → 3
111	3 → 2	(clade 15)		191	6 → 3	279	3 → 4
139	0 → 4	8	0 → 1	193	0 → 5	341	2 → 4
140	0 → 4	82	1 → 0	213	6 → 2	node_377 →	
141	0 → 3	111	3 → 2	247	2 → 1	<i>Pidorus corculum</i> (clade 8)	
142	0 → 3	120	0 → 1	254	5 → 3	33	2 → 1
153	3 → 4	124	3 → 1	257	5 → 9	34	2 → 1
154	3 → 4	154	3 → 4	329	0 → 3	145	0 → 1
167	1 → 2	247	2 → 3	403	9 → 2	173	4 → 3
169	3 → 4	257	5 → 8	410	1 → 2	213	0 → 3
193	3 → 4	266	3 → 2	node_369 → node_362		257	2 → 3
194	1 → 2	283	2 → 1	(<i>Eterusia</i>)		266	2 → 5
198	1 → 2	284	3 → 5	103	1 → 2	285	1 → 3
266	3 → 4	302	0 → 1	137	0 → 1	319	0 → 1
284	1 → 7	363	0 → 1	138	0 → 1	342	1 → 0
301	0 → 4	366	0 → 1	140	0 → 3	node_392 → node_391	
322	0 → 1	node_356 → node_313		153	3 → 0	(clade 7)	
node_304 → node_298		(clade 16)		154	3 → 4	13	2 → 0
(<i>Erasmiphlebohecta</i> + <i>Chalcophaedra</i>)		16	2 → 3	156	0 → 1	29	1 → 0
20	6 → 7	68	0 → 6	157	0 → 1	102	2 → 0
26	0 → 1	94	3 → 4	174	3 → 4	107	2 → 0
27	0 → 1	143	0 → 2	182	0 → 1	141	0 → 3
68	0 → 1	144	0 → 2	183	0 → 5	203	0 → 2
75	0 → 1	173	4 → 3	184	3 → 5	232	0 → 1
76	0 → 1	195	6 → 2	186	0 → 1	260	0 → 4
77	0 → 1	201	6 → 7	190	2 → 0	266	2 → 1
78	0 → 1	202	4 → 5	196	3 → 4	272	1 → 4
136	0 → 6	205	1 → 3	205	2 → 3	283	2 → 1
137	0 → 3	213	6 → 1	208	2 → 1	337	3 → 0
138	0 → 3	350	2 → 0	247	1 → 7	351	0 → 1
173	4 → 3	360	1 → 0	node_369 → node_368		node_396 → node_395	
174	4 → 3	365	2 → 0	(<i>Soritia</i>)		(clade 6)	
190	0 → 3	node_355 → node_332		12	1 → 2	5	2 → 0
196	7 → 1	(clade 17)		15	4 → 5	15	3 → 5
198	2 → 5	17	5 → 6	17	5 → 7	16	2 → 3
236	3 → 2	26	5 → 0	19	4 → 7	27	0 → 1
263	1 → 0	27	5 → 0	20	5 → 6	28	1 → 0
265	0 → 1	31	3 → 4	67	0 → 2	30	2 → 1
272	2 → 4	78	0 → 1	68	0 → 4	31	4 → 2
279	3 → 5	107	0 → 1	111	3 → 2	33	2 → 4
300	0 → 7	147	0 → 3	158	0 → 1	37	0 → 1
301	4 → 8	154	3 → 2	159	0 → 1	103	0 → 1
349	1 → 0	196	3 → 4	173	4 → 3	117	0 → 2
350	2 → 0	201	6 → 8	180	0 → 1	119	0 → 1
360	1 → 0	202	4 → 6	195	6 → 0	120	0 → 1
361	1 → 0	node_355 → node_354		228	5 → 8	130	0 → 1
365	1 → 0	(clade 18)		254	3 → 4	146	0 → 1
366	1 → 0	5	2 → 1	258	0 → 6	153	0 → 1
node_371 → node_306		30	3 → 2	261	5 → 1	174	4 → 3
(clade 13)		102	2 → 1	265	0 → 1	190	1 → 3
7	0 → 1	103	1 → 0	266	3 → 4	191	1 → 0
8	0 → 1	190	2 → 4	node_376 → node_375		248	0 → 1
17	5 → 6	213	6 → 7	(clade 9)		249	0 → 1
151	0 → 1	238	5 → 3	6	2 → 1	266	2 → 4
162	0 → 1	356	0 → 1	10	1 → 0	283	2 → 4
189	3 → 0	360	1 → 2	14	2 → 1	284	3 → 4
191	6 → 0	361	0 → 2	27	0 → 5	308	0 → 1
195	6 → 1	node_370 → node_369		29	1 → 0	320	2 → 1
218	0 → 4	(clade 14)		33	2 → 3	337	3 → 1
231	1 → 2	6	2 → 3	34	2 → 3	341	3 → 0
				68	0 → 6		

APPENDIX 6

Character change lists of the strict consensus tree (Fig. 63A) obtained from 72 taxa with data of immature stages available. Changes are listed only for the main clades. The apomorphies not present on the nodes of the 'compatible' clades in the analyses based on the whole data set are in bold. The immature characters are in pale tinted boxes.

node_265 → node_264		54	1 → 2	338	4 ⇒ 5	node_261 → node_233	
(Chalcosiinae)		104	0 ⇒ 2	361	0 ⇒ 1	(clade 5)	
5	1 → 2	153	0 → 5	362	0 ⇒ 2	6	3 → 2
14	0 → 2	154	0 → 5	node_263 → node_262		11	1 → 2
17	2 → 6	164	0 ⇒ 1	5	2 → 3	28	1 → 0
18	2 → 5	165	0 ⇒ 1	6	2 → 3	33	1 → 2
28	2 → 0	168	0 → 2	8	0 → 1	34	1 → 2
29	2 → 1	171	2 → 1	9	0 → 1	38	3 → 0
30	2 → 3	190	1 → 2	11	2 → 1	94	4 → 3
38	0 → 2	191	1 → 2	17	6 ⇒ 5	97	0 ⇒ 2
40	1 ⇒ 2	218	0 ⇒ 3	28	0 → 1	173	3 ⇒ 4
41	1 ⇒ 2	219	0 ⇒ 3	55	2 → 3	174	4 → 5
43	0 ⇒ 2	223	0 → 2	174	3 ⇒ 4	213	0 → 4
45	0 → 1	224	0 ⇒ 3	212	0 → 6	218	0 ⇒ 3
53	0 → 2	228	0 ⇒ 1	227	3 ⇒ 4	240	0 ⇒ 3
55	1 → 2	255	0 ⇒ 2	228	0 → 3	272	2 ⇒ 1
70	3 ⇒ 4	262	0 ⇒ 1	246	2 → 3	279	3 ⇒ 2
72	1 ⇒ 2	266	2 → 4	256	0 → 1	327	0 ⇒ 1
81	0 → 1	293	0 ⇒ 1	285	0 ⇒ 1	347	0 ⇒ 1
84	0 ⇒ 1	320	2 ⇒ 3	node_262 → node_232		348	0 ⇒ 1
87	0 ⇒ 1	324	0 ⇒ 1	(clade 4)		358	0 ⇒ 1
101	0 ⇒ 2	341	0 ⇒ 1	3	2 ⇒ 1	388	0 ⇒ 1
102	0 ⇒ 2	343	0 ⇒ 1	101	2 ⇒ 1	403	2 ⇒ 1
116	0 → 1	380	0 → 1	177	4 ⇒ 6	node_261 → node_260	
124	0 ⇒ 3	388	0 ⇒ 1	190	1 → 2	8	1 → 0
125	0 ⇒ 3	403	2 → 6	195	0 ⇒ 6	16	2 ⇒ 3
177	0 → 4	413	1 → 2	211	0 ⇒ 1	20	4 → 5
178	0 ⇒ 3	node_264 → node_263		218	0 ⇒ 1	55	3 → 2
227	0 → 3	6	1 → 2	219	0 ⇒ 1	82	0 → 1
233	0 ⇒ 1	7	0 ⇒ 1	249	0 ⇒ 1	143	0 ⇒ 2
246	0 → 1	12	2 → 1	268	1 ⇒ 0	144	0 ⇒ 2
250	0 ⇒ 1	13	0 ⇒ 2	269	1 ⇒ 0	176	1 → 2
253	0 → 3	38	2 → 3	270	2 ⇒ 0	189	2 → 3
268	0 → 1	48	2 → 3	283	1 → 0	195	0 → 2
269	0 → 1	49	1 → 2	284	3 → 0	196	2 ⇒ 4
270	0 ⇒ 2	73	0 ⇒ 1	341	0 ⇒ 3	197	0 → 1
272	0 → 2	107	0 → 2	367	0 ⇒ 1	209	1 → 2
313	0 → 2	167	3 ⇒ 1	368	0 ⇒ 1	216	0 → 1
337	0 ⇒ 3	189	0 → 2	403	2 ⇒ 5	221	0 ⇒ 1
338	0 ⇒ 4	196	1 → 2	node_262 → node_261		227	4 ⇒ 5
354	0 ⇒ 2	246	1 → 2	15	3 → 4	228	4 → 5
373	0 → 1	253	3 → 5	31	2 → 3	232	0 → 1
374	0 → 1	261	1 → 3	67	0 ⇒ 1	246	3 → 4
375	0 → 1	263	0 → 1	68	0 ⇒ 6	254	1 → 2
376	0 → 1	279	2 ⇒ 3	74	0 ⇒ 1	256	3 → 4
377	0 → 1	283	0 → 1	107	2 → 0	257	1 → 2
378	0 → 1	284	1 → 3	209	0 → 1	261	3 ⇒ 5
379	0 → 1	292	0 ⇒ 1	220	0 ⇒ 2	263	1 → 4
393	0 ⇒ 1	node_263 → node_230		228	3 → 4	267	0 ⇒ 1
394	1 → 3	(clade 2)		253	5 ⇒ 6	283	1 → 2
395	0 → 2	18	5 → 6	254	0 → 1	339	0 ⇒ 1
396	0 ⇒ 1	30	3 → 2	256	1 → 3	340	0 ⇒ 1
403	4 → 2	111	2 ⇒ 3	257	0 → 1	341	0 → 1
node_264 → node_225		144	0 ⇒ 1	266	2 → 3	342	0 ⇒ 1
(clade 1)		146	0 → 3	365	1 ⇒ 0	343	0 ⇒ 2
23	0 → 1	225	0 ⇒ 2	392	0 ⇒ 1	344	0 ⇒ 1
37	0 → 1	226	0 → 1	393	1 ⇒ 0	360	0 → 1
44	2 ⇒ 1	240	0 → 4			361	0 → 1
						362	0 ⇒ 3

APPENDIX 7

CHARACTER DIAGNOSIS OF THE EW ANALYSIS BASED ON THE WHOLE DATA SET

Character	Range	CI	RI	Character	Range	CI	RI	Character	Range	CI	RI
1	2	0.222	0.588	69	1	0.333	0.667	137	5	0.5	0.6
2	2	0.286	0.5	70	4	1	1	138	5	0.4	0.471
3	4	0.071	0.556	71	3	0.75	0.857	139	5	0.156	0.341
4	4	0.078	0.548	72	2	0.667	0.938	140	5	0.147	0.356
5	4	0.1	0.676	73	1	0.5	0.977	141	3	0.13	0.355
6	4	0.103	0.706	74	2	0.5	0.982	142	3	0.125	0.344
7	2	0.054	0.507	75	5	0.122	0.379	143	2	0.088	0.436
8	2	0.056	0.58	76	5	0.106	0.373	144	2	0.081	0.452
9	3	0.1	0.542	77	6	0.13	0.365	145	1	0.111	0.273
10	2	0.077	0.607	78	6	0.107	0.342	146	5	0.233	0.574
11	2	0.062	0.625	79	1	0.333	0.5	147	5	0.241	0.56
12	2	0.069	0.63	80	1	0.25	0.667	148	2	0.333	0
13	3	0.083	0.653	81	1	0.125	0.844	149	2	0.5	0
14	3	0.1	0.707	82	1	0.143	0.93	150	1	0.167	0.688
15	6	0.122	0.609	83	1	1	0/0	151	1	0.091	0.167
16	5	0.116	0.591	84	1	0.5	0.957	152	2	0.286	0.286
17	7	0.13	0.605	85	1	1	1	153	6	0.13	0.239
18	6	0.115	0.613	86	1	1	1	154	6	0.136	0.3
19	7	0.146	0.65	87	2	1	1	155	2	0.333	0.2
20	7	0.179	0.731	88	1	0.667	0	156	5	0.312	0.154
21	1	0.167	0.861	89	1	1	1	157	5	0.375	0.286
22	1	0.062	0.754	90	1	0.25	0.812	158	3	0.25	0.4
23	2	0.4	0.75	91	1	1	1	159	3	0.2	0.25
24	2	0.222	0.533	92	2	0.4	0.667	160	4	0.556	0.333
25	1	0.333	0.714	93	1	0.5	0.5	161	3	0.375	0.167
26	5	0.132	0.4	94	6	0.182	0.598	162	1	0.083	0.214
27	5	0.109	0.423	95	1	1	0/0	163	2	0.667	0.952
28	2	0.061	0.635	96	1	0.2	0.818	164	2	0.278	0.723
29	2	0.087	0.687	97	2	0.176	0.588	165	1	1	1
30	4	0.093	0.672	98	2	0.4	0.833	166	2	0.5	0.867
31	4	0.095	0.661	99	1	0.5	0.667	167	3	0.143	0.82
32	1	0.5	0	100	1	0.333	0.333	168	2	0.091	0.78
33	5	0.116	0.67	101	3	0.25	0.721	169	7	0.5	0.761
34	5	0.132	0.72	102	3	0.6	0.9	170	7	0.691	0.823
35	1	1	1	103	3	0.143	0.691	171	4	0.222	0.745
36	1	0.143	0.4	104	3	0.241	0.802	172	5	0.556	0.724
37	2	0.143	0.75	105	2	0.143	0.52	173	6	0.176	0.752
38	3	0.5	0.958	106	3	0.5	0.571	174	6	0.41	0.755
39	1	1	1	107	2	0.069	0.707	175	1	1	1
40	2	0.286	0.615	108	1	0.5	0	176	3	0.375	0.941
41	2	0.4	0.812	109	1	1	0/0	177	6	0.15	0.742
42	3	0.429	0.6	110	1	0.25	0.824	178	5	0.625	0.909
43	2	0.5	0.882	111	3	0.103	0.573	179	2	0.148	0.148
44	2	0.4	0.927	112	1	1	1	180	2	0.16	0.323
45	2	0.286	0.667	113	1	0.25	0.5	181	1	0.5	0
46	2	0.4	0.842	114	1	1	0/0	182	1	0.667	0.75
47	2	0.286	0.762	115	1	0.333	0	183	5	0.162	0.326
48	4	0.154	0.768	116	1	0.167	0.783	184	5	0.162	0.392
49	3	0.125	0.661	117	2	0.154	0.711	185	1	0.067	0.333
50	1	1	1	118	1	1	0/0	186	1	0.067	0.3
51	1	0.333	0.333	119	1	0.053	0.419	187	1	0.25	0.4
52	1	1	1	120	1	0.05	0.596	188	1	0.2	0.333
53	2	0.5	0.909	121	1	0.2	0.556	189	3	0.188	0.879
54	3	0.143	0.804	122	1	1	1	190	5	0.132	0.75
55	4	0.222	0.874	123	1	1	1	191	9	0.257	0.787
56	1	1	1	124	8	0.131	0.404	192	1	1	1
57	2	1	1	125	8	0.148	0.446	193	9	0.5	0.845
58	1	0.25	0.25	126	1	1	1	194	5	0.5	0.75
59	1	0.2	0.714	127	1	1	0/0	195	7	0.233	0.755
60	1	1	1	128	1	1	0/0	196	7	0.226	0.838
61	4	0.8	0.947	129	1	1	0/0	197	3	0.273	0.905
62	5	0.625	0.824	130	1	0.043	0.476	198	5	1	1
63	1	0.333	0.6	131	1	0.25	0	199	2	1	1
64	1	0.25	0.571	132	1	0.5	0.889	200	4	0.308	0.571
65	3	1	1	133	3	0.176	0.3	201	9	0.6	0.87
66	3	0.5	0.812	134	2	0.667	0.5	202	8	0.571	0.818
67	3	0.097	0.548	135	3	0.438	0.438	203	3	0.6	0.8
68	6	0.146	0.5	136	6	0.375	0.545	204	2	0.667	0.667

APPENDIX 7 *Continued*

Character	Range	CI	RI	Character	Range	CI	RI	Character	Range	CI	RI
205	4	0.267	0.788	275	1	1	1	345	1	1	1
206	1	0.333	0.6	276	1	1	1	346	1	0.5	0.5
207	1	0.25	0.5	277	1	1	1	347	1	1	1
208	3	0.5	0.864	278	1	0.5	0.95	348	1	1	1
209	2	0.4	0.964	279	5	0.185	0.761	349	1	0.333	0.571
210	1	1	1	280	1	1	1	350	2	0.5	0.913
211	1	0.5	0.5	281	3	1	1	351	1	0.333	0.778
212	6	0.316	0.649	282	2	1	1	352	1	0.5	0.5
213	9	0.257	0.671	283	4	0.154	0.815	353	1	1	1
214	1	1	0/0	284	8	0.229	0.779	354	2	0.5	0.833
215	1	1	1	285	3	0.143	0.757	355	1	0.5	0.909
216	3	0.273	0.917	286	1	1	1	356	1	0.333	0.5
217	1	1	0/0	287	1	0.333	0.6	357	1	0.5	0.875
218	4	0.267	0.788	288	2	0.5	0	358	1	0.2	0.692
219	3	0.333	0.778	289	2	0.333	0.2	359	1	1	1
220	2	0.667	0.988	290	2	0.667	0	360	2	0.222	0.759
221	2	0.286	0.949	291	1	1	0/0	361	2	0.154	0.686
222	3	0.273	0.765	292	1	0.5	0.982	362	3	0.6	0.946
223	3	0.75	0.95	293	1	1	1	363	1	0.333	0.6
224	6	0.857	0.941	294	1	1	1	364	2	0.5	0.895
225	4	1	1	295	1	1	1	365	2	0.154	0.686
226	3	1	1	296	1	0.333	0.333	366	2	0.2	0.652
227	5	0.625	0.966	297	1	1	1	367	1	1	1
228	9	0.643	0.947	298	1	0.5	0.917	368	1	1	1
229	1	1	1	299	1	1	1	369	1	0.143	0.647
230	2	0.333	0.5	300	7	0.233	0.558	370	1	1	1
231	2	0.25	0.936	301	8	0.258	0.596	371	1	1	0/0
232	2	0.333	0.959	302	1	0.5	0	372	1	1	0/0
233	2	0.286	0.953	303	1	0.5	0	373	1	1	1
234	3	0.6	0.973	304	1	0.333	0.5	374	1	1	1
235	7	0.583	0.933	305	1	0.5	0.5	375	1	1	1
236	3	0.375	0.93	306	1	0.167	0.5	376	1	1	1
237	1	1	1	307	1	0.5	0.909	377	1	1	1
238	6	0.462	0.863	308	3	0.3	0.462	378	1	1	1
239	3	0.25	0.83	309	1	1	0/0	379	1	1	1
240	7	0.583	0.865	310	1	1	0/0	380	1	0.5	0.9
241	1	1	1	311	1	1	1	381	2	0.5	0.833
242	1	1	1	312	1	0.5	0.8	382	1	0.5	0.5
243	2	1	1	313	3	0.429	0.81	383	2	1	1
244	3	0.375	0.375	314	1	0.5	0.96	384	1	1	0/0
245	7	1	1	315	2	0.5	0.5	385	1	1	0/0
246	7	0.7	0.972	316	1	1	1	386	2	1	1
247	6	0.75	0.964	317	2	0.167	0.231	387	1	0.5	0.5
248	1	0.333	0.833	318	1	0.5	0.667	388	1	0.2	0.826
249	1	0.25	0.864	319	1	0.333	0.5	389	2	0.5	0.778
250	1	0.143	0.846	320	4	0.133	0.662	390	1	0.5	0.857
251	2	0.667	0.5	321	1	1	0/0	391	1	0.333	0.333
252	1	1	0/0	322	2	0.25	0.769	392	1	1	1
253	6	0.545	0.938	323	2	0.333	0.333	393	1	0.2	0.84
254	9	0.562	0.929	324	1	1	1	394	3	0.75	0.909
255	3	0.3	0.708	325	1	1	0/0	395	2	1	1
256	8	0.333	0.824	326	1	0.25	0.4	396	1	1	1
257	9	0.562	0.923	327	1	1	1	397	1	1	1
258	6	0.545	0.881	328	1	1	1	398	1	0.333	0.5
259	1	0.5	0.986	329	3	0.231	0.756	399	1	1	1
260	4	0.667	0.818	330	4	0.8	0.5	400	2	0.5	0.5
261	5	0.143	0.748	331	1	1	0/0	401	4	0.667	0.857
262	1	0.333	0.938	332	1	1	1	402	1	1	1
263	7	0.175	0.732	333	1	0.5	0	403	9	0.333	0.881
264	1	0.2	0.733	334	1	1	1	404	1	0.333	0.75
265	3	0.2	0.4	335	1	1	0/0	405	1	0.333	0.957
266	8	0.17	0.695	336	1	1	0/0	406	1	1	1
267	1	0.333	0.977	337	3	0.158	0.807	407	1	0.5	0.5
268	1	0.5	0.966	338	6	0.207	0.787	408	1	0.333	0.8
269	1	0.333	0.929	339	1	0.167	0.932	409	2	0.5	0.818
270	2	0.286	0.848	340	2	0.286	0.94	410	2	0.667	0.947
271	1	0.333	0.889	341	4	0.091	0.685	411	1	0.333	0.8
272	7	0.149	0.675	342	1	0.091	0.894	412	1	0.5	0.889
273	1	1	1	343	2	0.154	0.892	413	2	0.667	0.933
274	1	0.167	0.545	344	2	0.143	0.852	414	1	0.5	0.5

APPENDIX 8

PAPUAPHLEBOHECTA YEN GEN. NOV.

Type species: Papuaphlebohecta bicolora Yen, sp. nov., designated here (see note 13, Appendix 1).

Adult: Head smoothly scaled; proboscis rudimentary, galeal lobes not fused; labial palpus short, 2-segmented; chaetosemata developed; antenna about half of forewing length, flagellomeres rather short, short bipectinate in male and serrate in female, apical part without enlarged or thickened flagellomeres. Forewing elongate, with apex rounded, termen straight; hindwing somewhat triangular, rounded at apex; r3 + r4 of forewing not stalked with r5, sc + r1 of hindwing connected to cell by a short cross veinlet; hindwing-abdomen scent organ absent, hindwing base of female with a bundle of short filiform scales; frenulum number 3.

Male genitalia and the associated abdominal segment. Uncus fused with tegumen, forming a ring-like structure, slender viewed laterally. Subscaphium absent. Vinculum fused with lower part of tegumen, saccus extending anteriorly. Valva with cucullus membranous, sacculus more sclerotized, forming an elongate process with apex rounded; sacculus with a curved digital long process. Tegumenal structure complex, a pair of beak-like processes arising near conjunction between valval bases and lower margins of tegumen, the paired processes extending posteriorly and curved downwards; anterior ends of beak-like structure connected to a cap-like structure, formed by anterior extension of tegumen, cap-like structure fused dorsomedially, running downwards to fuse with medial inner ridge of vinculum. Aedeagus slender, curved medially to be 'L'-shaped, phallobase not prominent, apical part attenuate, but not acute. Eighth tergite and sternite truncate at hind margin, no peculiar modification is found.

Female genitalia. Ovipositor present, slightly longer than seventh tergite. Eighth tergite sclerotized, lateral part extended downwards, forming a ring-like structure; apophyses anteriores slightly shorter than seventh tergite. Seventh sternite short, about half of tergite, upper margin rounded. A sclerotized and folded structure posterior to antrum. Antrum slightly sclerotized in the opening; ductus bursae short, not spiralled, as long as tergite, corpus bursae small, without specialized wrinkles or signa.

Diagnosis and relationships: The wing shape of this genus is somewhat similar to that of *Soritia* and *Eterusia*, but it can be easily distinguished by the slender antenna which has no enlarged apex and the reduced proboscis. The male genitalia of this new genus suggests its close relationships to the genus complex which contains *Caprima*, *Sciodoclea* and some other species currently placed in *Pidorus* and *Hemiscia*.

Etymology. The first half of the generic name is derived from Papua New Guinea, the type locality of the type species, the second from *Phlebohecta*, another chalcosiine genus which has a similar wing pattern and wing shape. The gender is feminine.

Distribution. One species found in Papua New Guinea.

PAPUAPHLEBOHECTA BICOLORA YEN SP. NOV.

Adult. External characters as described for the genus. Male chaetosemata black; in female tinged with some creamy white scales posteriorly. Scale ring in front of patagia creamy white. Tegula with white scales around outer margin. Upperside of male forewing dark grey, underside whitish near base, hindwing with broad grey margin extending from outer margin to medial line; ground colour of female forewing dark green, with a broad creamy white zone from sub-basal to medial line, basal patch on underside smaller than that of upperside, hindwing creamy white, with apex tinged dark green.

Male genitalia and the associated abdominal segment. As described for the genus.

Female genitalia. As described for the genus.

Type material. Holotype ♂, Papua New Guinea: West Highland district, Sirunke, 7.vi.1973 (G. Baker) (ex coll. Department Agr. Port Moresby, now in BMNH). Paratype, 1♀, same collection data (ex coll. Department Agr. Port Moresby, now in BMNH).

Diagnosis. According to the label, this species was identified as '*Pidorus* sp.' by W. H. T. Tams, probably due to the similarity of its wing pattern and that of the historically confusing *Pidorus*.

Etymology. The specific name refers to the wing pattern, which is formed by two colours.

Biology. The adults are possibly flying by June. The larvae feed on *Nothofagus grandis* Steen. (Nothofagaceae).

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