

# Entomologica scandinavica

## Supplements

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ENTOMOLOGICA SCANDINAVICA

SUPPLEMENT 46

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## Phylogeny and classification of the Liopteridae, an archaic group of cynipoid wasps (Hymenoptera)

FREDRIK RONQUIST

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## Phylogeny and classification of the Liopteridae, an archaic group of cynipoid wasps (Hymenoptera)

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The world fauna of the Liopteridae, a mainly tropical to subtropical group of cynipoid parasitoids of wood-boring insect larvae, was revised at the generic level based on the largest material of the family ever collated, including type specimens of most described species. The Liopteridae were found to be monophyletic once the previously included genera *Heteribalia* and *Eileenella* had been removed, and evidence supporting this conclusion is presented. Ground-plan character states of the Liopteridae are tabulated for 108 external skeletal features. The family was divided into eleven putatively monophyletic genera, and a key to these is presented. Each genus is described, possible autapomorphies discussed, and distributional and biological data summarized. All material studied is listed to species, and depositories and distribution records are given. It is estimated that the material (750 specimens) represents 130 species, of which 70 are new to science (not described here). Although the material probably constitutes a fair portion of the liopterids in world collections, most species are represented by very few specimens, suggesting that only a small fraction of the total world fauna has been collected.

A cladistic analysis of intergeneric relationships based on 54 morphological characters is presented, and a new classification of the Liopteridae into subfamilies is proposed. The historical biogeography of the group was analysed and used to date some of the speciation events in the phylogeny. The biogeographic patterns suggest that the family already existed in the Jurassic. The only fossil liopterid known, *Protoibalia connexiva* from the upper Eocene, is discussed and placed in the genus *Kiefferiella*.

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### Introduction

The Liopteridae are a family of cynipoid parasitoids of wood-boring insect larvae. Although unusually large and spectacular, they are sparsely represented in most insect collections. Part of the reason for this may be the distribution of liopterid diversity: although the family occurs in all major zoogeographic regions, liopterids are absent from the western Palaearctic, and most species occur in tropical or subtropical regions of the world. However, these insects also seem to be exceptionally rare and difficult to collect, in which respect they resemble other groups of hymenopterous parasitoids of wood-boring insect larvae.

Because many species of the Liopteridae are

restricted to tropical and subtropical regions, and to the more or less pristine forest habitats where their hosts thrive, it seems probable that liopterid diversity is being reduced by human activities. Thus, many liopterid species will likely go extinct before they can be described or even collected. At the same time, if trees from tropical and subtropical regions were to become cultivated extensively, some liopterids might become economically important as biocontrol agents.

The Liopteridae are particularly interesting in the context of analyzing the early evolution of the Cynipoidea. The family is usually treated early in higher classifications of the Cynipoidea (Weld 1952, Riek 1971, Quinlan 1979, Nordlander 1982), suggesting that they represent a basal lineage. A

basal position for the Liopteridae is also consistent with an old idea among hymenopterists that "primitive" lineages of parasitic wasps usually have retained the original apocritan habit of being parasitoids of wood-boring insect larvae (Cooper 1953, Brues 1921, Wheeler 1928). Liopterids show many structural and biological affinities with ibaliids, which are parasitoids of wood-boring siricid larvae. The Ibaliidae are considered to represent an archaic lineage of cynipoids (Ronquist & Nordlander 1989), but higher-level relationships within the Cynipoidea have not yet been analysed cladistically (Ronquist & Nordlander 1989; but see Ronquist in press).

The modern concept of the Liopteridae dates from Hedicke and Kerrich (1940), who placed groups previously considered as subfamilies within the Cynipidae (Dalla Torre & Kieffer 1910, Kieffer 1911, Hedicke 1922, Weld 1922) or Figitidae (Ashmead 1903a, b, Weld 1921) in a separate family, the Liopteridae, which they divided into three subfamilies: Liopterinae, Oberthuerellinae and Mesocynipinae. Their classification has essentially remained unchanged until now. The Liopterinae and Oberthuerellinae have both been revised at the species level, the Liopterinae by Hedicke and Kerrich (1940) and the Oberthuerellinae by Quinlan (1979). The Mesocynipinae have never been revised.

Although the Liopteridae have attracted the attention of several taxonomists, most workers have only had access to a few specimens and this has caused many problems in liopterid systematics. One of the most serious problems is that the family Liopteridae is so poorly defined that the inclusion of several genera has been in doubt. For instance, the genus *Heteribalia* was placed in the Liopteridae by Sakagami (1949) and Weld (1952), but Maa (1949), Ronquist and Nordlander (1989) and Liu and Nordlander (1994) included it in the Ibaliidae. The genus *Eileenella* was recently described by Fergusson (1992), who provisionally placed it in the Mesocynipinae (Liopteridae), but expressed doubts as to its real affinities. Hedicke (in Hedicke and Kerrich 1940) synonymized *Paraegilips* with the liopterid genus *Paramblynotus*, but Weld, uncertain about the family placement of *Paraegilips*

entered it under Anacharitininae (Figitidae) as well as under Mesocynipinae (Liopteridae) in the keys of his monograph on the Cynipoidea (Weld 1952). The genus *Kiefferiella* is generally considered to be a liopterid, but does not key out properly in most keys to the families of cynipoids (e.g., Weld 1952, Riek 1971, Quinlan 1979).

Another effect of the rarity of liopterid specimens has been that the extent and nature of intraspecific variation are poorly understood. Although the present study is based on more material of the Liopteridae than any previous study, this particular problem with liopterid scarcity remains. Most species are still represented by only one or a few specimens.

Taxonomic work on liopterids has been almost entirely restricted to the species level. There has been very little discussion concerning generic concepts (but see Hedicke and Kerrich 1940), and no phylogenetic studies have been attempted. One fossil species has been described, *Protoibalia connexiva* (Brues 1910) from the upper Eocene. This species was originally placed in the Ibaliidae, but actually belongs to the Liopteridae (Rasnitsyn 1980:97; see also discussion below).

This paper has two primary aims. First, it defines the family Liopteridae as a monophyletic group and lists ground-plan characters of the family in order to facilitate future studies of higher-level relationships within the Cynipoidea. Second, it provides a basis for future taxonomic work on the liopterids themselves by increasing our understanding of the external morphology, biology and evolution of the family.

## Materials and methods

### Insect material

The present study is based on 750 specimens of the Liopteridae borrowed from the insect collections listed below. Some collections were visited, while others were requested to send all their liopterid material. In a few cases, museums sent only holotype specimens (MNHN, MRAC, ZMAS); in most cases, however, the specimens examined presumably represent the entire culled material of the

family in these collections.

An effort was made to locate all type specimens of the Liopteridae. Of the 81 described species and two described subspecies, types of all but twelve species were located and examined. The types of the following species were not found:

- Baviana ferruginea* Barbotin, 1954. The type is apparently in the private collection of Mr. F. Barbotin (J. Casevitz-Weulersse, pers. comm.), but I was not able to confirm that with Mr. Barbotin.
- Holocynips nigra* Kieffer, 1916. The type of this species was apparently lost in the mail (Weld 1952:164).
- Allocynips flaviceps* Kieffer, 1916. This species was described in the same paper as *Holocynips nigra*, and it seems likely that the type suffered the same fate.
- Mesocynips insignis* Smith, 1858. Location of type not known. It is not in the Oxford University Museum (C. O'Toole, pers. comm.), nor in the Natural History Museum in London (N. Fergusson, pers. comm.)
- Oberthuerella lenticularis* Saussure, 1890. Kieffer (1903) redescribed this species from the type specimen, sent to him by de Saussure. Presumably the specimen was returned to de Saussure by Kieffer, but the specimen is not now in de Saussure's collection (C. Besuchet, pers. comm.)
- Oberthuerella nigra* Kieffer, 1910a. Originally in ZMHB but now missing (cf. Quinlan 1979:114).
- Liopterion brasiliense* Hedicke in Hedicke and Kerrich, 1940. The type was originally in Hedicke's private collection (Hedicke and Kerrich 1940), but the current location is not known. It could not be found in the University Museum in Berlin and it is not in the Deutsches Entomologisches Institut (A. Taeger, pers. comm.)
- Liopterion antennale*, *L. biroi*, *L. brevicorne* and *L. laticeps*, all described by Kerrich (in Hedicke and Kerrich 1940). The types were deposited in the Hungarian Natural History Museum in Budapest according to Hedicke and Kerrich (1940). The specimens could not be found in Budapest (J. Papp, pers. comm.), and they are not in the Natural History Museum in London (N. Fergusson, pers. comm.)
- Peras ruficeps* Kieffer, 1905. Location of type not known (cf. Hedicke and Kerrich 1940).

### List of depositories (curators in parentheses)

- AEIC - American Entomological Institute, Gainesville, FL, USA (D. Wahl).
- ANIC - Australian National Insect Collection, Canberra, Australia (I. Naumann).
- BMNH - The Natural History Museum, London, UK (T. Huddleston, N. Fergusson).
- BPBM - Bernice P. Bishop Museum, Honolulu, HI, USA (K. Arakaki).

- CASC - California Academy of Sciences, San Francisco, CA, USA (W. Pulawski).
- CFR - F. Ronquist, private collection, Stockholm, Sweden.
- CFB - F. Barbotin, private collection, Rennes, France.
- CMS - M. Söderlund, private collection, Kungälv, Sweden.
- CNCI - Canadian National Collection of Insects, Ottawa, ON, Canada (J. Read).
- DEIC - Deutsches Entomologisches Institut, Eberswalde, Germany (A. Taeger).
- EIHU - Hokkaido University, Sapporo, Japan (M. Suwa).
- HNHM - Hungarian Natural History Museum, Budapest, Hungary (J. Papp).
- IRCT - Institut de Recherches du Coton et des Textiles exotiques, Montpellier, France (G. Delvare).
- KUEC - Kyushu University, Fukuoka, Japan (K. Morimoto).
- MCZC - Museum of Comparative Zoology, Cambridge, MA, USA (D. Furth).
- MHNG - Muséum d'Histoire Naturelle, Geneva, Switzerland (C. Besuchet).
- MNHN - Muséum National d'Histoire Naturelle, Paris, France (J. Casevitz-Weulersse).
- MRAC - Musée Royal de l'Afrique Centrale, Tervuren, Belgium (E. De Coninck).
- NHMF - Naturhistorisches Museum, Wien, Austria (M. Fischer).
- NHRS - Naturhistoriska riksmuseet, Stockholm, Sweden (F. Ronquist).
- OXUM - The University Museum, Oxford, UK (C. O'Toole).
- QCAZ - Quito Catholic Zoology Museum, Quito, Ecuador (G. Onore).
- RMNH - Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands (C. van Achterberg).
- ROME - Royal Ontario Museum, Toronto, ON, Canada (C. Darling).
- UCDC - University of California at Davis, Davis, CA, USA (S. Heydon).
- USNM - Smithsonian Institution, Washington, DC, USA (A. Menke).
- ZLMU - Zoological Laboratory, Meijo University, Nagoya, Japan (K. Yamagishi).
- ZMAS - Zoological Museum, Academy of Sciences, St. Petersburg, Russia (O. Kovalev).
- ZMHB - Museum für Naturkunde der Humboldtuniversität, Berlin, Germany (F. Koch).
- ZSMC - Zoologische Staatssammlung, München, Germany (E. Diller).

### Methods

The material was first sorted to species. Most species were represented by very few specimens. About half of the 130 species were present only as singletons, and 70% of the species were represent-

ed by less than five specimens.

The species were grouped into genera based on synapomorphic features, and the relationships between these genera were then inferred. For character analyses, the Austrocynipidae and Ibalidae were used as outgroups, represented by material of *Austrocynips mirabilis* (female), the only species in the family Austrocynipidae, and *Ibalia rufipes* (male and female), *Ibalia anceps* (male and female), *Heteribalia divergens* (female), *Heteribalia subtilis* (male) and *Eileenella catherinae* (female), representing all genera and subgenera of the Ibalidae. Although it is possible that neither the Austrocynipidae nor the Ibalidae are the sister group of the Liopteridae, these three families are structurally and biologically similar, and undoubtedly closely related (Rasnitsyn 1980, 1988, Ronquist & Nordlander 1989, Ronquist in press). To obtain additional information concerning the polarity of some characters, representatives of all major groups of cynipoids were examined. In referring to these data, the classification of the Cynipoidea presented in Tab. 1 has been used. Representatives of the Diapriidae were also studied for some characters. The representatives were as follows: *Ismarus rugulosus*, *I. americanus* (Ismarinae); *Cinetus iridipennis*, *Belyta sanguinolenta* (Belytinae); *Spilomicrus atriclavus*, *Psilus* sp. (Diapriinae); and *Propsilomma columbianum* (Ambositrinae). Diapriids were selected as a reference group outside of the Cynipoidea because it has been suggested that the Diapriidae are the sister group of the Cynipoidea (Rasnitsyn 1988) and because diapriids are structurally similar to cynipoids in many respects.

PAUP version 3.1.1 (Swofford 1993) was used for the phylogenetic analyses. Character changes were traced on the resulting tree with MacClade version 3.01 (Maddison & Maddison 1992).

## Terminology

### Terms for skeletal structures

Terms for skeletal features follow Ronquist and Nordlander (1989) and Richards (1977), with some changes and additions as outlined below. Many of

Tab. 1. Higher classification of the Cynipoidea used in this paper, partly based on Ronquist (1994). Taxa that are clearly not monophyletic are put within inverted commas. The figitoid inquilines are listed in Ronquist (1994).

Austrocynipidae	
Ibalidae (including <i>Heteribalia</i> and <i>Eileenella</i> )	
Liopteridae	
Mayrellinae	
Dallatorrellinae	
Oberthuerellinae	
Liopterinae	
Cynipidae	
"Aylacini"	
Synergini	
Rhoditini	
Eschatocerini	
Pediastidini (including <i>Himalocynips</i> )	
Cynipini	
Figitidae (sensu lato)	
"Figitinae" (incl. the figitoid inquilines)	
Anacharitininae	
Charipinae	
Aspiceratinae	
Pycnostigmatinae	
Eucoilinae	

plained in Figures 6, 9, 11, 12, 20, 23, 38–40 and 73 (see also Tab. 2).

**Ocellar plate (op, Fig. 6).** Triangular area, distinctly raised in some liopterids, comprising ocelli and surrounding parts of the upper face, ventrally usually continued in the median frontal carina.

**Anterior flange of pronotum (afl, Figs. 11, 12; cf. also Figs. 31, 32).** Anterior, more or less horizontal part of the pronotum, projecting over the articulation between the head and mesosoma.

**Submedian depressions of pronotum (sd, Figs. 11, 12; cf. also Figs. 31, 32).** Submedian depressions on the anterior flange of the pronotum.

**Lateral pronotal carina (lnc, Figs. 11, 12).** Obliquely vertical carina located laterally on the pronotum.

**Anterior plate of pronotum (ap, Figs. 11, 12).** Anterior, vertical, more or less platelike area of the pronotum, anterior and mesal to the lateral pronotal

Tab. 2. List of abbreviations used in Figures 1–84. Subscripts 1–3 refer to segments of the thorax, prescripts 3–9 to segments of the abdomen. Abbreviations of wing veins in Figure 39 follow Ross (1936).

a	anterior basal process of metacoxa (Fig. 20)	lpc	lateral propodeal carina (Figs. 12, 36)
aas	anteroadmedian signum (Fig. 23)	ls	lateral surface of pronotum (Fig. 12)
ab	articular bulb of petiole (Fig. 73)	mc	marginal cell (Fig. 40)
ac	acetabulum (Fig. 38)	md	mandible (Fig. 6)
acc	acetabular carina (Fig. 38)	mes	metepisternum (Fig. 12)
afa	anterior flange of petiolar annulus (Fig. 73)	mfc	median frontal carina (Figs. 6–8)
afl	anterior flange of pronotum (Fig. 12)	mi	mesopleural impression (Fig. 12)
afo	antennal foramen (Fig. 6)	mmi	median mesoscutal impression (Fig. 23)
amp	anterior metapleural pit (Fig. 20)	mpa	median propodeal area (Fig. 36)
an	petiolar annulus (Fig. 73)	mpc	metapleural carina (Fig. 12)
ap	anterior plate of pronotum (Fig. 12)	mps	metapleural sulcus (Fig. 12)
ar	areolet (Fig. 40)	mpt	mesopleural triangle (Fig. 12)
as	antennal scrobe (Fig. 6)	ms	malar space (Fig. 6)
au	auricula (Fig. 12)	msc	mesoscutum (Fig. 12)
ax	axilla (Figs. 12, 23)	n	notum (Fig. 38)
ba	basalis (Fig. 39)	not	notaulus (Fig. 23)
br	basal ring of metafemur (Fig. 49)	nu	nucha (Fig. 12)
ca	calyptra (Fig. 12)	oc	occipital carina (Fig. 9)
cf	coxal foramen (Fig. 38)	op	ocellar plate (Fig. 6)
cl	clypeus (Fig. 6)	p	process from median frontal carina (Figs. 6, 8, 10)
d	depression beneath eye (Fig. 6)	pa	prespiracular area (Fig. 12)
do	dorsellum (Fig. 12)	pc	pronotal crest (Fig. 12)
em	metepimeron (Figs. 12, 20)	pi	parascutal impression (Fig. 23)
g	gena (Fig. 6)	pl	pleuron (Fig. 38)
h	ventral hump of petiolar annulus (Fig. 73)	ppp	posterolateral propodeal process (Fig. 12)
ip	intercoxal process (Figs. 19, 38)	ps	parapsidal signum (Fig. 23)
laf	lateral flap of abdominal sternum 7 (Figs. 65, 72)	psc	parascutal carina (Fig. 23)
lb	lateral bar (Figs. 12, 23)	psp	postsubpleuron (Figs. 12, 38)
lc	lateroventral carina of mesopectus (Figs. 12, 38)	sc	scutellum (Figs. 12, 23)
ld	lateral depression of dorsellum (Fig. 12)	scf	scutellar fovea (Fig. 23)
ldp	laterodorsal process of scutellum (Figs. 12, 23–26)	sd	submedian depression of pronotum (Fig. 12)
lf	lower face (Fig. 6)	sp	speculum (Fig. 12)
lfc	lateral frontal carina (Fig. 6)	spl	subpleuron (Fig. 38)
lnc	lateral pronotal carina (Fig. 12)	st	sternum (Figs. 38, 65, 72)
lp	lower pleuron (Fig. 12)	teg	tegula (Fig. 12)
lpa	lateral propodeal area (Fig. 12)	tg	abdominal tergum (Figs. 65, 70–72, 74, 76, 78)
		up	upper pleuron (Fig. 12)
		vx	vertex (Fig. 6)

**Lateral surface of pronotum (ls, Figs. 11, 12).** Lateral surface of the pronotum posterior to the lateral pronotal carina.

**Pronotal crest (pc, Figs. 11, 12).** Raised, trans-

**Dorsal pronotal area** (not illustrated). Narrow dorsal area of the pronotum posterior to the crest.

**Parascutal impression (pi, Fig. 23; cf. also Fig. 24).** Impression just mesad the parascutal carina

**Axilla (ax, Fig. 23; cf. also Figs. 11, 12, 24–26).** This term is used instead of dorsal axillar area for brevity.

**Auricula (au, Figs. 11, 12).** Semilunar, slightly impressed area bounded by carinae, present laterally on the scutellum in some liopterids.

**Laterodorsal process of scutellum (ldp, Figs. 11, 12, 23–26).** A usually rounded process along the dorsolateral margin of the scutellum in most liopterids.

**Mesopleural impression (mi, Figs. 11, 12; cf. also Figs. 17, 19).** Longitudinal impression medially on the mesopleuron present in most liopterids.

**Upper pleuron (up, Figs. 11, 12; cf. also Figs. 15–19).** Area of the mesopleuron between the mesopleural triangle and the mesopleural impression, including the impression when there is no sharp dorsal boundary to the latter.

**Lateroventral carina of mesopectus (lc, Figs. 11, 12, 38; cf. also Figs. 15–19).** Carina lateroventrally on the mesopectus, extending from the lateral part of the acetabulum towards the lateral part of the mesocoxal foramen.

**Lower pleuron (lp, Figs. 11, 12; cf. also Figs. 15–19).** Area of the mesopleuron between the mesopleural impression and the lateroventral carina.

**Intermesocoxal processes (ip<sub>2</sub>, Figs. 19, 38).** Pair of small processes situated between the mesocoxal foramina.

**Dorsellum (do, Figs. 11, 12; cf. also Figs. 33–35).** Median, elevated area of the metanotum, previously referred to as the metascutellum (Ronquist & Nordlander 1989). The term was changed to dorsellum because it is uncertain whether the structure is serially homologous to the mesoscutellum, and dorsellum is widely used for the structure in the Chalcidoidea (e.g., Graham 1969).

**Metapleural carina (mpc, Fig. 12; cf. also Figs. 20–22).** Carina associated with the metapleural sulcus (mps, Figs. 11, 12), usually present only on the lower part of the metapleuron in liopterids.

**Anterior metapleural pit (amp, Fig. 20).** Pit just below the point where the metapleural sulcus reaches the anterior metapleural margin.

**Calyptra (ca, Figs. 11, 12).** Lidlike process projecting over, and from lateral view hiding, the propodeal spiracle.

**Prespiracular area (pa, Figs. 11, 12; cf. also Figs. 20–22).** Rectangular area, of propodeal or metapleural origin, between the calyptra and the metepimeron (em, Figs. 11, 12, 20).

**Prespiracular process (not illustrated).** Usually blunt process or surface convexity present on the prespiracular area in many Liopteridae (and in *Heteribalia*).

**Lateral propodeal area (lpa, Figs. 11, 12; cf. also Figs. 20–22).** Propodeal area anterior to the lateral propodeal carina, excluding the prespiracular area.

**Posterolateral propodeal process (ppp, Figs. 11, 12; cf. also Figs. 20–22).** Usually ridgelike process on the lateral propodeal area.

**Median propodeal area (mpa, Fig. 36; cf. also Fig. 37).** Propodeal area between the lateral propodeal carinae (lpc, Figs. 11, 12, 36; cf. also Fig. 37).

**Intermetacoxal processes (ip<sub>3</sub>, Fig. 38).** Pair of small processes situated between the metacoxal foramina.

**Postsubpleuron (psp, Figs. 11, 12, 38).** Ventral area of the metapectal-propodeal complex posterior to the metacoxal foramina.

**Nucha (nu, Figs. 11, 12, 38).** Collarlike projection of the propodeum protecting the propodeal-petiole articulation.

**Basalis (ba, Fig. 39; cf. also Fig. 40).** Apparent crossvein in the forewing formed by sections of Rs and M.

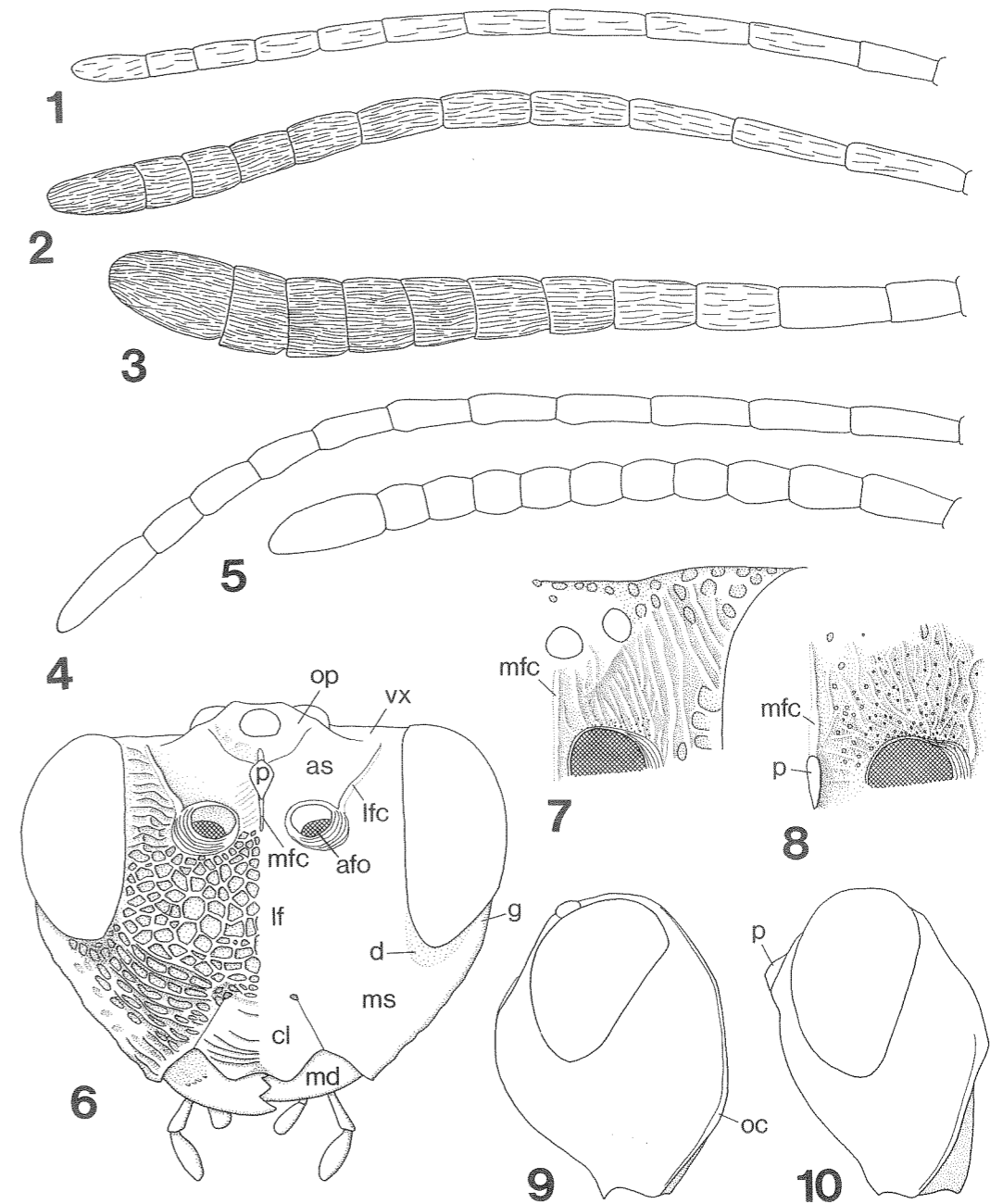
**Mesotibial lobe (not illustrated).** Subapical, lobelike projection on the anterior surface of the mesotibia.

**Metatibial lobe (Figs. 51–55).** Subapical, usually lobelike projection on the anterior surface of the metatibia.

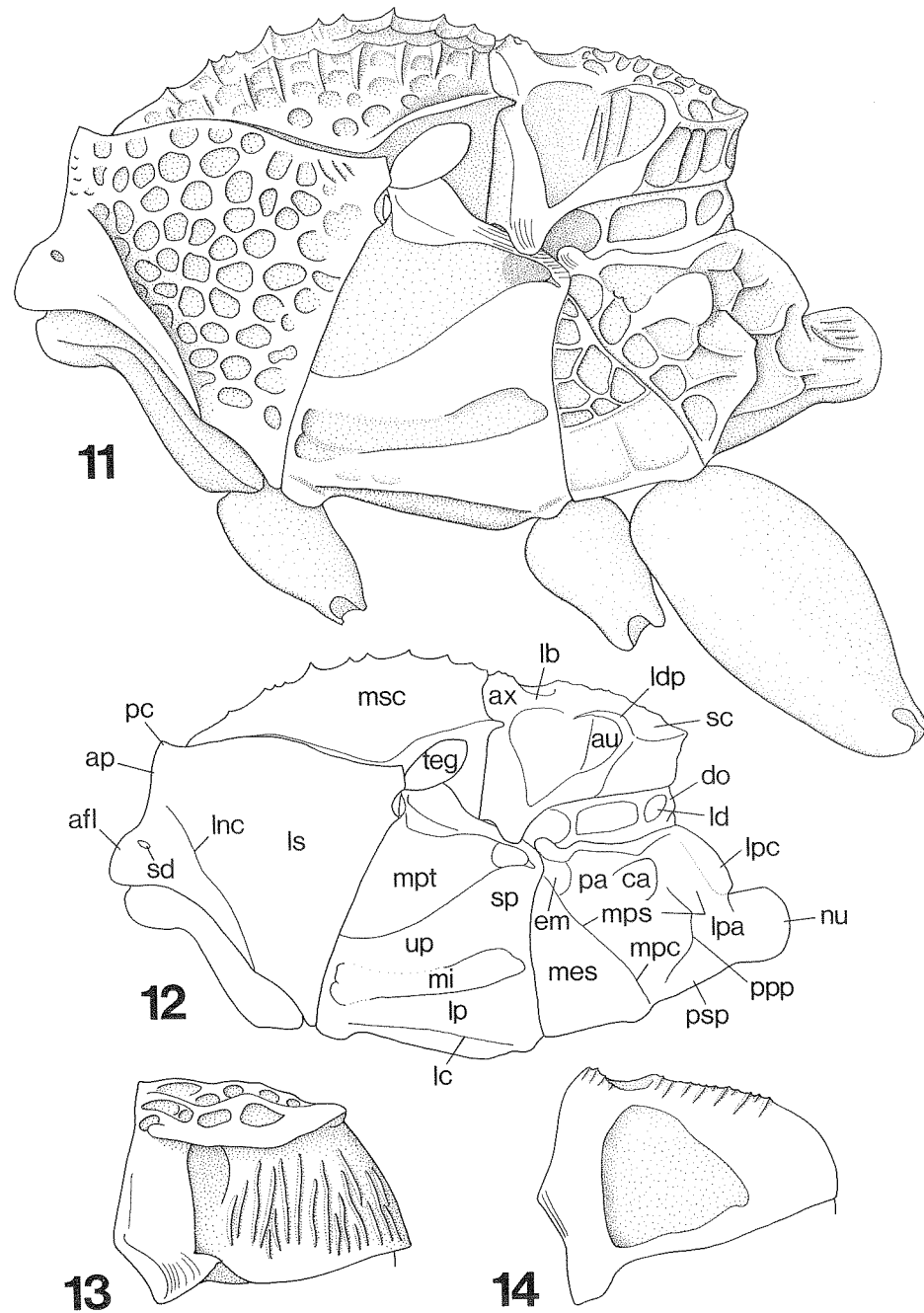
**Articular bulb of petiole (ab, Fig. 73).** Anterior bulblike part of the petiole, normally almost entirely inserted into the nucha of the propodeum.

**Annulus of petiole (an, Fig. 73; cf. also Figs. 63, 65–72, 74–82).** Posterior, abruptly widened, more or less cylindrical part of the petiole.

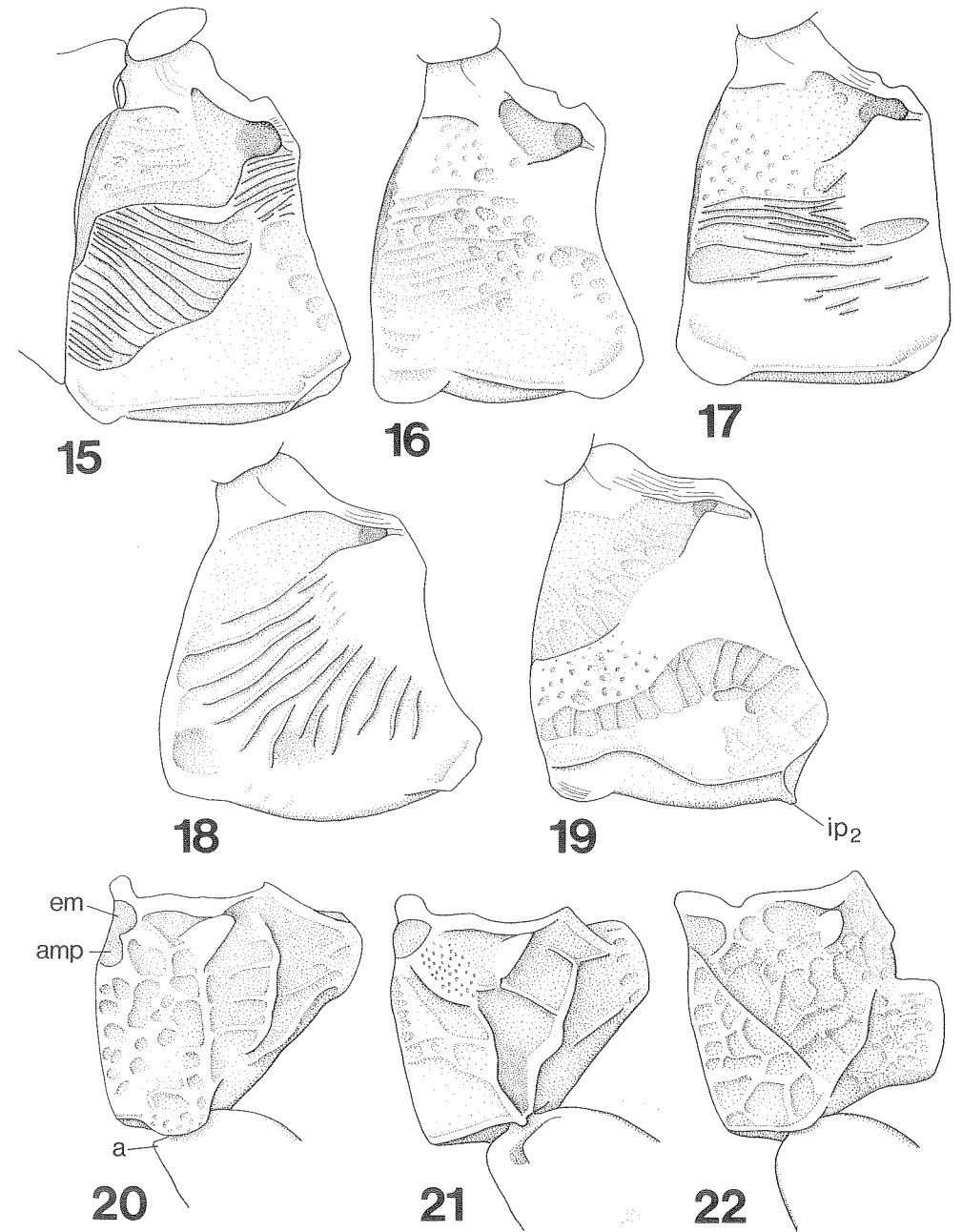
**Anterior flange of petiolar annulus (afa, Fig. 73).** Anterior, flangelike projection of the petiolar annulus, projecting over and protecting the articular bulb of the petiole.



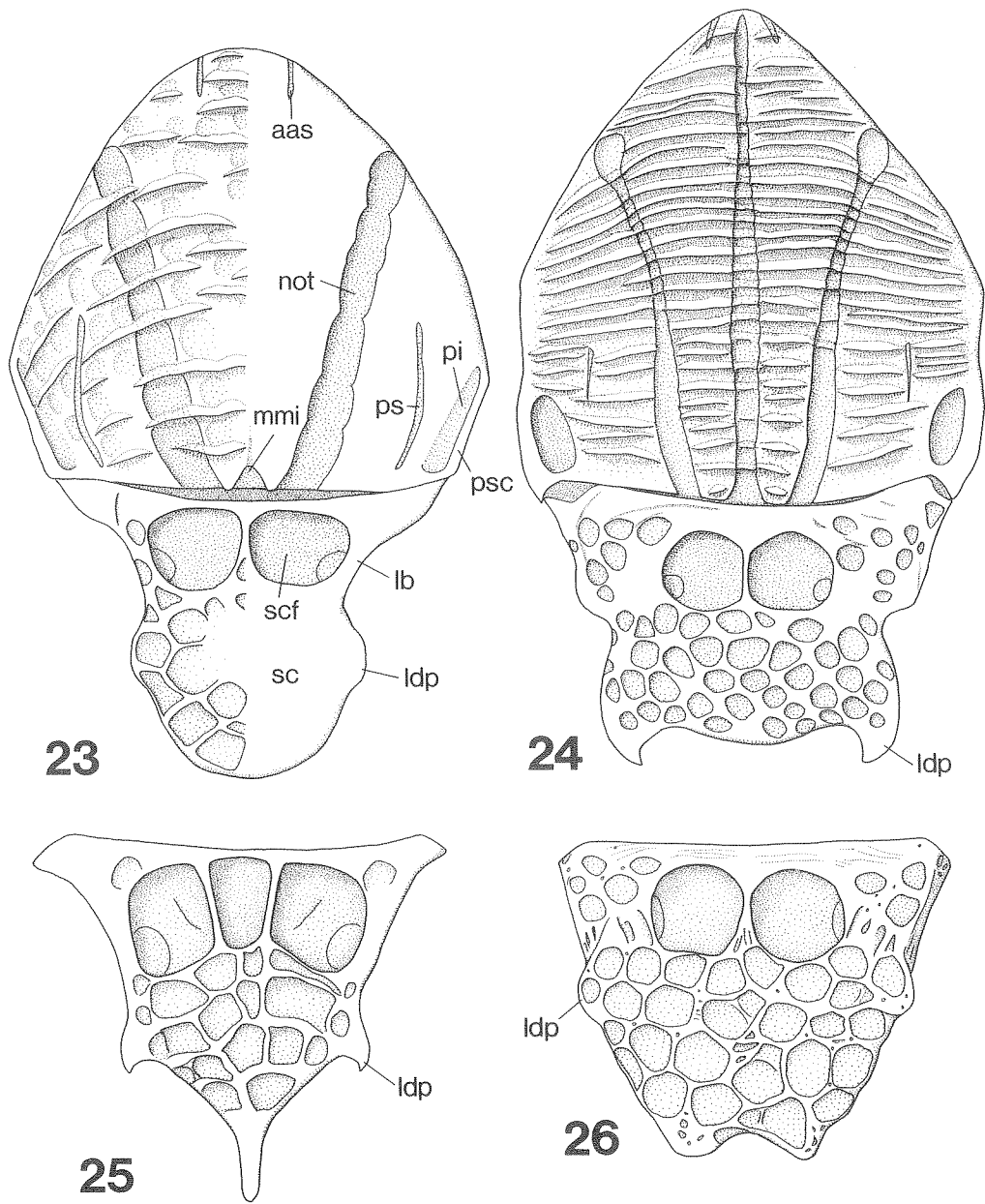
Figs. 1–10. — 1–3. Left flagellum of female, lateral view, pubescence omitted. — 1. *Kiefferiella* n. sp. 2. *Decellea yangambicola*. — 3. *Pseudibalia* n. sp. 1. — 4–5. Left flagellum of female, dorsal view, placodes and pubescence omitted. — 4. *Mesocynips insignis*. — 5. *Dallatorrella carinifrons*. — 6. Head, anterior view, pubescence omitted, *Paramblynotus* n. sp. 2 (nr *zonatus*). — 7. Left antennal scrobe and surrounding parts of the cranium, dorsoanterior view, pubescence omitted, *Liopteron nigripenne*. — 8. Left antennal scrobe, ventral half, anterior view, pubescence omitted, *Pseudibalia* n. sp. 11. — 9–10. Cranium, lateral view, sculpture and pubescence omitted. — 9. *Decellea yangambicola*. — 10. *Peras fenestratum*. Abbreviations explained in Tab. 2.



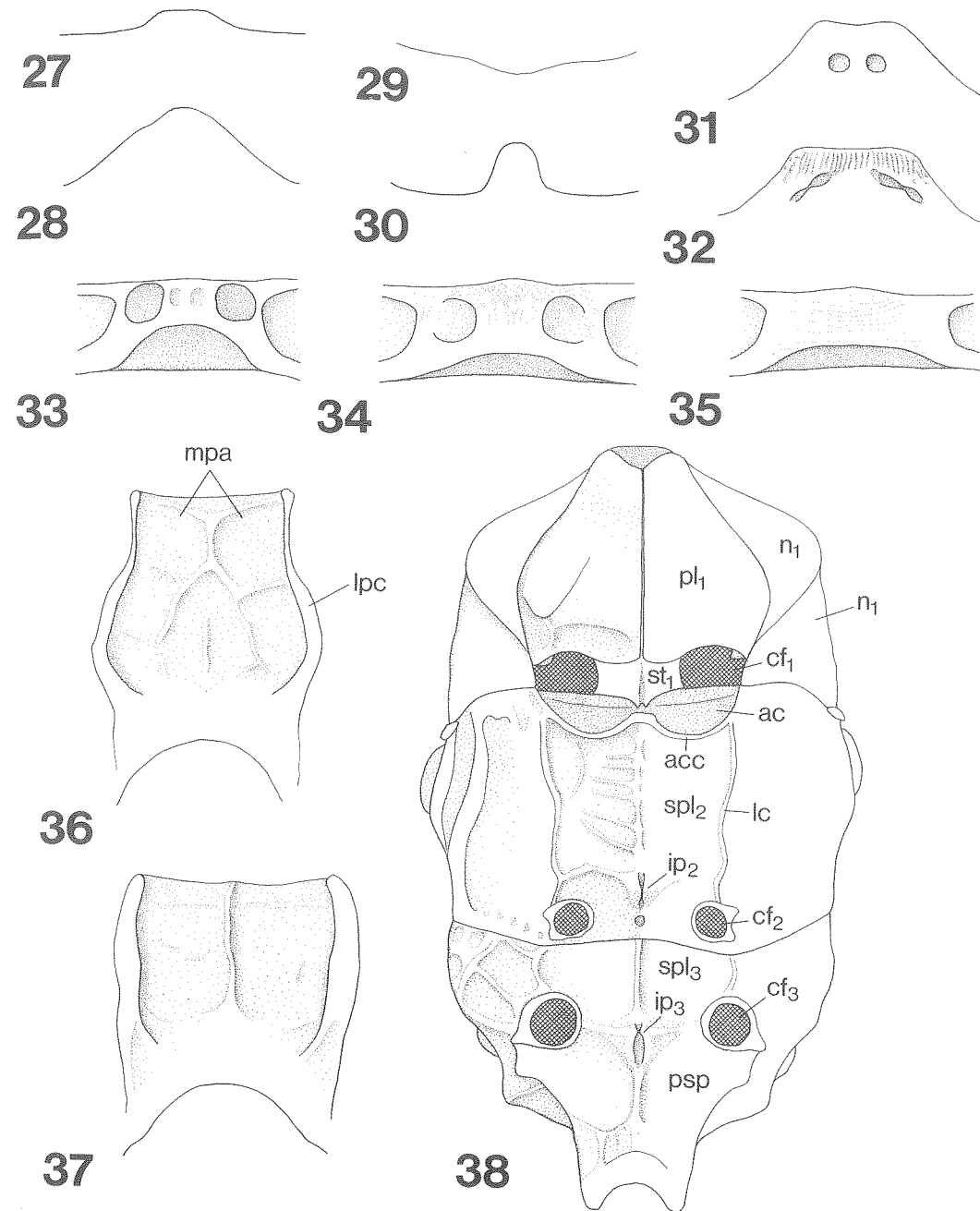
Figs. 11–14. — 11. Mesosoma with coxae, lateral view, pubescence omitted, *Paramblynotus* n. sp. 2 (nr *zonatus*). — 12. Same without coxae, sculpture omitted. — 13–14. Scutellar-axillar complex, lateral view, pubescence omitted. — 13. *Liopteron abdominale*. — 14. *Mesocynips insignis*. Abbreviations explained in Tab. 2.



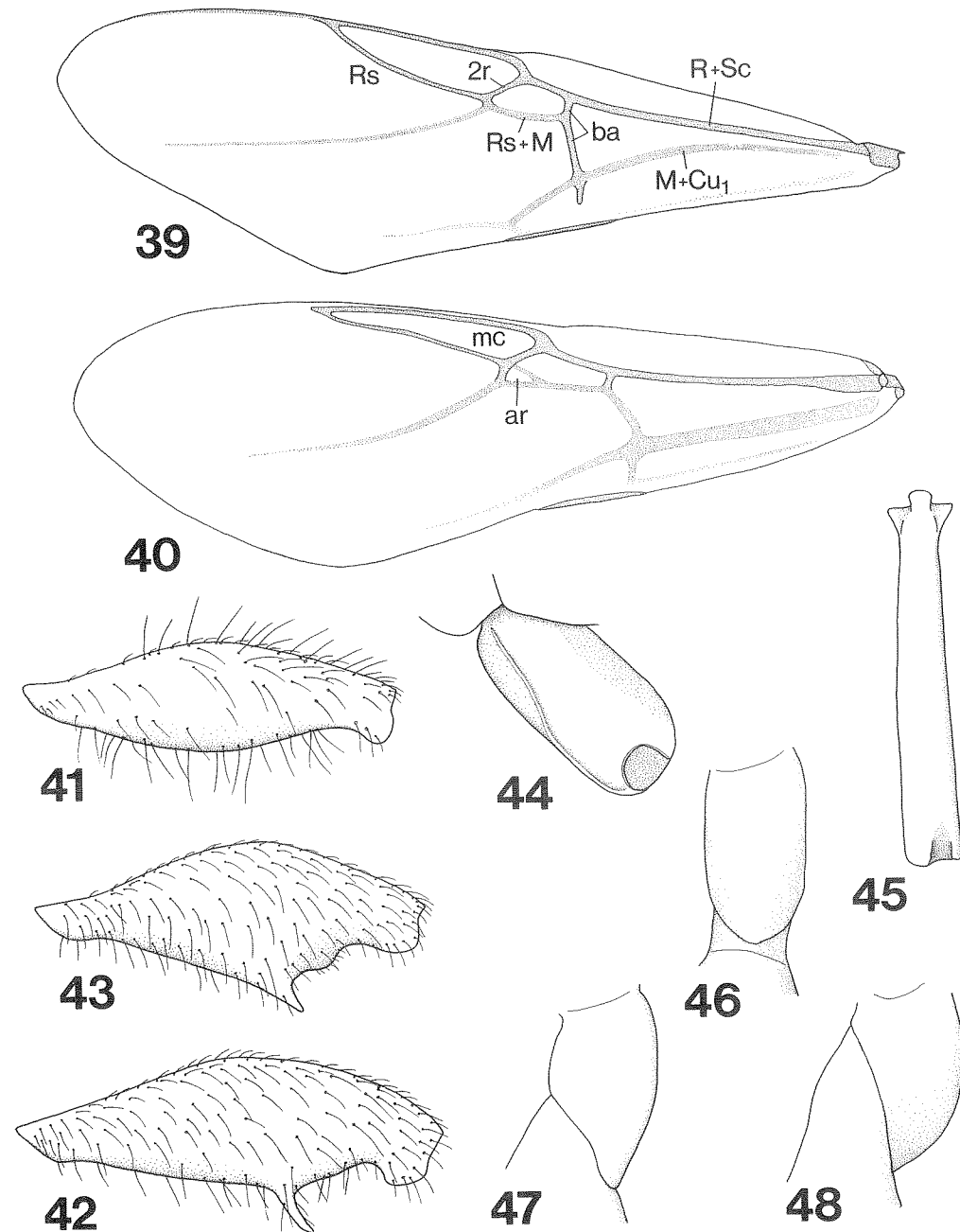
Figs. 15–22. — 15. Mesopleuron and adjacent part of pronotum, lateral view, pubescence omitted, *Tessmannella spinosa*. — 16–19. Mesopleuron, lateral view, pubescence omitted. — 16. *Oberthuerella* n. sp. 4. — 17. *Xenocynips* n. sp. 2. — 18. *Decellea yangambicola*. — 19. *Kiefferiella* n. sp. 2. — 20–22. Metapectal-propodeal complex and base of metacoxa, lateral view, pubescence omitted. — 20. *Peras fenestratum*. — 21. *Dallatorrella carinifrons*. — 22. *Kiefferiella* n. sp. 2.



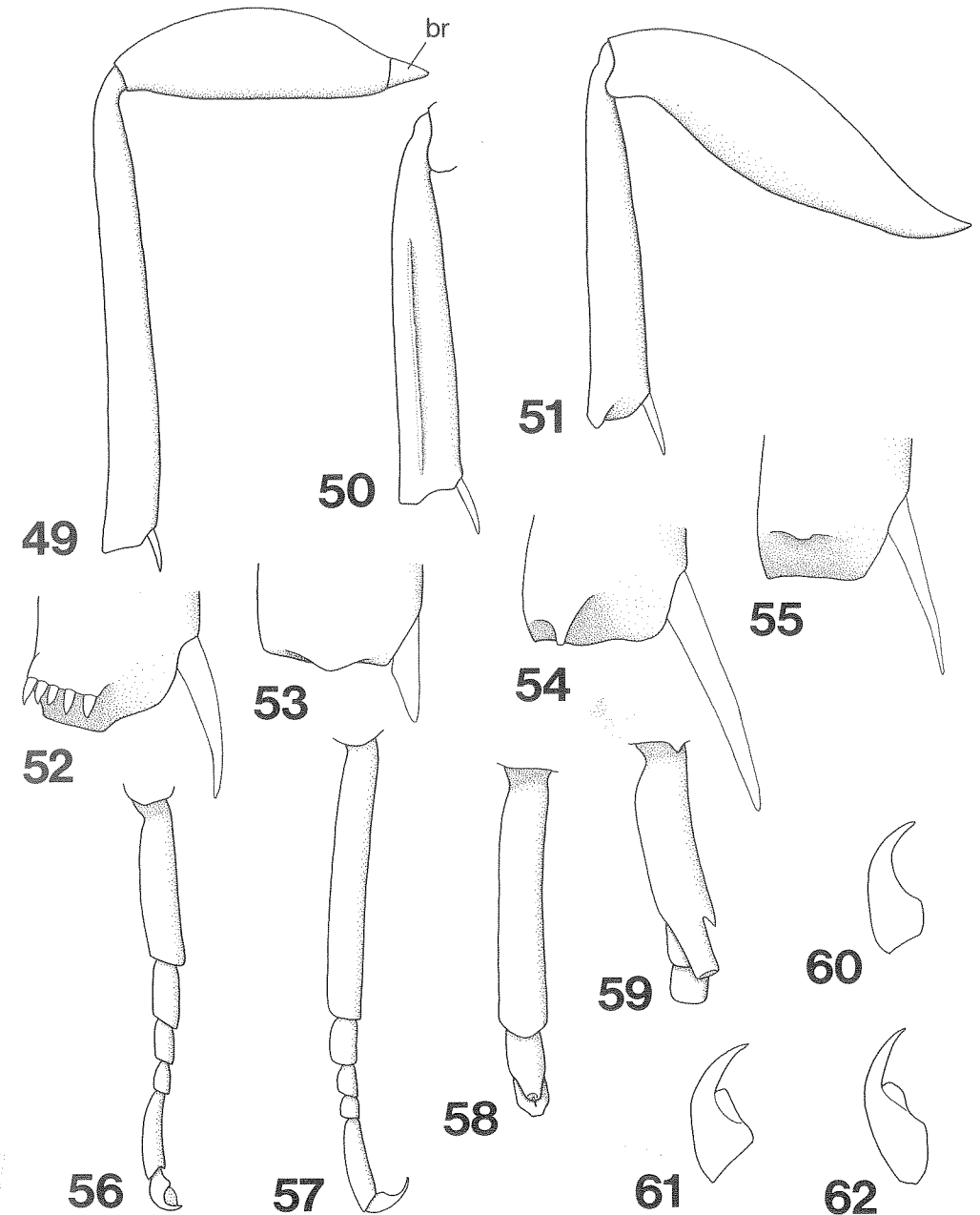
Figs. 23–26. — 23–24. Mesonotum, dorsal view, pubescence omitted. — 23. *Kiefferiella* n. sp. 2. — 24. *Liopteron nigripenne*. — 25–26. Scutellar-axillar complex, dorsal view, pubescence omitted. — 25. *Tessmannella spinosa*. — 26. *Pseudibalia* n. sp. 1. Abbreviations explained in Tab. 2.



Figs. 27–38. — 27–30. Dorsal margin of pronotum, anterior view, outline. — 27. *Kiefferiella* n. sp. 2. — 28. *Decellea yangambicola*. — 29. *Oberthuerella* n. sp. 5. — 30. *Tessmannella spinosa*. — 31–32. Anterior flange of pronotum, anterodorsal view, pubescence omitted. — 31. *Kiefferiella* n. sp. 2. — 32. *Decellea yangambicola*. — 33–35. Dorsellum, posterior view, pubescence omitted. — 33. *Kiefferiella* n. sp. 2. — 34. *Oberthuerella* n. sp. 5. — 35. *Tessmannella spinosa*. — 36–37. Median part of propodeum, dorsoposterior view, pubescence omitted. — 36. *Paramblynotus* n. sp. 2 (nr *zonatus*). — 37. *Peras fenestratum*. — 38. Mesosoma, ventral view, pubescence omitted, *Paramblynotus* n. sp. 2 (nr *zonatus*).

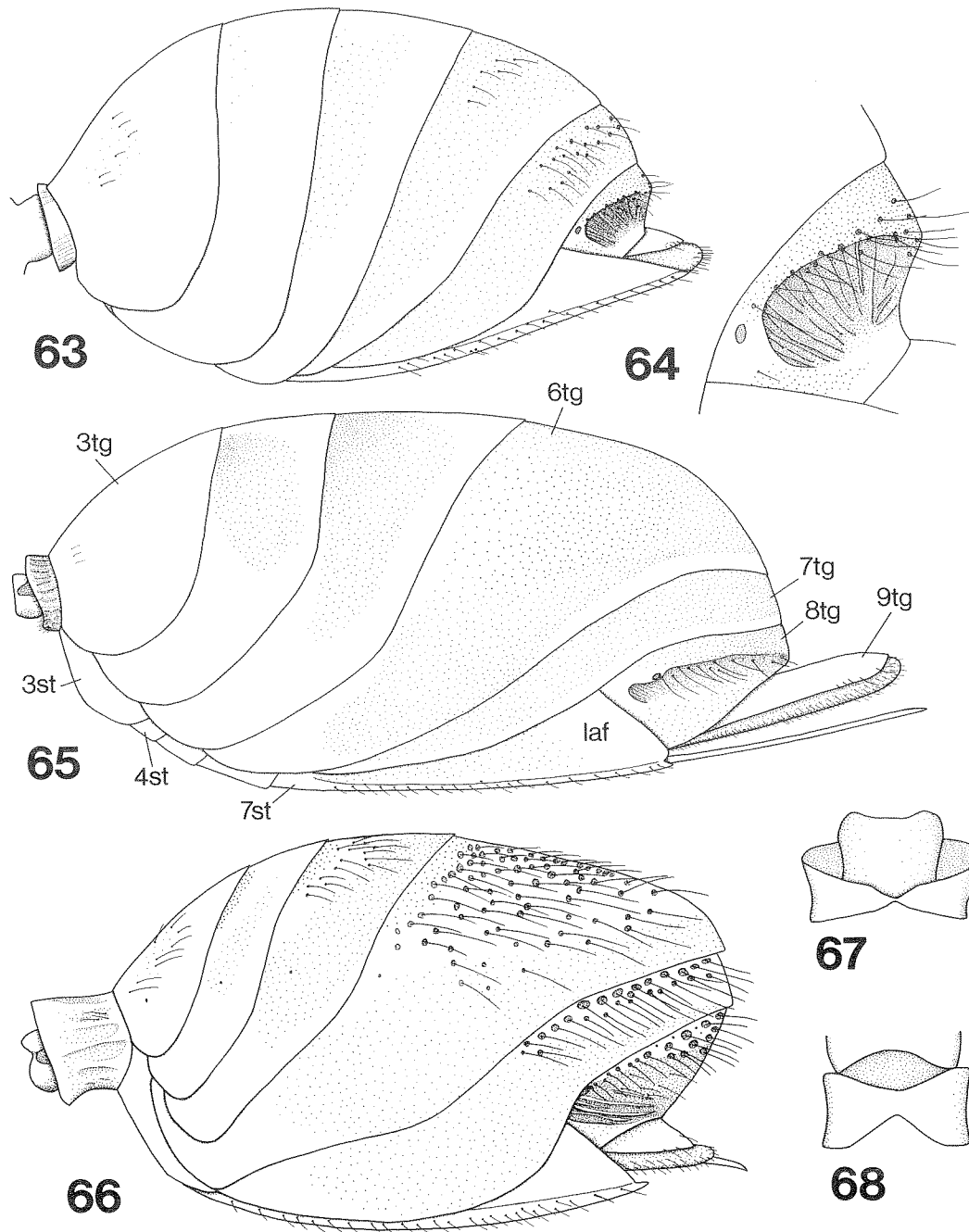


Figs. 39-48. — 39-40. Left forewing, dorsal view, pubescence omitted. — 39. *Dallatorrella rubriventris*. — 40. *Oberthuerella* n. sp. 4. — 41-43. Left metafemur, anterior view. — 41. *Peras fenestratum*. — 42. *Oberthuerella* n. sp. 3. — 43. *Tessmannella spinosa*. — 44. Left procoxa, lateral view, pubescence omitted, *Dallatorrella* n. sp. 2. — 45. Left protibia, dorsal (outer) view, pubescence omitted, *Peras fenestratum*. — 46-48. Left metatrochanter, dorsal view, pubescence omitted. — 46. *Ibalia anceps*. — 47. *Paramblynotus ruficeps*. — 48. *Peras fenestratum*. Abbreviations explained in Tab. 2.

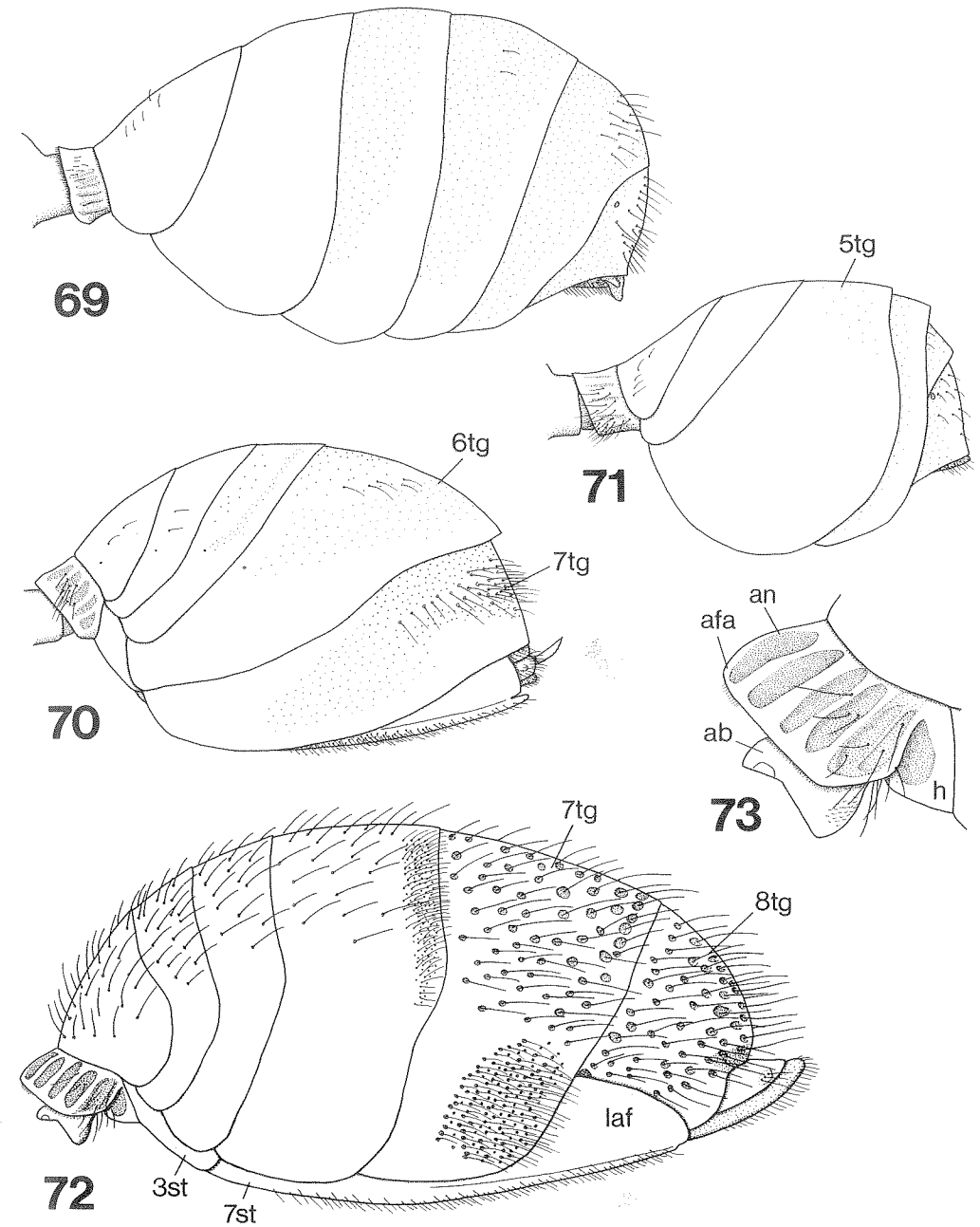


Figs. 49-62. — 49. Right metafemur and tibia, anterior view, pubescence omitted, *Ibalia rufipes*. — 50. Left metatibia, posterior view, pubescence omitted, *Liopteron apicale*. — 51. Right metafemur and tibia, anterior view, pubescence omitted, *Liopteron apicale*. — 52-55. Right metatibial apex, anterior view, pubescence omitted. — 52. *Decellea yangambicola*. — 53. *Xenocynips* n. sp. 2. — 54. *Dallatorrella* n. sp. 2. — 55. *Dallatorrella* n. sp. 5. — 56-57. Right metatarsus, anterior view, pubescence omitted. — 56. *Paramblynotus* n. sp. 2 (nr *zonatus*). — 57. *Decellea yangambicola*. — 58-59. Right metatarsomere 1-3, anterior view, pubescence omitted. — 58. *Liopteron nigripenne*. — 59. *Pseudibalia* n. sp. 11. — 60-62. Mesotarsal claw, anterior view, pubescence omitted. — 60. *Paramblynotus* n. sp. 2 (nr *zonatus*). — 61. *Pseudibalia* n. sp.

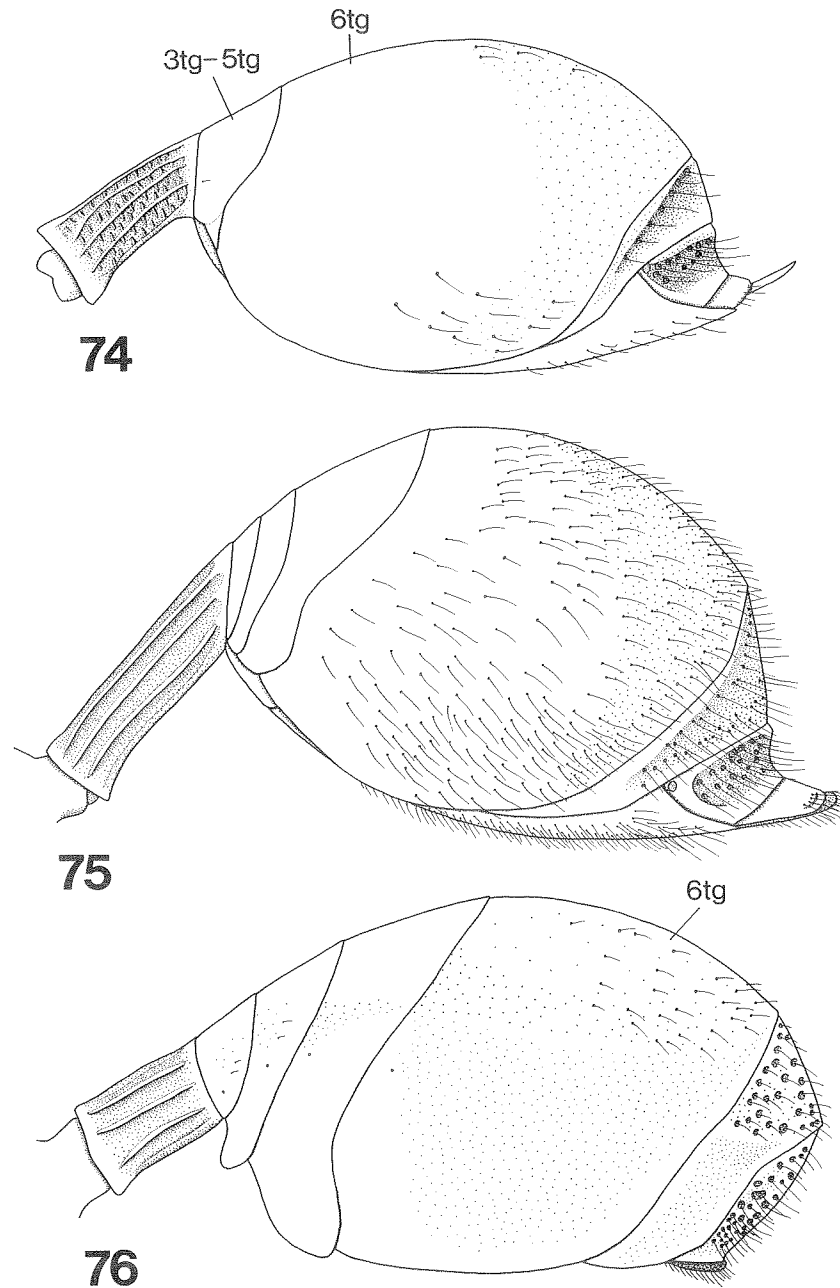




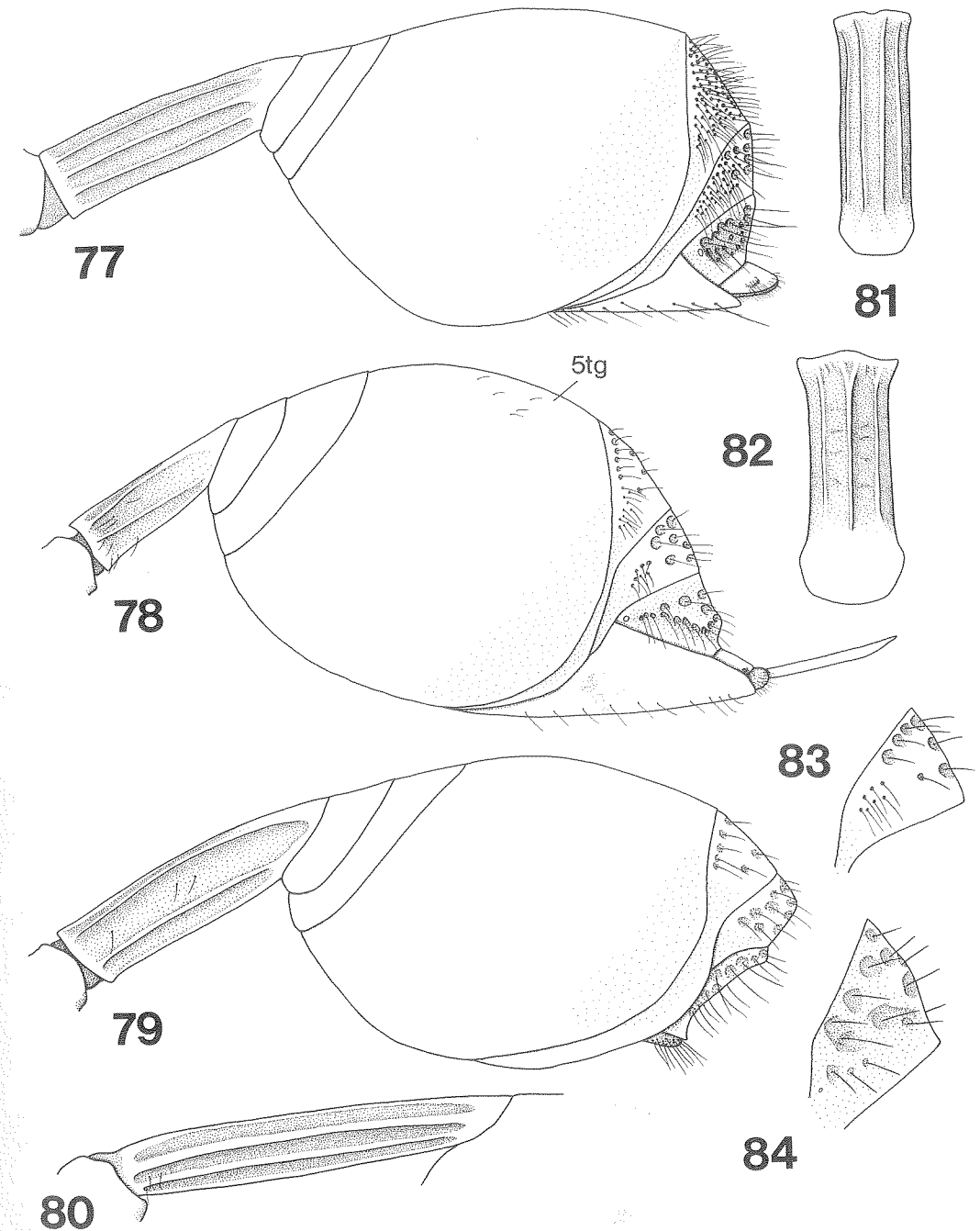
Figs. 63–68. Metasoma of the Mayrellinae. — 63. Female metasoma, lateral view, *Kiefferiella* n. sp. 2. — 64. Same, detail of abdominal tergum 8. — 65–66. Female metasoma, lateral view. — 65. *Decellea yangambicola*. — 66. *Paramblynotus zonatus* n. sp. 2 (nr *zonatus*). — 67–68. Female petiole, ventral view, sculpture and pubescence omitted. — 67. *Decellea*



Figs. 69–73. — 69–71. Metasoma of the Mayrellinae. — 69. Male metasoma, lateral view, *Kiefferiella* n. sp. 2. — 70. Female metasoma, lateral view, *Paramblynotus punctulatus*. — 71. Male metasoma, lateral view, *Paramblynotus* n. sp. 9. — 72–73. Metasoma of Dallatorrellinae. — 72. Female metasoma, lateral view, *Dallatorrella* n. sp. 2. — 73. Same, detail of petiole.



Figs. 74–76. Metasoma of the Oberthuerellinae. — 74. Female metasoma, lateral view, *Xenocynips subsquamata*. — 75. Female metasoma, lateral view, *Tessmannella spinosa*. — 76. Male metasoma, lateral view, *Oberthuerella* n. sp. 4. Abbreviations explained in Tab. 2.



Figs. 77–84. Metasoma of the Liopterinae. — 77–78. Female metasoma, lateral view. — 77. *Pseudibalia* n. sp. 1. — 78. *Peras fenestratum*. — 79. Male metasoma, lateral view, *Peras fenestratum*. — 80. Female petiole, lateral view, *Liopteron abdominale*. — 81–82. Annulus of female petiole, dorsal view. — 81. *Pseudibalia* n. sp. 1. — 82. *Peras fenestratum*. — 83–84. Dorsal half of female abdominal tergum 7, lateral view. — 83. *Peras fenestratum*. — 84. *Liopteron compressum*.

**Lateral flap of abdominal sternum 7 of females** (laf, Figs. 65, 72; cf. also Figs. 63, 66, 70, 74, 75, 77, 78). Lateral part of abdominal sternum 7 of females.

#### Descriptive terminology

Surface-sculpture terminology is from Harris (1979), except that "glabrous" and "glabrate" are used to describe surface texture regardless of the presence or absence of pubescence.

Antennae are described as if they were directed strictly forwards; wings and legs (except coxae) are described as if they were stretched out at right angles to the mesial plane.

The posterior margins of the abdominal terga have been described as follows: The dorsal part is described either as incised, straight, rounded or acute; the two latter terms being used as antonyms for "incised". The lateral part is either described as straight (e.g., the posterior margin of tergum 4 in Fig. 77), rounded (e.g., the posterior margin of tergum 3 in Fig. 69), sinuate (e.g., the posterior margin of tergum 6 in Figs. 65, 66) or ligulate (the posterior margin of tergum 5 in Figs. 74–76).

The lateral aspect of the eudorsal margin of abdominal tergum 8 is described as reclivous when it slopes inwards such that the centre of the body is closer to the lower end than to the upper end (e.g., Fig. 66). It is described as declivous when it slopes outwards such that the centre of the body is closer to the upper end than to the lower end (e.g., Figs. 74, 75).

Total body length has been measured from the anterior margin of the head to the posterior margin of abdominal tergum 8; other measures are explained below, under abbreviations.

To avoid redundancy in the generic descriptions, I have not repeated information given in the character analysis. Furthermore, ground-plan states

are not given for many characters; that is, if a character is not mentioned under a genus, the genus possesses the ground-plan state of the Liopteridae, given in Tab. 3, for that character.

#### Abbreviations

The following abbreviations have been used in the generic descriptions (x denotes an integer).

Fx = flagellomere x

mtx = metatarsomere x

xst = abdominal sternum x

xtg = abdominal tergum x

The following abbreviations have been used to refer to ratios:

F1/F2 = ratio of length of flagellomere 1 to length of flagellomere 2

l/w (in antenna) = ratio of maximum length to maximum width

l/w (in petiole) = ratio of median dorsal length to minimum dorsal width

Rs/2r = ratio of length of Rs, between the anterior wing margin and the junction with 2r, to length of 2r

mt1/mt2–5 = ratio of length of metatarsomere 1, excluding the articular bulb and any distal processes, to the length of metatarsomeres 2–5 combined, excluding the articular bulb of metatarsomere 2

The following abbreviations and symbol have been used in the checklists:

AT = allotype

HT = holotype

LT = lectotype

PT = paratype

PLT = paralectotype

T = syntype

\* = junior synonym

## Results

### Liopteridae

#### Monophyly of the Liopteridae sensu stricto

A long series of putative apomorphies supports the monophyly of the Liopteridae excluding *Heteribalia* and *Eileenella*, but including *Paraegilips* and *Kiefferiella*. However, many of the features show some homoplasy within the Cynipoidea, either because of secondary reductions within the Liopteridae or because of independent, parallel gains in other cynipoids. The apomorphies are listed below; only character states that are also informative about relationships among liopterid genera will recur in the character and phylogenetic analyses towards the end of the paper.

1. *Foveate sculpture on lateral surface of pronotum* (Fig. 11) and *dorsal surface of scutellum* (Figs. 23–26). Usually the foveate sculpture is also present on the lower face (Fig. 6), the vertex (Fig. 7) and at least the sides of the mesoscutum (Figs. 11, 23). This type of sculpture is unique among cynipoids and does not occur in the Diapriidae. The foveate sculpture has been secondarily lost almost completely in *Mesocynips insignis* and partly in some other species of the Liopteridae (see phylogenetic analysis, character 9).

2. *Acetabulum* (ac, Fig. 38) *more or less vertical, divided into two furrows for the procoxae by a strong median keel; acetabular carina* (acc, Fig. 38) *describing an ω-shape*. The acetabulum is more oblique and almost flat, and the acetabular carina more closely approximates a v-shape or u-shape in all other cynipoids and in the Diapriidae.

3. *Metapleural sulcus* (mps, Figs. 11, 12; cf. also Figs. 20–22) *reaches anterior metapectal margin far above mid-height of margin*. A somewhat similar, but not as extreme modification occurs in the Synergini (Ronquist 1994), but this is obviously an independently derived condition. In other cynipoids, as well as in the Diapriidae, the metapleural sulcus reaches the anterior metapectal margin further down.

4. *Intermetacoxal processes present* (ip, Fig.

38). These processes are unique for liopterids within the Cynipoidea and do not occur in the Diapriidae.

5. *Lateral pronotal carina* (lnc, Figs. 11, 12) *reaching raised ventral pronotal margin*. The ground-plan state of the Cynipoidea is very likely that seen in the Diapriidae, Ibaliidae and Austrocynipidae, where the lateral pronotal carina does not reach the ventral margin of the pronotum. This is also the primitive condition in the Figitidae and maybe in the Cynipidae as well, although most members of the Cynipidae lack the lateral pronotal carina. In some groups of the Figitidae and in some Synergini, the lateral pronotal carina has been secondarily modified such that it reaches the ventral pronotal margin, but the ventral margin is not raised like that of the Liopteridae.

6. *Laterodorsal process of scutellum* (ldp, Figs. 11, 12, 23–26) *present*. This process is unique for liopterids among cynipoids, and does not occur in diapriids. Within the Liopteridae, the process has been strongly reduced in *Dallatorrella*, and it has been lost entirely in the closely related genus *Mesocynips* (Fig. 14; see phylogenetic analysis, character 15).

7. *Lateroventral carina of mesopectus present* (lc, Figs. 11, 12; cf. also Figs. 15–19). This carina is at least partly present in all liopterids. There is a similar carina in the Eucoilinae, Aspiceratinae, Anacharitinae and some Figitinae, but this carina is probably not present in the ground plan of the Figitidae. Diapriids and other cynipoids lack such a carina, and this is the probable ground-plan state of the Cynipoidea.

8. *Nucha* (nu, Figs. 11, 12; cf. also Figs. 20–22) *long*. The nucha is shorter in most other cynipoids (except in the Pycnostigmatinae and some Eucoilinae) and in the Diapriidae, and this is the probable ground-plan state of the Cynipoidea. Within the Liopteridae, the nucha has secondarily been reduced in size in *Liopteron*.

9. *Metatibia shorter than metafemur* (Fig. 51). The metatibia is longer than (occasionally only as long as) the metafemur in all other cynipoids (Fig. 49), and this is also the condition in the Diapriidae. Within the Liopteridae, the metatibia has secondarily become longer in the genus *Decellea* (see

phylogenetic analysis, character 35).

10. *Petiolar annulus complete; tergal and sternal parts fused with no trace of a suture* (e.g., Figs. 63, 65, 66). The tergal and sternal parts of the annulus are separate or only partly fused with each other in the Austrocynipidae, Cynipidae and primitively in the Figitidae. In the Ibalidae the sternal part has been lost. Although the tergal and sternal parts of the annulus are fused with no trace of a suture in the Diapriidae, it seems likely that they are separate in the ground plan of the Cynipoidea because of the taxonomic distribution of the states within the superfamily. Furthermore, the tergal and sternal parts of the petiole are separated by a suture in many other parasitic wasps (e.g., Mason 1983, Naumann & Masner 1985), and they are independent sclerites in the ground plan of the Apocrita (Rasnitsyn 1988).

11. *Occipital carina present* (oc, Fig. 9; cf. also Fig. 10). This carina occurs in all liopterids. Within the Cynipoidea a similar carina occurs primitively in the Figitidae, but it is absent in the Ibalidae, Austrocynipidae and primitively in the Cynipidae. Diapriids, as well as many other groups of parasitic wasps, have an occipital carina. However, this carina is situated more mesally than that of cynipoids, making it uncertain whether these are actually homologous features. Because of the taxonomic distribution of the states within the Cynipoidea, I find it likely that the occipital carina is absent in the ground plan of cynipoids and has evolved independently in liopterids and figitids (see also Ronquist in press).

12. *Mesopleural impression present* (mi, Figs. 11, 12; cf. also Figs. 17, 19). The relatively distinct impression in liopterids is unique among cynipoids, although there are somewhat similar structures on the mesopleuron in many other groups in the superfamily. Eucoilines have a carina associated with a narrow furrow across the mesopleuron, and some charipines have a ledge in the same position. In the Rhoditini, Aspiceratinae, some Anacharitinae and some Figitinae there is an irregular, broader furrow or differently sculptured band across the lower part of the mesopleuron. *Eileenella* has a band of larger-than-usual punctures indicating the position of the mesopleural impression of liopterids. Despite this

variation, it seems likely that the distinct mesopleural impression is an autapomorphy for the Liopteridae. The impression has been secondarily lost twice within the Liopteridae (see phylogenetic analysis, character 21), but traces of the impression usually remain. In *Decellea yangambicola* there are two small impressed patches left (Fig. 18), and in *Tessmannella* the ventral margin of the impression is still visible (Fig. 15). The impression has been lost completely only in *Oberthuerella* (Fig. 16).

Where "Liopteridae" is used in the following text, it refers to the group defined by the characters listed above.

#### *Relationships and classification of Heteribalia and Eileenella*

Only one feature supports the monophyly of *Heteribalia* + Liopteridae, namely the presence of a metatibial lobe. This lobe is absent in all other cynipoids as well as in diapriids. However, the lobe of *Heteribalia* is smaller and situated more dorsally than the lobe of the Liopteridae, so it is uncertain whether these structures are actually homologous.

One character supports *Eileenella* + *Heteribalia* + Liopteridae as a monophyletic group; it is the metatrochanter, which is bent laterad towards the apex in these three taxa (Fig. 47). In other cynipoids the metatrochanter is straight (Fig. 46), and this is also the state found in the Diapriidae.

Two apparent synapomorphies support a sister-group relationship between *Eileenella* and the Liopteridae: (1) longitudinal sculpture present on the tergal part of the petiolar annulus (e.g., Fig. 73; the tergal part of the annulus is smooth in the Austrocynipidae, *Heteribalia*, *Ibalia* and primitively in the Cynipidae and Figitidae, but it is usually longitudinally sculptured in the Diapriidae), and (2) basal ring of metafemur invisibly fused to the rest of the femur (Fig. 51; the basal ring is distinct in the Diapriidae, Austrocynipidae, *Ibalia*, *Heteribalia* and primitively in the Cynipidae and Figitidae, cf. Fig. 49).

However, more convincing synapomorphies support the monophyly of a group consisting of *Eileenella*, *Heteribalia* and *Ibalia*, hereafter referred to as the Ibalidae. These characters include: (1) abdom-

Tab. 3. Ground-plan character states of the Liopteridae, inferred from the phylogeny given in Figs. 85–86 and using the Ibalidae and Austrocynipidae as outgroups, under the constraint that ibaliid relationships are (*Eileenella*, (*Heteribalia*, *Ibalia*)). Males of *Decellea* and *Tessmannella* are not known. Unless otherwise indicated, mention of a genus or a subfamily refers to all members of that genus or subfamily. No. = character number in the phylogenetic analysis.

Ground-plan state	No.	Secondary modifications in
<i>Head</i>		
1. Ocellar plate not raised (ocelli may be raised)	–	<i>Kiefferiella</i> , most <i>Paramblynotus</i>
2. Median frontal carina present	–	a few <i>Paramblynotus</i> , some <i>Xenocynips</i>
3. Antennal scrobe at least slightly impressed	–	<i>Decellea</i> , a few <i>Paramblynotus</i>
4. Lower face not protruding	–	<i>Decellea</i>
5. Lower face without impressions	–	some <i>Pseudibalia</i>
6. Malar space not impressed	–	<i>Paramblynotus</i> , some <i>Dallatorrella</i> , some <i>Oberthuerella</i> , some <i>Liopteron</i> , <i>Peras</i> , some <i>Pseudibalia</i>
7. Occipital carina present	–	–
8. Occipital carina dorsally reaching almost to vertex	–	<i>Mesocynips</i>
9. Occiput glabrous	–	some <i>Paramblynotus</i>
10. Postoccipt and gula set in cavity	–	–
<i>Female antenna</i>		
1. Antenna longer than length of head and mesosoma combined	–	<i>Dallatorrella</i> , some <i>Oberthuerella</i>
2. Flagellum with 11 articles	–	a few <i>Paramblynotus</i>
3. Flagellum not widened apically	2	<i>Decellea</i> , a few <i>Paramblynotus</i> , <i>Xenocynips</i> , some <i>Oberthuerella</i> , <i>Peras</i> , <i>Pseudibalia</i>
4. Flagellum not compressed	3	<i>Decellea</i> , <i>Peras</i> , most <i>Pseudibalia</i>
5. Median flagellomeres subcylindrical, not swollen	4	Dallatorrellinae
6. Placodes dense apically, covering entire surface of last flagellomere	–	<i>Kiefferiella</i> , some <i>Paramblynotus</i>
7. Last flagellomere without yellow spot apically	–	most <i>Pseudibalia</i>
<i>Male antenna</i>		
1. Antenna longer than length of head and mesosoma combined	–	<i>Dallatorrella</i>
2. Flagellum with 12 or 13 articles	–	–
3. Flagellum not widened apically	–	<i>Peras</i> , <i>Pseudibalia</i>
4. Flagellum not compressed	–	<i>Peras</i> , <i>Pseudibalia</i>
5. F1 subcylindrical, not swollen or excavated	–	some <i>Paramblynotus</i>
6. Median flagellomeres subcylindrical, not swollen	4	Dallatorrellinae
<i>Pronotum</i>		
1. Pronotal crest present	–	<i>Dallatorrella</i> , most <i>Oberthuerella</i>

Ground-plan state	No.	Secondary modifications in
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2. Dorsal pronotal area present, narrow	—	most <i>Oberthuerella</i>
3. Lateral pronotal carina present	—	—
4. Lateral pronotal carina ventrally joining raised ventral pronotal margin	—	—
5. Lateral surface flat, not produced	—	a few <i>Dallatorrella</i> , a few <i>Liopteron</i>
6. Lateral surface at least partly foveate	9	<i>Mesocynips</i> , one <i>Xenocynips</i> , one <i>Oberthuerella</i> , a few <i>Liopteron</i>
7. Posteriormost part of ventral margin short, concave	—	—
8. Posterior margin not incised, mesopleural triangle not impressed anteriorly	10	Dallatorrellinae, Oberthuerellinae, Liopterinae

*Mesonotum*

1. Scutum with transverse costae	—	some <i>Paramblynotus</i>
2. Median mesoscutal impression distinct only posteriorly	—	some <i>Xenocynips</i> , <i>Tessmannella</i> , <i>Oberthuerella</i> , Liopterinae
3. Notaulus percurrent	—	some <i>Liopteron</i>
4. Parascutal impression shallow, longitudinal, not margined	—	<i>Liopteron</i>
5. Parascutal carina not conspicuously raised	11	some <i>Paramblynotus</i> , Dallatorrellinae, Oberthuerellinae, Liopterinae
6. Lateral margin of axilla not raised	12	Liopterinae, Oberthuerellinae
7. Lateral bar narrow	13	some <i>Dallatorrella</i> , some <i>Oberthuerella</i> , Liopterinae
8. Scuto-scutellar sulcus dorsally divided by a median carina into two foveae	14	some <i>Paramblynotus</i> , <i>Dallatorrella</i> , Oberthuerellinae
9. Axillula without conspicuous white or yellow pubescence	—	some <i>Paramblynotus</i> , some <i>Dallatorrella</i>
10. Scutellum at least partly foveate or alveolate	—	<i>Xenocynips</i> , some <i>Oberthuerella</i>
11. Scutellum falling abruptly laterally and posteriorly	—	<i>Mesocynips</i> , <i>Liopteron</i>
12. Laterodorsal process present	15	<i>Mesocynips</i> , <i>Dallatorrella</i>
13. Laterodorsal process rounded	16	a few <i>Liopteron</i> , Oberthuerellinae
14. Scutellum posteriorly rounded, without processes	17, 18	<i>Decellea</i> , some <i>Paramblynotus</i> , Oberthuerellinae, most <i>Pseudibalia</i>
15. Auricula absent	19	Mayrellinae

*Mesopectus*

1. Mesopleural surface flat or slightly convex	20	<i>Tessmannella</i> , <i>Oberthuerella</i>
2. Posterior subalar pit present	—	—
3. Mesopleural triangle without conspicuous white or yellow pubescence	—	some <i>Paramblynotus</i> , some <i>Dallatorrella</i>
4. Mesopleural triangle not distinctly margined ventrally	—	<i>Paramblynotus</i>
5. Mesopleural impression present	21	<i>Decellea</i> , <i>Tessmannella</i> , <i>Oberthuerella</i>
6. Acetabulum almost vertical, divided medially, acetabular carina ω-shaped	—	—
7. Lateroventral carina at least partly present	—	—
8. Lateroventral carina without median protuberance	—	a few <i>Dallatorrella</i>

Ground-plan state	No.	Secondary modifications in
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9. Intermedesocoxal processes absent	22	<i>Kiefferiella</i> , <i>Paramblynotus</i> , some Liopterinae
10. Mesocoxa directed obliquely backwards	—	—

*Metanotum*

1. Lateral depression of dorsellum distinct	23	<i>Tessmannella</i> , a few <i>Pseudibalia</i>
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*Metapectal-propodeal complex*

1. Metapleural sulcus reaches anterior metapectal margin up high	—	—
2. Metapleural carina not produced ventrally	24	Dallatorrellinae
3. Posterolateral propodeal process present	—	some <i>Kiefferiella</i>
4. Metacoxal foramen and surrounding region not raised	25	Oberthuerellinae, Liopterinae
5. Metacoxa directed obliquely backwards	—	—
6. Intermetacoxal processes present	—	—
7. Calyptra present	—	—

*Wings*

1. Areolet absent	—	some <i>Oberthuerella</i>
2. Three hamuli on hind wing	—	—

*Legs*

1. Protibia with a longitudinal carina anterodorsally	—	—
2. Outer surface of protibia not impressed distally	29	Oberthuerellinae, Liopterinae
3. Mesofemur distinctly widened subbasally	—	—
4. Mesotibial lobe present	—	some <i>Paramblynotus</i>
5. Metacoxa without anterobasal process	30	<i>Xenocynips</i> , <i>Tessmannella</i> , Liopterinae
6. Laterobasal part of metacoxa rounded, without carina and pubescent patch	31	Dallatorrellinae
7. Metatrochanter slightly bent laterad towards apex	32	Liopterinae, Oberthuerellinae
8. No ventral process on metafemur	33	Oberthuerellinae
9. Metafemur without erect hairs dorsally	34	Dallatorrellinae, Liopterinae
10. Metatibia shorter than metafemur	35	<i>Decellea</i>
11. Metatibial lobe present	—	—
12. Metatarsomere 1 shorter than metatarsomeres 2–5 combined	—	<i>Decellea</i> , <i>Mesocynips</i> , most <i>Dallatorrella</i>
13. Metatarsomeres 1 and 2 without processes distally	—	one <i>Kiefferiella</i> , some <i>Paramblynotus</i> , <i>Xenocynips</i> , a few <i>Oberthuerella</i> , some <i>Liopteron</i> , some <i>Pseudibalia</i>
14. All claws simple	38	Dallatorrellinae, Oberthuerellinae, Liopterinae

*Female metasoma*

1. Petiolar annulus short, l/w < 0.9	39	some <i>Paramblynotus</i> , Oberthuerellinae, Liopterinae
2. Sternal and tergal parts of annulus fused with no trace of a suture	—	—
3. Annulus at least partly longitudinally sculptured	—	—
4. Anterior flange of annulus present	—	<i>Liopteron</i>

Ground-plan state	No.	Secondary modifications in
5. Annulus complete ventrally	—	<i>Decellea</i>
6. Annulus without ventral hump	40	Dallatorrellinae
7. Postpetiolar metasoma only slightly laterally compressed	—	one <i>Kiefferiella</i> , <i>Decellea</i>
8. 3tg–8tg subequal in size	45, 49	<i>Decellea</i> , <i>Paramblynotus</i> , Dallatorrellinae, Oberthuerellinae, Liopterinae
9. 3tg–8tg free, intertergal sutures distinct	—	<i>Xenocynips</i> , some <i>Pseudibalia</i>
10. Metasoma not truncate posteriorly	—	most <i>Pseudibalia</i>
11. 3tg–5tg not covered with erect hairs	41	Dallatorrellinae
12. Distinct angle between annulus and 3tg	42	Oberthuerellinae, Liopterinae
13. Lateral part of posterior margin of 3tg vertical	43	<i>Decellea</i> , <i>Paramblynotus</i> , Oberthuerellinae, Liopterinae
14. 4st–6st exposed, not membranous	44	<i>Paramblynotus</i> , Dallatorrellinae, Oberthuerellinae, Liopterinae
15. Dorsal part of posterior margin of 5tg straight or acute, not incised	46	Liopterinae
16. Lateral part of posterior margin of 5tg straight, rounded or sinuate; not ligulate	47	Oberthuerellinae
17. Pubescence dorsolaterally on 7tg in punctures of equal size	51	<i>Peras</i> , <i>Pseudibalia</i>
18. No ventrolateral hair patch on 7tg or on 6tg	52	Dallatorrellinae
19. 8tg not strigate close to spiracle	53	<i>Kiefferiella</i> , <i>Decellea</i> , many <i>Paramblynotus</i>
20. Eudorsal margin of 8tg not distinctly angled, vertical to declivous	54	<i>Kiefferiella</i> , <i>Decellea</i> , many <i>Paramblynotus</i> , <i>Dallatorrella</i>
21. 7tg and 8tg without dorsomedian carina and without processes	—	some <i>Oberthuerella</i> , some <i>Liopteron</i> , <i>Peras</i> , one <i>Pseudibalia</i>
22. 9tg slightly projecting beyond 8tg	—	<i>Decellea</i> , some <i>Paramblynotus</i> , some <i>Oberthuerella</i>
<b>Male metasoma</b>		
1. Petiolar annulus not specialized ventrally	—	Dallatorrellinae
2. 3tg–8tg subequal in size	—	many <i>Paramblynotus</i> , <i>Dallatorrella</i> , Oberthuerellinae, Liopterinae
3. 3tg–8tg free, intertergal sutures distinct	—	<i>Xenocynips</i>
4. 3tg–8tg not keeled medially	—	—
5. Eudorsal margin of 7tg dorsally rounded or straight, not angled	—	one <i>Liopteron</i> , <i>Peras</i>
6. 8tg without median keel and without processes	—	some <i>Liopteron</i> , <i>Peras</i>

inal tergum 7 of female conspicuously enlarged (unique among cynipoids and diapiroids), (2) a short and stout metafemur, about as long as the metacoxa (the metafemur is longer and more slender in all other cynipoids and in diapiroids), (3) loss of the sternal part of the petiolar annulus (the sternal part is present in the Diapiroidae, Austrocynipidae, Liopteridae and primitively in the Cynipidae and Figitidae), (4) dorsomedian part of pronotum pos-

cynipoids; the posterior pronotum is long in *Belyta* but short in the other diapiroids examined), (5) marginal cell of forewing long (it is also long in some Liopteridae, but not in the ground plan of the family; it is short in all other cynipoids, and presumably also in the ground plan of the Cynipoidea; the marginal cell of diapiroids is different and cannot be used for outgroup comparisons) and (6) pair of posterior scutellar processes present (similar pro-

Figitidae, but not primitively in either family; the processes are absent in other cynipoids and in the Diapiroidae).

Further apomorphies support a sister-group relationship between *Heteribalia* and *Ibalia*. These features include: (1) a long (wide) and transversely costate dorsal pronotal area (unique among cynipoids and diapiroids), (2) pronotum laterally with a distinct dorsal surface (unique among cynipoids and diapiroids), (3) a conspicuous, deep femoral groove on the mesopleuron (unique among cynipoids and diapiroids), (4) a deep median furrow on the mesosubpleuron (unique among cynipoids, but the state occurs in some diapiroids), and (5) a tubular process on the second metatarsomere (a similar process does occur in some liopterids, but is not a ground-plan feature of the Liopteridae; other cynipoids and diapiroids lack this process).

In view of the character evidence listed above, I have not included *Heteribalia* and *Eileenella* in the Liopteridae. Instead, I place them in the family Ibaliidae, together with the genus *Ibalia*. The relationships among the Liopteridae, Ibaliidae and other Cynipoidea will be discussed in detail elsewhere (Ronquist in press).

#### Ground-plan states

Ground-plan character states of the Liopteridae are listed in Tab. 3. These states were reconstructed *a posteriori* using the phylogeny given in Fig. 85, and employing the Austrocynipidae and Ibaliidae as outgroups under the constraint that the Ibaliidae are monophyletic and that relationships within the Ibaliidae are (*Eileenella*, (*Ibalia*, *Heteribalia*)). To avoid redundancy, the ground-plan states will usually not be given in the generic descriptions below. Thus, if a character is not mentioned under a genus, this implies that the genus possesses the ground-plan state, given in Tab. 3, for that character.

#### Diversity and distribution

Liopterids occur in all zoogeographic regions except the western Palaearctic, although most species are tropical or subtropical. There are 81 avail-

herein and six have been synonymized previously, yielding a total of 73 valid species. The material examined for this study comprised an additional 70 undescribed species.

#### Key to genera

1. Claws simple (Fig. 60). Scutellum laterally with semilunar, slightly impressed area set off by distinct carinae (the auricula; *au*, Figs. 11, 12). Posterolateral pronotal margin not incised, mesopleural triangle not deeply impressed anteriorly (Fig. 11; cf. also Figs. 18, 19). (Subfam. Mayrellinae) ..... 2
- Pro- and mesotarsal claws with basal, lamellate lobe (Figs. 61, 62). Scutellum laterally without impressed semilunar area (Figs. 13, 14). Posterolateral pronotal margin distinctly incised in front of mesopleural triangle, the latter deeply impressed anteriorly (Fig. 15; cf. also Figs. 16, 17) ..... 4
- 2 (1). Mesopleural triangle ventrally with distinct, evenly curved margin (Fig. 11). In females, abdominal sterna 4–6 entirely covered by sternum 3 (Fig. 66). All zoogeographic regions except western Palaearctic ..... *Paramblynotus* (p. 34)
- Mesopleural triangle ventrally not defined by distinct, evenly curved margin (Figs. 18–19). In females, abdominal sterna 4–6 at least partly exposed (Fig. 65). Afrotropical and Nearctic regions ..... 3
- 3 (2). Lower face not protruding (cf. Fig. 10). Submedian pronotal depressions closed laterally (Fig. 31). Pronotal crest not triangularly raised (Fig. 27). Upper pleuron foveolate; mesopleural impression present (Fig. 19). Metatibia shorter than metafemur. Metatarsomere 1 shorter than metatarsomeres 2–5 combined (cf. Fig. 56). Nearctic region ..... *Kiefferiella* (p. 29)
- Lower face distinctly protruding (Fig. 9). Submedian pronotal depressions open laterally (Fig. 32). Pronotal crest prominently triangularly raised (Fig. 28). Upper pleuron with widely spaced, oblique costulae; meso-

- longer than metafemur. Metatarsomere 1 longer than metatarsomeres 2–5 combined (Fig. 57). Afrotropical region .....  
 ..... *Decellea* (p. 32)
- 4 (1). Median flagellomeres distinctly swollen medially to subapically (Figs. 4, 5). Metapleural carina drawn out into ventral process; region laterad metacoxal foramen not distinctly raised (Fig. 21). Metacoxa basally with lateral carina and anterolateral depression (Fig. 21). Metatrochanter moderately bent laterad towards apex (cf. Fig. 47). Petiolar annulus ventrally with hump (Fig. 73) or distinctly marked, differently sculptured area. Abdominal terga 3–5 with long, erect pubescence; abdominal tergum 7 larger than terga 5 and 6 in lateral view; abdominal tergum 7 with patch of recumbent hairs ventrolaterally (Fig. 72). Australian and Oriental regions. (Subfam. Dallatorrellinae) ..... 5
- Median flagellomeres not swollen (Fig. 3; cf. also Figs. 1, 2). Metapleural carina not produced ventrally; region laterad metacoxal foramen distinctly raised (Fig. 20). Metacoxa basally without lateral carina and anterolateral depression (Fig. 20). Metatrochanter strongly bent laterad towards apex (Fig. 48). Petiolar annulus cylindrical, not specialized ventrally (Figs. 74–80). Abdominal terga 3–5 without erect pubescence, at most with a few semi-erect hairs; abdominal tergum 5 or 6 largest in lateral view; abdominal tergum 7 without patch of recumbent hairs ventrolaterally (Figs. 74–79). Afrotropical and Neotropical (occasionally Nearctic) regions ..... 6
- 5 (4). Specimen bright yellowish to reddish brown. Antenna long, much longer than length of head and mesosoma combined; flagellomeres elongate (Fig. 4). Foveate sculpture absent or almost absent from head, pronotum and scutellum (Fig. 14). Scuto-scutellar sulcus divided into two foveae by median carina (cf. Figs. 23, 24, 26). M+Cu<sub>1</sub> of forewing straight, not curved towards R+Sc (cf. Fig. 40). Procoxa laterally without vertical carina (cf. Fig. 11) .....  
 ..... *Mesocynips* (p. 38)
- Specimen variously coloured but never entirely bright yellowish to reddish brown

- Antenna short, distinctly shorter than length of head and mesosoma combined; flagellomeres more or less stout (Fig. 5). Foveate sculpture present on lower face, laterally on pronotum and dorsally on scutellum (cf. Figs. 6, 11, 23–26). Scuto-scutellar sulcus divided into 3 foveae by two longitudinal carinae, occasionally into more foveae by additional, weaker carinae (cf. Fig. 25). M+Cu<sub>1</sub> of forewing distinctly curved towards R+Sc (Fig. 39). Procoxa laterally with vertical carina (Fig. 44) .....  
 ..... *Dallatorrella* (p. 40)
- 6 (4). Scutellum posteriorly with median process (Fig. 25). Metafemur ventrally with spinelike process; dorsally only with recumbent pubescence, not with erect hairs (Figs. 42, 43). Abdominal tergum 6 largest in lateral view (Figs. 74–76). Afrotropical region. (Subfam. Oberthuerellinae) ..... 7
- Scutellum posteriorly without median process (Figs. 24, 26). Metafemur ventrally without process; dorsally with erect hairs in addition to recumbent pubescence (Fig. 41). Abdominal tergum 5 largest in lateral view (Figs. 77–79). Neotropical (occasionally Nearctic) region(s) (Subfam. Liopterinae) ... 9
- 7 (6). Mesopleural surface not concave; mesopleural impression present; lower pleuron at least partly horizontally strigate (Fig. 17). Anterior metatibial spur short and stout (Fig. 53). Abdominal terga 3–5 fused, intertergal sutures at least partly invisible (Fig. 74) ....  
 ..... *Xenocynips* (p. 42)
- Mesopleural surface distinctly concave, the concavity forming oblique, shallow femoral groove (indicated in Figs. 15 and 16); mesopleural impression absent; lower pleuron without horizontal, linear sculpture (Figs. 15, 16). Anterior metatibial spur not short and stout (cf. Figs. 52, 54, 55). Abdominal terga 3–5 not fused, intertergal sutures distinct (Figs. 75, 76) ..... 8
- 8 (7). Pronotal crest produced into conspicuous toothlike process (Fig. 30). Ventral margin of mesopleural impression visible as well defined ventral margin of obliquely costate area of mesopleuron (Fig. 15). Lateral depressions of dorsellum completely absent

- (Fig. 35). Metafemoral spine triangular, broad-based, oblique (Fig. 43) .....  
 ..... *Tessmannella* (p. 44)
- Pronotal crest not produced into conspicuous toothlike process; crest usually absent (Fig. 29), but occasionally present and produced into small, triangular process. Ventral margin of mesopleural impression not marked (Fig. 16). Lateral depressions of dorsellum clearly indicated (Fig. 34). Metafemoral spine elongate, narrow-based, erect (Fig. 42) ..... *Oberthuerella* (p. 46)
- 9 (6). Flagellum not widened towards apex, not compressed (cf. Figs. 1, 2). Mesoscutum at least medially with closely set, transverse costae; parascutal impression rounded, deep, well-defined (Fig. 24). Scutellum posteriorly falling gradually, drawn out posteroventrally (Fig. 13). Anterior flange of petiolar annulus (cf. *afa*, Fig. 73) absent, petiolar annulus usually more or less continuous with articular bulb dorsally (Fig. 80). Large insects, length at least 9.3 mm .....  
 ..... *Liopteron* (p. 49)
- Flagellum slightly to distinctly widened towards apex, often distinctly compressed (Fig. 3). Mesoscutum with costae less closely set;

- parascutal impression elongate, shallow, not well-defined (cf. Fig. 23). Scutellum posteriorly falling more abruptly, not drawn out posteroventrally (cf. Fig. 11). Anterior flange of petiolar annulus present, distinct (Figs. 77–79). Smaller insects, length at most 9.5 mm, usually much less ..... 10
- 10 (9). Petiolar annulus laterally with broad, slightly impressed area, broadened posteriorly (Figs. 78, 79); dorsally with distinct, median ridge (Fig. 82). Dorsal surface of scutellum without processes posteriorly. Metasoma with abdominal terga 3 or 4 moderately reduced and (in females) abdominal terga 6–8 never falling abruptly posteriorly (Fig. 78) ..... *Peras* (p. 52)
- Petiolar annulus laterally with several narrower and deeper furrows (Fig. 77); dorsally with median furrow (Fig. 81), occasionally with weak, short median ridge. Dorsal surface of scutellum with pair of small but distinct processes posteriorly (Fig. 26); if not, then metasoma with abdominal terga 3 and 4 more strongly reduced, occasionally abdominal terga 3–5 fused, and (in females) abdominal terga 6–8 falling abruptly posteriorly (Fig. 77) ..... *Pseudibalia* (p. 54)

## Mayrellinae

Mayrellinae Hedicke, 1922:190

### Genus *Kiefferiella* Ashmead

Figs. 1, 19, 22, 23, 27, 31, 33, 63, 64, 69.

*Kiefferia* Ashmead, 1903a:10. Type species *Kiefferia rugosa* Ashmead by original designation and monotypy. Name preoccupied by *Kiefferia* Mik, 1895:96 and *Kiefferia* Kunster & Chaîne, 1902:113.

*Kiefferiella* Ashmead, 1903c:159. Replacement name for *Kiefferia* Ashmead. See also Ashmead (1903d:221).

*Protoibalia* Brues, 1910:15. Type species *Protoibalia connexiva* Brues by original designation and monotypy.  
 New synonymy.

### Monophyly

Monophyly of *Kiefferiella* is indicated by the following anomorphies, although all of them show

at least some homoplasy within the Liopteridae.

1. *Flagellum of females with placodes sparse, not covering the entire surface of the apical flagellomeres* (Fig. 1). A state approaching that of *Kiefferiella* has apparently evolved independently in some *Paramblynotus* (some species in the *scaber*, *trisetosus* and *nigricornis* groups). In other liopterids, as well as in ibaliids and in *Austrocynips*, the placodes are more numerous, especially on the apical flagellomeres where they usually cover the entire surface (Figs. 2, 3).

2. *First flagellomere in female antenna distinctly shorter than second* (Fig. 1). The first flagellomere is long in *Austrocynips*, ibaliids and most liopterids, but short in the Liopterinae + Oberthuerellinae and in some species in the *Paramblynotus nunctulatus* group. The state in *Kiefferiella* is an

autapomorphy for that genus according to the phylogenetic analysis (character 5).

3. *Upper pleuron foveolate* (Fig. 19). A somewhat similar sculpture occurs in some species of the *Paramblynotus trisetosus* group, but is absent from all other liopterids. *Eileenella* has the upper pleuron glabrate with relatively large punctures, but the punctures are less distinct and more sparse than the foveolae of *Kiefferiella*; other ibaliids and *Austrocynips* have the upper pleuron glabrate or irregularly sculptured, without foveolae or large punctures.

4. *Mesopleural triangle rugulose* (Fig. 19). A somewhat similar sculpture occurs in *Oberthuerella*, and in *Austrocynips*, *Ibalia* and *Heteribalia*. However, the type of rugulose sculpture in *Kiefferiella* is different. A series of more or less vertical costulae along the ventral margin of the mesopleural triangle is particularly characteristic (Fig. 19). Other liopterids usually have the mesopleural triangle largely glabrate, and this is also the condition in *Eileenella*.

5. *Submedian pronotal depressions closed laterally* (Fig. 31). This state also occurs in the Liopterinae + Oberthuerellinae and in a few *Paramblynotus* (the *zonatus* and *borneanus* groups). In *Ibalia* the pronotal depressions are open laterally, but in *Heteribalia* they are closed. The depressions are absent in *Eileenella* and *Austrocynips*. Considering only the Austrocynipidae, Liopteridae and Ibalidae, it is impossible to infer whether this character state is an autapomorphy or a plesiomorphy for *Kiefferiella* (see phylogenetic analysis, character 8) However, since the depressions are open laterally in the Cynipidae and most Figitidae, I consider it likely that they were open in the ground plan of the Liopteridae and became closed in the stem species of *Kiefferiella*.

Further possible autapomorphies of *Kiefferiella*, for which present data are ambiguous, include: presence of intermesocoxal processes (character 22; Fig. 19), ocellar plate raised, nucha and petiolar annulus more or less smooth dorsally.

#### Description

Body length 3.3–5.2 mm.

*Head.* Lower face foveate-foveolate to rugu-

lose; not or weakly keeled medially. Median frontal carina distinct, slightly raised to form a blunt, pyramidal process. Ocellar plate distinctly raised. Antennal scrobe distinctly impressed; glabrate, punctate. Lateral frontal carina absent. Vertex foveate-reticulate. Gena foveate-reticulate. Occipital carina not angled midlaterally; not raised. Clypeus with vertical to slightly radiating strigae; distinctly projecting ventrally; ventral margin straight or slightly incised.

*Female antenna.* F1/F2 = 0.6–0.8; F3 l/w = 2.8–5.0. Placodes start on F2. Placodes sparse on entire flagellum; apically becoming denser but even on last flagellomere not close to covering entire surface.

*Male antenna.* Flagellum with 12 articles (n. sp. 1) or 13 articles (n. sp. 2). F1/F2 = 0.7–0.8; F3 l/w = 2.3–2.4 (n. sp. 1) or 4.1–4.3 (n. sp. 2).

*Pronotum.* Anterior flange glabrate, with or without some longitudinal strigae laterally; or entirely longitudinally strigate. Submedian depressions large, deep, isolated. Anterior plate foveolate. Lateral surface foveate-reticulate. Crest slightly raised medially, evenly curved. Dorsal pronotal area glabrate with some transverse strigae.

*Mesonotum.* Scutum with foveae and transverse, slightly undulating costae; the former superficial medially but distinct laterally. Median mesoscutal impression only indicated posteriorly. Notaulus distinct or indistinct. Parascutal carina not raised, rounded posteriorly. Scuto-scutellar sulcus divided into two foveae by strong median carina, sometimes also a few additional, weaker carinae present. Dorsal surface of scutellum foveate-areolate to rugose; laterally and posteriorly not or indistinctly margined; without processes posteriorly. Posterior and lateral surfaces of scutellum vertically costulate to rugose. Laterodorsal process small, rounded. Auricula broad, sometimes subdivided.

*Mesopectus.* Mesopleural triangle large, triangular, distinctly impressed; rugulose, pubescent. Upper pleuron glabrate, foveolate. Speculum glabrous. Mesopleural impression percurrent; subdivided by vertical ridges. Lower pleuron entirely glabrate; or glabrate, posteriorly rugulose; or glabrate, posteriorly with some horizontal costulae; sparsely pubescent. Lateroventral carina percur-

rent, strongly curved. Subpleuron transversely costulate. Intercostal processes peglike, directed obliquely posteriorly.

*Metanotum.* Dorsellum glabrate; lateral depressions distinct, deep, medium-sized.

*Metapectal-propodeal complex.* Anterior meta-pleural pit present or absent. Metepisternum rugose. Prespiracular area rugose; prespiracular process represented by slight surface convexity or absent. Lateral propodeal area rugose; posterolateral propodeal process absent; or (in n. sp. 2) present, low, ridgelike, oblique. Median propodeal area carinate to rugose; lateral propodeal carina only present dorsally, not raised or flattened above. Postsubpleuron glabrate. Nucha glabrate dorsally, with some costulae or punctures laterally.

*Wings.* Wings hyaline; in some species forewing slightly darker in the apical half, especially in and around the marginal cell. Marginal cell short,  $R_s/2r = 2.1-2.3$ .  $R_s+M$  from middle of basalis. Bulla in  $R_1+Sc$  present.

*Legs.* Protibia apically with one to two teeth. Mesotibial lobe blunt, not margined, with two teeth. Metatibial lobe margined, not produced, with four teeth. Longitudinal carina on posterior surface of metatibia indistinct or absent. Metatarsomere 1 not compressed;  $mt1/mt2-5 = 0.6$ . Distal margins of  $mt1$  and  $mt2$  not produced or (in n. sp. 2) slightly, bluntly produced anteroventrally.

*Female metasoma.* Petiolar annulus short,  $l/w = 0.3-0.5$ ; dorsally glabrate or (in n. sp. 2) superficially longitudinally ridged, laterally longitudinally costulate. Postpetiolar metasoma slightly laterally compressed or (in *K. rugosa*) very strongly compressed. 3tg–8tg subequal in size; 3tg largest in lateral view. 3tg–8tg entirely to 4tg posteriorly and 5tg–8tg entirely keeled medially. Posterior margins of terga: 3tg–4tg dorsally straight or slightly acute, 5tg–7tg dorsally slightly acute, 3tg–4tg laterally rounded or very slightly sinuate, 5tg–7tg laterally sinuate. 4tg–5tg or 5tg partly, 6tg–8tg entirely minutely punctate. 3tg with some hairs laterally, 4tg–5tg nude, 6tg with a row of hairs in coarse punctures, 7tg–8tg with more hairs in coarse punctures. 8tg with broad apical impression almost reaching to slightly surpassing spiracle; impression obliquely set, but at least close to spiracle

otherwise glabrate, punctate. Eudorsal margin of 8tg in lateral view angled close to upper end; ventrad angle reclivous or vertical, distinctly concave. 4st–6st partly covered by 3st in n. sp. 1, 4st–6st all well exposed in n. sp. 2; state unknown in *K. rugosa* and *K. acmaeodera*. 7st with irregular, double row of submedian hairs; posterior margin of lateral flap oblique, straight.

*Male metasoma.* Petiolar annulus short,  $l/w = 0.5-0.6$ ; dorsally glabrate or (in n. sp. 2) superficially longitudinally ridged, laterally longitudinally costulate. 3tg–8tg subequal in size; 3tg or 4tg largest in lateral view. Posterior margins of terga: 3tg dorsally straight, 4tg–6tg dorsally slightly, broadly incised, 7tg dorsally broadly incised, 3tg–6tg laterally rounded, 7tg laterally sinuate. 4tg not or partly, 5tg largely, 6tg–8tg entirely minutely punctate. 3tg laterally with a few hairs, 4tg–5tg nude, 6tg with a few hairs in coarse punctures, 7tg–8tg with more hairs in coarse punctures. Eudorsal margin of 8tg in lateral view almost straight.

*Coloration.* Black to brown; in *K. acmaeodera* with head, mesosoma and legs yellowish brown; in n. sp. 2 with head, mesosoma and legs partly reddish brown.

#### Diversity and distribution

Two described and two undescribed species from southwestern Nearctic (USA: ID, CA, TX).

#### Biology

Eighteen specimens of *Kiefferiella* n. sp. 1 reared from *Prosopis glandulosa* (Fabaceae) in Texas. One female of n. sp. 2 from California labelled: "On *Boccheris* sp. (common)", possibly referring to a species in the genus *Baccharis* (Asteraceae).

There are two published records of *Kiefferiella* being associated with buprestids (Weld 1956): three reared female specimens determined as *K. rugosa* exited from fresh tunnels of *Acmaeodera* sp. (Buprestidae), and the type female of *K. acmaeodera* was reared from *Eurotia lanata* (Chenopodiaceae) infested with *Acmaeodera pulchella*. What appears to be two of the three reared "*K. rugosa*" specimens



were present in a series of *Kiefferiella* specimens from the USNM examined after the main part of this study was completed. The reared specimens do not belong to *K. rugosa* or any of the other species listed in the appendix but to an additional, undescribed species of *Kiefferiella* from California.

#### Checklist of described species

*acmaeodera* Weld, 1956:291, ♀; USA: ID; USNM (HT♀, No. 63 269).  
*connexiva* (Brues, 1910:15, ♀); USA: CO, Florissant, upper Eocene; MCZC (HT♀, No. 2065, reverse piece, No. 2066). As *Protoibalia*; **new combination**.  
*rugosa* (Ashmead, 1903a:10, ♀); USA: CA; USNM (HT♀, No. 23 455). As *Kiefferia* Ashmead; combination by Ashmead (1903c:159).

#### Genus *Decellea* Benoit

Figs. 2, 9, 18, 28, 32, 52, 57, 65, 67.

*Decellea* Benoit, 1956:51. Type species *Decellea yangambicola* Benoit by original designation and monotypy. Synonymized with *Paramblynotus* by Weld (1962:279). **Status reestablished.**

#### Monophyly

The single species of *Decellea* is characterized by numerous autapomorphies.

1. *Lower face distinctly protruding* (Fig. 9). This feature is unique among the Liopteridae, Austrocynipidae and Ibaliidae. Some liopterids have the lower face keeled medially, but the entire lower face is never distinctly protruding.

2. *Petiolear annulus medioventrally interrupted* (Fig. 67). In all other liopterids the annulus is complete ventrally (Fig. 68). The sternal portion of the annulus has been lost in the Ibaliidae, but in *Austrocynips* it is present and complete medioventrally, and this is presumably the ground-plan state for the Liopteridae.

3. *Metatibia longer than metafemur* (cf. Fig. 49). All liopterids except *Decellea* have the metatibia shorter than the metafemur (Fig. 51). Although *Austrocynips* and Ibaliidae are similar to

*Decellea* in having a long metatibia, the phylogenetic analysis (character 35) indicates that the state in *Decellea* is due to secondary reversal to the primitive state.

4. *Flagellum slightly widened towards apex and slightly compressed apically* (Fig. 2). A similar, but more pronounced, modification occurs in *Peras* and some *Pseudibalia*, but the phylogenetic analysis (character 3) indicates that the state in *Decellea* is independently derived.

5. *Mesopleural impression absent* (Fig. 18). The mesopleural impression is present in most liopterids but absent in Ibaliids and *Austrocynips*. The phylogenetic analysis (character 21) indicates that the absence of the impression in *Decellea* is due to secondary loss. This hypothesis is further strengthened by the presence of superficial impressions in *Decellea* in the position where the mesopleural impression occurs in other liopterids. In the Liopteridae, the mesopleural impression has also been lost in the ancestor of *Oberthuerella* + *Tessmannella* (see phylogenetic analysis, character 21).

6. *Upper pleuron glabrous with horizontal to slightly oblique, broadly spaced costulae* (Fig. 18). A somewhat similar sculpture occurs in some *Oberthuerella*, but in those species the costulae are denser, more irregular and mixed with other sculptural components such as alveolae or rugosity (Fig. 16). Linear sculpture different from that in *Decellea* occurs in *Xenocynips* (Fig. 17), *Tessmannella* (Fig. 15) and some *Oberthuerella*; other liopterids, Ibaliids and *Austrocynips* have the upper pleuron largely glabrate, punctate-foveolate or rugulose, without parallel linear sculpture.

7. *Pronotal crest prominently triangularly raised* (Fig. 28). A similar modification has evolved independently in the *borneanus* group of *Paramblynotus*, as suggested by the distribution of other characters within *Paramblynotus*; otherwise, it is unique among the Liopteridae, Ibaliidae and Austrocynipidae.

Other possible autapomorphies for *Decellea* include: metatarsomere 1 longer than metatarsomeres 2–5 combined (Fig. 56), postpetiolear metasoma strongly laterally compressed, and abdominal tergum 6 devoid of pubescence (Fig. 65).

#### Description

Body length 6.0–8.7 mm.

*Head*. Lower face foveate-reticulate; not keeled medially. Entire lower face between antennal foramina, clypeus and inner orbits distinctly protruding. Median frontal carina distinct; not raised. Antennal scrobe not impressed; weakly longitudinally carinate. Lateral frontal carina present. Vertex foveate. Gena glabrate with more or less sparse, superficial foveae. Occipital carina not angled midlaterally; not raised. Clypeus punctate, ventrally coriaceous, with a median, vertical costula dorsally and an interrupted transverse carinula medially; distinctly projecting ventrally; ventral margin straight.

*Female antenna*. Flagellum slightly widened towards apex; slightly compressed towards apex.  $F1/F2 = 1.1$ ;  $F3\ l/w = 3.7$ . Placodes start on F1.

*Male antenna*. Unknown.

*Pronotum*. Anterior flange longitudinally strigate. Submedian depressions large, deep, open laterally. Anterior plate glabrate, dorsally punctate. Lateral surface dorsally foveate, ventrally foveolate. Crest prominently triangularly raised medially. Dorsal pronotal area transversely strigate, partly glabrate.

*Mesonotum*. Scutum with superficial foveae and transverse, slightly to distinctly undulating costulae to costae. Median mesoscutal impression absent. Notaulus indistinct. Parascutal carina not raised, rounded posteriorly. Dorsal surface of scutellum foveate-areolate; laterally and posteriorly margined; with a pair of broad and short processes posteriorly. Posterior and lateral surfaces of scutellum vertically costulate to rugose. Laterodorsal process small, rounded. Auricula narrow, not subdivided.

*Mesopectus*. Mesopleural triangle large, triangular, distinctly impressed; glabrate, pubescent. Upper pleuron glabrous with horizontal to oblique, broadly spaced costulae. Speculum glabrous, partly striolate. Mesopleural impression absent; in its place two superficial impressions, one medially and one anteriorly. Lower pleuron glabrate, with some fine punctures and weak costulae; sparsely pubescent. Lateroventral carina only present poste-

riorly, very short. Subpleuron transversely costulate.

*Metanotum*. Dorsellum glabrous medially, punctate laterally; lateral depressions distinct, deep, medium-sized.

*Metapectal-propodeal complex*. Anterior meta-pleural pit present. Metepisternum rugose. Prespiracular area rugose; prespiracular process represented by slight surface convexity. Lateral propodeal area rugose; posterolateral propodeal process low, ridgelike, oblique. Median propodeal area carinate; lateral propodeal carina present only dorsally, raised, flattened above, punctate and pubescent above. Postsubpleuron glabrate. Nucha with somewhat irregular, longitudinal costulae.

*Wings*. Forewing light brown, darker apically, especially in and around the marginal cell. Hind wing hyaline, brownish apically. Marginal cell short,  $Rs/2r = 3.6$ .  $Rs+M$  from middle of basalis. Bulla in  $R_1+Sc$  absent.

*Legs*. Protibia apically with 3 teeth. Mesotibial lobe blunt, not margined, with 3 teeth. Metatibial lobe margined, not produced, with 4–5 teeth. Longitudinal carina on posterior surface of metatibia present. Metatarsomere 1 slightly compressed;  $mt1/mt2-5 = 1.3$ . Distal margins of  $mt1$  and  $mt2$  not produced.

*Female metasoma*. Petiolear annulus short,  $l/w = 0.3$ ; longitudinally costulate; medioventrally narrowly interrupted. Postpetiolear metasoma strongly laterally compressed.  $3tg-5tg$  only slightly reduced in size,  $6tg$  conspicuously expanded dorsally but not ventrally.  $3tg$  posteriorly,  $4tg-8tg$  entirely keeled medially. Posterior margins of terga:  $3tg$  dorsally straight,  $4tg-7tg$  dorsally acute,  $3tg-4tg$  laterally slightly sinuate,  $5tg-7tg$  laterally sinuate.  $3tg$  posteriorly,  $4tg$  dorsolaterally,  $5tg-8tg$  largely to entirely minutely to more coarsely punctate.  $3tg$  with a few hairs anterolaterally,  $4tg-7tg$  nude,  $8tg$  with a row of long hairs from dorsal margin of impression.  $8tg$  with narrow apical impression surpassing spiracle; impression glabrate with some oblique longitudinal sculpture indicated close to the spiracle. Eudorsal margin of  $8tg$  in lateral view angled submedially, ventrad angle reclivous, slightly concave.  $9tg$  conspicuously projecting beyond  $8tg$ .  $4st-6st$  all well exposed.  $7st$  with single row of

submedian hairs; posterior margin of lateral flap oblique, slightly convex.

*Male metasoma.* Unknown.

*Coloration.* Black; postpetiolar metasoma yellow-red; legs partly brownish.

#### *Diversity and distribution*

One species recorded from the central part of the Ethiopian region.

#### *Biology*

Two females from Uganda labelled "ex Coleoptera"; two other females from Uganda labelled "ex Lepidoptera".

The type female of *Decellea yangambicola* was captured on a *Drypetes gossweileri* (Euphorbiaceae) log in Zaire (Benoit 1956).

#### *Checklist of described species*

*yangambicola* Benoit, 1956:52, ♀; Zaire; MRAC (HT♀). Transferred to *Paramblynotus* by Weld (1962:279); **combination reestablished.**

#### **Genus *Paramblynotus* Cameron**

Figs. 6, 11, 36, 38, 47, 56, 60, 66, 68, 70, 71.

*Paramblynotus* Cameron, 1908:299. Type species *Paramblynotus punctulatus* Cameron by subsequent designation (Rohwer & Fagan, 1917:372).

*Paraegilips* Kieffer, 1910b:335. Type species *Paraegilips reticulata* Kieffer by monotypy. Synonymized with *Paramblynotus* by Hedicke (in Hedicke and Kerrich 1940:179); resurrected as a valid genus by Weld (1952:164). **Synonymy reestablished.**

*Allocynips* Kieffer, 1914:185. Type species *Allocynips ruficeps* Kieffer [= *Paramblynotus ruficollis* Cameron] by original designation and monotypy. Synonymized with *Paramblynotus* by Weld (1930:137).

*Holocynips* Kieffer, 1916:284. Type species *Holocynips nigra* Kieffer by original designation and monotypy. Synonymized with *Paraegilips* by Weld (1952:164). Preoccupied by *Holocynips* Kieffer, 1910a:114. **New synonymy.**

*Diholocynips* Rohwer & Fagan, 1917:365. Replacement name for *Holocynips* Kieffer, 1916 nec Kieffer, 1910a. *Mayrella* Hedicke, 1922:190. Type species *Mayrella formosana* Hedicke by monotypy. Synonymized with *Paramblynotus* by Weld (1952:159).

*Paribalia* Weld, 1922:325. Type species *Paribalia borneana* Weld by monotypy. **New synonymy.**

*Stylobrachys* Belizin, 1951:572. Type species *Stylobrachys scaber* Belizin by original designation and monotypy. Synonymized with *Paramblynotus* by Kovalev (1994:414).

*Baviana* Barbotin, 1954:125. Type species *Baviana ferruginea* Barbotin by original designation and monotypy. Synonymized with *Paramblynotus* by Weld (1962:279).

#### *Monophyly*

*Paramblynotus* is supported as a monophyletic group by two shared derived features.

1. *Ventral margin of mesopleural triangle well defined, evenly curved* (Fig. 11). In all other liopterids, as well as in ibaliids and *Austrocynips*, the ventral margin of the mesopleural triangle is irregular and usually not well defined (Figs. 16–19); in the rare cases where it is defined, it is not evenly curved (Fig. 15).

2. *Abdominal sterna 4–6 entirely covered by sternum 3 in females* (Fig. 66). Among liopterids, a similar condition occurs in the Dallatorrellinae, Oberthuerellinae and Liopterinae (Fig. 72), but abdominal sterna 4–6 are exposed externally in *Kiefferiella* and *Decellea* (Fig. 65). The latter condition is also found in ibaliids and *Austrocynips*, and is the probable ground-plan state of the Liopteridae. The phylogenetic analysis (character 44) indicates that the condition in *Paramblynotus* evolved independently from that in the Dallatorrellinae + Oberthuerellinae + Liopterinae.

#### *Description*

Body length 1.4–9.0 mm.

*Head.* Lower face more or less distinctly foveate/foveolate-reticulate to rugulose, with or without smaller punctures; not keeled medially or (in *P. annulicornis* and n. sp. 16–20) with a lamellate median keel. Median frontal carina distinct; in some species in the *ruficollis* group indistinct or almost absent; not, slightly or distinctly raised to form a blunt, pyramidal; or triangular, lamellate; or oval, dorsally flattened process. Ocellar plate distinctly raised, occasionally indistinctly raised or not discernible. Antennal scrobe indistinctly or

distinctly impressed, occasionally not impressed; glabrate with punctures or foveolae. Lateral frontal carina present or absent. Vertex foveate to foveate-areolate; or rugose; occasionally with some longitudinal costulae. Occiput glabrous; in the *borneanus* group vertically strigate; in n. sp. 3 coriarius. Gena glabrous or more or less superficially sculptured, foveate to rugose, occasionally also coriarius; with or without smaller punctures. Occipital carina not angled midlaterally or occasionally weakly angled; not raised or sometimes slightly raised throughout. Malar space distinctly or occasionally only slightly impressed beneath eye. Clypeus ventrally usually glabrate; dorsally and medially glabrate, foveolate to foveate, punctate, foveolate-punctate or rugulose; with or without some transverse strigae; distinctly projecting ventrally; ventral margin straight or slightly incised, occasionally slightly acute.

*Female antenna.* Flagellum with 11 articles, occasionally with 10; not widened or occasionally slightly widened towards apex. F1/F2 = 0.7–1.2; F3 usually long, occasionally shorter, l/w = 1.5–3.0. Placodes start on F1, occasionally on F2. Placodes usually dense, covering entire surface of last flagellomere; occasionally less dense (some species in the *trisetosus*, *nigricornis* and *scaber* groups).

*Male antenna.* Flagellum with 12 articles, occasionally with 13 articles. F1/F2 = 0.7–1.0; F3 l/w = 2.5–4.1. In the *zonatus* and *nigricornis* groups F1 distinctly swollen and excavated laterally; excavated area glabrate, nude and without placodes. F1 similarly, but not as extremely, modified in the *trisetosus* group.

*Pronotum.* Anterior flange glabrate, punctate, transversely striolate or longitudinally strigate. Submedian depressions large, deep, open laterally; occasionally isolated (*zonatus* group). Anterior plate glabrous to glabrate, dorsally punctate, or entirely foveolate. Lateral surface foveate, foveate-reticulate or foveate-areolate, occasionally alveolate; with or without smaller punctures. Crest either (1) prominently triangularly raised medially (*borneanus* group), or (2) raised medially to form a more or less distinct triangular process (*ruficollis* group), or (3) raised into two separate, submedian, triangular

processes (*zonatus* group), or (4) only slightly raised medially, evenly curved (other species). Dorsal pronotal area coriarius, colliculate or glabrate.

*Mesonotum.* Scutum either with foveae and transverse, slightly to distinctly undulating costae; the former superficial medially but distinct laterally; or scutum entirely distinctly foveate with transverse ridges only indicated or entirely absent. Median mesoscutal impression only indicated posteriorly. Notaulus distinct to indistinct. Parascutal carina conspicuously raised, angulate or slightly produced posteriorly; or not raised, rounded posteriorly. Scuto-scutellar sulcus divided into two foveae by strong median carina, sometimes divided by additional, more or less strong carinae into four or more foveae (*zonatus* and *ruficollis* groups). Axillula in some species with conspicuous white or yellow pubescence. Dorsal surface of scutellum foveate-areolate to slightly scabrous; in n. sp. 3 foveate; laterally and posteriorly margined or not margined; usually without processes posteriorly but occasionally with two broad, short processes (*zonatus* group) or two smaller, triangular processes (some species in the *punctulatus* and *borneanus* groups). Lateral and posterior surfaces of scutellum vertically costulate or rugose. Laterodorsal process small, rounded. Auricula broad, occasionally subdivided.

*Mesopectus.* Mesopleural triangle large, triangular, distinctly impressed; occasionally only slightly impressed; glabrate, densely pubescent, in some species with conspicuous white or yellow pubescence; ventrally distinctly margined, margin usually evenly curved but occasionally slightly sinuate. Upper pleuron glabrous to glabrate, anteriorly with or without some punctures, a few foveae/foveolae or larger impressions; occasionally partly foveolate to foveolate-reticulate (*P. nigricornis*, n. sp. 10, n. sp. 13). Speculum glabrous; occasionally horizontally costulate. Mesopleural impression percurrent, occasionally very superficial; not subdivided or subdivided by vertical ridges. Lower pleuron glabrous to glabrate with more or less sparse hair-punctures; with one to two vertical impression(s) anteriorly; occasionally also with impressions posteriorly. Lateroventral carina percurrent, occasionally only present posteriorly; more

or less strongly curved. Subpleuron transversely costulate. Intercoxal processes peglike or occasionally more rounded, directed obliquely posteriorly.

*Metanotum.* Dorsellum glabrate, punctate, or vertically strigate; lateral depressions distinct, moderately deep or deep, medium-sized to large.

*Metapectal-propodeal complex.* Anterior meta-pleural pit absent; in the *scaber* group present. Metepisternum rugose, medially often with an elevated, glabrous patch. Prespiracular area rugose to rugulose; prespiracular process represented by slight to distinct surface convexity or absent. Lateral propodeal area rugose; posterolateral propodeal process absent or present; if present then low to moderately high, ridgelike to slightly triangularly raised ventrally, oblique. Median propodeal area carinate, often with a median longitudinal carina and one transverse carina; lateral propodeal carina percurrent, not raised, usually not flattened above but occasionally partly flattened; if flattened then glabrous and nude to punctate and pubescent above. Postsubpleuron glabrate. Nucha dorsally glabrous to more or less superficially longitudinally costulate, laterally rugose or longitudinally costulate.

*Wings.* Forewings hyaline, occasionally darker brown, with or without dark brown spot in and around marginal cell; in the *zonatus* group also with a dark brown transverse band along basalis; with or without an apical infuscate band. Hind wings hyaline with or without an apical infuscate band. In n. sp. 22 forewings and hind wings basally dark brown, apically hyaline. Marginal cell short,  $R_s/2r = 2.0-3.5$ .  $R_s+M$  from middle of basalis, occasionally from upper third. Bulla in  $R_1+Sc$  present or absent.

*Legs.* Protibia apically with one or two teeth. Mesotibial lobe blunt, not margined, with one or two teeth; or absent. Metatibial lobe margined, not produced, with or without three to six teeth. Longitudinal carina on posterior surface of metatibia present or absent. Metatarsomere 1 not compressed or slightly to distinctly compressed;  $mt1/mt2-5 = 0.4-0.9$ . Distal margin of  $mt1$  not produced, or (in most species in the *borneanus* group) produced into a blunt or tubular process anteroventrally; distal margin of  $mt2$  not produced

*Female metasoma.* Petiolar annulus short,  $l/w = 0.4-1.0$ ; longitudinally costate, sometimes only superficially dorsally. 3tg–5tg reduced in size, 6tg conspicuously expanded dorsally but not ventrally. In a few undescribed species in the *nigricornis* group 6tg also expanded ventrally, and 5tg enlarged, partly covering 6tg. 4tg–8tg keeled medially. Posterior margins of terga: 3tg–6tg dorsally acute, 7tg dorsally broadly and deeply incised, exposing 8tg; or (in the *borneanus*, *punctulatus* and *trisetosus* groups) 7tg dorsally straight, not incised, entirely covering 8tg; 3tg–6tg laterally slightly to strongly sinuate, occasionally rounded, 7tg laterally rounded. 3tg–8tg to 6tg–8tg minutely to more coarsely punctate; the punctures covering only the posterior part of the anterior terga but more of the surface of the posterior terga, becoming coarser posteriorly. 3tg with a few hairs laterally; 4tg nude, occasionally with a few hairs laterally; 5tg nude; 6tg–8tg with hairs in coarse punctures, occasionally densely pubescent. 8tg with broad apical impression surpassing to almost reaching spiracle; impression with oblique strigae throughout or at least close to spiracle, occasionally entirely punctate. In species with 8tg covered by 7tg, the impression on 8tg and the strigate sculpture may be reduced. Eudorsal margin of 8tg in lateral view angled close to upper end, ventrad angle reclivous to vertical, straight to slightly convex. In species with 8tg covered by 7tg, eudorsal margin of 8tg may be straight, vertical and not angled. 9tg not or slightly projecting beyond 8tg. 4st–6st covered by 3st. 7st with about three rows to a single row of submedian hairs, occasionally more broadly pubescent; posterior margin of lateral flap oblique to vertical, convex to almost straight.

*Male metasoma.* Petiolar annulus short to fairly long,  $l/w = 0.6-1.7$ ; longitudinally costulate, sometimes superficially dorsally. 3tg–8tg subequal in size or 5tg slightly to conspicuously enlarged; 4tg or 5tg largest in lateral view. Posterior margins of terga: 3tg–4tg dorsally straight or acute, 5tg–7tg dorsally broadly incised, 3tg–7tg laterally rounded. 3tg–8tg to 5tg–8tg posteriorly and laterally minutely to more coarsely punctate; punctate area more extensive on posterior terga. 3tg with some hairs laterally. 4tg nude, sometimes with a few

hairs laterally, 5tg nude, 6tg–8tg with hairs in coarse punctures. Eudorsal margin of 8tg in lateral view almost straight.

*Coloration.* Many species more or less uniformly coloured: black, brown, reddish brown or yellowish brown; in n. sp. 21 bright yellowish brown. Other species bicoloured: black with postpetiolar metasoma entirely and legs partly red; or black to brownish black with head, antennae, part of mesosoma and part of legs yellow, red, yellowish brown or reddish brown. In *P. annulicornis* and n. sp. 16–20 flagellum with a median, white band.

#### Diversity and distribution

Twenty described and 40 undescribed species in all zoogeographic regions except western Palaearctic. Centre of diversity in the eastern Palaearctic and Oriental regions. Apparently two different lineages present in Africa (the *trisetosus* and *nigricornis* groups), but only one (the *zonatus* group with two closely related species) in the New World.

#### Biology

Nine females of *P. trisectus* collected on tree trunk in Nepal, six females of n. sp. 37 on *Syzygium* (Myrtaceae) log in Papua New Guinea. Two males of n. sp. 3 reared from *Dalbergia fusca* (Fabaceae) in Burma, one female of n. sp. 13 from “Coleoptera” in Uganda.

Diaz (1973) recorded *P. zonatus* from Argentina, collected on *Nectandra* sp. (Lauraceae) attacked by *Oncideres* sp. (Cerambycidae). Judging from Diaz’s description of this material, the record actually refers to n. sp. 2 and not to *P. zonatus*. The type female of *P. zonatus* was taken by beating on *Ulmus crassifolia* (Ulmaceae) in Texas (Weld 1944). Yang (pers. comm.) observed females of an undescribed species of *Paramblynotus* ovipositing into the trunk of a recently killed tree of *Fraxinus mandshurica* (Oleaceae) attacked by *Mesosomyops* (Cerambycidae) and *Tremex simulacrum* (Siricidae).

#### Checklist of described species

*annulicornis* Cameron, 1910:132, ♂; Borneo;

BMNH (HT♂, No. 7.11).

*borneanus* (Weld, 1922:326, ♂ ♀); Borneo; USNM (HT♀, No. 24 375, PT♂). As *Paribalia*; **new combination**.

\**borneensis* (Weld, 1922:322, ♀); Borneo; USNM (HT♀, No. 24 380, 2 PT♀). As *Allocynips*, = *P. punctulatus* Cameron; combination and synonymy by Weld (1930b:137).

*clarus* (Weld, 1922:330, ♂); Mindanao; USNM (HT♂, No. 24 378). As *Allocynips*; combination by Weld (1930:137).

*dyak* (Weld, 1922:329, ♀); Borneo; USNM (HT♀, No. 24 376, PT♀). As *Allocynips*; combination by Weld (1930:137).

*esakii* (Yasumatsu, 1959:93, ♂); Japan: Honshu; KUEC (HT♂). As *Paribalia*; **new comb.**

*ferrugineus* (Barbotin, 1954:125, ♀); Indochina: Mont Bavi; CFB (HT♀); not seen. As *Baviana*; combination by Weld (1962:279).

*flaviceps* (Kieffer, 1916:286, ♀); Mindanao; location of type not known, probably lost (cf. Weld, 1952:164). As *Allocynips*; combination by Weld (1930:137).

*formosanus* (Hedicke, 1922:190, ♀); Taiwan; DEIC (HT♀). As *Mayrella*; combination by Weld (1930:137).

\**isosceles* (Weld, 1922:331, ♂ ♀); Singapore; USNM (HT♀, No. 24 379, 3 PT♂). As *Allocynips* = *P. ruficeps* Cameron; combination by Weld (1930:137), **new synonymy**.

*kosugii* Watanabe & Sakagami, 1951:129, ♂; Japan; EIHW (HT♂, 3 PT♂), BMNH (1 PT♂).

*malayensis* (Weld, 1922:329, ♂ ♀); Borneo; USNM (HT♀, No. 24 377, 1 PT♀, 2 PT♂). As *Allocynips*; combination by Weld (1930:137).

*niger* (Kieffer, 1916:285, ♂); Philippines: Palawan; location of type not known, probably lost (Weld, 1952:164). As *Holocynips* Kieffer, 1916 *nec* Kieffer, 1910a; transferred to *Paraegilips* by Weld (1952:164); **new combination**.

*nigricornis* Benoit, 1956:55, ♀; Zaire; MRAC (HT♀).

*punctulatus* Cameron, 1908:300, ♀; Borneo; BMNH (2T♀, in main coll.).

*reticulatus* (Kieffer, 1910b:335, ♂); Indonesia: Bintan; ZMHB (HT♂). As *Paraegilips*; combination by Hedicke in Hedicke and Kerrich (1940:179) by inference through generic syn-

*ruficeps* Cameron, 1908:300, ♂; Borneo; BMNH (HT♂, main coll.).

\**ruficeps* Kieffer, 1914:186, ♂; Luzon; USNM (HT♂, not numbered). = *P. ruficollis* Cameron; synonymy by Weld (1930:137).

*ruficollis* Cameron, 1909:18, ♂; Borneo; BMNH (4 T♂, No. 7.9 and in main coll.).

\**rufiventris* Cameron, 1910:131, ♀; Borneo; BMNH (HT♀, No. 7.8). = *P. punctulatus* Cameron; **new synonymy**.

*scaber* (Belizin, 1951:573, ♂ ♀); Russia: Primorskiy Kray [Khabarovsk, Irkutsk]; ZMAS (HT♀). As *Stylobrachys*; **new combination**.

*trisectus* Maa, 1962:126, ♀; Thailand; BPBM (HT♀).

*trisetosus* Benoit, 1956:53, ♀; Zaire; MRAC (HT♀, 3 PT♀).

*zonatus* Weld, 1944:56, ♀; USA: TX; USNM (HT♀, No. 56 811).

## Dallatorrellinae

Dallatorrellinae Kieffer, 1911:244.

Mesocynipinae Kerrich in Hedicke and Kerrich, 1940:178.

## Genus *Mesocynips* Cameron

Figs. 4, 14.

*Mesocynips* Cameron, 1903:91. Type species *Mesocynips insignis* Cameron by monotypy.

### Monophyly

The single species of *Mesocynips* possesses several autapomorphies.

1. *Scutellum falling gradually laterally as well as posteriorly* (Fig. 14). The scutellum is margined or falls abruptly laterally in all other liopterids as well as in *Austrocynips* and the Ibalidae (cf. Fig. 11). In *Liopteron* the scutellum falls gradually posteriorly (Fig. 13), but this condition is different and almost certainly evolved independently from that in *Mesocynips*.

2. *Pronotum laterally almost entirely glabrous; foveate sculpture completely absent*. In all other liopterids except for a few species of *Oberthuerella*, *Xenocynips* and *Liopteron*, the pronotum has at least some superficial foveae or alveolae laterally

(Fig. 11). The foveate sculpture does not occur in ibaliids and *Austrocynips*, but the phylogenetic analysis (character 9) indicates that the absence in *Mesocynips* is due to secondary loss.

3. *Occipital carina only present ventrally; dorsally the carina only reaches lower margin of compound eye*. The carina reaches further dorsally, usually almost to the vertex, in all other liopterids. Ibalids and *Austrocynips* do not have an occipital carina, but the results of the phylogenetic analysis of the Liopteridae (Fig. 86) indicate that the state in *Mesocynips* is derived relative to that of other liopterids.

4. *Scutellum anterodorsally transversely costulate, otherwise glabrate; foveate sculpture almost completely absent* (Fig. 14). The scutellum has at least some foveate or alveolate sculpture and is never transversely costulate in other liopterids. *Eileenella* and some species of *Ibalia* have a transversely costate scutellum, but the scutellum is never largely glabrate in the Ibalidae or in *Austrocynips*.

5. *Almost entire animal yellowish brown* This coloration is unique among liopterids and ibaliids, with the exception of some species of *Paramblynotus* that almost certainly acquired this coloration independently.

### Description

Body length 9.5–13.0 mm.

*Head*. Lower face glabrate, sparsely punctate; not keeled medially. Median frontal carina distinct; slightly raised to form an oblong, lamellate process. Antennal scrobe distinctly impressed; glabrous. Lateral frontal carina present. Vertex glabrate, sparsely punctate. Gena glabrate, sparsely punctate. Occipital carina present only ventrally, dorsally reaching to lower margin of eye; not angled midlaterally, not raised. Clypeus glabrate with a few oblique, indistinct costulae laterally; distinctly projecting ventrally; ventral margin incised.

*Female antenna*. Flagellomeres distinctly swollen subapically, especially ventrally. F1/F2 = 1.1; F3/F1 = 3.2. Placodes start on F1.

*Male antenna*. Flagellum with 13 articles. Flagellomeres distinctly swollen subapically, especial-

ly ventrally. F1/F2 = 1.0; F3 l/w = 3.0.

*Pronotum*. Anterior flange longitudinally strigate. Submedian depressions large, deep, open laterally. Anterior plate glabrate, sparsely punctate. Lateral surface glabrous with small, sparse punctures; dorsally sometimes a rim of transverse costae. Crest raised medially to form a low or high, rounded lobe. Dorsal pronotal area transversely strigate.

*Mesonotum*. Scutum with transverse, non-undulating costae; foveae completely absent. Median mesoscutal impression only indicated posteriorly. Notaulus indistinct. Parascutal carina conspicuously raised, angulate posteriorly. Dorsal surface of scutellum glabrate, with some transverse costulae anteriorly and a few foveae/foveolae; laterally and posteriorly not margined, falling gradually; without processes posteriorly. Laterodorsal process completely absent, not even indicated.

*Mesopectus*. Mesopleural triangle large, triangular, slightly impressed; glabrate, sparsely pubescent. Upper pleuron glabrous to glabrate with sparse hair-punctures. Speculum glabrous. Mesopleural impression distinct posteriorly and anteriorly, broadly interrupted medially; not subdivided. Lower pleuron glabrate to glabrous with sparse hair-punctures. Lateroventral carina only present posteriorly, very short. Subpleuron transversely costulate.

*Metanotum*. Dorsellum glabrate; lateral depressions distinct, deep, medium-sized.

*Metapectal-propodeal complex*. Anterior meta-pleural pit absent. Metepisternum glabrate. Meta-pleural carina produced ventrally into a prominent process laterad metacoxal foramen. Prespiracular area glabrate, foveolate, with long hairs; prespiracular process absent. Lateral propodeal area very sparsely rugose; posterolateral propodeal process high, lobelike, vertical. Median propodeal area glabrate, ecarinate; lateral propodeal carina percurrent, strongly raised dorsally and medially; where raised somewhat flattened and punctate-pubescent above. Postsubpleuron glabrate. Nucha longitudinally costate.

*Wings*. Both wings yellow basally, dark apically. Marginal cell short, Rs/2r = 2.6–3.2. Rs+M from upper tenth of basalis. Bulla in R<sub>1</sub>+Sc absent.

*Leos*. Protibia apically with one tooth. Mesotibi-

al lobe blunt, not margined, with one tooth. Metatibial lobe margined, produced into a conspicuous, fingerlike process, without teeth. Longitudinal carina on posterior surface of metatibia absent. Metatarsomere 1 slightly compressed; mt1/mt2–5 = 1.5. Distal margins of mt1–mt2 not produced.

*Female metasoma*. Petiolar annulus short, l/w = 0.2; longitudinally canaliculate; medioventrally with a conspicuous hump. 3tg–5tg subequal in size, 6tg–8tg larger, but not conspicuously enlarged; 7tg largest in lateral view. 4tg–8tg keeled medially. Posterior margins of terga: 3tg–7tg dorsally slightly acute, 3tg–7tg laterally slightly sinuate. No terga minutely punctate. 3tg–8tg with long, erect, yellow hairs in fine punctures on 3tg–6tg, in coarse punctures on 7tg–8tg. 7tg ventrolaterally with a large patch of recumbent pubescence; a similar but smaller patch on 6tg. 8tg with narrow apical impression ending far from spiracle; impression glabrate with some foveae. Eudorsal margin of 8tg in lateral view almost straight, declivous. 4st–6st covered by 3st. 7st laterally broadly pubescent; posterior margin of lateral flap oblique, convex.

*Male metasoma*. Petiolar annulus short, l/w = 0.2; longitudinally canaliculate; medioventrally with a conspicuous hump. 3tg–8tg subequal in size; no tergum obviously largest in lateral view. Posterior margins of terga: 3tg dorsally straight, 4tg–7tg dorsally slightly, broadly incised, 3tg–7tg laterally rounded. No terga minutely punctate. 3tg–8tg with long, erect, yellow hairs in fine punctures on 3tg–5tg, in coarse punctures on 6tg–8tg. 6tg and 7tg ventrolaterally with a large patch of recumbent pubescence; similar but smaller patches on 5tg and 8tg. Eudorsal margin of 8tg in lateral view distinctly rounded.

*Coloration*. Bright reddish to yellowish brown with flagellum, compound eye, apex of mandible and metatarsus dark brown to black.

### Diversity and distribution

One described species in the Oriental region.

### Biology

Unknown.

## Checklist of described species

*insignis* (Smith, 1858:117, ♀); Borneo; location of type not known. As *Cynips*; combination by Cameron (1903:93).

\**insignis* Cameron, 1903:92, ♀; Borneo; BMNH (HT♂, No. 7.45). Synonymy by Cameron (1903:93).

Genus *Dallatorrella* Kieffer

Figs. 5, 21, 39, 44, 54, 55, 72, 73.

*Dallatorrella* Kieffer, 1911:244. Type species *Dallatorrella rubriventris* Kieffer by monotypy.

## Monophyly

Several derived features support the monophyly of *Dallatorrella*.

1.  $M+Cu_1$  of forewing venation strongly curved towards  $R+Sc$  (Fig. 39).  $M+Cu_1$  is straight in all other liopterids (Fig. 40) as well as in ibaliids and *Austrocynips*.

2. *Procoxa* anterolaterally with a vertical carina (Fig. 44). This carina is absent in other liopterids as well as in the Ibaliidae and *Austrocynipidae*.

3. Scuto-scutellar sulcus divided by two submedian carinae into three foveae; median carina absent (cf. Fig. 25). The structure of the scuto-scutellar sulcus in *Austrocynips* is not directly comparable to that in the Liopteridae. However, in the Ibaliidae and most Liopteridae the scuto-scutellar sulcus is divided by a median carina into two foveae (Figs. 23, 24, 26), and this is the probable ground-plan state for the Liopteridae. In the Oberthuerellinae and some species of *Paramblynotus* there is a state similar to that of *Dallatorrella*; the state in *Dallatorrella*, however, appears to be independently derived (see phylogenetic analysis, character 14).

4. Antenna short in both sexes, shorter than the length of head and mesosoma combined. The antenna is longer than the length of head and mesosoma combined in all other Liopteridae except for some females of *Oberthuerella*. The antenna is long also in the Ibaliidae, and this is probably the

ground-plan condition of the Liopteridae, although the antenna is short in *Austrocynips*.

5. Median, ventral hump on petiolar annulus present in females but absent in males. The hump is present in both sexes in *Mesocynips*; in all other liopterids it is absent. Ibaliids have lost the sternal part of the annulus, so they cannot be used for outgroup comparisons. However, the ventral hump is absent from the sternal part of the annulus in *Austrocynips*, and this is likely to be the ground-plan state of the Liopteridae. The condition in *Mesocynips* might have been derived from that in *Dallatorrella*, in which case the character does not hold as an autapomorphy for *Dallatorrella*. However, in contrast to other liopterids, the ventral region is separated from the rest of the annulus and differently sculptured in male *Dallatorrella*; this indicates that the absence of a hump in *Dallatorrella* males is derived rather than primitive. Furthermore, although the length of the annulus is commonly sexually dimorphic in the Liopteridae, the structure is usually not. This provides additional support for the absence of the hump in males as an autapomorphy for *Dallatorrella*.

## Description

Body length 5.5–15.0 mm.

**Head.** Lower face sparsely to very sparsely foveate and sparsely to densely punctate; weakly to distinctly keeled medially. Median frontal carina distinct; strongly raised to form a triangular, more or less lamellate process. Antennal scrobe distinctly impressed; glabrate to glabrous. Lateral frontal carina usually present, occasionally absent. Vertex glabrate, more or less sparsely foveate/foveolate. Gena sparsely and more or less superficially foveate, sometimes also sparsely punctate. Occipital carina weakly angled midlaterally; not raised. Malar space with or without a vertical, more or less linear impression beneath eye. Clypeus with vertical to radiating costulae; or glabrate medially with a few radiating costulae laterally; distinctly projecting ventrally; ventral margin incised.

**Female antenna.** Antenna short, shorter than length of head and mesosoma combined. Flagellomeres distinctly swollen submedially to sub-

apically.  $F1/F2 = 1.0-1.3$ ;  $F3l/w = 1.2-1.6$ ; in n. sp. 4  $F3l/w = 2.2$ . Placodes start on  $F1$ .

**Male antenna.** Antenna short, shorter than dorsal length of head and mesosoma combined. Flagellum with 13 articles.  $F1/F2 = 1.2-1.4$ ;  $F3l/w = 1.4-1.7$ .

**Pronotum.** Anterior flange glabrous, with or without punctures laterally. Submedian depressions large, deep, open laterally. Anterior plate sparsely foveolate-punctate. Lateral surface foveate to foveate-reticulate, with a glabrate region ventrally; in n. sp. 4 and n. sp. 5 the glabrate region large, covering almost half the lateral surface; in the other species the glabrate region smaller or almost absent. Lateral surface in n. sp. 4 and n. sp. 5 conspicuously produced in front of the mesothoracic spiracle; in the other species not produced. Crest absent. Dorsal pronotal area glabrate.

**Mesonotum.** Scutum with sparse foveae and transverse, slightly undulating or non-undulating costae; the former superficial medially but distinct laterally. Median mesoscutal impression only present as a deep impression posteriorly. Notaulus distinct. Parascutal carina conspicuously raised, produced posteriorly. Lateral margin of axilla not raised or (in *D. albata*) very slightly raised. Lateral bar narrow to rather broad. Scuto-scutellar sulcus divided by two strong submedian carinae into three foveae, sometimes also additional, more or less weaker carinae present. Axillula in some species with conspicuous white or yellow pubescence. Dorsal surface of scutellum foveate-reticulate/areolate to slightly scabrous; laterally and posteriorly not margined; without processes posteriorly. Posterior and lateral surfaces of scutellum foveate-areolate to rugose, sometimes lateral surface partly vertically costulate. Laterodorsal process absent but indicated by blunt, protruding part of scutellum.

**Mesopectus.** Mesopleural triangle large or (in n. sp. 4 and n. sp. 5) small, triangular, slightly impressed; glabrate, pubescent; in some species with conspicuous white or yellow pubescence. Upper pleuron glabrate to glabrous with a few hair-punctures. Speculum glabrous. Mesopleural impression percurrent; not subdivided. Lower pleuron glabrate, with a few hair-punctures to sparsely pubes-

cent. Lateroventral carina percurrent, almost straight; in n. sp. 4 and n. sp. 5 with a distinct protuberance medially. Subpleuron glabrate or transversely costulate; with a stronger transverse carina anterior to coxal foramina.

**Metanotum.** Dorsellum glabrous or (in n. sp. 5) striolate; with or without two small, lateral pits; lateral depressions distinct, deep to moderately deep, medium-sized to very large.

**Metapectal-propodeal complex.** Anterior meta-pleural pit absent. Metepisternum glabrate, very sparsely rugose. Meta-pleural carina produced ventrally into a prominent process laterad metacoxal foramen; in n. sp. 4 and n. sp. 5 with an additional process just anterior to the process from the meta-pleural carina. Prespiracular area glabrate, foveolate, with long hairs; prespiracular process absent. Lateral propodeal area rugose; posterolateral propodeal process low to moderately high, ridge-like or lobelike, oblique or (in n. sp. 4 and n. sp. 5) vertical. Median propodeal area carinate, usually with two submedian longitudinal carinae; lateral propodeal carina percurrent, strongly raised dorsally and medially; where raised somewhat flattened above, punctate and pubescent above. Post-subpleuron glabrate. Nucha longitudinally costate.

**Wings.** Forewings more or less uniformly dark; or (in n. sp. 2) hyaline to yellowish with an apical, transverse, dark brown band; or (in n. sp. 4) hyaline with a median and an apical, transverse, dark brown band. Hind wings yellowish or more or less uniformly dark brown. Marginal cell short,  $Rs/2r = 2.3-4.7$ .  $Rs+M$  from upper third of basalis. Bulla in  $R_1+Sc$  absent.

**Legs.** Protibia apically with one tooth. Mesotibial lobe rounded, not margined, with one tooth. Metatibial lobe margined, produced into a conspicuous, fingerlike process; in n. sp. 4 the process reduced, in n. sp. 5 the process almost absent; without teeth. Longitudinal carina on posterior surface of metatibia present; in n. sp. 5 absent. Metatarsomere I distinctly compressed or not compressed;  $mt1/mt2-5 = 0.9-1.2$ . Distal margins of  $mt1-mt2$  not produced.

**Female metasoma.** Petiolar annulus short,  $l/w = 0.2-0.7$ ; longitudinally canaliculate; medioventrally with a conspicuous hump; in n. sp. 4 this hump

considerably reduced in size. 3tg–5tg subequal in size, 6tg–8tg larger but not conspicuously enlarged; 7tg largest in lateral view. 4tg–8tg keeled medially. Posterior margins of terga: 3tg–7tg dorsally slightly acute, 3tg–7tg laterally slightly sinuate. 5tg–7tg to only 7tg posteriorly, 8tg posteriorly and laterally minutely punctate. 3tg–8tg with long, erect, yellow or black hairs in moderately coarse punctures on 3tg–6tg, in coarse punctures on 7tg–8tg. 7tg ventrolaterally with a large patch of recumbent pubescence. In some species with a band of dense, white or yellow pubescence apically on 6tg; in *D. albata* such bands also on 5tg and 7tg. 8tg with narrow apical impression ending far from spiracle; impression glabrate with some foveolae. 8tg in n. sp. 4 with a median angulate, raised carina. Eudorsal margin of 8tg in lateral view rounded, declivous; near lower end roundedly angled; ventrad angle reclivous, concave. 4st–6st covered by 3st. 7st laterally broadly pubescent, narrowly pubescent or with a single row of submedian hairs; posterior margin of lateral flap oblique, convex.

**Male metasoma.** Petiolar annulus short, l/w = 0.3–0.5; longitudinally canaliculate; ventrally with a separated area; this area longitudinally strigate in n. sp. 5, glabrate in *D. rubriventris*. 3tg–5tg subequal in size, 6tg–8tg larger, but not conspicuously enlarged; 7tg largest in lateral view. Posterior margins of terga: 3tg dorsally straight, 4tg–7tg dorsally slightly, broadly incised, 3tg laterally rounded, 4tg–7tg laterally slightly sinuate or rounded. 5tg–8tg or 6tg–8tg laterally minutely punctate. 3tg–8tg with long, erect, yellow or black hairs in moderately coarse punctures on 3tg–6tg (*D. rubriventris*) or on 3tg–5tg (n. sp. 5), in coarse punctures on 7tg–8tg (*D. rubriventris*) or on 6tg–8tg (n. sp. 5). In n. sp. 5 also with a band of less coarse, dense punctures without hairs anteriorly on 6tg. 7tg ventrolaterally with a small patch of recumbent pubescence; in n. sp. 5 similar but smaller patches present also on 6tg and 8tg. Eudorsal margin of 8tg in lateral view distinctly rounded.

**Coloration.** Entirely black; or black with antenna, head, legs and metasoma partly or entirely red.

#### Diversity and distribution

Three described and five undescribed species

from the Australian and Oriental regions.

#### Biology

Three females of n. sp. 1 collected on *Syzygium* (Myrtaceae) log in Papua-New Guinea.

#### Checklist of described species

*albata* (Weld, 1944:55, ♀); Mindanao; USNM (HT♀, No. 56 810). As *Mesocynips*; **new combination**.

*carinifrons* (Cameron, 1910:132, ♀); Borneo; BMNH (HT♀, No. 7.10). As *Paramblynotus*; combination by Weld (1952:162).

*rubriventris* Kieffer, 1911:244, ♂; Australia; BMNH (HT♂, No. 7.12).

#### Oberthuerellinae

Oberthuerellinae Kieffer, 1903:88.

#### Genus *Xenocynips* Kieffer

Figs. 17, 53, 74.

*Xenocynips* Kieffer, 1910b:340. Type species *Xenocynips subsquamata* Kieffer by monotypy.

#### Monophyly

Several apomorphies unite members of *Xenocynips*.

1. *Abdominal terga 3–5 fused; intertergal sutures invisible, at least middorsally* (Fig. 74). Although the postpetiolar terga are probably more or less rigidly attached to each other in most liopterids, the intertergal sutures are always distinct. The only exception is a couple of species of *Pseudibalia*, but the general structure of the metasoma of these species is sufficiently different from that of *Xenocynips* to preclude any possibility of homology. All postpetiolar terga are free in ibaliids and in *Austrocynips*, and this is apparently the ground-plan state for the Liopteridae.

2. *Lower pleuron at least partly horizontally strigate* (Fig. 17). No other liopterid (cf. Figs. 11, 15, 16, 18, 19) has horizontal strigae on the lower

pleuron. The lower pleuron is horizontally strigate in some ibaliids and in *Austrocynips*, but this sculpture is more irregular, and has the strigae closer set than in *Xenocynips*. Because of these structural differences, I find it likely that the strigate lower pleuron of *Xenocynips* is an autapomorphy for that genus.

3. *Anterior metatibial spur short and stout* (Fig. 53) In other liopterids, as well as in ibaliids (except *Eileenella* that lacks the spur) and *Austrocynips*, this spur is more slender (cf. Figs. 52, 54, 55).

4. *Petiolar annulus dull, with colliculate to rugulose sculpture in addition to the longitudinal furrows and ridges* (Fig. 74). Other liopterids have the annulus more or less smooth except for the furrows and ridges. The annulus or its tergal part is more or less smooth except for occasional furrows and ridges in the Ibalidae and in *Austrocynips*.

#### Description

Body length 9.3–14.0 mm.

**Head.** Lower face foveate-areolate to rugulose, colliculate; weakly keeled medially. Median frontal carina indistinct or absent; not raised. Antennal scrobe indistinctly impressed; obliquely to longitudinally strigate ventrally, glabrate or finely coriarius dorsally. Lateral frontal carina present or absent. Vertex foveate-rugose. Gena foveate to foveate-rugose, colliculate. Occipital carina weakly angled midlaterally; slightly raised dorsad angle, not raised ventrad angle. Clypeus rugulose-colliculate with some transverse, irregular strigae; slightly projecting ventrally; ventral margin straight.

**Female antenna.** Flagellum moderately widened towards apex. F1/F2 = 0.5; F3 l/w = 2.6. Placodes start on F3.

**Male antenna.** Flagellum with 12 articles; last article partly subdivided in one specimen. F1/F2 = 0.4; F3 l/w = 2.8.

**Pronotum.** Anterior flange longitudinally strigate. Submedian depressions small, deep or shallow, isolated. Anterior plate colliculate or coriarius, dorsally punctate. Lateral surface superficially foveate and slightly coriarius, ventrally with some horizontal costulae; in *X. subsquamata* without foveae, with superficial, vertical costulae

dorsally and horizontal costulae ventrally. Crest raised medially to form a large, triangular process. Dorsal pronotal area colliculate to glabrate.

**Mesonotum.** Scutum with transverse, distinctly undulating costae; without foveae. Median mesoscutal impression percurrent and distinct or only indicated posteriorly. Notaulus indistinct. Parascutal carina conspicuously raised, produced posteriorly. Lateral margin of axilla conspicuously raised anteriorly but not medially or posteriorly. Scuto-scutellar sulcus divided into three foveae by two strong submedian carinae; also with some additional, weaker carinae. Dorsal surface of scutellum sparsely rugose; laterally and posteriorly margined; with a median, short and blunt or fairly long and slender process posteriorly. Lateral and posterior surfaces of scutellum rugulose or vertically costulate. Laterodorsal process large, produced posteriorly into a pointed process.

**Mesoplexus.** Mesopleural triangle large, triangular, anteriorly and posteriorly distinctly impressed, otherwise only slightly impressed; glabrate with or without some horizontal strigae and some foveolae; punctate, more or less sparsely pubescent. Upper pleuron horizontally strigate. Speculum horizontally strigate, sometimes partly glabrous. Mesopleural impression more or less broadly interrupted medially or percurrent; not subdivided. Lower pleuron more or less superficially horizontally strigate; sparsely pubescent. Lateroventral carina percurrent, almost straight. Subpleuron transversely costulate.

**Metanotum.** Dorsellum coriarius; lateral depressions distinct or barely indicated, shallow, medium-sized to small.

**Metapectal-propodeal complex.** Anterior metapectal pit present. Metepisternum ventrally rugulose, dorsally rugose. Prespiracular area rugose; prespiracular process present, blunt, rugulose. Lateral propodeal area rugose; posterolateral propodeal process low, ridgelike, vertical; or indistinct, almost absent. Median propodeal area carinate; lateral propodeal carina percurrent, not raised, flattened above throughout or almost throughout, glabrate with a few hair-punctures or coriarius above. Postsubpleuron rugulose or colliculate. Nucha longitudinally strigate.

*Wings.* Wings hyaline; forewing with a dark brown transverse band subapically from anterior margin at marginal cell. Marginal cell long,  $Rs/2r = 5.3-5.7$ .  $Rs+M$  from upper third of basalis. Bulla in  $R_1+Sc$  absent.

*Legs.* Protibia apically without teeth. Mesotibial lobe rounded, margined, without teeth. Metatibial lobe margined, produced into a subtriangular process, without teeth. Longitudinal carina on posterior surface of metatibia present. Metatarsomere 1 distinctly compressed;  $mt1/mt2-5 = 0.7$ . Distal margin of  $mt1$  slightly or distinctly produced into a flat process anteroventrally. Distal margin of  $mt2$  sometimes also slightly produced into a flat process anteroventrally.

*Female metasoma.* Petiolar annulus long,  $l/w = 1.9$ ; longitudinally costate and colliculate to rugulose.  $3tg-5tg$  reduced in size,  $6tg$  conspicuously enlarged.  $3tg-5tg$  fused, intertergal sutures absent.  $6tg$  posteriorly,  $7tg-8tg$  entirely keeled medially. Posterior margins of terga: syntergum ( $3tg-5tg$ ) and  $6tg-7tg$  dorsally straight, syntergum laterally ligulate,  $6tg$  laterally slightly sinuate,  $7tg$  laterally sinuate.  $6tg$  posteriorly,  $7tg$  and  $8tg$  entirely minutely to more coarsely punctate. Syntergum with a few hairs anterolaterally;  $6tg$  posterodorsally and posteroventrally with sparse pubescence in indistinct, moderately coarse punctures;  $7tg-8tg$  with hairs in indistinct, coarse punctures.  $8tg$  with broad apical impression not reaching spiracle; impression punctate. Eudorsal margin of  $8tg$  in lateral view almost straight, declivous. State of  $4st-6st$  unknown.  $7st$  with single row of submedian hairs; posterior margin of lateral flap oblique, straight to slightly concave.

*Male metasoma.* Petiolar annulus long,  $l/w = 2.9$ ; longitudinally costate and colliculate to rugulose.  $3tg-5tg$  reduced in size,  $6tg$  conspicuously enlarged.  $3tg-5tg$  fused, intertergal sutures at least absent middorsally; in one species (n. sp. 2)  $3tg-6tg$  fused, intertergal sutures  $3tg-4tg$ ,  $4tg-5tg$  and  $5tg-6tg$  absent middorsally, present laterally; in the other species (n. sp. 1)  $3tg-5tg$  fused, intertergal suture  $3tg-4tg$  entirely absent, suture  $4tg-5tg$  visible laterally, close to ventral margin, suture  $5tg-6tg$  distinct throughout. Posterior margins of terga:  $3tg$  dorsally straight,  $4tg-5tg$  dorsally acute or

straight,  $6tg-7tg$  dorsally broadly incised,  $3tg$  laterally rounded,  $4tg-5tg$  laterally ligulate,  $6tg$  laterally slightly sinuate,  $7tg$  laterally rounded.  $6tg$  posteriorly,  $7tg$  and  $8tg$  laterally minutely to more coarsely punctate.  $3tg$  with a few hairs laterally,  $4tg-5tg$  nude,  $6tg$  posteriorly with some hairs in coarse punctures,  $7tg$  and  $8tg$  with more hairs in coarse punctures. Eudorsal margin of  $8tg$  in lateral view almost straight.

*Coloration.* Black to brownish black; head and antennae may be entirely or partly yellow.

#### Diversity and distribution

One described and two undescribed species from the central part of the Ethiopian region.

#### Biology

Unknown.

#### Checklist of described species

*subsquamata* Kieffer, 1910b:340, ♀; Cameroon; DEIC (HT♀).

#### Genus *Tessmannella* Hedicke

Figs. 15, 25, 30, 35, 43, 75.

*Tessmannella* Hedicke, 1912:303. Type species *Tessmannella spinosa* Hedicke by original designation.

#### Monophyly

Monophyly of *Tessmannella* is supported by the following apomorphies.

1. *Abdominal tergum 6 in females broadly incised posteriorly* (Fig. 75). The posterior margin of abdominal tergum 6 is dorsally straight or acute in all other liopterids, as well as in ibaliids and *Austrocynips*.

2. *Lateral depressions of dorsellum completely absent, not even indicated* (Fig. 35). The depressions are distinctly, albeit sometimes very shallowly, impressed in almost all other liopterids (Figs. 33, 34); the only exception is a few species of *Pseudibalia*. The depressions are absent in *Ibalia* and *Heteribalia*, and the structure of the dorsellum

of *Eileenella* and *Austrocynips* is such that it is difficult to determine whether the depressions are absent or present. However, the phylogenetic analysis (character 23) indicates that the depressions are present in the ground plan of the Liopteridae; hence, the absence in *Tessmannella* must be due to secondary loss.

3. *Distinct lobe with median row of short hairs subapically on the ventral surface of the metafemur* (Fig. 43). In *Oberthuerella abscinda* there is a similar, but more irregular and nude, lobe; in *Xenocynips* n. sp. 1 the lateral margin of the metafemoral spine is basally joined with a lobe with a median row of short hairs. The structure of these lobes, as well as other character data, suggest that they are not homologous with the lobe of *Tessmannella*. Other liopterids, ibaliids and *Austrocynips* do not have a lobe on the metafemur.

4. *Pronotal crest with a conspicuous, toothlike process* (Fig. 30). Other liopterids, ibaliids and *Austrocynips* lack such a process; if the pronotal crest is produced, it is always formed into a rounded or triangular process (cf. Figs. 27, 28).

5. *Metafemoral spine triangular, broad-based, oblique* (Fig. 43). The metafemoral spine is more slender and erect in *Xenocynips* and *Oberthuerella* (Fig. 42). The polarity of this character is difficult to determine because the metafemoral spine is absent in other liopterids, in ibaliids and in *Austrocynips*. However, the relationships implied by the phylogenetic analysis (Fig. 86) suggest that the *Tessmannella* state is apomorphic.

#### Description

Body length 6.5–8.8 mm.

*Head.* Lower face foveate/foveolate-reticulate, coriarius; not or weakly keeled medially. Median frontal carina indistinct; not raised. Antennal scrobe indistinctly impressed; with weak longitudinal to oblique costulae. Lateral frontal carina absent. Vertex weakly foveate-reticulate to areolate. Gena glabrate with sparse, weak horizontal costulae and some foveae. Occipital carina strongly angled midlaterally; strongly raised dorsad angle, not raised ventrad angle. Clypeus dorsally glabrate to coriarius, medially transversely strigate with some fo-

veolae, ventrally glabrate; slightly projecting ventrally; ventral margin bilobed.

*Female antenna.*  $F1/F2 = 0.6$ ;  $F3 l/w = 3.1-3.8$ . Placodes start on  $F2$ .

*Male antenna.* Unknown.

*Pronotum.* Anterior flange longitudinally strigate. Submedian depressions small, shallow, isolated. Anterior plate coriarius, dorsally punctate. Lateral surface superficially foveate-reticulate to alveolate with a few vertical costulae. Crest prominently produced medially into a high, toothlike process. Dorsal pronotal area colliculate.

*Mesonotum.* Scutum with transverse, distinctly undulating costae, laterally with a few superficial foveae. Median mesoscutal impression percurrent or almost so, indistinct. Notaulus distinct. Parascutal carina conspicuously raised, produced posteriorly. Lateral margin of axilla conspicuously raised throughout. Scuto-scutellar sulcus divided into three foveae by two strong, submedian carinae. Dorsal surface of scutellum irregularly alveolate to rugose; laterally and posteriorly margined; with a median, fairly long and slender process posteriorly. Lateral and posterior surfaces of scutellum glabrate to rugulose. Laterodorsal process large, produced posteriorly into a pointed process.

*Mesopectus.* Mesopleural triangle large, triangular, distinctly impressed ventrally and posteriorly, otherwise only slightly impressed; glabrate with some horizontal, more or less irregular costae anteriorly; very sparsely pubescent. Upper pleuron with regular, somewhat oblique, vertical costulae. Speculum horizontally strigate. Mesopleural impression virtually absent, only ventral margin left as ventral margin of vertically costulate area. Lower pleuron glabrate with sparse hair-punctures. Lateroventral carina percurrent, almost straight. Subpleuron glabrate with one angled, transverse costula anterior to coxal foramina.

*Metanotum.* Dorsellum coriarius or glabrate; lateral depressions completely absent, dorsellum laterally glabrate.

*Metapectal-propodeal complex.* Anterior meta-pleural pit present. Metepisternum more or less sparsely rugose, partly also coriarius to colliculate. Prespiracular area colliculate or glabrate; prespiracular process present blunt rugulose. Lat-

eral propodeal area sparsely rugose; posterolateral propodeal process moderately high, lobelike, vertical. Median propodeal area with median carina; lateral propodeal carina percurrent, not raised, dorsally and medially flattened above, partly punctate and pubescent above. Postsubpleuron colliculate. Nucha longitudinally costate to costulate; in *T. spinosa* dorsally largely glabrate.

**Wings.** Wings uniformly dark brown. Marginal cell long,  $Rs/2r = 5.5-7.3$ .  $Rs+M$  from upper third of basalis. Bulla in  $R_1+Sc$  absent.

**Legs.** Protibia apically with a lobelike projection but no teeth. Mesotibial lobe rounded, margined, without teeth. Metatibial lobe margined, produced into a subtriangular process, without teeth. Longitudinal carina on posterior surface of metatibia present. Metatarsomere 1 distinctly compressed;  $mt1/mt2-5 = 0.7-0.8$ . Distal margins of  $mt1-2$  not produced.

**Female metasoma.** Petiolar annulus long,  $l/w = 3.3-4.5$ ; longitudinally costate.  $3tg-5tg$  reduced in size,  $6tg$  conspicuously enlarged.  $6tg-8tg$  keeled medially. Posterior margins of terga:  $3tg-4tg$  dorsally slightly, broadly incised,  $5tg$  dorsally straight,  $6tg$  dorsally broadly, subangulately incised,  $7tg$  dorsally straight,  $3tg$  laterally rounded,  $4tg-5tg$  laterally ligulate,  $6tg$  laterally slightly sinuate,  $7tg$  laterally sinuate.  $6tg$  posteriorly and  $7tg-8tg$  entirely minutely to more coarsely punctate.  $3tg$  laterally with a few hairs,  $4tg-5tg$  nude,  $6tg$  with hairs in moderately coarse punctures,  $7tg-8tg$  with hairs in coarse punctures.  $8tg$  with broad apical impression not reaching spiracle; impression rugulose to colliculate/coriarius. Eudorsal margin of  $8tg$  in lateral view almost straight, vertical.  $4st-6st$  covered by  $3st$ .  $7st$  with about three rows of submedian hairs; posterior margin of lateral flap oblique, distinctly concave.

**Male metasoma.** Unknown.

**Coloration.** Black to brownish black with legs partly brown or reddish brown.

#### Diversity and distribution

Three described species from the central part of the Ethiopian region.

#### Biology

Unknown

#### Checklist of described species

*expansa* Quinlan, 1979:116, ♀; Gabon; MNHN (HT♀).

*nigra* Hedicke, 1912:304, ♀; Zaire; ZMHB (HT♀).

*spinosa* Hedicke, 1912:303, ♀; Zaire, ZMHB (2 T♀).

#### Genus *Oberthuerella* Saussure

Figs. 16, 29, 34, 40, 42, 76.

*Oberthuerella* Saussure, 1890: Pl. 20, Fig 20. Type species *Oberthuerella lenticularis* Saussure by monotypy.

#### Monophyly

Three derived features support the monophyly of *Oberthuerella*.

1. *Pronotal crest strongly reduced or completely absent* (Fig. 29). Most liopterids as well as *Austrocynips* and all ibaliids have a distinct crest. Within the Liopteridae the crest has been strongly reduced or lost independently in *Oberthuerella*, *Dallatorrella* and some *Liopterion*.

2. *Ventral margin of mesopleural impression not marked* (Fig. 16). The mesopleural impression is one of the ground-plan features of the Liopteridae, but in *Oberthuerella* and *Tessmannella* the impression has been secondarily lost (see phylogenetic analysis, character 21). The ventral margin of the impression remains as the lower margin of the obliquely costulate mesopleural area in *Tessmannella* (Fig. 15). In *Oberthuerella*, however, also the ventral margin has been lost (Fig. 16).

3. *Anterolateral, basal metacoxal process absent*. This process is present in all other Oberthuerellinae and Liopterinae (Fig. 20), but absent in the Mayrellinae, Dallatorrellinae, Ibaliidae and *Austrocynips*. The phylogenetic analysis (character 30) indicates that the process has been secondarily lost in *Oberthuerella*.

#### Description

Body length 7.0–13.0 mm.

**Head.** Lower face foveate-reticulate to rugose;

with transverse or oblique strigae to aciculae; weakly to distinctly keeled medially or not keeled. Median frontal carina indistinct; not raised. Antennal scrobe indistinctly impressed; ventrally usually transversely costulate, but sometimes rugose to rugulose, glabrate, or vertically costulate to strigate; dorsally usually areolate but sometimes rugose. Lateral frontal carina absent. Vertex foveate, areolate, alveolate or rugose. Gena more or less superficially foveate, alveolate, or foveate-areolate; with or without oblique costulae. Occipital carina strongly angled midlaterally; strongly raised dorsad angle, not raised ventrad angle. Malar space not impressed or slightly impressed beneath eye. Clypeus dorsally and dorsomedially foveolate or glabrate, laterally and medially more or less distinctly transversely strigate, ventrally glabrate; slightly projecting ventrally; ventral margin bilobed.

**Female antenna.** Antenna short, not or only slightly longer than length of head and mesosoma combined. Flagellum slightly to moderately widened towards apex.  $F1/F2 = 0.7-0.9$ ;  $F3 l/w = 1.1-2.3$ . Placodes start on F3.

**Male antenna.** Antenna long, distinctly longer than length of head and mesosoma combined. Flagellum with 12 articles.  $F1/F2 = 0.5-0.7$ ;  $F3 l/w = 1.8-2.6$ .

**Pronotum.** Anterior flange longitudinally strigate; or medially glabrate, laterally longitudinally strigate. Submedian depressions small, shallow, isolated. Anterior plate usually largely coriarius; sometimes medially glabrate, laterally horizontally strigate and only dorsally coriarius; dorsally also with punctures to foveolae. Lateral surface superficially or distinctly foveate, foveate-reticulate or alveolate; with or without vertical to horizontal costulae or aciculae; in *O. breviscutellaris* with vertical, curved costulae but no foveae. Crest present as a small median, subtriangular process (*O. transiens*) or completely absent (other species). Dorsal pronotal area coriarius or absent.

**Mesonotum.** Scutum with transverse, distinctly undulating costae; laterally with a few to several superficial or distinct foveae, medially with or without some superficial foveae. Median mesoscutal impression percurrent, distinct posteriorly and indistinct otherwise, or distinct throughout. Notaul-

lus distinct. Parascutal carina conspicuously raised, produced posteriorly. Lateral margin of axilla conspicuously raised throughout. Scuto-scutellar sulcus divided into three foveae by two strong submedian carinae; usually also with some additional, weaker or equally strong carinae. Dorsal surface of scutellum foveate-areolate, foveate-alveolate or rugose; laterally and posteriorly margined; with a median, short and blunt to long and slender process posteriorly. Lateral and posterior surfaces of scutellum largely glabrate, with or without a few vertical or oblique costulae. Laterodorsal process large, produced posteriorly into a pointed process.

**Mesopectus.** Mesopleural triangle sometimes large and triangular, but usually small and oblong; slightly impressed anteriorly, distinctly impressed posteriorly; or not impressed anteriorly except for narrowly ventrally and sometimes also narrowly anteriorly; rugulose to coriarius, occasionally partly glabrate; sparsely pubescent. Upper pleuron in *O. transiens* and *O. breviscutellaris* obliquely vertically costulate as in *Tessmannella*; in other species irregularly horizontally costulate to rugose, often with some foveae. Speculum either (1) more or less distinctly coriarius, or (2) rugose to rugulose, or (3) horizontally strigate, or (4) largely glabrate, with or without some horizontal strigae dorsally, or (5) partly glabrate, partly coriarius. Mesopleural impression completely absent, ventral margin not marked. Lower pleuron medially glabrate, anteriorly coriarius, posteriorly with a few foveae; sometimes also with short, horizontal costulae posteriorly; sparsely pubescent. Lateroventral carina percurrent, almost straight; or (usually) only present anteriorly and posteriorly, broadly interrupted medially. Subpleuron transversely costulate; or glabrate, with one transverse carina anterior to coxal foramina.

**Metanotum.** Dorsellum coriarius; lateral depressions distinct, shallow or moderately deep, small or large.

**Metapectal-propodeal complex.** Anterior meta-pleural pit usually indistinct or absent, occasionally present. Metepisternum sparsely horizontally costulate/costate to rugose; in *O. transiens* partly coriarius. Prespiracular area rugose; prespiracular process present, blunt, rugose to foveate; occa-



sionally lobelike, polished. Lateral propodeal area rugose; posterolateral propodeal process high to very high, lobelike or occasionally ridgelike, vertical. Median propodeal area carinate; lateral propodeal carina percurrent or almost so, not raised, dorsally and medially slightly to distinctly flattened above, punctate and pubescent or almost glabrate and nude above. Postsubpleuron colliculate to glabrous. Nucha longitudinally costulate to costate.

**Wings.** Wings more or less uniformly dark brown; forewings in *O. transiens* hyaline basally and with a hyaline spot subapically at the anterior margin. Marginal cell long in some species, short in others;  $Rs/2r = 4.0-7.2$ .  $Rs+M$  from upper third of basalis. Bulla in  $R_1+Sc$  absent. Some species with areolet.

**Legs.** Protibia apically with one tooth (*O. breviscutellaris*) or without teeth (other species). Mesotibial lobe rounded, margined, triangularly produced. Metatibial lobe margined, produced into a subtriangular process, without teeth. Longitudinal carina on posterior surface of metatibia present; in n. sp. 3 only indicated. Metatarsomere 1 distinctly compressed;  $mt1/mt2-5 = 0.7-1.0$ . Distal margins of  $mt1-2$  usually not produced, occasionally slightly produced into flat processes anteroventrally.

**Female metasoma.** Petiolar annulus moderately long,  $l/w = 0.9-1.7$ ; longitudinally costate. 3tg-5tg reduced in size, 6tg conspicuously enlarged. 3tg-8tg entirely to 6tg posteriorly and 7tg-8tg entirely keeled medially. Posterior margins of terga: 3tg and 4tg dorsally straight, 5tg dorsally straight or acute, 6tg-7tg dorsally straight or slightly acute, 3tg laterally rounded, 4tg-5tg laterally ligulate, 6tg-7tg laterally sinuate. 6tg posteriorly, sometimes also 4tg and 5tg posteriorly, 7tg-8tg entirely minutely to more coarsely punctate. 3tg laterally with some hairs, 4tg nude, sometimes with a few hairs laterally, 5tg nude, 6tg posteriorly or more or less entirely, 7tg-8tg entirely with hairs in coarse, more or less distinct punctures; in *O. aureopilosa* with dense yellow pubescence in coarse hair-punctures on 3tg-8tg. 8tg with narrow apical impression almost reaching spiracle; impression punctate to foveolate. 8tg with or without a median carina produced into a triangular, lamellate process. Eudorsal margin of 8tg in lateral view almost straight

vertical or declivous. 9tg slightly to conspicuously projecting. 4st-6st covered by 3st. 7st with about two to four rows of submedian hairs; posterior margin of lateral flap oblique, straight or slightly to distinctly concave, occasionally convex.

**Male metasoma.** Petiolar annulus moderately long;  $l/w = 0.7-1.8$ ; in *O. transiens* long,  $l/w = 3.5$ ; longitudinally costate. 3tg-5tg reduced in size, 6tg conspicuously enlarged. Posterior margins of terga: 3tg-4tg dorsally straight or slightly rounded, 5tg dorsally straight, slightly acute or rounded, 6tg-7tg dorsally broadly incised, 3tg laterally rounded, 4tg-5tg laterally ligulate, 6tg laterally slightly sinuate, 7tg laterally rounded. 4tg not or posteriorly, 5tg posteriorly, 6tg posteriorly and laterally, 7tg-8tg laterally minutely to more coarsely punctate. 3tg-4tg laterally with some hairs, 5tg nude, 6tg posteriorly and 7tg-8tg entirely with hairs in coarse punctures. Eudorsal margin of 8tg in lateral view almost straight.

**Coloration.** Entirely black; or black with legs and metasoma partly brownish; or black with post-petiolar metasoma red or yellow and legs entirely or partly brownish black, reddish brown or red.

#### Diversity and distribution

Twelve described and five undescribed species in the Ethiopian region.

#### Biology

Unknown.

#### Checklist of described species

*abscinda* Quinlan, 1979:111, ♂ ♀; Zambia, Zaire; BMNH (HT♀, main coll., 1 PT♂), MRAC (1 PT♂).

*aureopilosa* Benoit, 1955:290; ♀; Zaire; MRAC (HT♀).

*breviscutellaris* Benoit, 1955:286; ♀; Zaire; MRAC (HT♀).

*\*compressa* Benoit, 1955:292; ♀; Zaire; MRAC (HT♀). = *O. crassicornis* Benoit; synonymy by Quinlan (1979:112).

*crassicornis* Benoit, 1955:289; ♀; Zaire; MRAC (HT♀).

*lenticularis* Saussure, 1890: Pl. 20: Fig. 20, ♀; Madagascar; location of type not known.

*longicaudata* Benoit, 1955:291, ♀; Zaire; MRAC (HT♀).

*longispinosa* Benoit, 1955:290, ♂; Zaire; MRAC (HT♂).

*nigra* Kieffer, 1910a:110, ♂; Equatorial Guinea; ZMHB (HT♂, now missing (cf. Quinlan 1979:114)).

*nigrescens* Benoit, 1955:288, ♀; Zaire; MRAC (HT♀).

*tibialis* Kieffer, 1904:107, ♀; Cameroon; NHRS (HT♀).

*transiens* (Benoit, 1955:283, ♂); Zaire; MRAC (HT♂). As *Tessmannella*; **new combination**.

*triformis* Quinlan, 1979:115, ♀; Tanzania; BMNH (HT♀, main coll.).

## Liopterinae

Liopterinae Ashmead, 1895:175.

### Genus *Liopteron* Perty

Figs. 7, 13, 24, 50, 51, 58, 62, 80, 84.

*Liopteron* Perty, 1833:140. Type species *Liopteron compressum* Perty by monotypy.

*Liopteron* Westwood, 1837:1. Unjustified emendation.

*Liopteron* Agassiz, 1846:212. Unjustified emendation.

*Plastibalia* Kieffer, 1911:249. Type species *Plastibalia violaceipennis* Kieffer [= *Liopteron nigripenne* Westwood] by monotypy. **New synonymy**.

#### Monophyly

Members of *Liopteron* share several apomorphies.

1. *Mesoscutum with numerous closely set, transverse costae* (Fig. 24). In all other liopterids the transverse ridges on the mesoscutum are more broadly spaced (Fig. 23), and this is also the state in the Ibalidae and *Austrocynips*.

2. *Scutellum sloping gradually posteriorly, drawn out posteroventrally* (Fig. 13). In the Ibalidae, *Austrocynips* and other liopterids the scutellum falls more or less abruptly posteriorly (cf. Fig. 11). The only exception is *Mesocynips* (Fig. 14), where the scutellum falls gradually posteriorly, but

is not drawn out posteroventrally.

3. *Anterior flange of petiolar annulus absent; anterior margin of the annulus not projecting forwards* (Fig. 80). In all other liopterids the anterior margin of the annulus is equipped with a well developed, anteriorly projecting flange, at least dorsally (cf. Figs. 63, 65, 66, 69-79). A well developed anterior flange also occurs in *Austrocynips*, and dorsally in the Ibalidae.

4. *Parascutal impression rounded, deep, distinctly margined* (Fig. 24). In *Austrocynips*, the Ibalidae and all other Liopteridae the parascutal impression is more superficial and not distinctly margined (cf. Fig. 23).

5. *Antennal scrobe and adjacent parts of upper face and vertex coarsely longitudinally costate* (Fig. 7). This condition is unique among the Liopteridae, Ibalidae and *Austrocynipidae*. The sculpture is absent in *L. apicale* and *L. levilaterale*, but other characters indicate that this is due to secondary loss.

#### Description

Body length 9.3-13.9 mm. **Head.** Lower face foveate, with or without smaller punctures, usually also more or less distinctly, transversely or obliquely aciculate; weakly or distinctly keeled medially. Median frontal carina distinct; strongly raised to form a blunt tooth (*L. bispinosum*) or not raised (other species). Antennal scrobe indistinctly impressed; usually longitudinally costate, but in some species partly or entirely glabrate. Lateral frontal carina present or absent. Vertex medially foveate, laterally longitudinally costate; in *L. apicale* and *L. levilaterale* glabrate with only one lateral, broad costa and in *L. apicale* also some weaker strigae. Gena more or less superficially foveate, ventrally sometimes with oblique aciculae or costulae. Occipital carina strongly angled midlaterally; strongly raised dorsad angle, not raised ventrad angle. Malar space not or very slightly impressed beneath eye. Clypeus medially more or less glabrate or vertically strigate, laterally with radiating or horizontal strigae and some punctures of varying size; or (in *L. bicolor*) glabrate, punctate; or (in *L. immarginatum*) glabrate, sparsely foveolate; slightly

projecting ventrally; ventral margin bilobed.

*Female antenna.* F1/F2 = 0.5–0.8; F3 l/w = 2.2–3.4. Placodes start on F2 (*L. bispinosum*) or on F3 (all other species).

*Male antenna.* Flagellum with 12 articles. F1/F2 = 0.4–0.7; F3 l/w = 2.3–4.5.

*Pronotum.* Anterior flange laterally coriarius or punctate, medially glabrate to glabrous. Submedian depressions small, deep or shallow, isolated. Anterior plate glabrate, dorsally coriarius or transversely strigate, dorsally with some foveolae. Lateral surface dorsally foveate-scabrous to superficially foveate, more or less densely costate, ventrally glabrate; or (in *L. levilaterale* and *L. bispinosum*) entirely glabrous with a few more or less superficial foveae. Lateral surface conspicuously produced, bulging laterodorsally in some species. Crest raised medially into a small to medium-sized, triangular process; or only slightly raised medially, evenly curved. Dorsal pronotal area glabrate or transversely strigate.

*Mesonotum.* Scutum with very closely set transverse, non-undulating to distinctly undulating costae; with or without some foveae laterally; in *L. levilaterale* laterally glabrous, without costae or foveae. Median mesoscutal impression percurrent and distinct or absent. Notaulus distinct. Parascutal carina conspicuously raised, produced posteriorly. Lateral margin of axilla conspicuously raised throughout. Lateral bar broad. Scuto-scutellar sulcus divided into two foveae by strong median carina; sometimes an additional, weak or strong carina in each fovea; in *L. levilaterale* median carina reduced and additional carina absent. Dorsal surface of scutellum foveate-reticulate to scabrous; laterally margined or not margined; posteriorly not margined, falling gradually, drawn out posteroventrally; without processes posteriorly. Posterior and lateral surfaces of scutellum vertically costate to costulate, sometimes glabrate. Laterodorsal process small to large, rounded or produced into a blunt process posteriorly.

*Mesopectus.* Mesopleural triangle moderately large to small, triangular to oblong, slightly impressed; glabrate with sparse hairs or somewhat denser pubescence. Upper pleuron glabrous with a few hair-punctures. Speculum glabrous. Mesopleu-

ral impression percurrent; not subdivided or subdivided by vertical ridges. Lower pleuron largely glabrous; with a few small to large hair-punctures or (in *L. nigripenne*) sparsely pubescent. Lateroventral carina percurrent or interrupted medially, almost straight. Subpleuron transversely costulate. Intercostal processes absent or present; if present then small or large, rounded, directed posteriorly.

*Metanotum.* Dorsellum entirely glabrate; or glabrate with some aciculations laterally and punctures medially; lateral depressions distinct, shallow, medium-sized to large.

*Metapectal-propodeal complex.* Anterior meta-pleural pit present. Metepisternum entirely rugose; or anteriorly glabrous or coriarius with a few foveae and small punctures, and only posteriorly rugose. Prespiracular area rugose; prespiracular process absent or present; if present then blunt and rugulose or lobelike and polished. Lateral propodeal area rugose; in *L. nigripenne* only superficially; posterolateral propodeal process high; ridgelike, lobelike or blunt triangular; vertical. Median propodeal area carinate, usually with a median, longitudinal carina and a dorsal, transverse carina; lateral propodeal carina percurrent, distinctly raised throughout, flattened above, pubescent or glabrous/glabrate and nude above. Postsubpleuron transversely costulate or glabrate. Nucha laterally superficially rugulose to longitudinally costate, dorsally glabrate.

*Wings.* Fore and hind wings uniformly dark brown; or dark with a hyaline transverse band subapically on the forewing; or (in *L. levilaterale*) dark with a yellow spot subapically at anterior margin of forewing. Marginal cell long, Rs/2r = 5.5–6.3; in *L. levilaterale* short, Rs/2r = 3.4. Rs+M from upper third of basalis. Bulla in R<sub>1</sub>+Sc absent.

*Legs.* Protibia apically with one tooth. Mesotibial lobe blunt, not margined, with one tooth or without teeth. Metatibial lobe margined or not margined, produced into a subtriangular process or not produced, with one tooth (*L. levilaterale*) or without teeth; metatibial lobe in some species strongly reduced. Longitudinal carina on posterior surface of metatibia present. Metatarsomere 1 distinctly compressed or not compressed; mt1/mt2–5 = 0.5–0.8. Distal margin of mt1 not produced.

Distal margin of mt2 usually not produced; sometimes produced into a tubular or blunt process anteroventrally.

*Female metasoma.* Petiolar annulus long, l/w = 3.4–7.0; longitudinally costate with a more or less shallow dorsomedian furrow. Anterior flange of annulus absent or (in *L. bispinosum*) very reduced; anterior margin of annulus dorsally distinctly set off from articular bulb of petiole in *L. bispinosum* and *L. immarginatum*, more or less continuous with the bulb in the other species. 3tg–4tg reduced in size, 5tg conspicuously enlarged. 4tg–8tg or 5tg–8tg keeled medially. Posterior margins of terga: 3tg–4tg dorsally straight, occasionally acute, 5tg dorsally broadly incised, 6tg–7tg dorsally straight, 3tg–4tg laterally rounded, occasionally slightly sinuate, 5tg laterally rounded, 6tg–7tg laterally slightly sinuate. 3tg–5tg posteriorly or only 5tg posteriorly, 6tg–8tg largely minutely punctate. 3tg usually with some hairs laterally, sometimes nude, 4tg–5tg nude, 6tg–8tg with hairs in coarse punctures. 7tg in *L. bispinosum* with a submedian pair of tubercles; in *L. levilaterale* with a median spinelike process; in other species unarmed. 8tg with or without narrow apical impression not reaching spiracle; impression or corresponding area punctate-foveate or colliculate. 8tg in *L. immarginatum* with a median small, triangular, lamellate process; in *L. compressum* with a similar but larger process; in *L. bispinosum* with a pair of submedian, spine-like processes; in other species not armed. Eudorsal margin of 8tg in lateral view almost straight, vertical or slightly declivous; in *L. abdominale* strongly declivous. 4st–6st covered by 3st. 7st with single row of submedian hairs; posterior margin of lateral flap oblique, slightly sinuate or convex.

*Male metasoma.* Petiolar annulus long, l/w = 5.7–8.5; longitudinally costate with a more or less shallow dorsomedian furrow. 3tg–4tg reduced in size, 5tg conspicuously enlarged. Posterior margins of terga: 3tg–4tg dorsally straight, occasionally acute, 5tg–7tg dorsally broadly incised, 3tg–4tg laterally rounded, occasionally slightly sinuate, 5tg–7tg laterally rounded. 6tg posterolaterally, 7tg–8tg laterally to entirely minutely punctate. 3tg with or without some hairs laterally, 4tg–6tg nude, 7tg–8tg with hairs in coarse punctures. Eudorsal margin

of 7tg in lateral view angled mediadorsally in *L. compressum*, rounded in other species. 8tg in *L. compressum* with a median, large, spinelike process; in *L. immarginatum* with a median, distinct keel; in other species without armature. Eudorsal margin of 8tg in lateral view almost straight.

*Coloration.* Black or brownish black; in *L. abdominale* with petiole reddish brown and postpetiolar metasoma red; in *L. bicolor* with mesosoma red; in *L. levilaterale* with reddish brown tint to meso- and metasoma.

#### Diversity and distribution

Eight described species in the central part of the Neotropics up to Panama.

#### Biology

Unknown.

#### Checklist of described species

- abdominale* Westwood, 1874:132, ♀; Brazil; OXUM (HT♀).
- apicale* Westwood, 1874:133, ♂; Brazil; OXUM (HT♂). Transferred to *Plastibalia* by Hedicke and Kerrich (1940:221); **combination reestablished.**
- bicolor* Hedicke in Hedicke and Kerrich, 1940:198, ♂; Bolivia; ZMHB (HT♂).
- bispinosum* Kerrich in Hedicke and Kerrich, 1940:194, ♀; French Guiana; MNHN (HT♀).
- compressum* Perty, 1833:140, ♀; Brazil; ZSMC (HT♀).
- compressum minus* Kerrich in Hedicke and Kerrich, 1940:194, ♀; Brazil, Peru; NHRS (HT♀), HNHM (1 PT♀, now prob. lost). As variety; deemed to be of subspecific status.
- immarginatum* Kerrich in Hedicke and Kerrich, 1940:195, ♂♀; Brazil; NHMV (HT♂, 1 PT♀), BMNH (1 PT♂), HNHM (AT♀, now prob. lost).
- levilaterale* Kerrich in Hedicke and Kerrich, 1940:199, ♀; Brazil; MNHN (HT♀).
- nigripenne* Westwood, 1874:132, ♂; Brazil; OXUM (HT♂). Transferred to *Plastibalia* by Hedicke and Kerrich (1940:220); **combination**

**reestablished.**

\**violaceipenne* (Kieffer, 1911:249, ♀); Brazil; BMNH (2 T♀, No. 7.5a, b). As *Plastibalia*, = *Liopterion nigripenne* Westwood; synonymy by Hedicke and Kerrich (1940:220), **new combination.**

**Genus *Peras* Westwood**

Figs. 10, 20, 37, 41, 45, 48, 78, 79, 82, 83.

*Peras* Westwood, 1837:2. Type species *Peras nigra* Westwood by monotypy. Synonymized with *Liopterion* by Hedicke and Kerrich (1940:188). **Status reestablished.**

*Perus* Scudder, 1882:255. Unjustified emendation.

**Monophyly**

Several derived features support the monophyly of *Peras*.

1. *Petiolar annulus laterally with a broad, superficial impression devoid of longitudinal grooves or ridges* (Figs. 78, 79). The lack of longitudinal ridges and grooves on a broad segment of the lateral surface of the petiolar annulus is unique within the Liopteridae. This character cannot be polarized using ibaliids or *Austrocynips* because these taxa either lack longitudinal sculpture on the petiolar annulus or have only the tergal part of the annulus present. However, the analysis of liopterid relationships (Fig. 86) indicates that the structure in *Peras* is an autapomorphy for that genus.

2. *Petiolar annulus medially on the dorsal surface with a longitudinal ridge* (Fig. 82). In *Mesocynips* and *Mayrellinae* it is difficult to determine whether the annulus is ridged or grooved medially because of the large number of ridges and grooves. In all other liopterids the annulus has a groove medially on the dorsal surface and this should be the ground-plan condition for the Liopterinae + Oberthuerellinae according to the relationships suggested by the phylogenetic analysis (Fig. 86). *Eileenella* also has a median furrow on the petiolar annulus, but other ibaliids and *Austrocynips* lack longitudinal sculpture on the annulus, and it is uncertain whether the longitudinal sculpture of *Eileenella* is homologous to that of the Liopteridae

(see discussion of liopterid monophyly above).

3. *Abdominal tergum 7 in males abruptly falling mediodorsally; angled in profile* (Fig. 79). A somewhat similar, but less pronounced angulation of the male abdominal tergum 7 occurs in *Liopterion compressum*; otherwise this structure is unique among liopterids and ibaliids (males unknown in *Austrocynips*).

**Description**

Body length 3.9–8.6 mm.

**Head.** Lower face foveate-reticulate, punctate and, at least partly, superficially transversely or obliquely aciculate; distinctly keeled medially. Median frontal carina distinct; strongly raised to form a prominent, triangular, lamellate process. Antennal scrobe indistinctly impressed; glabrate. Lateral frontal carina present. Vertex foveate. Gena foveate. Occipital carina weakly angled midlaterally; more or less strongly raised dorsad angle, not raised ventrad angle. Malar space slightly impressed beneath eye. Clypeus punctate; slightly projecting ventrally; ventral margin slightly or distinctly bilobed.

**Female antenna.** Flagellum strongly widened towards apex; strongly compressed towards apex. F1/F2 = 0.7–0.8; F3 l/w = 2.4–2.7. Placodes start on F3, sometimes on F2.

**Male antenna.** Flagellum with 12 articles; strongly widened towards apex; strongly compressed towards apex. F1/F2 = 0.8; F3 l/w = 1.9–3.1, the lower values in species with F3 compressed.

**Pronotum.** Anterior flange laterally longitudinally strigate, medially glabrate. Submedian depressions small, deep or shallow, isolated. Anterior plate glabrate, dorsally transversely strigate with some foveolae. Lateral surface foveate-reticulate or foveate-areolate. Crest raised medially into a small to very small, triangular process. Dorsal pronotal area transversely strigate.

**Mesonotum.** Dorsal surface with foveae and transverse, distinctly undulating costae; the former superficial medially, but distinct laterally. Median mesoscutal impression percurrent, distinct. Notaulus distinct. Parascutal carina conspicuously raised, produced posteriorly. Lateral margin of axilla con-

spicuously raised throughout. Lateral bar broad. Dorsal surface of scutellum foveate-areolate to slightly scabrous; laterally and posteriorly indistinctly margined or not margined, posteriorly rounded; without processes posteriorly; occasionally weakly emarginate posteriorly. Posterior and lateral surfaces of scutellum vertically costulate. Laterodorsal process small to medium-sized, rounded.

**Mesopectus.** Mesopleural triangle large, triangular, slightly impressed anteriorly, more distinctly impressed posteriorly; glabrate, more or less sparsely pubescent. Upper pleuron glabrous with two superficial or deep impressions. Speculum glabrous. Mesopleural impression percurrent; more or less distinctly subdivided by vertical ridges. Lower pleuron glabrate with some foveolae-foveae, some smaller punctures, and anteriorly with two larger impressions; sparsely pubescent. Lateroventral carina percurrent, almost straight. Subpleuron transversely costulate; or rugulose with one transverse carina anterior to coxal foramina. Intercoxal processes absent or present; if present then small, rounded, directed posteriorly.

**Metanotum.** Dorsellum glabrous, sometimes slightly sculptured medially; lateral depressions distinct, shallow, medium-sized.

**Metapectal-propodeal complex.** Anterior metapectal pit present. Metepisternum foveate-rugose; or anteriorly foveate, posteriorly rugose. Prespiracular area rugose; prespiracular process more or less distinct, lobelike, polished. Lateral propodeal area rugose; posterolateral propodeal process low, ridgelike, vertical. Median propodeal area with a median carina; lateral propodeal carina percurrent, distinctly raised throughout, flattened above, glabrous and nude above. Postsubpleuron transversely costulate. Nucha longitudinally costulate.

**Wings.** Forewings basally brown, apically hyaline; or hyaline with a brown transverse band medially and another one subapically. Hind wings hyaline; or basally brown, apically hyaline. Marginal cell long, Rs/2r = 5.5–6.7. Rs+M from upper third of basalis. Bulla in R<sub>1</sub>+Sc absent.

**Legs.** Protibia apically with one tooth. Mesotibial lobe rounded, margined, with one tooth. Metatibial lobe margined, produced into a subtriangular process, without teeth. Longitudinal carina on pos-

terior surface of metatibia present. Metatarsomere 1 distinctly compressed; mt1/mt2–5 = 0.6–0.7. Distal margins of mt1–2 not produced.

**Female metasoma.** Petiolar annulus long, l/w = 2.0–3.1; with longitudinal, broadly set costae; dorsally with a median carina, this carina occasionally medially subdivided; in some species also with short transverse carinae dorsally; laterally with a broad, shallow impression broadened medially to posteriorly, this area without longitudinal grooves or ridges. 3tg–4tg reduced in size, 5tg conspicuously enlarged. 4tg–8tg keeled medially. Posterior margins of terga: 3tg–4tg dorsally straight, 5tg dorsally broadly incised, 6tg–7tg dorsally straight, 3tg–5tg laterally rounded, 6tg–7tg laterally sinuate. 5tg posterolaterally, 6tg–7tg laterally, 8tg entirely minutely punctate. 3tg–4tg nude, 5tg posterodorsally with or without a few long or short hairs, 6tg–8tg dorsally with hairs in coarse punctures, 6tg–7tg also with more lateral hairs in smaller punctures. 8tg with or without narrow apical impression almost reaching or not reaching spiracle; impression or corresponding area foveolate. 8tg with a median lamellate keel; this keel slightly to distinctly triangularly produced. Eudorsal margin of 8tg in lateral view almost straight, slightly declivous. 4st–6st covered by 3st. 7st with single row of submedian hairs; posterior margin of lateral flap oblique, slightly sinuate.

**Male metasoma.** Petiolar annulus long, l/w = 2.7–3.5; transverse carinae on dorsal surface more pronounced than in female; structure otherwise as in female. 3tg–4tg reduced in size, 5tg conspicuously enlarged. Posterior margins of terga: 3tg dorsally straight, 4tg dorsally slightly acute or straight, 5tg–7tg dorsally broadly incised, 3tg–7tg laterally rounded. 5tg posterolaterally, 6tg–8tg laterally minutely punctate. 3tg–5tg nude, 6tg–8tg with hairs in coarse punctures. Eudorsal margin of 7tg in lateral view distinctly angled medially. 8tg with short keel medially from the anterior margin. Eudorsal margin of 8tg in lateral view almost straight.

**Coloration.** Black; or black with head reddish brown; or black to brown with head, antennae, legs and mesosoma partly yellowish brown to reddish brown.

## Diversity and distribution

Eleven described and three undescribed species from the central Neotropics up to Mexico.

## Biology

Unknown.

## Checklist of described species

*biroi* (Kerrich in Hedicke and Kerrich, 1940:201, ♂); Peru; HNHM (HT♂, now probably lost). As *Liopteron*; **new combination**.

*brasiliense* (Hedicke in Hedicke and Kerrich, 1940:217, ♀); Brazil; types originally in coll. Hedicke, current location not known (HT♀, 1 PT♀). As *Liopteron*; **new combination**.

*clavicorne* (Westwood, 1874:132, ♀); Brazil; OXUM (HT♀). As *Liopteron*; **new combination**.

*fenestratum* (Ashmead, 1895:177, ♂); Brazil; USNM (HT♂, No. 23 644). As *Liopteron*; **new combination**.

*fuscicorne* (Westwood, 1874:132, ♀); Brazil; OXUM (HT♀). As *Liopteron*; **new combination**.

*laticeps* (Kerrich in Hedicke and Kerrich, 1940:203, ♂); Brazil; HNHM (HT♂, now probably lost). As *Liopteron*; **new combination**.

*nigrum* Westwood, 1837:2, ♀; French Guiana; ZMHB (HT♀). Transferred to *Liopteron* Perty by Hedicke and Kerrich (1940:206); **combination reestablished**.

\**reticulatum* Kieffer, 1910a:108. Isotypic with *P. nigra* Westwood; discovered by Hedicke (in Hedicke and Kerrich 1940:207).

*ruficeps* Kieffer, 1905:110, ♂; Brazil; location of type not known. Transferred to *Liopteron* by Hedicke and Kerrich (1940:217); **combination reestablished**.

*scaberrimum* Kieffer, 1911:250, ♂; Brazil [Mexico]; BMNH (LT♂, No. 7.3a, 1 PLT♂, No. 7.3b); lectotype designation by Hedicke and Kerrich (1940:205). Transferred to *Liopteron* by Hedicke and Kerrich (1940:204); **combination reestablished**.

*subpetiolatum* (Westwood, 1874:133, ♀); Brazil; OXUM (HT♀). As *Liopteron*; **new combination**.

Genus *Pseudibalia* Kieffer

Figs. 3, 8, 26, 59, 61, 77, 81.

*Pseudibalia* Kieffer, 1911:246. Type species *Pseudibalia fasciatipennis* Kieffer by monotypy.

*Heterocynips* Kieffer, 1911:247. Type species *Heterocynips rufipes* Kieffer by monotypy. Synonymized with *Liopteron* by Kerrich (in Hedicke and Kerrich 1940:188). **New synonymy**.

## Monophyly

The following synapomorphies for members of *Pseudibalia* all have exceptions within the genus, but the exceptions occur in different species so that the features taken together seem to support the monophyly of *Pseudibalia*.

1. *Female metasoma falling more or less abruptly posteriorly; eudorsal margins of abdominal terga 6 and 7 in lateral view straight, distinctly angled relative to each other.* In most species this character is very striking, the metasoma being truncate posteriorly with eudorsal margins of abdominal terga 7 and 8 in lateral view almost vertical (Fig. 77). This structure of the female metasoma is unique among liopterids, ibaliids and *Austrocynips*. *P. intermedia*, *P. weldi*, n. sp. 3 and n. sp. 13 have the metasoma less conspicuously, but still visibly, truncate posteriorly. However, in *P. confusa* the female metasoma is not truncate posteriorly, and the eudorsal margins of abdominal terga 6 and 7 are rounded and only slightly angled relative to each other in lateral view. It is uncertain whether the structure in *P. confusa* is primitive for *Pseudibalia* or secondarily derived within the genus.

2. *Dorsal surface of scutellum posteriorly with two small to relatively large, distinct, triangular processes* (Fig. 26). Within *Austrocynips*, the Ibaaliidae and Liopteridae, similar processes can only be found in some species of *Paramblynotus* (in the *punctulatus* and *borneanus* groups), but these processes are probably not present in the ground plan of *Paramblynotus*. Ibaaliids, *Decellea* and the *zonatus* group of *Paramblynotus* also have a pair of scutellar processes posteriorly, but these are broader and/or more lateral than the processes in *Pseudibalia*, and must have been derived independently (see also phylogenetic analysis, character 17). The

scutellar processes are absent in one group of closely related *Pseudibalia* species comprising *P. antennalis* (cf. Hedicke and Kerrich, 1940:219), n. sp. 6 and n. sp. 7, but the distribution of other character states within *Pseudibalia* suggests that this is due to secondary loss.

3. *Last flagellomere of female antenna with a bright yellow spot apically.* In *Austrocynips*, ibaliids and most liopterids the last flagellomere is uniformly coloured. In *Decellea*, a few *Dallatorrella*, a few *Oberthuerella* and a few *Paramblynotus* the last article is brighter apically, but never with a bright yellow spot. Within *Pseudibalia* the spot is absent in *P. weldi*, n. sp. 6, n. sp. 7 and n. sp. 12.

4. *Antennal scrobe ventrally with a punctate and striate, pubescent area* (Fig. 8). Although the antennal scrobe may be pubescent ventrally in other liopterids and in ibaliids, the pubescence never occurs on a well defined, differently sculptured area. The only possible exception is *Liopteron apicale*, which has a pubescent patch ventrally in the antennal scrobe similar to the one found in *Pseudibalia*, but less well defined. Within *Pseudibalia* the patch is reduced in females of n. sp. 12, n. sp. 6 and n. sp. 7, and in males of n. sp. 8 and n. sp. 9. The patch is completely absent in the male of *P. unifasciata*.

## Description

Body length 3.7–9.4 mm.

*Head.* Lower face foveate to foveate-reticulate, punctate, sometimes also superficially obliquely striolate; weakly to distinctly keeled medially. Lower face in n. sp. 9 (male) with a pair of conspicuous lateral, oblique, glabrate impressions converging ventrally onto the clypeus; in *P. bifasciata* (male) with a pair of lateral, glabrate, rounded impressions with a few costulae; in the other species such impressions absent. Median frontal carina distinct; strongly raised to form a triangular, lamellate process; in n. sp. 9 strongly raised to form a cylindrical process. Lateral frontal carina present or absent. Antennal scrobe indistinctly impressed; dorsally glabrate or foveate, sometimes with a few oblique costulae; ventrally with a punctate and

striate, pubescent patch; the structure of this patch variable: in n. sp. 10 (male) striae superficial; in n. sp. 12 (female) patch strongly reduced in size; in n. sp. 6 (female) and n. sp. 8 (male) patch strongly reduced in size, and hairs absent; in n. sp. 7 (female) hairs and punctures lost, but striae left; in n. sp. 9 (male) punctures and hairs strongly reduced in number and restricted to ventral margin of scrobe, but striae distinct; in *P. unifasciata* (male) patch completely absent. Lateral frontal carina present or absent. Vertex foveate to foveate-reticulate; or foveate-areolate; or rugose. Gena sparsely foveate to foveate-rugose, with a few to many smaller punctures. Occipital carina weakly to strongly angled midlaterally; more or less strongly raised dorsad angle, not raised ventrad angle. Malar space not impressed or slightly, occasionally distinctly, impressed beneath eye. Clypeus ventrally punctate, otherwise rugulose, punctate or glabrate; with or without some foveolae; with or without radiating or transverse strigae; slightly projecting ventrally; ventral margin bilobed or straight.

*Female antenna.* Flagellum moderately to strongly widened towards apex; subcylindrical to strongly compressed towards apex; last article with a bright yellow spot apically (absent in n. sp. 6, n. sp. 7, n. sp. 12 and *P. weldi*). F1/F2 = 0.5–0.9; F3 l/w = 1.4–2.9. Placodes start on F2 or F3, occasionally a few placodes also present on F1.

*Male antenna.* Flagellum with 12 articles; slightly widened towards apex; slightly compressed towards apex; last article without a bright yellow spot apically. F1/F2 = 0.6–0.8; F3 l/w = 2.1–2.9, the lower values in species with F3 compressed.

*Pronotum.* Anterior flange longitudinally strigate; or partly longitudinally strigate, partly glabrate; or entirely glabrate. Submedian depressions small, shallow, isolated. Anterior plate dorsally horizontally strigate to coriarius, foveolate; otherwise glabrate. Lateral surface more or less distinctly foveate to foveate-reticulate, with or without sparse punctures. Crest raised medially into a small, triangular process; or only slightly raised, evenly curved. Dorsal pronotal area glabrate; or transversely strigate; or colliculate.

*Mesonotum.* Scutum with foveae and transverse, distinctly undulating costae; the former superficial

medially but distinct laterally. Median mesoscutal impression percurrent, distinct. Notaulus distinct. Parascutal carina conspicuously raised, produced posteriorly. Lateral margin of axilla conspicuously raised throughout. Lateral bar broad. Scuto-scutellar sulcus divided into two foveae by strong, median carina; in n. sp. 9 and n. sp. 10 with an additional carina in each fovea. Dorsal surface of scutellum foveate-areolate to slightly scabrous; laterally and posteriorly indistinctly margined or not margined; with two small to relatively large, triangular processes posteriorly; these processes absent in *P. antennalis* (cf. Hedicke and Kerrich, 1940:219), n. sp. 6 and n. sp. 7. Lateral and posterior surfaces of scutellum vertically costulate to rugose-rugulose. Laterodorsal process small, rounded.

*Mesopectus*. Mesopleural triangle large, triangular, slightly impressed; glabrate, more or less sparsely pubescent. Upper pleuron glabrous, with or without a few foveae and a few larger impressions; in n. sp. 6 rugose. Speculum glabrous. Mesopleural impression percurrent; not subdivided or subdivided by more or less distinct vertical ridges. Lower pleuron glabrous to glabrate, with an anterior vertical row of larger impressions and some hair-punctures to foveae; sparsely pubescent. Lateroventral carina percurrent, almost straight. Subpleuron transversely costulate; or glabrate with one transverse carina anterior to coxal foramina. Intercostal processes present or absent; if present then small to moderately large, rounded, directed posteriorly.

*Metanotum*. Dorsellum either coriarius, or horizontally strigate, or vertically striolate, or glabrate; lateral depressions distinct or indistinct, shallow, medium-sized; in specimens of n. sp. 3 and n. sp. 10 the depression absent on one side; on the other side the depression barely indicated (n. sp. 3) or distinct (n. sp. 10).

*Metapectal-propodeal complex*. Anterior metapectal pit present. Metepisternum glabrate with some foveae to rugose. Prespiracular area rugose; prespiracular process conspicuous to absent; if present then blunt and rugulose or lobelike and polished. Lateral propodeal area rugose; posterolateral propodeal process low to moderately high, ridgelike or slightly lobelike, vertical. Median

propodeal area carinate; with a median longitudinal carina and one transverse carina, occasionally with some additional transverse carinae; lateral propodeal carina percurrent, distinctly raised throughout, flattened above, glabrate/glabrous and nude above. Postsubpleuron anteriorly glabrate, posteriorly transversely costulate; in n. sp. 6 and 7 colliculate. Nucha longitudinally costulate, dorsally often glabrate.

*Wings*. Forewings hyaline, usually with two brown, transverse bands, one medially and one subapically; occasionally the median or both bands missing. Hind wings hyaline, with or without a darker band apically. Marginal cell long,  $Rs/2r = 5.2-7.0$ .  $Rs+M$  usually from upper third of basalis, occasionally from slightly above middle of basalis. Bulla in  $R_1+Sc$  absent.

*Legs*. Protibia apically with one tooth. Mesotibial lobe rounded, margined, with one tooth or without teeth. Metatibial lobe margined, produced into a subtriangular process or not produced, without teeth. Longitudinal carina on posterior surface of metatibia present. Metatarsomere 1 distinctly compressed;  $mt1/mt2-5 = 0.5-0.9$ . Distal margin of  $mt1$  not, slightly or strongly produced anterovertrally; if produced then process flat or semitubular. Distal margin of  $mt2$  not or slightly produced anterovertrally; if produced then process flat.

*Female metasoma*. Petiolar annulus long,  $l/w = 3.1-4.4$ ; longitudinally costate; furrows about equal-sized, rather narrow; dorsomedially with a furrow and occasionally with a minute median keel anteriorly (*P. antennalis* (cf. Hedicke and Kerrich, 1940:219), n. sp. 6 and n. sp. 7). 3tg-4tg reduced in size, 5tg conspicuously enlarged. In *P. antennalis* (Hedicke and Kerrich 1940:219) and n. sp. 6 3tg-5tg fused, intertergal sutures absent. In all species except *P. confusa* the metasoma more or less abruptly truncated posteriorly, with eudorsal margins of 6tg and 7tg in lateral view straight, distinctly angled relative to each other, and eudorsal margin of 7tg in lateral view more or less vertical. In *P. confusa* the metasoma rounded posteriorly, eudorsal margins of 6tg and 7tg in lateral view slightly rounded, only slightly angled relative to each other, and eudorsal margin of 7tg in lateral view more oblique, declivous. 4tg-8tg to only 8tg keeled me-

dially; usually 6tg-8tg keeled medially. Posterior margins of terga: 3tg dorsally straight, 4tg dorsally straight, rounded or slightly acute, 5tg dorsally broadly incised, 6tg-7tg dorsally straight, 3tg-4tg laterally straight or rounded, 5tg laterally rounded, 6tg-7tg laterally sinuate. 5tg posterolaterally. 6tg-8tg laterally minutely punctate. 3tg-4tg nude, 5tg nude, in *P. confusa* with a submedian hair patch posteriorly, 6tg-8tg dorsally with hairs in coarse punctures, 6tg-7tg also with more lateral hairs in smaller punctures. 8tg with broad or narrow apical impression not reaching or almost reaching spiracle; impression rugulose to foveolate. 8tg in *P. confusa* with a low, roundedly angled carina; in the other species without ridges and processes. Eudorsal margin of 8tg in lateral view almost straight, vertical or slightly declivous. 9tg slightly to conspicuously projecting beyond 8tg. 4st-6st covered by 3st. 7st with single row of submedian hairs; posterior margin of lateral flap oblique, straight or slightly to strongly concave.

*Male metasoma*. Petiolar annulus long,  $l/w = 3.7-4.9$ ; longitudinally costate; furrows rather narrow, about equal-sized; dorsomedially with a furrow. 3tg-4tg reduced in size, 5tg conspicuously enlarged. Posterior margins of terga: 3tg-4tg dorsally straight or slightly rounded, 5tg-7tg dorsally broadly incised, 3tg-4tg laterally straight, 5tg-7tg laterally rounded. 5tg sometimes glabrate but usually posterolaterally minutely punctate, 6tg-8tg laterally minutely punctate. 3tg nude, occasionally with a few hairs laterally, 4tg-5tg nude, 6tg-8tg with hairs in coarse punctures. Eudorsal margin of 8tg in lateral view almost straight.

*Coloration*. Entirely black to brownish black; or black with head and legs reddish brown to yellowish brown; or black with legs yellow, red or reddish brown; or entirely yellowish brown to reddish brown, with or without metasoma darker brown; or black, partly tinted with reddish brown.

#### Diversity and distribution

Twelve described and thirteen undescribed species from the central Neotropical region and up to Mexico

#### Biology

Unknown.

#### Checklist of described species

- antennalis* (Kerrich in Hedicke and Kerrich, 1940:218, ♀); Brazil; HNHM (HT♀, now probably lost). As *Liopterion*; **new combination**.
- bifasciata* (Westwood, 1874:132, ♂); Brazil; OXUM (HT♂). As *Liopterion*; **new combination**.
- brevicornis* (Kerrich in Hedicke and Kerrich, 1940:211, ♀); Brazil; HNHM (HT♀, now prob. lost). As *Liopterion*; **new combination**.
- confusa* (Hedicke in Hedicke and Kerrich, 1940:216, ♀); Peru; ZMHB (HT♀). As *Liopterion*; **new combination**.
- fasciatipennis* Kieffer, 1911:247, ♀; Mexico; BMNH (HT♀, No. 7.4).
- intermedia* (Kerrich in Hedicke and Kerrich, 1940:200, ♀); Brazil; USNM (HT♀, No. 53 568). As *Liopterion*; **new combination**.
- intermedia autazense* (Kerrich in Hedicke and Kerrich, 1940:201, ♂); Brazil; NHRS (HT♂, 1 PT♂). As *Liopterion*; **new combination**. As variety, deemed to be of subspecific status.
- rufa* (Ashmead, 1895:178, ♂ ♀); Brazil; USNM (1 T♀, No. 23 642, 1 T♂); lectotype designated by Hedicke and Kerrich (1940:214). As *Liopterion*; **new combination**.
- rufipes* (Kieffer, 1911:252, ♀); Brazil; BMNH (HT♀, No. 7.2). As *Heterocynips*; transferred to *Liopterion* by Kerrich (in Hedicke and Kerrich 1940:188); **new combination**.
- tarsalis* (Ashmead, 1895:177, ♀); Brazil; USNM (HT♀, No. 23 643). As *Liopterion*; **new combination**.
- unifasciata* (Westwood, 1874:133, ♂); Brazil; OXUM (HT♂). As *Liopterion*; **new combination**.
- weldi* (Kerrich in Hedicke and Kerrich, 1940:209, ♀); Brazil; USNM (HT♀, No. 53 569). As *Liopterion*; **new combination**.
- westwoodii* (Cameron, 1883:75, ♀); Panama; BMNH (HT♀, main coll.). As *Liopterion*; **new combination**.

## Character analysis

The following list includes only the informative characters used to infer intergeneric relationships within the Liopteridae. After each multistate character the hypothesized order of the states, if any, is specified. The character consistency index (ci) and the character retention index (ri) on the minimum-length tree, with ibaliid relationships constrained to be (*Eileenella*, (*Ibaliia*, *Heteribalia*)), are given for all characters. In some cases, a polymorphic genus was coded for the estimated ground-plan state, rather than being coded as polymorphic. This was done only in cases where the distribution of other characters within the genus clearly indicated which one of the states was the ground-plan state for the genus. These cases have been noted below under the respective characters. The observed states for the characters are given in Tab. 4.

1. *Shape of median frontal carina*: (0) raised to form a more or less distinct process (Figs. 6, 8, 10); (1) not raised, ridgelike throughout (Figs. 7, 9). (ci = 0.60, ri = 0.60).

2. *Shape of flagellum (females)*: (0) not or only slightly widened towards apex (Figs. 1, 2, 4, 5); (1) distinctly widened towards apex (Fig. 3). (ci = 0.67, ri = 0.50).

3. *Shape of apical part of flagellum (females)*: (0) cylindrical or subcylindrical (Figs. 1, 4, 5); (1) weakly compressed (Fig. 2); (2) distinctly compressed (Fig. 3). Ordered 012. (ci = 0.80, ri = 0.00).

4. *Shape of median flagellomeres*: (0) cylindrical or subcylindrical (Figs. 1–3); (1) distinctly swollen submedially to subapically, especially ventrally (Figs. 4, 5). (ci = 1.00, ri = 1.00).

5. *Length of F1 (females)*: (0) long, subequal to or longer than F2 (Figs. 2, 4, 5); (1) short, distinctly shorter than F2 (Figs. 1, 3). (ci = 0.67, ri = 0.80).

6. *Placodes on F1 (females)*: (0) absent (Figs. 1, 3); (1) present (Fig. 2). (ci = 0.33, ri = 0.50).

7. *Number of flagellomeres (males)*: (0) 12; (1) 13. (ci = 1.00, ri = 1.00).

8. *Submedian pronotal depressions*: (0) open laterally (Fig. 32); (1) closed laterally (Fig. 31). (ci = 0.50, ri = 0.33).

9. *Sculpture on lateral surface of pronotum*: (0)

glabrous or punctate, sometimes partly costate-strigate; (1) at least partly foveate (Fig. 11). In *Xenocynips*, *Oberthuerella* and *Liopterion* there are a few species with the foveate sculpture completely absent, but other characters indicate that these species have lost the foveate sculpture secondarily. (ci = 0.50, ri = 0.75).

10. *Shape of posterolateral margin of pronotum and adjacent part of mesopleuron*: (0) pronotal margin straight, abutting with mesopleuron, mesopleural triangle not deeply impressed anteriorly (Fig. 11; cf. also Figs. 18, 19); (1) pronotal margin distinctly excavated in front of mesopleural triangle, not abutting with mesopleuron, mesopleural triangle deeply impressed anteriorly (Fig. 15; cf. also Figs. 16, 17). (ci = 1.00, ri = 1.00).

11. *Posterior part of parascutal carina*: (0) not conspicuously raised, posterolateral corner of anterior mesoscutal sclerite rounded (Fig. 23); (1) conspicuously raised, posterolateral corner of anterior mesoscutal sclerite angled or produced posteriorly into a point (Figs. 11, 24). (ci = 1.00, ri = 1.00).

12. *Lateral margin of axilla*: (0) not raised (Fig. 14); (1) conspicuously raised anteriorly; (2) conspicuously raised throughout (Fig. 13). Ordered 012. (ci = 0.67, ri = 0.89).

13. *Width of lateral bars*: (0) narrow (Figs. 23, 25), occasionally moderately broad (a few *Dallatorrella*); (1) broad (Figs. 24, 26). Some species of *Oberthuerella* have the lateral bars broad, but other characters indicate that the bars are narrow in the ground plan of *Oberthuerella*. (ci = 1.00, ri = 1.00).

14. *Scuto-scutellar sulcus*: (0) divided into two foveae by a strong median carina, occasionally also weaker carinae present in the foveae (Figs. 23, 24, 26); (1) divided into three or more foveae by two or more strong carinae, median carina absent or weak (Fig. 25). (ci = 0.67, ri = 0.67).

15. *Laterodorsal process of scutellum*: (0) absent (Fig. 14); (1) indicated; (2) present, distinct (Figs. 11, 13, 23–26). Ordered 012. (ci = 0.50, ri = 0.78).

16. *Shape of laterodorsal process of scutellum*: (0) rounded, not or only slightly projecting (Figs. 23, 26); (1) pointed, distinctly projecting (Fig. 25). In two species of *Liopterion* the laterodorsal process has secondarily become pointed and conspicuously

projecting (Fig. 24), but the distribution of other character states within *Liopterion* indicates that the process is rounded in the ground plan of the genus. (ci = 1.00, ri = 1.00).

17. *Pair of submedian posterior processes from the dorsal surface of the scutellum*: (0) absent (Figs. 23–25); (1) present (Fig. 26). (ci = 0.50, ri = 0.50). The processes are absent in some species of *Pseudibalia*, but other characters indicate that this is due to secondary loss within the genus.

18. *Median posterior process from the dorsal surface of the scutellum*: (0) absent (Figs. 23, 24, 26); (1) present (Fig. 25). (ci = 1.00, ri = 1.00).

19. *Auricula (semilunar, slightly impressed, glabrous area defined by carinae, situated posterior to axillula)*: (0) absent (Figs. 13, 14); (1) present (Fig. 11). (ci = 1.00, ri = 1.00).

20. *Shape of mesopleural surface*: (0) flat or slightly convex (Figs. 11, 17–19); (1) distinctly concave anteriorly, concavity obliquely vertical, may function as a shallow mesofemoral groove (indicated in Figs. 15, 16, but difficult to see). (ci = 1.00, ri = 1.00).

21. *Mesopleural impression*: (0) absent (Figs. 15, 16, 18); (1) present (Figs. 11, 17, 19). (ci = 0.33, ri = 0.67).

22. *Intermesocoxal processes*: (0) absent (Figs. 15–18); (1) small, narrow processes directed obliquely posteriorly (Figs. 19, 38); (2) broader, lobe-like processes directed posteriorly. Unordered. (ci = 0.80, ri = 0.00).

23. *Lateral depressions of dorsellum*: (0) absent or only indicated (Fig. 35); (1) shallow but distinct (Fig. 34); (2) deep (Fig. 33). Ordered 012. (ci = 0.50, ri = 0.67).

24. *Ventral end of metapleural carina*: (0) not produced (Figs. 11, 20, 22); (1) produced into a prominent process laterad metacoxal foramen (Fig. 21). (ci = 1.00, ri = 1.00).

25. *Structure of metapectal-propodeal complex laterad metacoxal foramen*: (0) only slightly raised (Figs. 11, 21, 22); (1) conspicuously raised (Fig. 20). (ci = 0.50, ri = 0.83).

26. *Shape of lateral propodeal carina*: (0) curved, not or only partly flattened dorsally (Fig. 36); (1) straight, flattened dorsally throughout (Fig. 37). (ci = 1.00, ri = 1.00)

27. *Insertion of metasoma on propodeum*: (0) low, postsubpleuron short (Fig. 22); (1) high, postsubpleuron long (Figs. 11, 20, 21). (ci = 0.50, ri = 0.67).

28. *Shape of marginal cell*: (0) short,  $Rs/2r = 2.0-4.7$ ; (1) long, ratio 5.2–7.3; (2) very long, ratio  $> 10.0$ . Ordered 012. Some species of *Oberthuerella* and one species of *Liopterion* have a short marginal cell, but the cell is hypothesized to be long in the ground plan of these genera based on other evidence. (ci = 0.67, ri = 0.80).

29. *Longitudinal impression apically on dorsal (outer) surface of protibia*: (0) absent; (1) present (Fig. 45). (ci = 1.00, ri = 1.00).

30. *Anterior, basal process of metacoxa*: (0) absent (Figs. 21, 22); (1) present (Fig. 20). (ci = 0.50, ri = 0.75).

31. *Shape of laterobasal part of metacoxa*: (0) rounded, not specialized (Figs. 20, 22); (1) with a lateral ridge and an anterolateral, pubescent depression (Fig. 21). (ci = 1.00, ri = 1.00).

32. *Shape of metatrochanter*: (0) long, not bent laterad towards apex, anteriormost part of metafemur well removed from base of trochanter (Fig. 46); (1) short, slightly bent laterad towards apex, anteriormost part of metafemur inserted closer to base of trochanter (Fig. 47); (2) very short, strongly bent laterad towards apex, anteriormost part of metafemur inserted very close to base of trochanter (Fig. 48). Ordered 012. (ci = 0.67, ri = 0.83).

33. *Ventral spinelike process on metafemur*: (0) absent (Fig. 41); (1) present (Figs. 42, 43). (ci = 1.00, ri = 1.00).

34. *Pubescence dorsally on metafemur*: (0) no erect hairs, pubescence more or less recumbent (Figs. 42, 43); (1) with long, erect hairs in addition to the more recumbent pubescence (Fig. 41). (ci = 0.50, ri = 0.75).

35. *Length of metatibia*: (0) longer than metafemur (Fig. 49); (1) shorter than metafemur (Fig. 51). (ci = 0.50, ri = 0.75).

36. *Longitudinal carina on posterior surface of metatibia*: (0) absent; (1) present (Fig. 50). (ci = 0.60, ri = 0.50).

37. *Shape of metatibial lobe*: (0) triangularly produced or not produced (Figs. 51–53); (1) produced into a distinct, slender, toothlike process

(Fig. 54), occasionally only the base of the tooth present (Fig. 55). (ci = 1.00, ri = 1.00).

38. *Shape of claws*: (0) all claws simple (Fig. 60); (1) fore and middle claws with a basal, lamellate lobe (Figs. 61, 62). (ci = 1.00, ri = 1.00).

39. *Length of petiolar annulus (females)*: (0) short, ratio of median dorsal length to minimum dorsal width < 1.6 (Figs. 63, 65, 66, 70, 72, 73); (1) long, ratio > 1.7 (Figs. 74, 75, 77, 78, 80–82). (ci = 0.50, ri = 0.75).

40. *Ventral hump on petiolar annulus (females)*: (0) absent (Figs. 63, 65, 66, 70, 74, 75, 77, 78, 80); (1) present (Figs. 72, 73). (ci = 1.00, ri = 1.00).

41. *Pubescence on abdominal terga 3–5*: (0) without erect hairs (Figs. 63, 65, 66, 69–71, 74–79), occasionally with a few erect hairs laterally (*Eileenella*); (1) covered with conspicuous, erect hairs (Fig. 72). (ci = 1.00, ri = 1.00).

42. *Relationship between abdominal tergum 3 and petiole*: (0) anterior margin of 3tg projecting over posterior part of petiole, distinct angle between dorsal margins of 3tg and petiole (Figs. 63, 65, 66, 69–72); (1) margins abutting, dorsal margins of 3tg and petiole more or less continuous (Figs. 74–80). (ci = 0.50, ri = 0.83).

43. *Shape of lateral part of posterior margin of abdominal tergum 3 (females)*: (0) more or less vertical (Figs. 63, 72); (1) oblique (Figs. 65, 66, 70, 75, 77, 78). (ci = 0.50, ri = 0.83).

44. *Abdominal sterna 4–6 (females)*: (0) at least partly exposed (Fig. 65); (1) entirely covered by abdominal sternum 3 (Figs. 66, 72). (ci = 0.50, ri = 0.75).

45. *Size of abdominal tergum 5 (females)*: (0) not enlarged, subequal in size to abdominal tergum 4 (Figs. 63, 65, 66, 70, 72, 74, 75); (1) conspicuously enlarged, much larger than abdominal tergum 4 (Figs. 77, 78). (ci = 1.00, ri = 1.00).

46. *Shape of dorsal part of posterior margin of abdominal tergum 5 (females)*: (0) straight or slightly acute, not incised (Figs. 63, 65, 66, 70, 72, 74, 75); (1) broadly incised (Figs. 77, 78). (ci = 1.00, ri = 1.00).

47. *Shape of lateral part of posterior margin of abdominal tergum 5*: (0) rounded or almost straight (Figs. 63, 65, 66, 69–72, 77–79); (1) ligulate (Figs. 74–76). (ci = 1.00, ri = 1.00).

48. *Size of abdominal tergum 5 (males)*: (0) not enlarged, subequal in size to other (not enlarged) postpetiolar terga (Figs. 69, 76); (1) conspicuously enlarged (Fig. 79). Some males of *Paramblynotus* have abdominal tergum 5 enlarged (Fig. 71), but other evidence indicates that the tergum is not enlarged in the ground plan of *Paramblynotus*. (ci = 1.00, ri = 1.00).

49. *Size and shape of abdominal tergum 6 (females)*: (0) not or only slightly enlarged, subequal in size to other (not enlarged) postpetiolar terga (Figs. 63, 72, 77, 78); (1) conspicuously enlarged dorsally but not ventrally, euposterior margin oblique (Figs. 65, 66, 70); (2) conspicuously enlarged both dorsally and ventrally, euposterior margin not so oblique (Figs. 74, 75). Unordered. (ci = 1.00, ri = 1.00).

50. *Size of abdominal tergum 6 (males)*: (0) not enlarged, subequal in size to other (not enlarged) postpetiolar terga (Figs. 69, 71, 79); (1) conspicuously enlarged (Fig. 76). (ci = 1.00, ri = 1.00).

51. *Pubescence dorsolaterally on abdominal tergum 7 (females)*: (0) with hairs in more or less coarse punctures of about equal size (Fig. 84); (1) with hairs in punctures of two different sizes; coarse above, fine below (Fig. 83; cf. also Figs. 77, 78). (ci = 1.00, ri = 1.00).

52. *Patch with recumbent pubescence ventrolaterally on abdominal tergum 7*: (0) absent (Figs. 63, 65, 66, 69–71, 74–79); (1) present (Fig. 72). (ci = 1.00, ri = 1.00).

53. *Sculpture on posterolateral region of abdominal tergum 8 (females)*: (0) with or without an impression, without parallel, linear sculpture (Figs. 72, 74, 75, 77, 78); (1) with a distinct impression, at least close to spiracle with oblique, parallel strigae (Fig. 64; cf. also Figs. 63, 65, 66). Some species of *Paramblynotus* do not have a deep, strigate impression, but other characters indicate that this is due to secondary loss of the strigate impression. (ci = 1.00, ri = 1.00).

54. *Shape of eudorsal margin of abdominal tergum 8 in lateral view (females)*: (0) more or less straight, slightly rounded or slightly angled, vertical to declivous (Figs. 74, 75, 77, 78); (1) distinctly angled submedially or close to dorsal (euanterior) margin, ventrad angle reclivous (Figs. 63–66); (2)

Tab. 4. Observed states of morphological characters used to infer intergeneric relationships within the Liopteridae. Characters 3, 12, 15, 23, 28 and 32 were ordered in the sequence 012; other characters were unordered. Explanation of symbols: 0-2 = observed monomorphic states, p = 0/1 polymorphism, q = 0/1/2 polymorphism, r = 0/2 polymorphism, ? = state unknown, - = character not applicable.

Genus	Character										
	1	6	11	16	21	26	31	36	41	46	51
<i>Austrocynips</i>	00000	0?-00	00--0	-0000	00?00	-0000	00000	0-000	00000	00?0?	0000
<i>Eileenella</i>	0000?	0?-00	0-000	-1000	00?01	0-100	01000	0-00-	010?0	00?0?	000?
<i>Ibalia</i>	10000	0p000	00000	-1000	00000	00200	00000	1-00-	00000	00000	0000
<i>Heteribalia</i>	-0000	11100	00000	-1000	00000	00100	01000	0-00-	00000	00000	0000
<i>Kiefferiella</i>	10001	0p110	00002	00010	11200	00000	01001	00000	00000	00000	0011
<i>Decellea</i>	10100	1?010	00002	01010	00200	-1000	01000	10000	00100	00?1?	?011
<i>Paramblynotus</i>	p000p	1pp10	p00p2	0p010	11200	01000	01001	p0000	00110	00010	0011
<i>Mesocynips</i>	00010	11001	10000	-0000	10210	01000	11011	01101	10010	00000	0100
<i>Dallatorrella</i>	00010	11011	10p11	00000	10210	01000	11011	p1101	10010	00000	0102
<i>Xenocynips</i>	11001	00111	11012	10100	10101	p1111	02101	10110	011?0	01021	0000
<i>Tessmannella</i>	10001	0?111	12012	10101	00001	01111	02101	10110	01110	01?2?	0000
<i>Oberthuerella</i>	1p001	00111	12012	10101	00101	01110	02101	10100	01110	01021	0000
<i>Liopterion</i>	p0001	00111	12102	00000	1r101	11111	02011	10110	01111	10100	0000
<i>Peras</i>	01201	00111	12102	00000	1r101	11111	02011	10110	01111	10100	1000
<i>Pseudibalia</i>	01q01	00111	12102	01000	1r101	11111	02011	10110	01111	10100	1000

roundedly angled close to ventral (euposterior) margin, ventrad rounding reclivous (Fig. 72). Unordered. Both states 0 and 1 occur in *Paramblyno-*

*tus*, but the distribution of other features indicates that state 1 is plesiomorphic for the genus (ci = 1.00, ri = 1.00).

## Phylogenetic analysis

Parsimony analysis using the branch-and-bound algorithm of PAUP, and constraining ibaliid relationships to (*Eileenella*, (*Heteribalia*, *Ibalia*)), resulted in one minimum-length tree of length 116, consistency index 0.71 and retention index 0.81 (Fig. 85). The most parsimonious tree was robust with respect to alternative methods of analyzing the data. It was stable to successive weighting, whether based on the consistency index, retention index or rescaled consistency index. Removing the constraints on outgroup relationships or treating all characters as unordered, irrespective of whether or not outgroup relationships were constrained, resulted in the same minimum-length tree.

Support for the branches in the tree was assessed using bootstrapping (Felsenstein 1985, Swofford

1993) and the decay index or Bremer support (Källersjö et al. 1992). These analyses were constrained in that the ingroup had to appear as monophyletic, and ibaliid relationships were specified as (*Eileenella*, (*Ibalia*, *Heteribalia*)). The result of these analyses, as well as the proposed classification of the Liopteridae into subfamilies, is given in Figure 86. Several of the clades were well supported by the data: the monophyly of the subfamilies Liopterinae, Oberthuerellinae and Dallatorrellinae, and the sister-group relationship between the Liopterinae and Oberthuerellinae. Less well supported were the monophyly of the Mayrellinae, the assemblage Dallatorrellinae + Liopterinae + Oberthuerellinae and the relationships within the subfamilies; alternative groupings occurred in trees that were only two or three steps longer than the shortest tree.

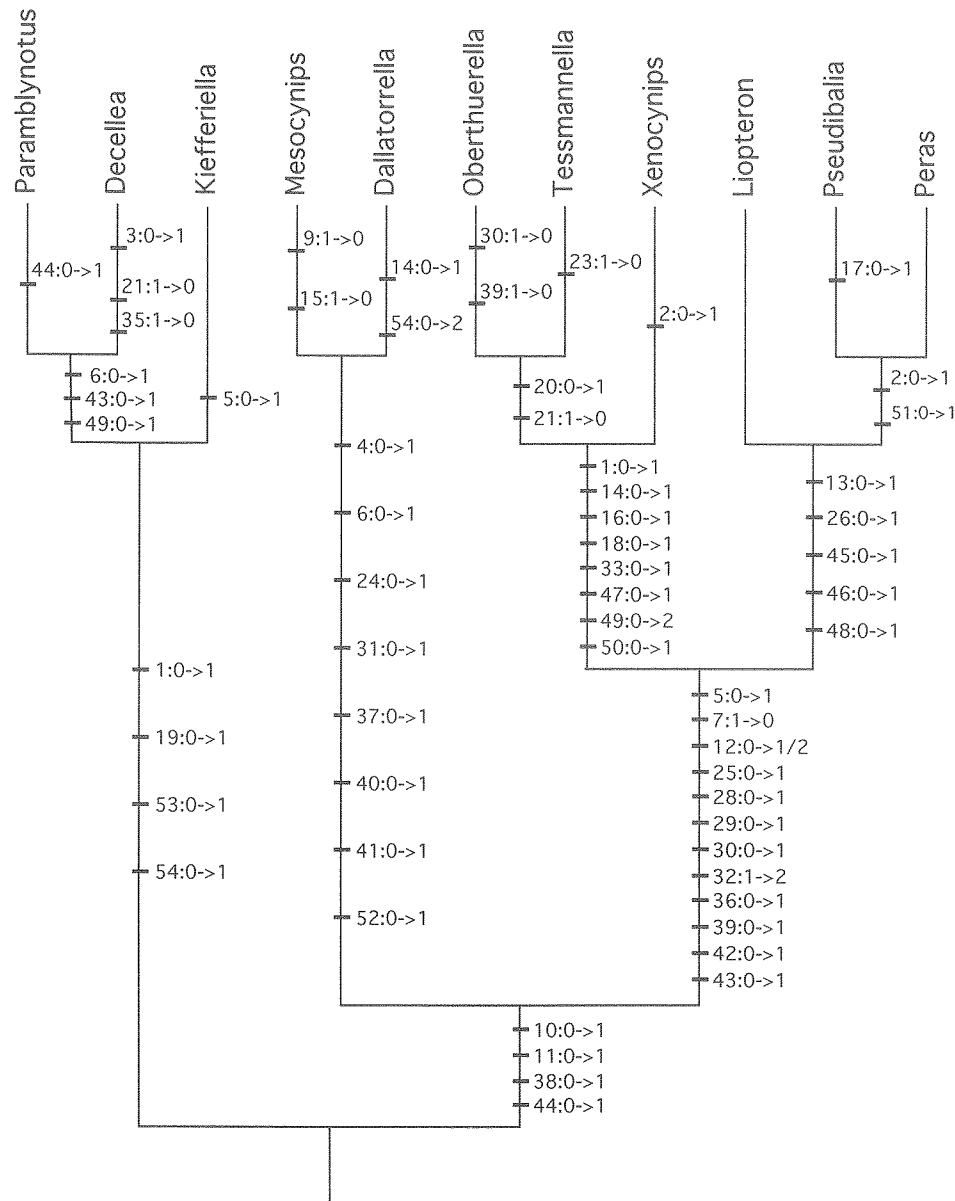


Fig. 85. Most parsimonious hypothesis of intergeneric relationships within the Liopteridae (length 116, consistency index 0.71, retention index 0.81). All unambiguous character changes, with ibaliid relationships constrained to (*Eileenella*, (*Ibalia*, *Heteribalia*)), are indicated on the tree.

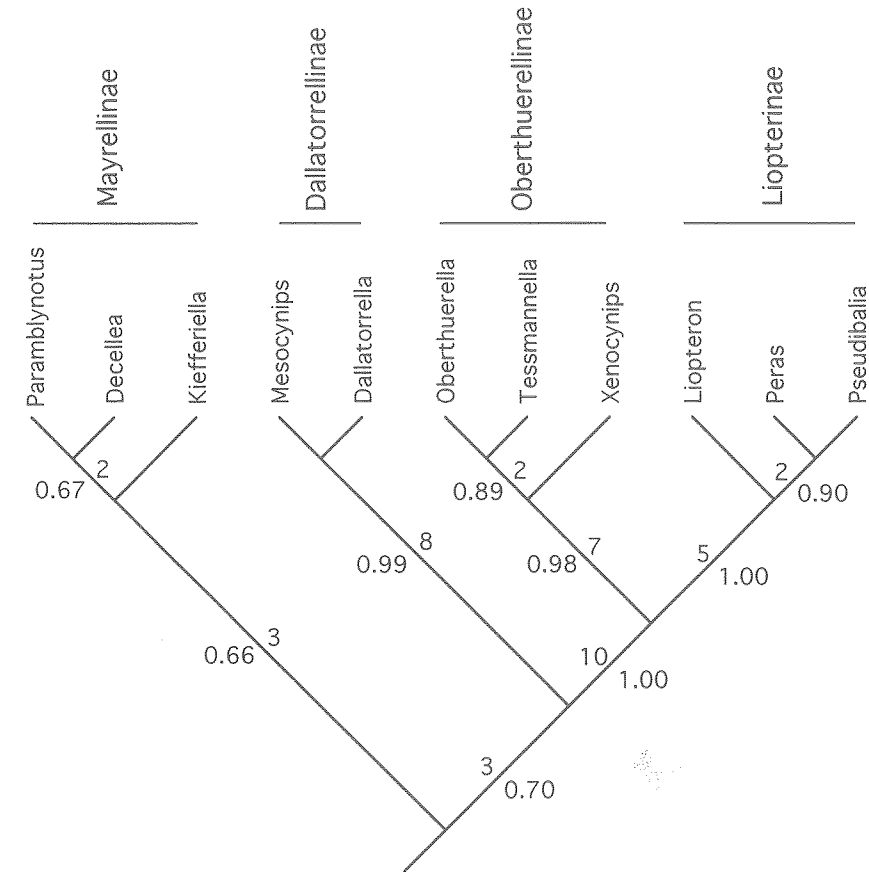


Fig. 86. Most parsimonious hypothesis of intergeneric relationships within the Liopteridae. The number of extra steps needed to break up the monophyly of a group (the decay index or Bremer support) is given above the corresponding branch; the frequency with which a particular group occurred among the shortest trees generated in 1000 bootstrap replications of the analysis is given below the corresponding branch. Proposed classification of the family into subfamilies is indicated above the genera.

**Biogeographic analysis**

An area cladogram for the Liopteridae based on the most parsimonious hypothesis of intergeneric relationships is presented in Figure 87. A few of the distribution areas in the cladogram seem to result from recent dispersal. The subfamily Liopterinae occurs exclusively in the central part of the Neotropics, except for a few species of *Pseudibalia* and *Peras* that stretch into the southernmost part of the Nearctic region. Therefore, it seems likely that the subfamily was originally present in the Neotropics and that a few species spread relatively recently to

The genus *Paramblynotus* is currently widespread, but an analysis of the distribution of *Paramblynotus* diversity suggests that the genus was originally present in the eastern Palearctic or Oriental region, and secondarily dispersed into other areas. One of the *Paramblynotus* groups that occurs in the eastern Palearctic (the *scaber* group) has retained many ground-plan features of the genus and may be the sister group to all the other species. Furthermore, *Paramblynotus* is more speciose and phylogenetically diverse in the eastern Palearctic and Oriental regions than anywhere else. The genus is only represented by two very



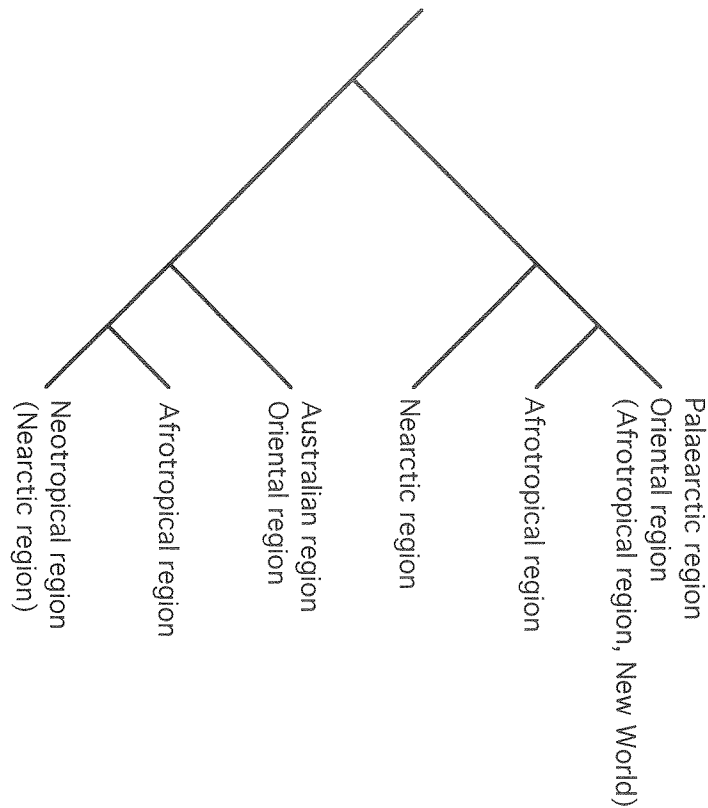


Fig. 87. Area cladogram for the Liopteridae. Distribution areas in parentheses are believed to be the result of recent dispersal events. The terminal branches correspond to the following liopterid taxa (from left to right): *Paramblynotus*, *Decellea*, *Kiefferiella*, Dallatorrellinae, Oberthuerellinae, Liopterinae.

*zonatus* group) and, apparently, by only two lineages in the Afrotropical region (the *trisetosus* and *nigricornis* groups).

Looking at the presumed original distribution areas (Fig. 87), the historical biogeography of the Liopteridae corresponds fairly closely to the break-up of Pangaea during the Mesozoic inferred from geological data (Owen 1983, Denham & Scotese 1989). Thus, it is possible to use geological data to date some of the speciation events in the phylogeny of the Liopteridae.

The split between Liopterinae and Oberthuerellinae can be dated to the lower Cretaceous (about 110 Ma), when central Africa drifted away from central South America. The separation of the Dallatorrellinae from the stem species of the Liopterinae + Oberthuerellinae possibly corresponds to the formation of a deep oceanic trench between

west Gondwana (South America + Africa) and east Gondwana (Australia + Antarctica) in the upper Jurassic (about 150 Ma). This dating assumes that the Dallatorrellinae were originally present in the Australian region and eastern Antarctic, and secondarily dispersed into the Oriental region. The split between *Kiefferiella* and the stem species of *Decellea* + *Paramblynotus* may correlate with the separation of North America from western Africa in the middle Jurassic (about 180 Ma). Alternatively, *Kiefferiella* might have been separated from *Decellea* + *Paramblynotus* later in the Jurassic or in the Cretaceous by the successive formation of the northern part of the Atlantic Ocean; this assumes that *Decellea* is an African remnant of a primitively western Palaearctic group that dispersed into Africa.

## Discussion

### Phylogeny and classification

In keys to the families of the Cynipoidea, liopterids were previously recognized mainly on the size of the metasomal terga, abdominal tergum 5, 6 or 7 being the largest in lateral view (Weld 1952, Riek 1971, Quinlan 1979). This does not hold as a good diagnostic character for the family, because members of *Kiefferiella* have tergum 3 or 4 largest in lateral view. Part of the problem in defining the family in previous studies was the uncertainty in the placement of some genera. The Liopteridae as delimited here form a distinctive family of cynipoids, and can easily be recognized on combinations of features such as the foveate sculpture on the pronotum and scutellum, the presence of laterodorsal processes on the scutellum, and the short metatibia.

The generic classification of the Liopteridae proposed in this paper is not dramatically different from that used previously (Hedicke and Kerrich 1940, Weld 1952), but the definitions of genera have changed with the inclusion of more species, and a few species have been transferred between closely related genera in order to create monophyletic groups. A notable exception is the generic classification of the subfamily Liopterinae. This subfamily was previously divided into three genera (Hedicke and Kerrich 1940): *Liopteron*, *Pseudibalia* and *Plastibalia*. Of these, *Pseudibalia* was defined based on the presence of a distal process on metatarsomere 1, and included a single species, whereas *Plastibalia* comprised two closely related species possessing a distal process on metatarsomere 2. The remaining species of the subfamily were grouped into the genus *Liopteron* (Hedicke and Kerrich 1940, Weld 1952), a group that was clearly paraphyletic relative to the other genera. In the classification proposed in this paper, Liopterinae is divided into three monophyletic genera of roughly the same size: *Liopteron sensu stricto* and the redefined genera *Peras* and *Pseudibalia*. The species falling under the previous definition of *Plastibalia* now appear as a minor lineage characterized by some striking anomorphies within the genus

*Liopteron sensu stricto*. Likewise, the genus *Pseudibalia* in the old sense constitutes an apomorphic subgroup within the redefined *Pseudibalia*.

In the former classification of the Liopteridae, several genera were characterized by the presence of distal processes on metatarsomere 1 or on metatarsomere 2 (Hedicke and Kerrich 1940, Weld 1952). However, these processes appear to be unreliable as diagnostic characters of genera, because they are expressed to varying degrees in several species that are not particularly closely related (see Table 3). The taxonomic distribution of these processes within the family suggests that the processes were absent in the ground plan of the Liopteridae, and evolved several times independently within the family. A well developed, tubular process on metatarsomere 1 has apparently evolved three times in the Liopteridae: once in the *borneanus* group of *Paramblynotus*, once within *Xenocynips* and once within *Pseudibalia*. A well developed, tubular process on metatarsomere 2 has evolved once, within *Liopteron*. Despite considerable structural similarity between the latter and the tubular process on metatarsomere 2 in *Ibalia* and *Heteribalia*, these structures cannot be homologous unless they were lost many times independently in the Liopteridae and Ibaliidae.

*Decellea* was synonymized with *Paramblynotus* by Weld (1962:279). Although *Paramblynotus* and *Decellea* together appear to form a monophyletic group (Figs. 85, 86), there are several reasons not to include *Decellea* in *Paramblynotus*. First, it is the phenetic distinctness of *Decellea*, the single species of that genus being very different from all other species of *Paramblynotus*. Second, it is the possession by *Decellea* of several apparent, striking plesiomorphies, such as the exposed abdominal sterna 4–6 and the long metatibia. Third, the inclusion of *Decellea* in *Paramblynotus* would obscure the biogeographic relationships because the African genus *Decellea* is not closely related to the African species of *Paramblynotus*.

*Paramblynotus* is in obvious need of more taxonomic research. It is, by far, the most speciose genus in the Liopteridae. *Paramblynotus* is composed of several distinct groups, but it was not possible during the current study to find a satisfac-

tory division of the genus into smaller units that were all monophyletic. The *borneanus* group, part of it formerly recognized as the separate genus *Paribalia*, is undoubtedly monophyletic. This group is characterized by the occiput being vertically strigate and the pronotal crest being prominently triangularly raised medially; most species also have a tubular process on metatarsomere 1. The *borneanus* group is nested within a larger group of *Paramblynotus* comprising the *borneanus*, *punctulatus* and *trisetosus* groups. This assemblage is united by the female metasoma having abdominal tergum 8 entirely covered by tergum 7. The *zonatus* and *ruficollis* groups may form a monophyletic lineage characterized by the scuto-scutellar sulcus being divided into more than two foveae. Finally, an assemblage consisting of all species groups except the *scaber* group appears to be monophyletic based on the parascutal carina being conspicuously raised posteriorly. However, most of the hypotheses about intrageneric relationships presented here are based on single characters and need to be confirmed through further work on *Paramblynotus*.

The proposed classification of the Liopteridae into subfamilies (Fig. 86) has the advantage that it recognizes as subfamilies morphologically and biogeographically distinct groups that were also well supported as monophyletic in the phylogenetic analysis. Furthermore, it represents the minimum amount of change to the old classification of Hedicke and Kerrich (1940) needed to obtain monophyletic subfamilies. Two of the three subfamilies of Hedicke and Kerrich, the Liopterinae and Oberthuerellinae, were monophyletic according to the present analysis. However, their third subfamily, the Mesocynipinae, came out as paraphyletic, with the sister genera *Mesocynips* and *Dallatorrella* being more closely related to the Oberthuerellinae and Liopterinae than to the remaining genera of the subfamily, which grouped together. The Mesocynipinae therefore had to be divided into two subfamilies, the Dallatorrellinae and Mayrellinae, to obtain monophyletic groups; the alternative would have been to let the entire family go into a single subfamily. The name Mesocynipinae was proposed by Kerrich (in Hedicke and Kerrich 1940), and subsequently used

by Weld (1952) and others, but falls as a junior synonym of Dallatorrellinae Kieffer, 1911.

#### Biology and diversity

The scanty biological data available indicate that liopterids are parasitoids of wood-boring or stem-boring insect larvae, probably mainly cerambycid and buprestid larvae in deciduous trees and bushes, but few specific details about liopterid biology are known. There are only two published rearing records (Weld 1956): the type female of *Kiefferiella acmaeodera* was reared from *Eurotia lanata* (Chenopodiaceae) infested with a buprestid beetle, *Acmaeodera pulchella*, and three reared females of *Kiefferiella rugosa* were observed to exit from fresh *Acmaeodera* tunnels. A few additional rearing records were obtained from label data in the material examined for the present study: one species of *Kiefferiella* was reared from *Prosopeis glandulosa* (Fabaceae), one species of *Paramblynotus* from *Dalbergia fusca* (Fabaceae), another species of *Paramblynotus* from "Coleoptera", and *Decellea yangambicola* from "Coleoptera" and "Lepidoptera." Several species have also been collected on tree trunks of various deciduous trees, some of which were dead or dying. Diaz (1973) reported one species of *Paramblynotus* collected from tree attacked by cerambycid larvae, and Z. Yang (pers. comm.) observed females of another species of *Paramblynotus* ovipositing into a recently killed tree attacked by cerambycid and sirioid larvae. Unfortunately, the available biological data refer only to the Mayrellinae, with one exception: three females of one species of *Dallatorrella* (Dallatorrellinae) collected on a log of *Syzygium* (Myrtaceae). There are no observations made on the biology of the Liopterinae and Oberthuerellinae.

Several morphological features of adult liopterids appear to be specific adaptations for boring in wood. The strong mandibles are well suited for chewing wood, and other features, such as the transversely ridged mesoscutum, the processes on the tibiae and tarsi and the short and stout hind legs, appear to serve to propel the animal in the tunnel and brace it against the tunnel walls. It is possible

that the foveate sculpture so characteristic of liopterids is also associated with a wood-boring habit. The foveate sculpture may simply be a cheap way of making a strong exoskeleton, needed for attachment of strong muscles and for bracing the action of the mandibles on the wood. In the closely related family Ibalidae, adults of *Ibalia* are known to chew their own exit tunnels (Chrystal 1930, Spradbery 1970), and there is one observation of a liopterid, *Kiefferiella rugosa*, behaving similarly (Weld 1956).

It is not known whether liopterid females are "pokers" that poke into existing holes when they lay their eggs, or "drillers" that actively drill through the wood. The structure of the apical part of the terebra suggests that liopterid females are pokers. Drillers, e.g., *Orussus* (Cooper 1953) and *Rhyssa* (Gardiner 1966), usually have both the united second valvulae and the first valvulae equipped with distinct teeth. This makes the drilling efficient, in that at least one valvula can always support the action of the others. Liopterids, on the other hand, lack teeth on the first valvulae, and the united second valvulae usually have rather weak teeth. An additional structural feature that seems to indicate a poking habit for the Liopteridae is the extremely long, coiled terebra (Fergusson 1988, own obs.). In both respects, liopterids are similar to other pokers, such as the Ibalidae (Chrystal 1930, Spradbery 1970, Ronquist & Nordlander 1989) and the Megalyridae (Rodd 1951). Fergusson (1988) suggested that some liopterids were borers and others pokers based on interspecific variation in the strength of the teeth on the united second valvulae. Z. Yang observed females of an undescribed species of *Paramblynotus* apparently drilling into a tree trunk, but it is conceivable that the females were actually poking into small preexisting holes that were not observed (Z. Yang, pers. comm.).

Nordlander (1984) estimated that the total number of liopterid species in the world was in the range of 160-400. Unfortunately, it is not possible to estimate the total number of existing liopterid species from the specimens examined for the present study because of the high proportion of species represented by single specimens in the material. However, it is clear that the total number of species

far exceeds 130. From the material studied, it appears that the Afrotropical region is particularly poorly sampled, but it is difficult to find any region of the world where the liopterid fauna has been adequately sampled.

#### Fossils, biogeography, and the age of the Liopteridae

The single specimen of *Kiefferiella connexiva* is the only fossil liopterid known. It was originally described in a separate genus, *Protoibalia*. Brues (1910) stated that the fossil is of Miocene origin, but later radiometric dating places the Florissant beds in the upper Eocene, on the border to Oligocene (34.1 Ma ago; Epis & Chapin 1974).

I examined the fossil without being able to add anything to the original description (Brues 1910:15-16). Together with biogeographic evidence, the characters that can be clearly seen in the specimen indicate that it belongs to the genus *Kiefferiella*. The fossil has a distinctly transversely ridged mesoscutum, a condition that only occurs in the Austrocynipidae, Ibalidae and Liopteridae among extant cynipoids (a few Eucoilinae also have this sculpture on the mesoscutum, but the fossil lacks the scutellar plate characteristic of the Eucoilinae). The short metatibia (cf. Brues 1910: fig. 8) indicates that the fossil is a liopterid, and the sculpture laterally on the pronotum seems to support this conclusion. The short marginal cell in combination with the simple antenna suggest the Mayrellinae, and the short first flagellomere is indicative of *Kiefferiella*, although some species of *Paramblynotus* also have a short first flagellomere. However, the species of *Paramblynotus* occurring in the New World have a long first flagellomere, and the biogeographic analysis indicates that *Kiefferiella* has had a long history in the Nearctic region, whereas *Paramblynotus* dispersed into the area relatively recently. Furthermore, *Paramblynotus* presently occurs only in the southernmost portion of the Nearctic, whereas *Kiefferiella* species occur as far north as Idaho, and *K. connexiva* was found in Colorado. Therefore, it seems likely that the fossil belongs to the genus *Kiefferiella*, to which it is transferred in this paper.

Although the only known fossil liopterid is from the upper Eocene, the biogeographic analysis suggested that the Liopteridae existed as early as the Jurassic. This conclusion may be construed as surprising, because the oldest known cynipoid fossils are from the lower Cretaceous (Rasnitsyn & Kovalev 1988), and parasitic wasps in general are rare in the Jurassic (Königsmann 1976, 1978, Rasnitsyn 1980, 1988). However, unless major liopterid lineages have gone extinct, it is likely that the family was represented by only a few species in the Jurassic and Cretaceous. Furthermore, if liopterids were as rare then as they are now, it is maybe not surprising that no liopterid fossils have been recovered from the Mesozoic. If the suggested dating is correct, the liopterids must be one of the oldest groups of cynipoids, and hence would be likely to represent one of the basal lineages of the superfamily. The early evolution of the Cynipoidea and the relationships between liopterids and other cynipoids will be discussed in detail elsewhere (Ronquist in press).

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## Appendix

List of material studied, sorted to species, with depositories. Distribution records in parentheses are from Hedicke and Kerrich (1940), Belizin (1951) or Quinlan (1979); other distribution records are from material studied. The order of the species is more or less arbitrary, except in *Paramblynotus* where some grouping according to perceived relationships has been attempted. Acronyms for insect collections are explained in "Materials and methods". In the southeastern Palearctic and Australian regions, distribution records are given in terms of islands rather than countries. T = Type specimens.

Genus, species	No.	Sex	Distribution records	Depositories
<i>Kiefferiella</i>				
<i>acmaeodera</i>	1	♀	USA: ID	USNM (1T)
<i>rugosa</i>	2	♀	USA: CA	USNM (1T), BMNH (1)
n. sp. 1	18	♂	USA: TX	USNM (18)
n. sp. 2	10	♂ ♀	USA: CA	CASC (9), AEIC (1)
<i>Decellea</i>				
<i>yangambicola</i>	6	♀	Zaire, Uganda	BMNH (5), MRAC (1T)
<i>Paramblynotus</i>				
<i>scaber</i> group				
<i>scaber</i>	1	♀	Russia: Primorskij Kraj, [Khabarovsk, Irkutsk]	ZMAS (1T)
n. sp. 1	1	♀	Russia: Vladivostok	NHRS (1)
<i>zonatus</i> group				
<i>zonatus</i>	4	♀	US: TX, Guatemala, Costa Rica	CNCI (2), BMNH (1), USNM (1T)
n. sp. 2	225	♂ ♀	Brazil MCZC (7), CMS (6), NHRS (4)	AEIC (117), BMNH (81), CNCI (10),
<i>ruficollis</i> group				
<i>malayensis</i>	4	♂ ♀	Borneo	USNM (4T)
<i>ruficollis</i>	18	♂ ♀	Laos, Malaya, Singapore, Borneo, Sibuyan, Negros (3), RMNH (2), AEIC (1)	BMNH (2+4T), USNM (5+1T), BPBM
<i>trisectus</i>	13	♀	Nepal, Thailand CNCI (1)	CMS (9), BPBM (1+1T), BMNH (1),
n. sp. 3	3	♂ ♀	Burma, Laos	BMNH (2), BPBM (1)
n. sp. 4	1	♀	Borneo	BPBM (1)
n. sp. 5	1	♀	Borneo	BMNH (1)
n. sp. 6	4	♀	Malaya	AEIC (4)
n. sp. 7	1	♀	Laos	BPBM (1)
<i>nigricornis</i> group				
<i>nigricornis</i>	1	♀	Zaire	MRAC (1T)
n. sp. 8	1	♀	South Africa	BMNH (1)
n. sp. 9	4	♂ ♀	Angola, Zimbabwe, South Africa	BMNH (2), CNCI (2)
n. sp. 10	1	♀	Zaire	BMNH (1)
n. sp. 11	1	♀	Namibia	BMNH (1)
n. sp. 12	1	♀	South Africa	BMNH (1)
n. sp. 13	3	♀	Zaire, Uganda, South Africa	AEIC (1), BMNH (1), IRCT (1)
<i>punctulatus</i> group				
<i>punctulatus</i>	87	♀	Malaya, Borneo, Sulawesi, Ogasawara, American Samoa	AEIC (63), BMNH (9+3T), USNM

Genus, species	No.	Sex	Distribution records	Depositories
n. sp. 14	3	♀	Malaya	AEIC (3)
n. sp. 15	1	♀	Taiwan	AEIC (1)
<i>reticulatus</i>	8	♂ ♀	Laos, Malaya, Bintan	BMNH (5), BPBM (2), ZMHB (1T)
<i>ruficeps</i>	31	♂ ♀	Malaya, Singapore	AEIC (23), USNM (3+4T), MCZC (1)
<i>annulicornis</i>	21	♂ ♀	Sumatera, Malaya, Borneo, Sulawesi	AEIC (11), RMNH (4), ROME (3), BMNH (1T), BPBM (1)
n. sp. 16	1	♀	Vietnam	BPBM (1)
n. sp. 17	1	♀	Malaya	AEIC (1)
n. sp. 18	2	♀	Sumatera, Malaya	AEIC (1), ROME (1)
n. sp. 19	3	♀	Sulawesi	BMNH (3)
n. sp. 20	2	♂ ♀	Malaya, Borneo	AEIC (1), RMNH (1)
<i>clarus</i>	3	♂ ♀	Sri Lanka, Mindanao	USNM (1+1T), CASC (1)
<i>formosanus</i>	1	♀	Taiwan	DEIC (1T)
n. sp. 21	3	♀	Vietnam, Malaya, Sumatera	BMNH (2), NHRS (1)
n. sp. 22	1	♀	Laos	BPBM (1)
n. sp. 23	2	♂	China: Hainan	BMNH (2)
<i>trisetosus</i> group				
<i>trisetosus</i>	1	♀	Zaire	MRAC (1T)
n. sp. 24	7	♀	Zimbabwe, South Africa	AEIC (4), BMNH (2), CNCI (1)
n. sp. 25	8	♂ ♀	Cameroun, Zaire	BMNH (8)
n. sp. 26	2	♀	Zaire	BMNH (2)
n. sp. 27	2	♀	Zaire	BMNH (2)
n. sp. 28	1	♀	Cameroun	BMNH (1)
<i>borneanus</i> group				
<i>borneanus</i>	2	♂ ♀	Borneo	USNM (2T)
<i>dyak</i>	24	♂ ♀	Malaya, Borneo, Sulawesi (2T), CFR (1), RMNH (1)	AEIC (12), BPBM (5), BMNH (3), USNM
<i>esakii</i>	1	♂	Japan: Honshu	KUEC (1T)
<i>kosugii</i>	4	♂	Japan: Hokkaido	EIHU (3T), BMNH (1T)
n. sp. 29	8	♀	Malaya	AEIC (7), CFR (1)
n. sp. 30	4	♀	Malaya	AEIC (3), CFR (1)
n. sp. 31	1	♀	Malaya	AEIC (1)
n. sp. 32	1	♀	Vietnam	BPBM (1)
n. sp. 33	1	♂	Laos	BPBM (1)
n. sp. 34	1	♀	Borneo	BMNH (1)
n. sp. 35	1	♀	Mindoro	AEIC (1)
n. sp. 36	4	♂ ♀	Borneo, Palawan, Mindanao	BPBM (2), BMNH (1), USNM (1)
n. sp. 37	9	♀	Laos, Sulawesi, New Guinea	BMNH (8), BPBM (1)
n. sp. 38	1	♀	Laos	BPBM (1)
n. sp. 39	1	♀	New Guinea	BMNH (1)
n. sp. 40	6	♀	Malaya, Borneo, Sulawesi	AEIC (3), RMNH (2), BMNH (1)
<i>Mesocynips insignis</i>	10	♂ ♀	Malaya, Borneo, Negros, Mindanao	BMNH (5+1T), USNM (3), ZLMU (1)
<i>Dallatorrella albata</i>	2	♀	Mindanao	BMNH (1), USNM (1T)
<i>rubriventris</i>	6	♂ ♀	Australia: WA, NSW	MCZC (3), BMNH (1+1T), ANIC (1)
<i>carinifrons</i>	4	♀	Malaya, Singapore, Borneo	BMNH (2+1T), AEIC (1)
n. sp. 1	4	♀	New Guinea, ?Aru	BMNH (4)
n. sp. 2	8	♀	Sulawesi, Bacan	BMNH (7), USNM (1)
n. sp. 3	1	♀	New Guinea	BPBM (1)

Genus, species	No.	Sex	Distribution records	Depositories
n. sp. 5	1	♂	Malaya	BMNH (1)
<i>Xenocynips subsquamata</i>	1	♀	Cameroun	DEIC (1T)
n. sp. 1	1	♂	Zaire	CASC (1)
n. sp. 2	1	♂	Cameroun	BMNH (1)
<i>Tessmannella expansa</i>	1	♀	Gabon	MNHN (1T)
<i>nigra</i>	1	♀	Zaire	ZMHB (1T)
<i>spinosa</i>	2	♀	Zaire	ZMHB (2T)
<i>Oberthuerella absinda</i>	3	♂ ♀	Zaire, Zambia	BMNH (1+2T)
<i>aureopilosa</i>	2	♀	Zaire	BMNH (1), MRAC (1T)
<i>breviscutellaris</i>	2	♀	Zaire, Zimbabwe	BMNH (1), MRAC (1T)
<i>crassicornis</i>	5	♂ ♀	Zaire, Malawi	BMNH (3), MRAC (2T)
<i>lenticularis</i>	8	♂ ♀	Malawi, Madagascar, [South Africa]	BMNH (7), USNM (1)
<i>longicaudata</i>	1	♀	Zaire	MRAC (1T)
<i>longispinosa</i>	3	♂ ♀	[Ivory Coast, Gabon], Zaire, Malawi	BMNH (2), MRAC (1T)
<i>nigrescens</i>	1	♀	Zaire	MRAC (1T)
<i>transiens</i>	1	♂	Zaire	MRAC (1T)
<i>triformis</i>	2	♂ ♀	Tanzania	BMNH (1+1T)
n. sp. 1	1	♀	Zaire	MCZC (1)
n. sp. 2	1	♂	Zaire	MCZC (1)
n. sp. 3	1	♂	South Africa	MHNG (1)
n. sp. 4	1	♂	Liberia	USNM (1)
n. sp. 5	1	♀	South Africa	CNCI (1)
<i>Liopteron abdominale</i>	4	♀	Brazil	BMNH (2), OXUM (1T), USNM (1)
<i>apicale</i>	2	♂	Panama, Brazil	OXUM (1T), UCDC (1)
<i>bicolor</i>	1	♂	Bolivia	ZMBH (1T)
<i>bispinosum</i>	2	♀	French Guiana, Brazil	AEIC (1), MNHN (1T)
<i>compressum</i>	8	♂ ♀	Peru, Brazil (1), NHMV (1), ZSMC (1T)	ZMBH (2), OXUM (2), CASC (1), MCZC
<i>immarginatum</i>	5	♂ ♀	Brazil	BMNH (1+1T), NHMV (2), CNCI (1)
<i>levilaterale</i>	1	♀	Brazil	MNHN (1T)
<i>nigripenne</i>	4	♂ ♀	Brazil	BMNH (2T), AEIC (1), OXUM (1T)
<i>Peras clavicornis</i>	1	♀	Brazil	OXUM (1T)
<i>fenestratum</i>	8	♂ ♀	Brazil (1T)	CFR (4), MCZC (2), CNCI (1), USNM
<i>fuscicornis</i>	7	♀	Brazil	OXUM (3+1T), BMNH (3)
<i>nigra</i>	3	♀	Guiana, Peru	BMNH (1), CASC (1), ZMHB (1T)
<i>scaberrimum</i>	13	♂ ♀	Mexico, Brazil	BMNH (8+2T), AEIC (3)
<i>subpetiolatum</i>	2	♀	Brazil	OXUM (1T), USNM (1)
n. sp. 1	1	♂	Surinam	USNM (1)
n. sp. 2	1	♀	Brazil	OXUM (1)
n. sp. 3	1	♀	Colombia	BMNH (1)
<i>Pseudibalia bifasciata</i>	1	♂	Brazil	OXUM (1T)
<i>confusa</i>	1	♀	Brazil	ZMHB (1T)
<i>fasciatipennis</i>	1	♀	Mexico [Brazil]	BMNH (1T)
<i>intermedia</i>	1	♀	Brazil	USNM (1T)

Genus, species	No.	Sex	Distribution records	Depositories
<i>tarsalis</i>	1	♀	Brazil	USNM (1T)
<i>unifasciata</i>	1	♂	Brazil	OXUM (1T)
<i>westwoodii</i>	1	♀	Panama	BMNH (1T)
n. sp. 1	2	♀	Brazil	AEIC (2)
n. sp. 2	1	♀	Brazil	CNCI (1)
n. sp. 3	1	♀	Brazil	AEIC (1)
n. sp. 4	1	♀	Mexico	USNM (1)
n. sp. 5	1	♀	Ecuador	QCAZ (1)
n. sp. 6	1	♀	Brazil	CNCI (1)
n. sp. 7	1	♀	Brazil	OXUM (1)
n. sp. 8	1	♂	Brazil	AEIC (1)
n. sp. 9	1	♂	Brazil	AEIC (1)
n. sp. 10	1	♂	Mexico	CNCI (1)
n. sp. 11	1	♀	Brazil	AEIC (1)
n. sp. 12	1	♀	Bolivia	USNM (1)
n. sp. 13	2	♀	Panama	USNM (2)

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