

# Phylogeny and classification of the Orussidae (Insecta: Hymenoptera), a basal parasitic wasp taxon

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The Orussidae is a small family of parasitic wasps, comprising 75 species worldwide. It occupies a key position within the Hymenoptera, being the sistergroup of the Apocrita, a taxon containing all other parasitic wasps. In total, 163 morphological characters were scored for 74 species of Orussidae and five outgroup taxa. The dataset was analysed under different weighting schemes. The results do not support a single phylogenetic hypothesis, but most relationships were retrieved in the majority of the cladistic analyses. Earlier attempts at tribal and subfamily classifications of the Orussidae are not corroborated. Enforcing a strictly cladistic classification at these levels would require the recognition of many redundant taxa without enhancing the information content. It is proposed that formal recognition of tribes and subfamilies within the Orussidae be abandoned. The generic concepts of the family are revised. Sixteen genera are recognized; detailed descriptions and illustrations of each are provided, as is a key to the genera. The monophyly of most genera as defined here is well supported, with the exception of *Guiglia* Benson, 1938. *Guiglia* is retained because alternatives to monophyly of this genus are not well supported either. *Heliorussus* Benson, 1955, **syn. nov.**, is incorporated in *Orussus* Latreille, 1796; the species formerly included in *Heliorussus*, *Orussus schoutedeni* Guiglia, 1937, **combination reestablished**, *O. scutator* (Benson, 1955) **comb. nov.** and *O. spinifer* (Benson, 1955), **comb. nov.** are transferred to *Orussus*. *Leptorussus kwazuluensis* **sp. nov.** is described; *Pseudoryssus emanuelis* Guiglia, 1956 **syn. nov.** is considered a junior synonym of *Pseudoryssus henschii* (Mocsáry, 1910). An annotated key to the world species of *Orussus* is included as an appendix. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, 139, 337–418.

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## INTRODUCTION

The Orussidae is a small family of parasitic wasps, unique among the Hymenoptera in being the only non-apocritan parasitoid taxon. They possess a combination of advanced and plesiomorphic traits (Vilhelmsen *et al.*, 2001), the absence of the ‘wasp-waist’ of the Apocrita being the most striking example of a retained plesiomorphy. The Apocrita with more than 100 000 described species, the majority of which are parasitoids, comprise the bulk of the Hymenoptera. Indeed, the main reason for the present day diversity of the Apocrita is probably their successful exploitation of the parasitoid lifestyle. In the most recent cladistic treatments of the phylogeny of the basal hymenopteran lineages (previously known as the sub-

order ‘Symphyta’), the Orussidae comes out strongly supported as the sistergroup of the Apocrita (Ronquist *et al.*, 1999; Vilhelmsen, 2001a). This implies that parasitism arose in the common ancestor of Orussidae and Apocrita. Therefore, understanding the lifestyle of the Orussidae is crucial in elucidating the evolution of parasitism within Hymenoptera.

Biological information for any species of Orussidae is scarce, most having been obtained from a few species of *Orussus*. Latreille (1811) provided the first detailed account of the morphology and lifestyle of any orussid (*Orussus abietinus*); he noted the close association with wood (p. 559: ‘...leurs larves vivent certainement dans l’intérieur du bois.’). The interpretation of the evidence accumulated since then has been contentious. Everyone agrees that orussid larvae are associated with galleries in dead wood made by other woodliving insect larvae. Most workers favour an ectoparasitic lifestyle for Orussidae, usually with

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Buprestidae (Coleoptera) as the (presumed) host (e.g. Burke, 1917; Rawlings, 1957; Powell & Turner, 1975; Nutall, 1980); in contrast, Cooper (1953) suggested that *Orussus* is feeding mainly on the frass in the galleries of wood-boring insects. However, the available evidence considered as a whole supports the parasitoid hypothesis (see Vilhelmsen *et al.*, 2001 for further discussion). Remarkable adaptations for ovipositing in wood includes an echolocation system involving the antennae and the forelegs in the female and a very long (at least twice the body length) concealed ovipositor (Vilhelmsen *et al.*, 2001).

Larval adaptations for the parasitoid lifestyle in a confined habitat include the reduction of the sensory apparatus (eyes and antenna), mouthparts (maxillae and labium), and locomotory apparatus (thoracic legs and suranal process (Vilhelmsen, 2003; see Rohwer & Cushman, 1917 and Parker, 1935 for further information about anatomy of the immature stages of the Orussidae). These features are all shared with apocritan larvae. An apparently unique feature is the presence of dorsal transverse rows of small cuticular backward curving spines on all thoracic and abdominal segments throughout larval development. These spines have also been reported in late instar larvae of *Schlettererius cinctipes* (Cresson) (Stephanidae, see Taylor, 1967). In Orussidae, they presumably facilitate moving in galleries inside the wood in order to seek out hosts that the ovipositing female was unable to reach (Vilhelmsen, 2003). Another feature not reported for any other Hymenoptera is the presence of cuticular folds in the hindgut which perhaps allow the orussid larva to clamp it shut during development; anatomically, the mid- and hindgut are continuous throughout most of larval development, contrary to the condition in virtually all Apocrita examined (Vilhelmsen, 2003). Shutting the hindgut and the postponement of defecation until just prior to pupation prevent fouling and subsequent putrefaction of the host; this is thought to be an important adaptation to the parasitoid lifestyle in Hymenoptera, especially endoparasitism (Gauld & Hanson, 1995).

The unique status of the Orussidae was recognized at an early stage in higher-level hymenopteran systematics. In precladistic days, this was translated by some authors into assigning them an 'intermediate' position between 'Symphyta' and Apocrita. Rohwer & Cushman (1917) erected the suborder Idiogastra solely to accommodate the Orussidae, and Bischoff (1926) argued that they should be placed in a separate superfamily among the 'Symphyta'. Others united them with the Apocrita (Börner, 1919; Rasnitsyn, 1988; [his Vespina]) or placed them among the 'Symphyta', usually in the Siricoidea (woodwasps) (Dalla Torre, 1894; Konow, 1905a,b; Ross, 1937; Benson, 1938a; Königsmann, 1977), depending on whether

apomorphic or plesiomorphic features were emphasized in the classification. Only with the application of quantitative cladistics did the systematic position of the Orussidae become firmly established. Currently, they are placed in a separate superfamily (Orussoidea), the most inclusive formal category below order level currently employed by hymenopterists (Vilhelmsen, 2001a).

In contrast to the present well corroborated phylogenetic position of the Orussidae within the Hymenoptera, the internal phylogeny of the family is entirely uncharted. The most recent comprehensive effort in orussid systematics on a global level is Guiglia's (1965) catalogue of the world species. It is a useful embarkation point for further exploration, but it was of course not done within a cladistic context, and no attempt was made to accumulate material for an exhaustive study. Regional surveys of most local faunas exist: Africa (Benson, 1935a; Guiglia, 1937a: *Chalinus*; Guiglia, 1937b: *Orussus*), Australia (Benson, 1938b; Riek, 1955), Europe (Guiglia, 1954a; Kraus, 1998), Far East/South-eastern Asia (Yasumatsu, 1954), North America (Ross, 1937; Middlekauff, 1983), Neotropical (Smith, 1988); these are all limited geographically.

The main obstacle to further progress in orussid systematics is the scarcity of material. Orussidae are uncommon and rarely collected. The most fortuitous record is that of the holotype of *Orussella dentifrons* (Philippi, 1873), which was plucked from a cobweb. The somewhat incomplete condition of this specimen led Konow (1897a) to conclude that it 'entschieden besser in den Papierkorb gewandert wäre' ['It would have been better to have thrown it in the paper bin.']. Abuse notwithstanding, the species is currently regarded as valid and placed in its own genus, attesting to the distinctiveness of the taxon. Only a few major collections hold material of more than half a dozen species of Orussidae. Furthermore, many species are represented by only a handful of specimens, spread in collections all over the world. Significantly, the only previous revisions of the higher-level classification were undertaken by R. B. Benson (1935a, 1955a) who worked in the NHML, which holds the largest and most diverse collection of Orussidae in the world by far.

The present revision is the most comprehensive effort in orussid systematics to date: 75 species in 16 genera are recognized. Material from about 50 collections from all over the world has been examined, including 57 primary types. This represents all but one to two of the species considered valid. A large morphological dataset has been compiled and analysed with cladistic computer software. The generic classification is revised in accordance with the results of the cladistic analysis, and the relevance of the subfamily and tribal classifications is discussed.

In addition to the extant species of Orussidae, two fossil taxa (*Mesorussus taimyrensis* Rasnitsyn, 1977; *Minyorussus luzzi* Basibuyuk, Quicke & Rasnitsyn, 2000) from the Upper Cretaceous have been assigned to the family. Furthermore, the family Paroryssidae from the Late Jurassic has traditionally been regarded as constituting the ancestors of the Orussidae (Rasnitsyn, 1969, 1980, 1988, 2002). These taxa and their relationships with extant Orussidae are reviewed and discussed in Vilhelmsen (in press).

The Orussidae are widely distributed, with the main diversity in the southern hemisphere, but representatives are found in all major biogeographical regions: the Afrotropical (16 species), Australian (17), Nearctic (8), Neotropical (16), Oriental (6), and Palearctic (14 (two species occur in two regions)). The presence of several disparate lineages in each of these regions indicates that the biogeography of the Orussidae is highly complex. The distributional history of the family is discussed in relation to major events in the tectonic history of the Earth (e.g. the breakup of the supercontinent Gondwana in the late Mesozoic) in Vilhelmsen (in press).

#### SYSTEMATIC HISTORY

The first species of Orussidae to be described was *Orussus abietinus* (Scopoli, 1763), as *Sphex abietinus*. Curiously, neither of the two outstanding 18th century entomologists described what is today considered a valid species. Linné failed to describe any orussids at all, whereas Fabricius described the species *Sirex vespertilio* (Fabricius, 1793) and *Oryssus coronatus* Fabricius, 1798; both these names have long since been synonymized with *O. abietinus*. Latreille (1796) placed *O. abietinus* in its own genus, *Orussus*. The alternate spelling *Oryssus*, from Fabricius (1798), was used well into the 20th century (e.g. Tosawa, 1930; Guiglia, 1962), but *Orussus* is the original. The first family group name derived from *Orussus*, *Oryssites*, was introduced by Newman (1834). The family name in its present form was apparently first employed by Haliday (1839; 'Oryssidae') (see Guiglia, 1965 for an exhaustive list of family group names).

For more than a century after the description of *O. abietinus*, additional species were discovered at a sluggish rate. Westwood (1874) was the first to describe more than a single species. Since then, new species descriptions have accumulated more rapidly. The 'golden age' in the systematics of Orussidae was from the mid-1930s through the 1950s (with a notable hiatus around WWII; no new names were published between 1938 and 1950), where 25 new species were

described. This was mainly due to the efforts of Guiglia and Benson. They hold the joint record for published species group names in the Orussidae, having proposed 12 each (not all valid; see below and Vilhelmsen, 2001b; Vilhelmsen & Smith, 2002). The problems with acquiring material for comparison (see above) and the publication of many descriptions in obscure journals has led to a high degree of synonymy in certain genera. For example, *Stirocorsia trifasciata* (Cameron, 1906) and *S. rossi* (Yasumatsu, 1952) were both described from New Guinea, the type locality being identical; both are currently considered junior synonyms of *S. maculipennis* (Smith, 1859) (Vilhelmsen & Smith, 2002).

At the moment, a renaissance in orussid systematics is taking place. Genera are being revised at the global level, instead of being treated piecemeal as part of regional surveys (see above). To date, the following genera have been revised: *Orussobaius* (Schmidt & Vilhelmsen, 2002), *Orussonia* (Schmidt & Gibson, 2001), *Chalinus* and *Mocsarya* (Vilhelmsen, 2001b), and the 'ophrynopine' genera (*Argentophrynopus*, *Guiglia*, *Kulcania*, *Ophrella*, *Ophrynon*, *Ophrynopus*, *Stirocorsia*; Vilhelmsen & Smith, 2002). With the present paper, all valid orussid genera except *Orussus* (but see Appendix) will be revised. The current pace of description of new species indicates that there are still many left to be discovered. Promising areas to look for additional species are the Neotropics and the Pacific islands, which have only been superficially sampled so far.

As the exploration of the diversity of Orussidae gained momentum in the second half of the 19th century, the need to develop a higher-level classification of the family arose. Kirby (1882) and Dalla Torre (1894) provided the first worldwide overviews of the family, accommodating all species within *Orussus* (as '*Oryssus*'). Konow (1897a,b) erected four new genera (*Chalinus*, *Mocsarya*, *Ophrynopus*, *Stirocorsia*) in addition to *Orussus*, employing this arrangement in his systematic surveys (Konow, 1897a, 1905a,b). Benson (1935a) added *Kulcania*, *Orussella* and *Pedicrista*; furthermore, he proposed the first subfamily classification of the family (see Table 1), erecting four subfamilies (Mocsaryinae, Ophrynopinae, Orussinae, Pedicristinae). He later revised this classification (Benson, 1955a), retaining only the Ophrynopinae and the Orussinae, but introducing six tribes (Guigliini, Leptorussini, Mocsaryini, Ophrynopini, Orussini, Pedicristini). This was adopted by Guiglia (1957, 1965), replacing Benson's earlier four-subfamily scheme employed in previous world cataloguing efforts (Guiglia, 1943).

Additional genera proposed in the Orussidae since Benson (1935a) are: *Ophrynella* (Ross, 1937), *Guiglia* and *Orussobaius* (Benson, 1938b), *Pseudoryssus*

**Table 1.** Previous higher-level classifications of the Orussidae

Benson (1935a)	Benson (1955a)/Guiglia (1965)
Mocsaryinae	Orussinae
	Mocsaryini
<i>Chalinus</i>	<i>Chalinus</i>
<i>Mocsarya</i>	<i>Mocsarya</i>
Orussinae	Orussini
	<i>Heliorussus</i>
<i>Orussus</i>	<i>Orussus</i>
	<i>Pseudoryssus</i>
	Leptorussini
	<i>Leptorussus</i>
<i>Orussella</i>	<i>Orussella</i>
	<i>Orussobaius</i>
	<i>Orussonia</i>
Pedicristinae	Pedicristini
<i>Pedicrista</i>	<i>Pedicrista</i>
Ophrynopinae	Ophrynopinae
	Ophrynopini
<i>Ophrynopus</i>	<i>Ophrynopus</i>
(incl. <i>Stirocorsia</i> )	<i>Stirocorsia</i>
	(+ <i>Ophrella</i> ; Middlekauff, 1985a)
	(+ <i>Ophrynon</i> ; Middlekauff, 1983)
	Guigliini
	<i>Guiglia</i>
<i>Kulcania</i>	<i>Kulcania</i>

(Guiglia, 1954a), *Heliorussus* and *Leptorussus* (Benson, 1955a), *Orussonia* (Riek, 1955), *Ophrynon* (Middlekauff, 1983), *Ophrella* (Middlekauff, 1985a), and *Argentophrynopus* (Vilhelmsen & Smith, 2002). Sixteen out of the 18 genera proposed in Orussidae are considered valid here, the exceptions being *Heliorussus* and *Ophrynella*. *Heliorussus* was erected for two very distinct African species which turn out to be deeply nested within the larger genus *Orussus* (see below). *Ophrynella* was proposed in the generic treatment of Nearctic sawflies by Ross (1937); it is based on a conflation of the genera *Kulcania* and *Ophrynopus*, caused by the neglect to study the type species, which do not occur within the range of Ross' survey (see Vilhelmsen & Smith, 2002 for further discussion). Most of the valid genera have undergone at most moderate changes in circumscription since they were erected. The comparative robustness of the genera contrasts starkly with the labile higher-level phylogeny (see discussion of generic relationships) and the considerable synonymy occurring at the species level; this emphasises the usefulness of current generic concepts for establishing a stable classification of the Orussidae.

## MATERIAL AND METHODS

### OUTGROUP MATERIAL

Five outgroup exemplars were included (see Tables 2 and 3), representing the 'woodwasp' superfamilies Siricoidea and Xiphydriodea (see Vilhelmsen, 2001a) and the apocritan superfamilies Megalyroidea, Stephanoidea and Trigonaloidea (see Goulet & Huber, 1993). Siricoidea and Xiphydriodea are the closest living relatives of the Orussidae + Apocrita, and the selected apocritan taxa are apparently basal within the Apocrita (Ronquist *et al.*, 1999). All but the Trigonaloidea are associated with wood, a substrate that was probably inhabited by the common ancestor of all parasitic Hymenoptera (Dowton & Austin, 2001). Some of the outgroup material was preserved in 70–95% ethanol and was dissected during previous studies (see Vilhelmsen, 2001a), after which it was stored in glycerol; this material was examined in the medium it was stored in.

### MATERIAL OF ORUSSIDAE

More than 900 specimens of Orussidae were examined for the present study (Table 2); almost all were pinned. Abbreviations for type depositories and collections providing material are listed below (curators in brackets); they follow those used in the Insect and Spider Collections of the World Web Site (<http://www.bishopmuseum.org/bishop/ento/codens-r-us.html>).

AEIC	American Entomological Institute, Gainesville, Florida, USA (D. Wahl).
AMNH	American Museum of Natural History, New York, New York, USA (J. M. Carpenter).
AMS	Australian Museum, Sydney, Australia (M. Moulds).
ANIC	Australian National Insect Collection, Canberra, Australia (S. Schmidt).
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
BLFU	Biological Laboratory, Fukui University, Japan.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA (G. Nishida).
CASC	California Academy of Sciences, San Francisco, California, USA (R. Zuparko).
CNCI	Canadian National Collection of Insects and Arachnids, Ottawa, Ontario, Canada (H. Goulet).
DEIE	Deutsches Entomologisches Institut, Eberswalde, Germany (S. Blank, A. Taeger).
EITH	Entomologisches Institut, Technische Hochschule, Zürich, Switzerland (S. Bieri, M. Schindler).

**Table 2.** Material examined. See Materials and Methods for abbreviations of depositories

Taxon	Author, date	No. of specimens (♀/♂)	Depositories
<i>Urocerus gigas</i> (SIR)	(Linné, 1758)	1/1 (excl. primary type)	ZMUC
<i>Xiphydria camelus</i> (XIP)	(Linné, 1758)	4/1 (excl. primary type)	ZMUC
<i>Schlettererius cinctipes</i> (STE)	(Cresson, 1880)	2/2 (excl. primary type)	ZMUC
<i>Megalyra fasciipennis</i> (MEG)	Westwood, 1832	4/2 (excl. primary type)	ZMUC
<i>Orthogonalys pulchella</i> (TRI)	(Cresson, 1867)	2/3 (excl. primary type)	ZMUC
<i>Argentophrynopus enigmus</i>	Vilhelmsen & Smith, 2002	1/0 (incl. primary type)	NMNH
<i>A. gauldi</i>	Vilhelmsen & Smith, 2002	2/2 (incl. primary type)	NHML, NMNH
<i>Chalinus berlandi</i>	Guiglia, 1935a	1/1 (incl. primary type)	MNHN, MRAC
<i>C. braunsi</i>	(Enslin, 1911)	11/15 (incl. primary type)	CNCI, EITH, EMEC, MCSN, NHML, NHMW, OLML, TMSA, ZMHB, ZMUC, ZSMC
<i>C. haugi</i>	du Buysson, 1902	1/0 (incl. primary type)	MNHN
<i>C. imperialis</i>	(Westwood, 1874)	12/5 (incl. primary type)	MCSN, MNHN, MRAC, NHML, OXUM
<i>C. orientalis</i>	Guiglia 1937a	4/2 (incl. primary type)	MNHN, OLML, ZMHB
<i>C. purpureiventris</i>	Cameron, 1912	0/1 (incl. primary type)	MRAC
<i>C. somalicus</i>	Guiglia, 1935b	1/4 (incl. primary type)	MCSN, NHML, OLML
<i>C. timnaensis</i>	Kraus, 1998	3/2 (incl. primary type)	ANIC, NHRS, NMNH, ZMSC
<i>Guiglia bombycinis</i>	Benson, 1938b	12/11 (incl. primary type)	ANIC, MNHN, MVMA, NHML, ZMHB
<i>G. chiliensis</i>	Benson, 1955b	1/3 (excl. primary type)	DEIE, MNNC, NHML
<i>G. coracina</i>	Benson, 1955a	1/0 (incl. primary type)	ANIC
<i>G. rubicunda</i>	Schmidt in Vilhelmsen & Smith, 2002	0/1 (incl. primary type)	CNCI
<i>G. rubricata</i>	Riek, 1955	4/6 (incl. primary type)	ANIC, MCSN, NHML, NHRS, ZMUC
<i>G. schauinslandi</i>	(Ashmead, 1903)	20/24 (excl. primary type)	ANIC, MNHN, NHML, NZAC, ZMUC
<i>G. sericata</i>	(Mocsáry, 1900)	18/5 (incl. primary type)	ANIC, CNCI, DEIE, HNHM, MVMA, NHML, RMNH, QMBA
<i>Kulcania mexicana</i>	(Cresson, 1879)	1/13 (excl. primary type)	DEIE, EMEC, NHML, NHRS, ZMHB, ZMUC
<i>K. tomentosa</i>	(Middlekauff, 1983)	3/3 (incl. primary type)	AMNH, CASC, EMEC, UCDC
<i>Leptorussus africanus</i>	Benson, 1955a	1/0 (incl. primary type)	NHML
<i>L. kwazuluensis</i>	Vilhelmsen <b>sp. nov.</b>	0/1 (incl. primary type)	CNCI
<i>Mocsarya metallicus</i>	(Mocsáry, 1896)	2/1 (incl. primary type)	HNHM, NHML, OXUM
<i>M. syriaca</i>	Benson, 1936	2/5 (incl. primary type)	NHML, NHMW, ZSMC
<i>Ophrella amazonica</i>	(Westwood, 1874)	1/0 (incl. primary type)	OXUM
<i>O. lingulata</i>	Middlekauff, 1985a	1/0 (incl. primary type)	CASC
<i>Ophrynon levigatus</i>	Middlekauff, 1983	2/1 (incl. primary type)	CASC
<i>Ophrynopus andrei</i>	Konow, 1897a	3/0 (incl. primary type)	DEIE, NHML
<i>O. batesianus</i>	(Westwood, 1874)	2/0 (incl. primary type)	NHML, NMNH
<i>O. carinatus</i>	Vilhelmsen & Smith, 2002	0/1 (incl. primary type)	NMNH
<i>O. depressatus</i>	Smith, 1988	4/2 (excl. primary type)	AEIC, AMNH, ANIC, CASC, DEIE
<i>O. fulvostigmus</i>	(Westwood, 1874)	5/1 (incl. primary type)	NHML, NHRS, OXUM
<i>O. hansonii</i>	Vilhelmsen & Smith, 2002	1/1 (incl. primary type)	CNCI, NMNH
<i>O. nigricans</i>	(Cameron, 1883)	7/3 (incl. primary type)	EMEC, NHML, TAMU
<i>O. plaumanni</i>	Smith, 1988	5/5 (excl. primary type)	CNCI, EMEC, NHML, NHMW, NMNH, ZMHB
<i>O. wagneri</i>	du Buysson, 1910	3/2 (incl. primary type)	MNHN, NHML, NHRS
<i>Orussella dentifrons</i>	(Philippi, 1873)	3/2 (excl. primary type)	CNCI, EMEC, HNMN, MNNC
<i>Orussobaius badius</i>	Schmidt & Vilhelmsen, 2002	1/0 (incl. primary type)	QMBA

Table 2. Continued

Taxon	Author, date	No. of specimens (♀/♂)	Depositories
<i>O. caligneus</i>	Schmidt & Vilhelmsen, 2002	1/0 (incl. primary type)	WAMP
<i>O. mesembrinus</i>	Benson, 1938b	5/1 (incl. primary type)	AMS, ANIC, NHML
<i>O. minutissimus</i>	Schmidt & Vilhelmsen, 2002	2/0 (incl. primary type)	ANIC
<i>O. minutus</i>	Benson, 1938b	35/24 (incl. primary type)	AMS, ANIC, CNCI, EMEC, MVMA, NHML, QDPI, QMBA, TAMU, UCDC, UQIC, ZMUC
<i>O. paniculus</i>	Schmidt & Vilhelmsen, 2002	0/1 (incl. primary type)	ANIC
<i>O. wilsoni</i>	Benson, 1938b	5/1 (incl. primary type)	MVMA, NHML, QDPI, QMBA
<i>Orussonia depressa</i>	Riek, 1955	2/2 (incl. primary type)	ANIC, NHML, OLML
<i>O. ruficaudata</i>	Schmidt & Gibson, 2001	1/0 (incl. primary type)	ANIC
<i>Orussus abietinus</i>	(Scopoli, 1763)	65/52 (excl. primary type)	ANIC, DEIE, EMEC, MNHN, NHMW, NSMT, OLML, OXUM, RMNH, SBPC, SMFD, ZMHB, ZMUC, ZSMC
<i>O. afer</i>	Guiglia, 1937b	1/0 (incl. primary type)	MRAC
<i>O. bensoni</i>	Guiglia, 1937d	0/1 (incl. primary type)	EITH
<i>O. boninensis</i>	Yasumatsu, 1954	1/0 (incl. primary type)	KUEC
<i>O. brunneus</i>	Shinohara & Smith in Shinohara, 1983	1/0 (incl. primary type)	NSMT
<i>O. coreanus</i>	Takeuchi, 1938	1/2 (incl. primary type)	NSMT, UOPJ
<i>O. decoomani</i>	Maa, 1950	5/2 (excl. primary type)	NHML
<i>O. japonicus</i>	Tosawa, 1930	6/8 (excl. primary type)	NMNH, NSMT, UOPJ, ZMUC
<i>O. loriae</i>	Mantero, 1899	1/0 (incl. primary type)	MCSN
<i>O. minutus</i>	Middlekauff, 1983	13/11 (excl. primary type)	ANIC, CASC, CNCI, EMEC, NMNH, TAMU, UCDC, ZMUC
<i>O. moroi</i>	Guiglia, 1954a	1/1 (incl. primary type)	MCSN
<i>O. occidentalis</i>	Cresson, 1879	67/167 (excl. primary type)	CASC, DEIE, NHML, NHMW, UCDC, ZMUC
<i>O. rufipes</i>	Tsuneki, 1963	4/1 (excl. primary type)	NSMT
<i>O. sayii</i>	Westwood, 1830	9/5 (incl. primary type)	AMNH, EMEC, NHML, NMNH, OXUM
<i>O. schoutedeni</i>	Guiglia, 1937b	2/1 (incl. primary type)	EMEC, MRAC, NMNH
<i>O. scutator</i>	(Benson, 1955a)	0/1 (incl. primary type)	NHML
<i>O. spinifer</i>	(Benson, 1955a)	1/0 (incl. primary type)	NHML
<i>O. striatus</i>	Maa, 1950	1/0 (excl. primary type)	UOPJ
<i>O. taorminensis</i>	Trautmann, 1922	2/1 (incl. primary type)	EITH, GFTC, ZMHB
<i>O. terminalis</i>	Newman, 1838	14/17 (excl. primary type)	CASC, CNCI, EMEC, NHMW, NMNH, UCDC, ZMUC, ZSMC
<i>O. tessmanni</i>	Enslin, 1913	1/0 (incl. primary type)	ZMHB
<i>O. thoracicus</i>	Ashmead, 1898	11/38 (incl. primary type)	CASC, NMNH, UCDC, ZMUC
<i>O. unicolor</i>	Latreille, 1811	8/14 (excl. primary type)	EITH, MHNG, SBPC, ZMHB, ZMUC
<i>Pedicrista hyalina</i>	Benson, 1935a	2/3 (incl. primary type)	NHML, SAMC
<i>Pseudoryssus henschii</i>	(Mocsáry, 1910)	9/5 (incl. primary type)	DEIE, HNHM, MNHN, MRAC, NHML, OLML, ZMHB
<i>P. niehuisorum</i>	Kraus, 1998	1/0 (excl. primary type)	DEIE
<i>Stirocorsia kohli</i>	Konow, 1897b	15/15 (incl. primary type)	AIEC, BPBM, CASC, EITH, MCSN, MNHN, NHML, NHMW, NMNH, NSMT, RMNH, ZOMU
<i>S. maculipennis</i>	(Smith, 1859)	19/5 (incl. primary type)	ANIC, CASC, EMEC, HNHM, KUEC, MCSN, MNHN, NHML, NMNH, NSMT, OXUM, RMNH, ZOMU
<i>S. tosensis</i>	(Tosawa & Sugihara, 1934)	8/8 (excl. primary type)	AIEC, DEIE, NMNH, UOPJ, ZMUC

Abbreviations: MEG, Megalyridae; SIR, Siricidae; STE, Stephanidae; TRI, Trigonalidae; XIP, Xiphydriidae.

**Table 3.** Distribution of character states. -, inapplicable; ?, unknown or uncertain; p, 0/1 polymorphism; q, 1/2 polymorphism; r, 0/2 polymorphism. Other abbreviations as in Table 1

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667
<i>Urocerus gigas</i> (SIR)	1234567890	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667
<i>Xiphydria camelus</i> (XIP)	0-----0-	-0-000000-	--0000-000	0001000--0	-000020100	1000100000	000-000010
<i>Schlettererius cinctipes</i> (STE)	0-----0-	-0-000000-	--00010000	0001000--0	-000000100	1000000000	0000101100
<i>Megalyra fascipennis</i> (MEG)	111101000-	-0-000100-	--00010000	0000000--0	-001100001	1000100010	0110101100
<i>Orthogonalys pulchella</i> (TRI)	0-----0-	-0-000000-	--00010000	2000000--0	-000000001	0001000010	0100101100
<i>Argentophrynopus enigmus</i>	0-----0-	-0-001101-	--00100000	0000000--0	-010000001	1000000000	0100000000
<i>A. gauldi</i>	111011000-	-1-000?030	1001010000	2??0000011	000110?100	100?011?10	1101000111
<i>Chalinus berlandi</i>	111011000-	-1-0000030	0102010000	2??0000011	000110?100	100?011010	1101000111
<i>C. braunsi</i>	111000011	00-2000030	0012010000	2100011101	0001120001	100?0?0110	1100011101
<i>C. haugi</i>	1110000p1	10-2000031	00p2010000	2102101111	0101120000	0001101110	1100010100
<i>C. imperialis</i>	111000011	00-200?030	0012010000	2100011101	0001120001	100?01?10	1100011101
<i>C. orientalis</i>	1110000p1	p0-2000031	0000010000	2102201111	0101120001	100?101110	1100010100
<i>C. purpureiventris</i>	1110000p1	10-2000031	0012010000	2102101111	0101120000	0001101110	1100010100
<i>C. somalicus</i>	111000011	00-20?0031	0000010000	2??220????	?0?112?000	100??0?110	?1000?0100
<i>C. timnaensis</i>	11100000-	-0-2000031	0012010000	2102101111	0101120000	0001101110	1100010100
<i>Guiglia bombycinis</i>	1110000p1	00-2000030	p012010000	2102001111	0101120000	0001101110	1100010100
<i>G. chilensis</i>	111011010-	-200000030	1102pp1000	2000000101	0001100000	0011001010	1110020102
<i>G. coracina</i>	111011010-	-210000030	110200--00	2000000101	0001100100	0011001010	1100010101
<i>G. rubicunda</i>	111001000-	-0-00?0030	1102111000	20?0000101	000110?100	0011001?10	1100021102
<i>G. rubricata</i>	111011010-	-200000030	1002011100	20?000????	?0?110?100	001?0?0?10	?1000?1101
<i>G. schauinslandi</i>	111001000-	-2-0000030	11021p1000	2000000101	000110?000	0011001010	1100020102
<i>G. sericata</i>	111p00010-	-210000030	1102p11000	2000000101	0001100000	1011001010	110002010q
<i>Kulcanea mexicana</i>	111111010-	-200000030	p1p2111000	2000000101	0001100000	0011001010	1100020102
<i>K. tomentosa</i>	111111010-	-200000030	0111010000	2000000011	000112?100	1101001010	1100010111
<i>Leptorussus africanus</i>	101110000-	-0-?00?130	000000--00	2000000p11	000112?100	1101001010	1100010111
<i>L. kwazuluensis</i>	101110000-	-0-00?0130	000000--00	10?0000001	000110?000	000?001?1?	1101001101
<i>Mocsarya metallicus</i>	110-010110	1212000030	0111010000	0?0000????	?0110?001	000??0?010	?010?1101
<i>M. syriaca</i>	110-011pp0	1212000030	110100--00	2000001101	0001120100	1001101010	1100010?01
<i>Ophrella amazonica</i>	111011100-	-0-010?030	0012010000	20?00000?1	00?210?001	1001001?10	110000??01
<i>O. lingulata</i>	111011100-	-0-010?030	0012010000	20?0000011	000110?001	1001001?10	1100000111
<i>Ophrynon levigatus</i>	1p1011010-	-210000030	010200--00	2000000011	000110?100	0001101010	11p000010p
<i>Ophrynopus andrei</i>	101100010-	-1-100?030	0012010100	20?0000011	000110?101	1001001?1?	1100011111
<i>O. batesianus</i>	111100000-	-11100?030	0112010100	20?0000011	000?10?101	1001001?11	1100011111
<i>O. carinatus</i>	111110000-	-0-00?0030	0002010000	2??0000????	?0?110?000	0001??0?0?	?1010?1102
<i>O. depressatus</i>	1011000p0-	-0-1000030	p012010100	2000000011	000110?001	1011001010	110002p101
<i>O. fulvostigmus</i>	101100010-	-1-1000030	0012010100	2000000011	000110?101	1001001011	1100011111
<i>O. hansonii</i>	1011p00p0-	-1-1000030	0012010100	20?0000011	000110?100	1001001011	1100011111
<i>O. nigricans</i>	101100000-	-0-1000030	p012010100	2000000011	000110?001	1011001010	1100020101
<i>O. plaumanni</i>	101100000-	-0-1000030	0012010100	2000000011	0001100001	1011001010	1100020101

Table 3. Continued

	1	111111112	222222223	333333334	444444445	555555556	666666667
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>O. wagneri</i>	111100000-	-0-1000030	0012010100	2000000011	000110?00p	1011001010	1100020101
<i>Orussella dentifrons</i>	110-11000-	-0-000001-	--0000--00	000p000101	0001100000	0000001010	1100p00001
<i>Orussobaius badius</i>	100-11000-	-0-000?01-	--0000--01	0?00000101	000110?000	1101001?10	11010000100
<i>O. caligneus</i>	100-11000-	-0-000?01-	--0000--00	0000000101	000110?100	0001001?10	1100001101
<i>O. mesembrinus</i>	100-11000-	-0-000001-	--0000--00	0000000101	000110?100	0001001?10	11000000101
<i>O. minutissimus</i>	100-11000-	-0-000?01-	--0000--01	0000000101	000110?000	1101001?10	1101001100
<i>O. minutus</i>	1p0-01000-	-0-000001-	--0000--01	0000000101	0001100p00	01010001010	1101000010p
<i>O. paniculus</i>	100-11000-	-0-000?01-	--0000--01	000000????	??1110?001	01010?010	?010000101
<i>O. wilsoni</i>	1p0-p1000-	-0-000001-	--1000--01	0000000101	000110?000	00010001010	11010000101
<i>Orussonia depressa</i>	110-01000-	-0-0000020	100000--10	00110000101	10011010001	1000101010	1100010100
<i>O. ruficaudata</i>	110-01000-	-0-000?020	1000?0--10	00110000101	10011010001	1000010?10	11000000000
<i>Orussus abietinus</i>	111p11000-	-0-0011030	p112010000	2000001101	00111000001	1001101010	11100000101
<i>O. afer</i>	10111000-	-0-000?030	1102010?00	2?00001101	000110?0?1	000?11?10	11100001101
<i>O. bensoni</i>	11111000-	-0-000?0030	1002010000	2?0000????	??1?0?0000	0001?000?00	??100?1?01
<i>O. boninensis</i>	10111000-	-0-000?030	0012010000	2000001001	000110?000	000?11?10	11100001111
<i>O. brunneus</i>	10111000-	-0-000?030	0002010000	2000001001	00011000000	000111?10	11100001101
<i>O. coreanus</i>	11111000-	-0-0011030	1p1000-000	2000001101	00111000000	0001101010	11100000101
<i>O. decoomani</i>	1?111000-	-0-?000?30	1102010000	2000001101	001110?000	000110101?	11100000101
<i>O. japonicus</i>	11111000-	-0-0011030	1112010000	2000001101	00011000000	1001101010	11100000101
<i>O. loriae</i>	11110000-	-0-000?030	00?2010000	2?00001101	000?1?100	100?101?00	11100001111
<i>O. minutus</i>	111011000-	-0-000p030	100000-000	2000001101	00111000000	1001101010	11100000101
<i>O. moroi</i>	11111000-	-0-000?030	1002??0?0	2?00001001	000110?000	000??1?10	11100000101
<i>O. occidentalis</i>	11111000-	-0-0001030	p00200--00	2000001101	00111000000	1001101010	11100000101
<i>O. rufipes</i>	11101000-	-0-0000030	1112010000	2000001101	0001100000p	10011p1010	11100001101
<i>O. sayii</i>	111p11000-	-0-001103p	00p200--00	2000001101	00111000000	1001101010	11100000100
<i>O. schoutedeni</i>	111100000-	-0-000?030	1102010000	2000001101	000110?001	000111?10	1110020111
<i>O. scutator</i>	1?1100000-	-0-?0?0?30	1002010000	2?0000????	?0110?001	000?11?01?	?110020101
<i>O. spinifer</i>	1?1100000-	-0-?00?030	1002010000	2000001101	000110?001	000111?1?	1110020101
<i>O. striatus</i>	11111000-	-0-000?030	1102010000	20?0001101	000110?100	?0?111?10	11110001101
<i>O. taorminensis</i>	11111000-	-0-000?030	100200--00	2000001001	00011000000	100111?10	11100001101
<i>O. terminalis</i>	111p11000-	-0-0000030	1010010000	2000001101	00111000001	1001101010	11100000111
<i>O. tessmanni</i>	10111000-	-0-000?030	1102010000	20?0001101	000110?001	000?11?10	11100000101
<i>O. thoracicus</i>	111p11000-	-0-0000030	p00r010000	2000001101	00111000000	1001101010	11100000101
<i>O. unicolor</i>	11111000-	-0-0011030	p0p200-000	2000001101	00111000000	1001101010	11100000101
<i>Pedicrista hyalina</i>	100-010011	10-0000030	010200--00	1000000001	0001110100	10010001010	1111011101
<i>Pseudoryssus henschii</i>	11111000-	-0-0000030	p002010000	2000000101	0001100100	00010001010	11010001101
<i>P. niehuisorum</i>	101101000-	-0-000?030	1102010000	2000000101	000110?100	010?001?10	11010001101
<i>Stirocorsia kohli</i>	1111p0010-	-200000030	0112010100	2000000011	00011000111	10110001010	1100021101
<i>S. maculipennis</i>	111100010-	-r10000003p	0112010100	2000000011	000110?111	10110001010	1100021101
<i>S. tosenisi</i>	111100010-	-200000030	0112010100	2000000011	0001100111	10110001010	110002p101



Table 3. Continued

777777778	888888889	999999990	111111111	111111111	111111111	111111111	111111111	111111111	111111111
123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789	123456789
010021-001	07000001--	1000000000	0000000000	0000000000	0107100111	111000-0-0	111000-0-0	111000-0-0	11111100000
110110-001	07010001--	1000000001	1000000000	1000000000	0100000101	110000-0-0	110000-0-0	11111100000	11111100000
11001--001	1210010000	0100001000	1000110010	1000110010	1010010101	0002201100	0002201100	00000010001	00000010001
11001--001	12000101--	01000100p1	1000010001	1000010001	0000100-11	0002111000	0002111000	00000010001	00000010001
11001-001	12000101--	0110000001	1000010001	1000010001	0000100111	110200-0-0	110200-0-0	000??10001	000??10001
1101100111	101?012000	100102?11	?120?10001	000?000001	000?000001	00012?1111	000?012000	000?012000	000?012000
1101100111	10?1012000	10pp020110	0120110001	0100000001	0010000001	0001221111	0000112000	0000112000	0000112000
1010110120	1210012000	1001011002	202111010-	0000110022	0000110022	000122-111	0000110000	0000110000	0000110000
010011012p	1210012000	1001010002	202011000p	0000110022	0000110022	0001110100	0000110000	0000110000	0000110000
1010110120	1210012000	1001011002	?02111010-	000?110022	000?110022	00012?-111	0000110000	0000110000	0000110000
0100110120	1210012000	1000010002	2020110000	0000110022	0000110022	000133-101	0000110000	0000110000	0000110000
0100110120	1210012000	1001010002	2020110000	000011p022	000011p022	0001110100	0000110000	0000110000	0000110000
0100110120	121?0?0000	10000?000?	2020?10000	00?0110022	00?0110022	0001?3-101	0000110000	0000110000	0000110000
010011012p	1210012000	1001010001	1020110000	000011p022	000011p022	0001110100	0000110000	0000110000	0000110000
010010r120	1010012000	100p01000r	r020110000	0000110022	0000110022	0001110100	0000110000	0000110000	0000110000
1101101110	1011012000	1011011011	0020110001	1022000001	1022000001	0001211001	0000112000	0000112000	0000112000
10-1101110	1011012000	1000010110	0020110001	0000000001	0000000001	0001221101	0000111000	0000111000	0000111000
10-1101110	10?0?1000	1001010010	?020110001	000?000001	000?000001	00012?1001	0000112000	0000112000	0000112000
1101101111	1011102001	101102?01?	1020110001	00?00001001	00?00001001	0001?21001	0000112000	0000112000	0000112000
1101101110	1011012000	101101p011	1020110001	0022000001	0022000001	0001211001	0000112000	0000112000	0000112000
1001101110	1011p12000	1011010010	0020110001	0000000001	0000000001	0001111100	0000112000	0000112000	0000112000
1101101110	1011012000	10110101p11	0020110001	0022000001	0022000001	0001211001	0000112000	0000112000	0000112000
10-1101111	1011112000	100p010100	0020110001	0000000001	0000000001	0001111100	0000110010	0000110010	0000110010
10-p101111	1011112000	1000010100	0020110001	0000000001	0000000001	000100-0-0	0000110110	0000110110	0000110110
1101102111	1111012011	1001020000	?020010011	000?101001	000?101001	00012???0	0000110000	0000110000	0000110000
110110211?	10?1012011	101102000?	0020010011	00?0101001	00?0101001	0011?0-0-0	000?01?000	000?01?000	000?01?000
1100212121	1010012001	1000010001	1020010000	0000110022	0000110022	0001111100	0000110000	0000110000	0000110000
0100112121	1010012001	1000010000	0020010000	0000110022	0000110022	0001110100	0000110000	0000110000	0000110000
1101000110	1?01012001	10?0?0?0?0?	?0?0?0?0?0?	000?000001	000?000001	00112?1001	0000112000	0000112000	0000112000
1101000110	1?01012001	1011010010	?020110?1?	000?000001	000?000001	00112?1001	0000112000	0000112000	0000112000
10-1101111	1011012000	1000010010	0020110001	r0200001001	r0200001001	0001201100	0000110000	0000110000	0000110000
1101000110	1211112011	1001021111	?022110001	002?000001	002?000001	00012?1001	0000112100	0000112100	0000112100
1100000110	1211112001	1001021111	?022110001	001?000001	001?000001	00012?1001	0000112100	0000112100	0000112100
110100?0?0?	?0111?01?	100112101?	0022110001	00?000?001	00?000?001	0001?21000	0000112100	0000112100	0000112100
110p000110	1211112001	100002111p	0022?0001	0011000001	0011000001	0001221001	0000112100	0000112100	0000112100
1101000110	1211112011	1001021111	1022110001	0022000001	0022000001	0001221001	0000112100	0000112100	0000112100
1101000110	121111201?	100102111?	1022?10001	0021000001	0021000001	0001221001	0000112100	0000112100	0000112100
110p000110	1211112001	10000q1110	0022110001	0011000001	0011000001	0001221001	0000112100	0000112100	0000112100
110p000110	1211112001	1000021110	0022110001	0011000001	0011000001	0001221000	0000112100	0000112100	0000112100



Table 3. Continued

<i>Urocerus gigas</i> (SIR)	1111111111	1111111111	111
<i>Xiphidria camelus</i> (XIP)	4444444445	5555555556	666
<i>Schlettererius cinctipes</i> (STE)	1234567890	1234567890	123
<i>Megalura fasciipennis</i> (MEG)	00-000000	0000?02000	000
<i>Orthogonalys pulchella</i> (TRI)	011011?11?	1101??1?0	?00
<i>Argentophrynopus enigmus</i>	0110112110	1101121120	000
<i>A. gauldi</i>	01000?2?20	0201000?0	000
<i>Chalinus berlandi</i>	0100012100	0211000120	000
<i>C. braunsi</i>	010001?12?	0201??1?0	?00
<i>C. haugi</i>	0100012100	0211000120	000
<i>C. imperialis</i>	0100012100	0211000120	000
<i>C. orientalis</i>	?1000?2?0	??0000?2?	0?0
<i>C. purpureiventris</i>	0100012100	0211000120	000
<i>C. somalicus</i>	0100012100	0211000120	000
<i>C. timnaensis</i>	0110012110	1101111120	010
<i>Guiglia bombycinis</i>	1110012110	1101021120	000
<i>G. chiliensis</i>	011011?11?	1101??1?0	?10
<i>G. coracina</i>	?1100?2?0	??0102???	000
<i>G. rubicunda</i>	0110012110	1101111120	010
<i>G. rubricata</i>	0110012110	1101012120	000
<i>G. schauinslandi</i>	1110112110	1101012120	010
<i>G. sericata</i>	011112110	1101021120	0?0
<i>Kulcania mexicana</i>	011112110	1101021120	000
<i>K. tomentosa</i>	011001?110	0101??3?0	?00
<i>Leptorussus africanus</i>	??00?2?0	??0101?2?	000
<i>L. kwazuluensis</i>	0100012110	0201000120	000
<i>Mocsarya metallicus</i>	01000121p0	0201000121	100
<i>M. syriaca</i>	0??001?1??	1101??1?0	?00
<i>Ophrella amazonica</i>	?11001?11?	1101??1?0	?00
<i>O. lingulata</i>	011011?11?	1101??1?0	?00
<i>Ophrynon levigatus</i>	111011?11?	1101??1?0	?00
<i>Ophrynopus andrei</i>	111011?11?	1101??1?0	?00
<i>O. batesianus</i>	??00?2?0	??0102???	0?0
<i>O. carinatus</i>	?110012110	1101022120	000
<i>O. depressatus</i>	1110112110	1101022120	000
<i>O. fulvostigmus</i>	?110112110	1101022?20	000
<i>O. hansonii</i>	?110012110	1101012120	000
<i>O. nigricans</i>	1110012110	1101022120	000
<i>O. plaumanni</i>			

Table 3. Continued

	1111111111	1111111111	111
	4444444445	5555555556	666
	1234567890	1234567890	123
<i>O. wagneri</i>	1110012110	11101022120	000
<i>Orussella dentifrons</i>	1100012110	0101001120	000
<i>Orussobaius badius</i>	01100?11?	0101??2?0	?00
<i>O. caligneus</i>	011001?11?	0101??2?0	?00
<i>O. mesembrinus</i>	0110012110	0101101220	000
<i>O. minutissimus</i>	011001?11?	0101??2?0	?00
<i>O. minutus</i>	0110012110	0101101220	000
<i>O. paniculus</i>	?1100?2?0	???101?2?	000
<i>O. wilsoni</i>	0110012110	0101101220	000
<i>Orussonia depressa</i>	1110012110	0101002120	001
<i>O. ruficaudata</i>	?11001?11?	0101??1?0	?01
<i>Orussus abietinus</i>	0110012111	11101001122	100
<i>O. afer</i>	011001?11?	??1???	?00
<i>O. bensoni</i>	??00?2?0	???001?2?	000
<i>O. boninensis</i>	011001?11?	1101??1?0	?00
<i>O. brunneus</i>	?11001?11?	1101??1?0	?00
<i>O. coreanus</i>	0110012111	11101001120	000
<i>O. decoomani</i>	0110012110	1101101120	000
<i>O. japonicus</i>	01p0012111	1101001120	000
<i>O. loritae</i>	01100?2?2?	????	?00
<i>O. minutus</i>	0110012111	1101001120	000
<i>O. moroi</i>	011001?11?	1101??1?0	?00
<i>O. occidentalis</i>	0110012111	11101001122	100
<i>O. rufipes</i>	0110012110	1101101120	000
<i>O. sayii</i>	0110012111	110100112f	000
<i>O. schoutedeni</i>	0110012110	11?001?0	?00
<i>O. scutator</i>	?1100?2?0	???01?2?	000
<i>O. spinifer</i>	011101?11?	1101??1?0	?00
<i>O. striatus</i>	011001?12?	0101???	?00
<i>O. taorminensis</i>	011001?11?	1101??1?0	?00
<i>O. terminalis</i>	0110012110	1101001121	000
<i>O. tessmanni</i>	011001?11?	0101??1?0	?00
<i>O. thoracicus</i>	011001211p	1101001120	000
<i>O. unicolor</i>	0110012110	1101001120	000
<i>Pedicularia hyalina</i>	0110012110	0101000120	000
<i>Pseudoryssus henshii</i>	0110012110	0101101320	000
<i>P. niehuisorum</i>	011001?11?	0101??3?0	?00
<i>Stiropora kohli</i>	0110012110	1101012120	000
<i>S. maculipennis</i>	0110012110	1101012120	000
<i>S. tosenis</i>	0110012110	1101012120	000

- EMEC Essig Museum of Entomology, University of California, Berkeley, California, USA (C. B. Barr, R. Zuparko).
- GFTC G. F. Turrisi private collection, Italy.
- HNHM Hungarian Natural History Museum, Budapest, Hungary (L. Zombori).
- IEAS Academia Sinica, Institute of Entomology, Shanghai, China.
- INPA Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil.
- KUEC Kyushu University, Fukuoka, Japan (J. Yukawa).
- MACN Museo Argentina de Ciencias Naturales, Buenos Aires, Argentina.
- MCSN Museo Civico di Storia Naturale, Genova, Italy (R. Poggi, V. Raineri).
- MCZH Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
- MHNG Muséum d'Histoire Naturelle, Genève, Switzerland (B. Merz).
- MNHN Muséum National d'Histoire Naturelle, Paris, France (C. Villemant).
- MNNC Museo Nacional de Historia Natural, Santiago, Chile (F. Rojas).
- MRAC Musée Royal de l'Afrique Centrale, Tervueren, Belgium (E. de Coninck).
- MVMA National Museum of Victoria, Melbourne, Australia (K. Walker).
- NHML The Natural History Museum, London, UK (S. Lewis, M. G. Fitton).
- NHMW Naturhistorisches Museum, Wien, Austria (S. Schödl).
- NHRS Naturhistoriska Riksmuseet, Stockholm, Sweden (K. A. Johanson, T. Pape).
- NMNH National Museum of Natural History, Smithsonian Institution, Washington D. C., USA (D. R. Smith).
- NSMT National Science Museum (Natural History), Tokyo, Japan (A. Shinohara).
- NZAC New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand (J. Berry).
- OLML Oberösterreichisches Landesmuseum, Linz, Austria (F. Gusenleitner).
- OXUM The University Museum, Oxford, UK (D. Mann).
- QDPI Queensland Department of Primary Industries, Brisbane, Australia (J.F. Donaldson).
- QMBA Queensland Museum, Brisbane, Australia (C. Burwell).
- RMNH Nationaal Natuurhistorisch Museum, Leiden, the Netherlands (C. van Achterberg).
- SAMC South African Museum, Cape Town, South Africa (S. van Noort).
- SBPC S. Blank private collection, Germany.
- SMFD Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany (J.-P. Kopelke).
- TARI Taiwan Agricultural Research Institute, Taipei, Taiwan.
- TAMU Texas A & M University, College Station, Texas, USA (E. G. Riley, R. A. Wharton).
- TMSA Transvaal Museum, Pretoria, South Africa (P. Bayliss).
- UCDC R.M. Bohart Museum of Entomology, University of California, Davis, California, USA (S. L. Heydon).
- UMBB Übersee-Museum, Bremen, Germany (P.-R. Becker).
- UOPJ University of Osaka Prefecture, Osaka, Sakai, Japan (T. Hirowatari).
- UQIC University of Queensland Insect Collection, Brisbane, Australia (G. Daniels).
- WAMP Western Australian Museum, Perth, Australia (T. Houston).
- ZMHB Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (F. Koch).
- ZMUC Zoological Museum, University of Copenhagen, Denmark.
- ZOMU Zoologisch Museum, Amsterdam, the Netherlands (W. Hogenes).
- ZSMC Zoologische Staatssammlung, München, Germany (E. Diller).

#### METHODS OF EXAMINATION

Specimens were studied under a Leitz dissection microscope. Measurements were taken with the aid of an ocular scale. Templates for drawings were made by applying a digital camera to a stereomicroscope and using printouts of pictures to provide a rough outline of structures to be illustrated; details were filled in by hand while constantly cross-checking specimens in the dissection microscope. The pencil drafts were inked and scanned; the final illustrations were made in Corel Photo House ver. 2. and Adobe Illustrator ver. 8.0. The sculptural nomenclature follows Harris (1979).

Abbreviations used are: A = antennomere; S = abdominal sternum; T = abdominal tergum.

#### RESULTS AND DISCUSSION

##### CHARACTER ANALYSIS

In total, 163 characters were defined and scored for the 74 orussid and five outgroup taxa examined for the present study (Table 3). Orussidae display considerable sexual dimorphism, not only in the male and female genitalia, but also in characters (40, 57, 61) associated with the female echolocation system (Vilhelmsen *et al.*, 2001), among others. Twenty-three

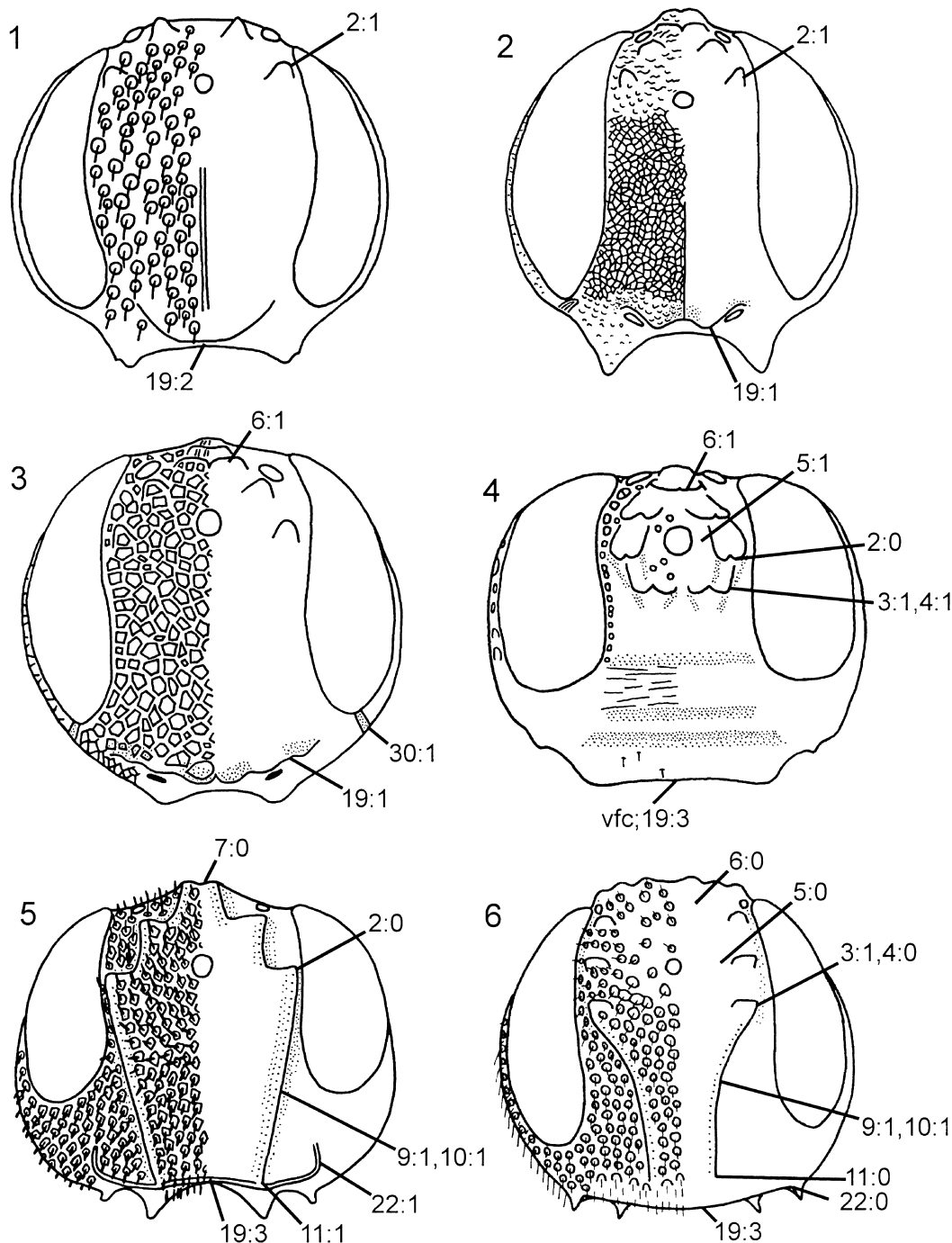
characters are specific for females and 12 for males, as indicated in the character list. Of these, 12 represent six pairs of characters (16–17, 100–101, 113–114, 125–126, 146–147, 160–161) exhibiting sufficient variation between the sexes to require them to be scored separately (see below); most of these deal with coloration of different body parts. The material available for many species is insufficient, with 28 represented by material of only one sex (see Table 2). This has resulted in a substantial number of missing entries. Additional lack of data is caused by the inability to score some characters in specimens unsuitably mounted (e.g. if the wings are folded over the abdomen in the usual resting position, examination of both hindwing and dorsal abdominal characters is impaired).

Earlier classifications and identification manuals (Konow, 1897a; Benson, 1935a, 1938b, 1955a; Middlekauff, 1983; Smith, 1988) emphasized a rather limited sample of characters: the configuration of carinae on the head (8–12, 19, 24, 26), the relative length of some antennal segments (37), the development of the maxillary palps (46), the configuration of the mesoscutellum (75), the relative length of the hindtibial apical spurs (110), selected wing venational characters (115, 119–120, 123), and the development of tubercles on the male S9 (156); these comprise only 10% of the dataset analysed here. Additional characters previously employed for separating orussid genera not included in the present study are the length/width ratio of the hindfemur (more/less than three times longer than broad), the relative length of the hindbasitarsus (longer/shorter than the following tarsomeres), and the relative length of the 2nd abdominal tergum (shorter/longer than T3 + 4). These characters were examined but found to be too variable over a large sample of orussid taxa to allow distinct states to be delimited.

For each character, all unambiguous changes and the consistency index (CI) and retention index (RI) are listed. These were computed after the distribution of the characters on the preferred topology (Fig. 107).

#### Head

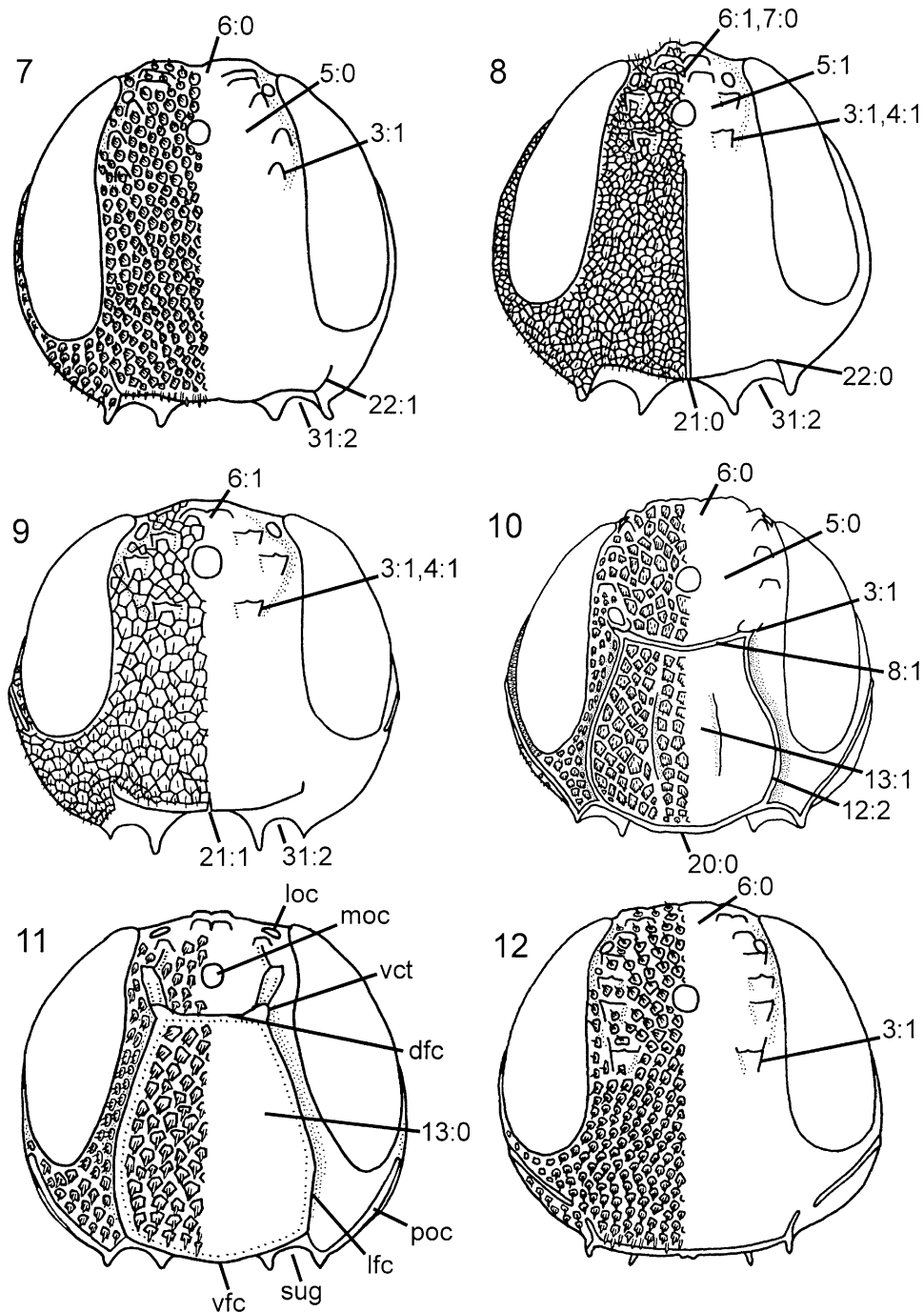
- (1) *Ocellar corona*: absent = 0; present = 1. *Unambiguous changes*: 148: 0–1. CI: 1.000, RI: 1.000. The cirlet (corona) of cuticular (coronal) teeth around the median ocellus (Figs 1–12) is only present in the Orussidae and Stephanidae within the Hymenoptera (e.g. Goulet & Huber, 1993). In the following, the lateral coronal teeth refers to the pair more or less level with the median ocellus, the ventral teeth are the pair ventral to the median ocellus, and the posterior teeth are the several pairs dorsoposterior to the median ocellus and medial to the lateral ocelli.
- (2) *Configuration, lateral coronal tooth*: situated below level of median ocellus (Fig. 4) = 0; situated at level or above the median ocellus (Figs 1, 2) = 1. *Unambiguous changes*: 74: 1–0; 76: 1–0; 82: 1–0; 84: 1–0; 122: 1–0; 128: 1–0. CI: 0.125, RI: 0.611.
- (3) *Ventral coronal tooth*: absent, ventralmost pair of coronal teeth (the lateral teeth) level with median ocellus (Figs 1–3, 5) = 0; ventralmost pair of coronal teeth situated well below median ocellus (Figs 4, 6, 7–12) = 1. *Unambiguous changes*: 137: 0–1. CI: 0.250, RI: 0.750. *Schlettererius* and other Stephanidae have only one unpaired ventral coronal tooth situated medially; *Schlettererius* was assigned state 1, as the ventral paired teeth present in most Orussidae could have arisen by subdivision of the single tooth in the former, or vice versa. However, the absence of ventral teeth in *Orussonia*, *Orussella* and *Orussobaius* indicates that absence is the ground plan state in Orussidae, but with reversals in *Pedicrista* and *Mocsarya*. Hence, the ventral tooth in Stephanidae is probably not homologous with the pair in Orussidae.
- (4) *Configuration, ventral coronal tooth*: situated laterally or at level with lateral coronal teeth (Fig. 6) = 0; ventral teeth situated medial to lateralmost coronal teeth (Figs 4, 8, 9) = 1. *Unambiguous changes*: 17: 0–1; 60: 1–0; 90: 0–1; 93: 0–1; 112: 1–0. CI: 0.200, RI: 0.778. Inapplicable when the ventral coronal teeth are absent.
- (5) *Size, ocellar corona*: large, distance between median ocellus and coronal teeth at least 1.5× the diameter of median ocellus (Figs 6, 7, 10) = 0; small, distance between median ocellus and coronal teeth not more than 1.5× diameter of median ocellus (Fig. 8) = 1. *Unambiguous changes*: 16: 1–0; 63: 1–0; 76: 1–0; 126: 1–0; 145: 0–1. CI: 0.091, RI: 0.697. The scorings for this character were measured along a horizontal line going through the median ocellus.
- (6) *Posterodorsal extent, ocellar corona*: extends dorsally from lateral ocelli to dorsal margins of eyes (Figs 6, 7, 10, 12) = 0; closed ventral to dorsal margins of eyes (level with lateral ocellus), although paired teeth may extend further dorsally (Figs 3, 4, 8, 9) = 1. *Unambiguous changes*: 22: 1–0; 90: 1–0; 108: 1–0; 126: 1–0. CI: 0.250, RI: 0.875.
- (7) *Configuration, posterior coronal teeth*: not separated medially (Figs 5, 8, 11) = 0; separated medially by narrow longitudinal furrow (see Vilhelmsen, 2001b: fig. 4 and Vilhelmsen & Smith, 2002: fig. 3) = 1. *Unambiguous changes*: 28: 0–1; 81: 0–1. CI: 0.500, RI: 0.500.
- (8) *Dorsal frontal transverse carina*: absent (Figs 7–9, 12) = 0; present (Figs 10, 11) = 1. *Unambiguous changes*: 82: 0–1; 89: 0–1; 92: 1–0; 99: 1–0; 102: 0–1. CI: 0.167, RI: 0.615. This carina is



**Figures 1–6.** Head, anterior view. 1. *Orussonia depressa* Riek; 2. *Orussella dentifrons* (Philippi); 3. *Orussobaius minutus* Benson; 4. *Leptorussus kwazuluensis* Vilhelmsen *sp. nov.*; 5. *Pedierista hyalina* Benson; 6. *Chalinus berlandi* Guiglia. Not to scale.

unpaired and extends between the ventral coronal teeth (when present) ventral to the median ocellus. In *Mocsarya*, the ventral coronal teeth are not distinct, but have probably been incorporated in the dorsal transverse frontal carina (see Vilhelmsen, 2001b: fig. 3)

(9) *Median longitudinal frontal carina*: absent (Figs 1–4) = 0; present (Figs 5, 6) = 1. *Unambiguous changes*: 18: 0–1; 111: 0–1. CI: 0.333, RI: 0.667. These paired carinae extend from the lateral (Fig. 5) or ventral (Fig. 6) coronal teeth medioventrally to reach the ventral frontal



**Figures 7–12.** Head, anterior view. 7. *Orussus schoutedeni* Guiglia; 8. *Orussus occidentalis* Cresson; 9. *Pseudoryssus henschii* (Mocsáry); 10. *Guiglia sericata* (Mocsáry); 11. *Kulcania mexicana* (Cresson); 12. *Ophrynopus plaumanni* Smith. Not to scale. dfc, dorsal transverse frontal carina; lfc, lateral longitudinal frontal carina; loc, lateral ocellus; moc, median ocellus; poc, postocular carina; sug, subantennal groove; vct, ventral coronal tooth; vfc, ventral transverse frontal carina.

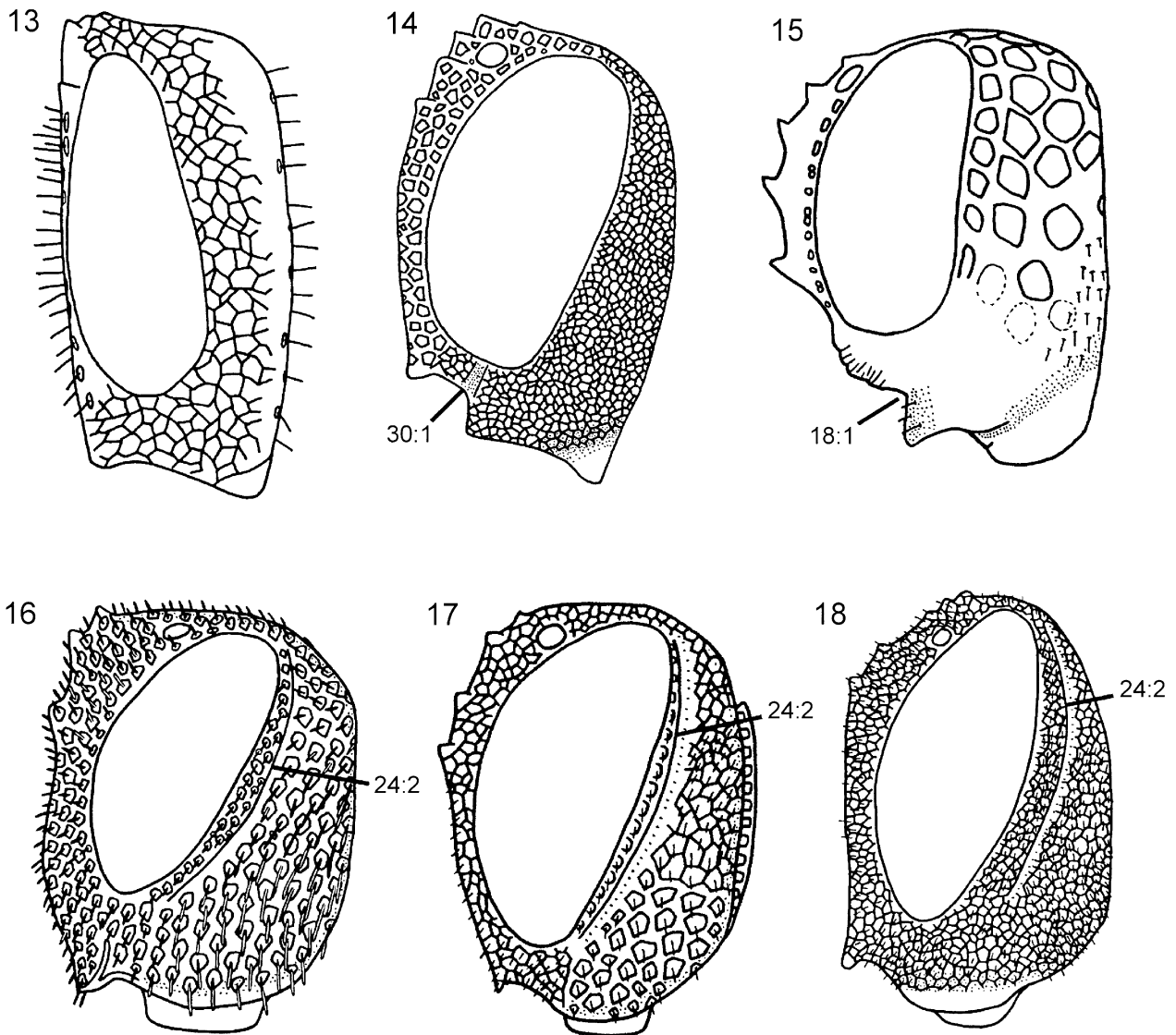
transverse carina well medial to the lateral ends of the latter. In some species (e.g. *Guiglia sericata*, Fig. 10), a pair of weakly developed swellings are present medially on the frons; this condition has been treated as state 0. The devel-

opment of the carinae is very variable within several *Chalinus* spp. (see Vilhelmsen, 2001b).

(10) *Configuration, median longitudinal frontal carina*: not converging medially (see Vilhelmsen, 2001b: fig. 3) = 0; converging medially (Figs 5, 6)



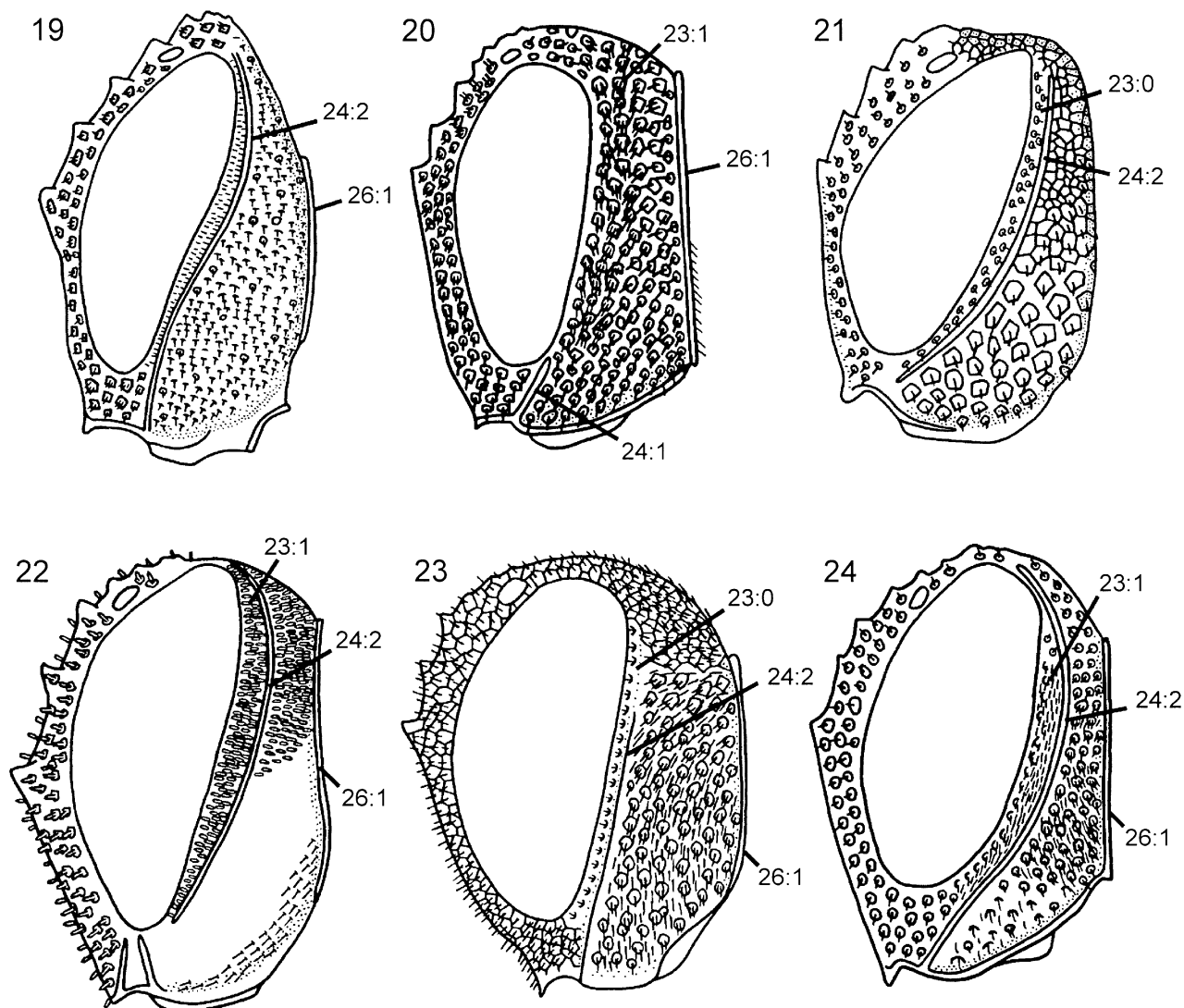
- = 1. *Unambiguous changes*: 109: 1–0. CI: 1.000, RI: 1.000. This and the following character are inapplicable when the median longitudinal frontal carinae are absent.
- (11) *Ventral extent, median longitudinal frontal carina*: does not reach ventral transverse frontal carina (Fig. 6) = 0; reaches ventral transverse frontal carina (Fig. 5) = 1. *Unambiguous changes*: 104: 0–1. CI: 0.333, RI: 0.500.
- (12) *Lateral longitudinal frontal carina*: absent (Figs 1–9, 12) = 0; well developed dorsally, but ventralmost part absent (see Vilhelmsen & Smith, 2002: fig. 4) = 1; present along entire distance between ventral coronal tooth and ventral transverse frontal carinae (Figs 10, 11) = 2 (ordered). *Unambiguous changes*: 19: 2–0; 92: 2–1; 102: 0–2; 109: 0–2. CI: 0.182, RI: 0.700. These carinae extend from the ventral coronal teeth ventrally along the inner margins of the eyes and, if fully developed, to the lateral ends of the ventral transverse frontal carina. The carinae are variously developed in *Stirocorsia maculipennis*, some having it faintly developed along the entire length, others wholly absent (see Vilhelmsen & Smith, 2002); this species was therefore scored as polymorphic.
- (13) *Shape, frons*: area delimited by lateral longitudinal frontal carinae and dorsal and ventral transverse frontal carinae higher than wide (Fig. 11) = 0; just as wide as high or wider (Fig. 10) = 1. *Unambiguous changes*: 88: 1–0; 93: 1–0. CI: 0.250, RI: 0.500. The height was measured medially as the shortest distance between the dorsal and ventral transverse frontal carinae, the width as the maximum distance in a straight horizontal line between the lateral longitudinal frontal carinae; the character is inapplicable if the dorsal transverse and/or the lateral longitudinal frontal carinae are absent.
- (14) *Colour, frons*: nonmetallic, usually dark brown or black = 0; with faint metallic sheen, very dark green = 1; brightly metallic green or bluegreen = 2 (unordered). *Unambiguous changes*: 86: 0–1; 110: 0–2. CI: 1.000, RI: 1.000. State 2 refers to the condition in *Chalinus* and *Mocsarya*, that have not only the head but the entire body entirely or predominantly green or bluegreen metallic. It was decided to incorporate this condition in the present character, as treating body colour as a separate character would weight it unduly.
- (15) *Flattened hairs, frons*: hairs on frons might be present, but not shaped as in state 1 = 0; distinctly flattened hairs present on frons (see Smith, 1988: fig. 111, and Vilhelmsen & Smith, 2002: fig. 3) = 1. *Unambiguous changes*: 81: 0–1. CI: 1.000, RI: 1.000.
- (16) *Markings, frons* (♀): absent = 0; white markings of various extent present = 1. *Unambiguous changes*: 5: 0–1; 60: 1–0; 62: 1–0; 116: 0–1. CI: 0.250, RI: 0.400. This and the following character varies between sexes in several *Orussus* spp.; hence it was decided to score each sex separately.
- (17) *Markings, frons* (♂): absent = 0; white markings of various extent present = 1. *Unambiguous changes*: 3: 0–1; 5: 0–1; 116: 0–1. CI: 0.333, RI: 0.714.
- (18) *Transverse frontal furrow*: absent (Figs 13, 14, 16–18) = 0; distinct furrow present just dorsal to ventral frontal transverse carina (Fig. 15) = 1. *Unambiguous changes*: 136: 0–1. CI: 1.000, RI: 1.000. The transverse frontal furrow is situated just dorsal to the ventral transverse frontal carina, when present.
- (19) *Ventral transverse frontal carina*: entirely absent, torulus not overlapped dorsally by carina = 0; torulus overlapped dorsally by carina, these are not continuous medially (Figs 2, 3) = 1; carinae dorsal to toruli continuous medially through narrow ridge (Fig. 1; see also Schmidt & Gibson, 2001: figs 1, 3) = 2; broad carina present along entire frons (Figs 4–6) = 3 (ordered). *Unambiguous changes*: 5: 0–1; 137: 1–3; 146: 1–2; 147: 0–1. CI: 0.600, RI: 0.931. This carina when fully developed (state 3) extends across the entire width of the frons just dorsal to the toruli, hiding the antennal bases in anterior view.
- (20) *Configuration, ventral transverse frontal carina*: straight (Fig. 10) = 0; with more or less developed triangular projection medially (see Vilhelmsen, 2001b: fig. 1) = 1. *Unambiguous changes*: 106: 0–1. CI: 1.000, RI: 1.000. This and the following two characters are only applicable when the ventral transverse frontal carina is well developed (19 : 2 & 3).
- (21) *Notch medially on ventral transverse frontal carina*: absent (Fig. 8) = 0; ventral transverse frontal carina with indentation medially (Fig. 9) = 1. *Unambiguous changes*: 6: 0–1; 21: 1–0; 28: 0–1; 59: 1–0; 64: 1–0; 128: 1–0. CI: 0.111, RI: 0.667.
- (22) *Lateral end, ventral transverse frontal carina*: straight (Figs 6, 8) = 0; upturned (Figs 5, 7) = 1. *Unambiguous changes*: 19: 1–0; 33: 0–1; 51: 0–1; 57: 0–1; 58: 0–1; 65: 0–1; 75: 1–0; 108: 1–0; 122: 0–1; 130: 1–0; 135: 0–1. CI: 0.071, RI: 0.480. All taxa with the lateral longitudinal frontal carinae extending all the way to the ventral transverse frontal carina were scored as state 1.
- (23) *Hairs posterior to eye*: at most a few scattered hairs present (Figs 21, 23) = 0; dense pilosity of fine hairs present (Figs 20, 22, 24) = 1. *Unambiguous changes*: 34: 1–0; 48: 0–1; 54: 0–1; 60: 1–0; 62: 1–0; 63: 0–1; 105: 1–0; 117: 0–1. CI: 0.083, RI: 0.593. This character refers to the hairs



**Figures 13–18.** Head, lateral view. 13. *Orussonia depressa* Riek; 14. *Orussobaius minutus* Benson; 15. *Leptorussus kwazuluensis* Vilhelmsen **sp. nov.**; 16. *Pedicrista hyalina* Benson; 17. *Pseudoryssus henschii* (Mocsáry); 18. *Orussus occidentalis* Cresson. Not to scale.

immediately posterior to the eye, i.e. between the eye and the postocular carina when the latter is present, not to hairs on the gena in general.

- (24) *Postocular carina*: entirely absent (Figs 13–15) = 0; present only ventrally (Fig. 20) = 1; present along entire length of eyes (Figs 16–19, 21–24) = 2 (ordered). *Unambiguous changes*: 6: 2–1; 70: 2–0; 93: 2–1; 105: 2–0; 109: 2–1; 114: 2–0; 135: 0–2. CI: 0.182, RI: 0.809.
- (25) *Mediodorsal line on occiput*: absent (Figs 25, 26, 28) = 0; narrow median line/groove present between ocellar corona and occipital foramen (Fig. 27) = 1. *Unambiguous changes*: 98: 0–1. CI: 1.000, RI: 1.000.
- (26) *Occipital carina*: absent (Figs 13–16, 21, 25, 26) = 0; present (Figs 19, 20, 22–24, 27, 28) = 1. *Unambiguous changes*: 1: 0; 51: 0–1; 58: 0–1; 116: 1–0; 147: 1–0. CI: 0.091, RI: 0.545.
- (27) *Configuration, occipital carina*: situated laterally, ventrally often continuous with lateral border of subantennal groove (Fig. 28) = 0; situated medially, never continuous with lateral border of subantennal groove (Fig. 27) = 1. *Unambiguous changes*: None. CI: 1.000, RI: 1.000. This and the following character are inapplicable when occipital carina is absent.
- (28) *Occipital concavity*: absent (Fig. 27) = 0; occipital carina dorsally with distinctly deflected



**Figures 19–24.** Head, lateral view. 19. *Guiglia sericata* (Mocsáry); 20. *Kulcania mexicana* (Cresson); 21. *Ophryon levigatus* Middlekauff; 22. *Ophrella lingulata* Middlekauff; 23. *Argentophrynopus gauldi* Vilhelmsen & Smith; 24. *Stirocorsia kohli* Konow. Not to scale.

margin, delimiting concavity dorsoposteriorly on head (Fig. 28) = 1. *Unambiguous changes*: 19: 0–1. CI: 0.333, RI: 0.818.

(29) *Position of occipital foramen*: about in the middle of the head capsule (Fig. 26) = 0; at least two-thirds of the height of the head capsule from the ventral margin of the latter (Fig. 25) = 1. *Unambiguous changes*: 146: 0–1. CI: 1.000, RI: 1.000.

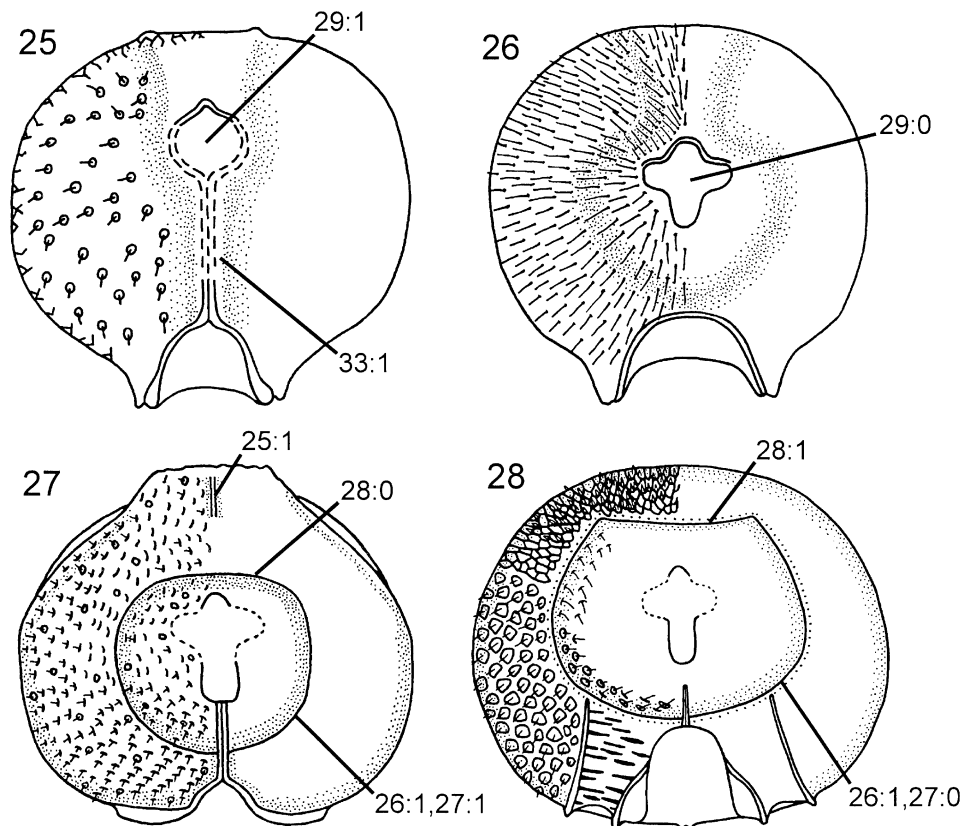
(30) *Malar groove*: absent (Figs 1, 2, 13, 15) = 0; distinct groove extends between ventral margin of eye and mandibular base (Figs 3, 14) = 1. *Unambiguous changes*: 141: 0–1. CI: 1.000, RI: 1.000.

(31) *Subantennal groove*: at most shallow depressions not delimited laterally, present posteroventrally of toruli (Figs 1–3) = 0; grooves

present, lateral margin only delimited by short carina not extending to postocciput = 1; grooves distinct, lateral margin delimited by carina continuous with the occipital carina (Figs 7–9; see also Vilhelmsen, 1997b: figs 4a, 5a) = 2 (ordered). *Unambiguous changes*: 4: 0–2; 74: 2–1; 135: 1–2. CI: 0.333, RI: 0.867.

(32) *Suboccipital trough*: absent, at most slight depression present along sulcus between the occipital and the oral foramina = 0; deep, short trough present, posterior margin of head capsule in ventral view distinctly V-shaped = 1. *Unambiguous changes*: 108: 0–1. CI: 1.000, RI: 1.000.

(33) *Suboccipital groove*: absent (Figs 26–28) = 0; distinct groove accommodating maxillary palps



**Figures 25–28.** Head, posterior view. 25. *Orussonia depressa* Riek; 26. *Orussella dentifrons* (Philippi); 27. *Guiglia sericata* (Mocsáry); 28. *Ophrynopus plaumanni* Smith. Not to scale.

present medioventrally between occipital and oral foramina (Fig. 25) = 1. *Unambiguous changes*: 146: 0–1. CI: 1.000, RI: 1.000.

#### Head appendages

(34) *Shape, scapus*: short, subcylindrical (Figs 31–33, 35, 36) = 0; elongate, cylindrical (Fig. 29) = 1; elongate, at least slightly flattened (Fig. 34; see also Vilhelmsen, 2001b: figs 6–8) = 2 (ordered). *Unambiguous changes*: 107: 0–2; 146: 0–1; 150: 1–0. CI: 0.500, RI: 0.857.

(35) *Ventral margin, scapus*: at most with slight projection distally in males (see Vilhelmsen, 2001b: fig. 6) = 0; distinct projection present distally, extends beyond base of pedicellus in males (see Vilhelmsen, 2001b: fig. 7) = 1; distal projection present, continuous with ventral carina along the entire margin of scapus (especially well developed in the males (see Vilhelmsen, 2001b: fig. 8) = 2 (ordered). *Unambiguous changes*: 105: 1–2; 106: 0–1. CI: 1.000, RI: 1.000.

(36) *Shape, antennomeres*: might be flattened, but not strongly constricted basally (Figs 29–36) = 0; most (male) or some (female) segments con-

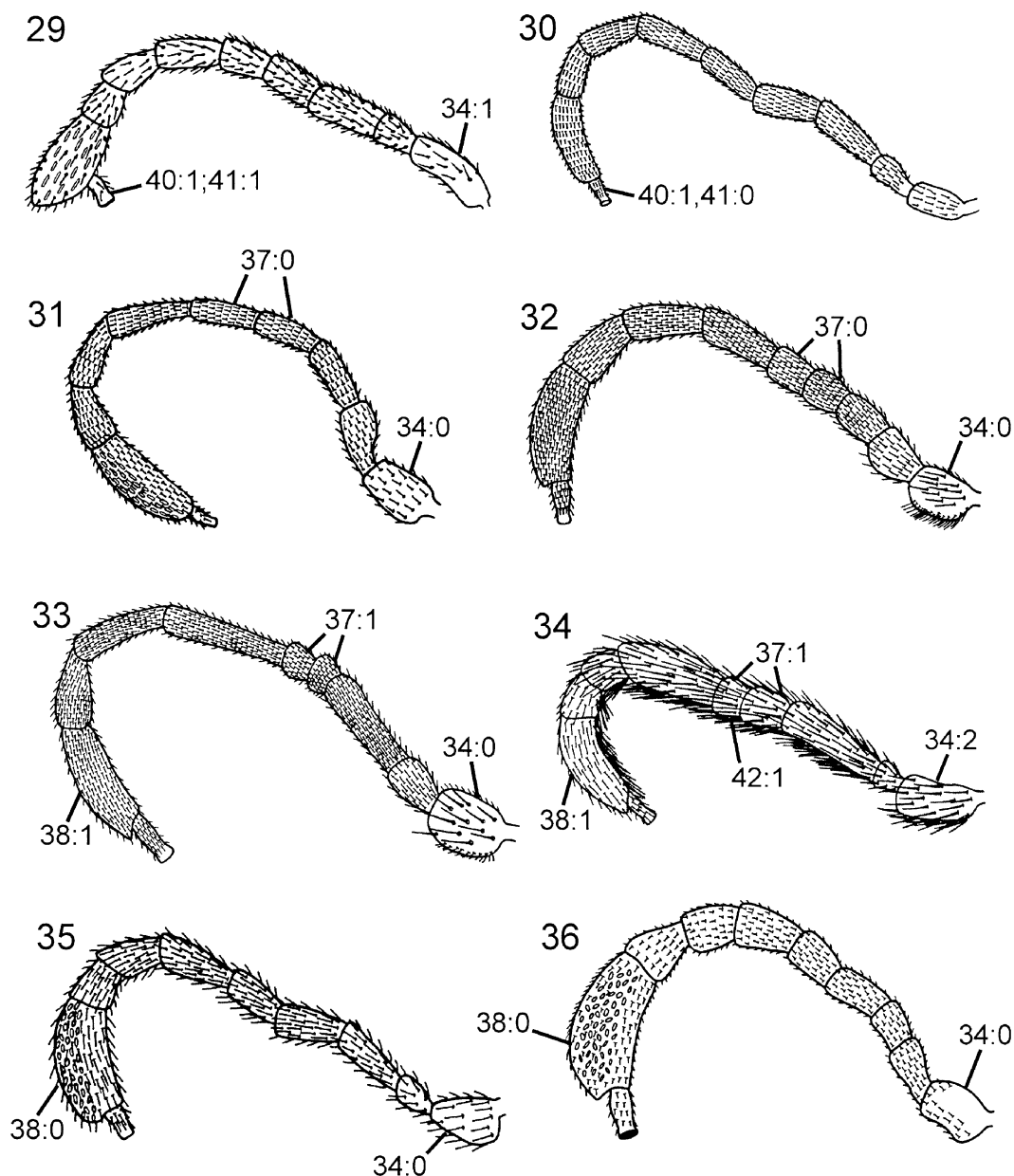
stricted basally and very flattened, also in females (see Vilhelmsen, 2001b: figs 9, 11) = 1. *Unambiguous changes*: 103: 0–1. CI: 1.000, RI: 1.000.

(37) *Configuration, antennomere 3–6* (♀): combined length of A4 + 5 longer than A3 and/or A6 (Figs 31, 32) = 0; A4 + 5 same length or shorter than A3 and/or A6 (Figs 33, 34) = 1. *Unambiguous changes*: 110: 0–1; 132: 0–1. CI: 0.500, RI: 0.966.

(38) *Configuration, antennomere 9* (♀): swollen subapically (Figs 35, 36) = 0; not swollen subapically, broadest proximal to the middle (Figs 33, 34) = 1. *Unambiguous changes*: 74: 1–0; 95: 1–0; 120: 1–0; 128: 1–0. CI: 0.200, RI: 0.818.

(39) *Carina, antennomere 9* (♀): absent = 0; with slight carina on outer distal margin = 1. *Unambiguous changes*: 95: 0–1; 107: 0–1. CI: 0.500, RI: 0.952.

(40) *Configuration, apical antennomere (A10)* (♀): not modified, subequal in size to preceding antennomere = 0; greatly diminished, distinctly subcylindrical, with flattened apex (Figs 29, 30) = 1. *Unambiguous changes*: 147: 0–1. CI: 1.000, RI: 1.000.



**Figures 29–36.** Female antenna of 29. *Orussonia depressa* Riek; 30. *Orussella dentifrons* (Philippi); 31. *Orussobaius minutus* Benson; 32. *Pseudoryssus henschii* (Mocsáry); 33. *Orussus occidentalis* Cresson; 34. *Chalinus braunsi* (Enslin); 35. *Ophrynon levigatus* Middlekauff; 36. *Argentophrynopus gauldi* Vilhelmsen & Smith. Not to scale.

(41) *Insertion, antennomere 10* (♀): inserted subapically on A9 (Fig. 30) = 0; inserted about midway along inner margin of A9 (Fig. 29) = 1. *Unambiguous changes*: None. CI: 1.000, RI: 1.000. Not applicable to non-orussids, which do not have state 1 for the preceding character.

(42) *Hairs on antenna* (♀): hairs inconspicuous = 0; stout, spine-like hairs present and densely placed, especially ventrally (Fig. 34) = 1. *Unambiguous changes*: 107: 0–1. CI: 1.000, RI: 1.000.

(43) *Markings on antenna*: absent = 0; white markings present on at least two of antennomeres 3–7 = 1. *Unambiguous changes*: 5: 0–1; 47: 0–1; 53: 0–1; 58: 1–0; 119: 0–1. CI: 0.200, RI: 0.636.

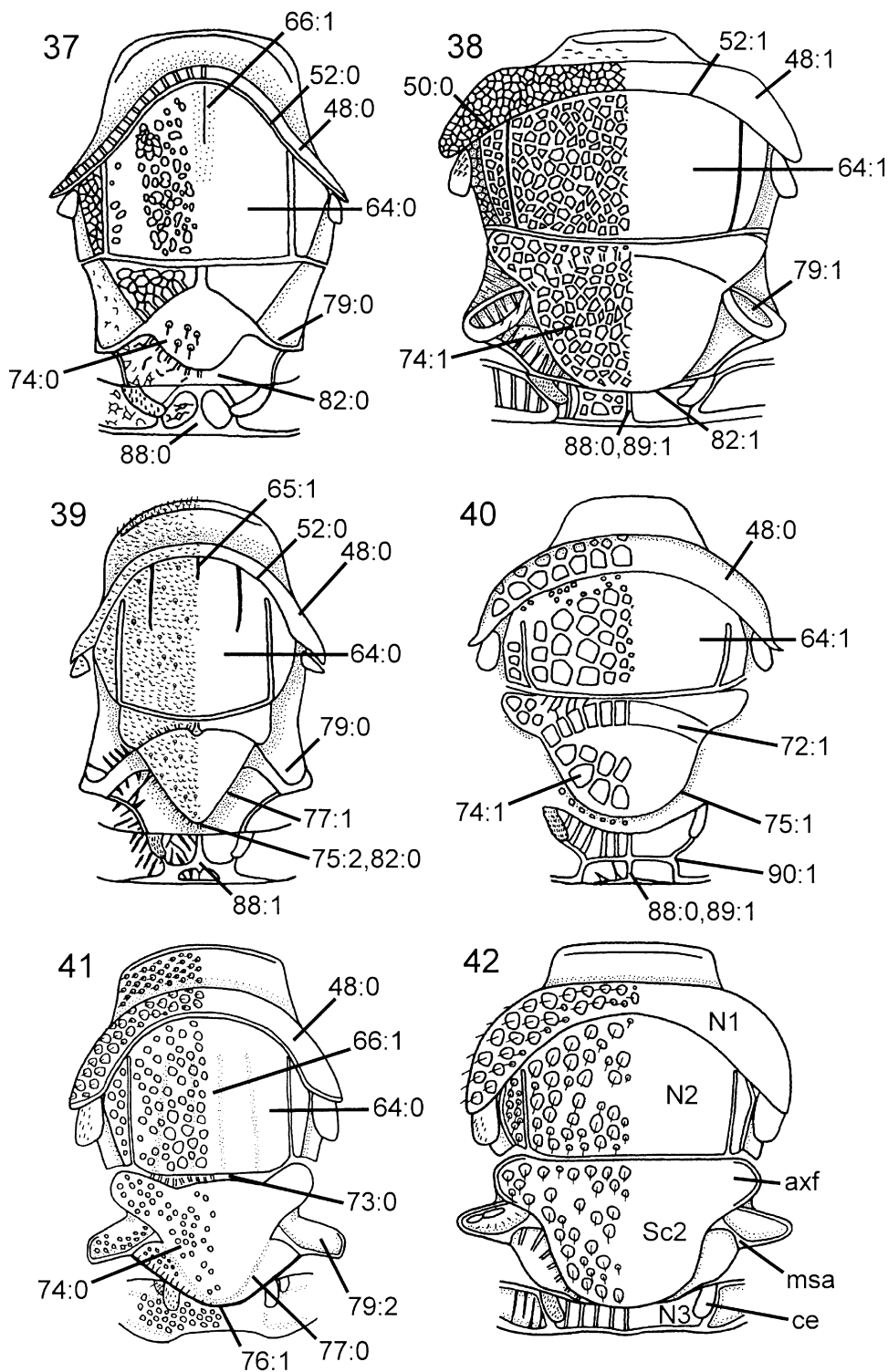
(44) *Shape, labrum*: labrum not conspicuously modified, usually hidden behind mandibles (see Vilhelmsen, 1996: fig. 3e, f, i) = 0; labrum comma-shaped, with stout spines anteroventrally, visible between mandibles (see Vilhelmsen, 1996:

fig. 3g, h) = 1. *Unambiguous changes*: 148: 0–1. CI: 1.000, RI: 1.000.

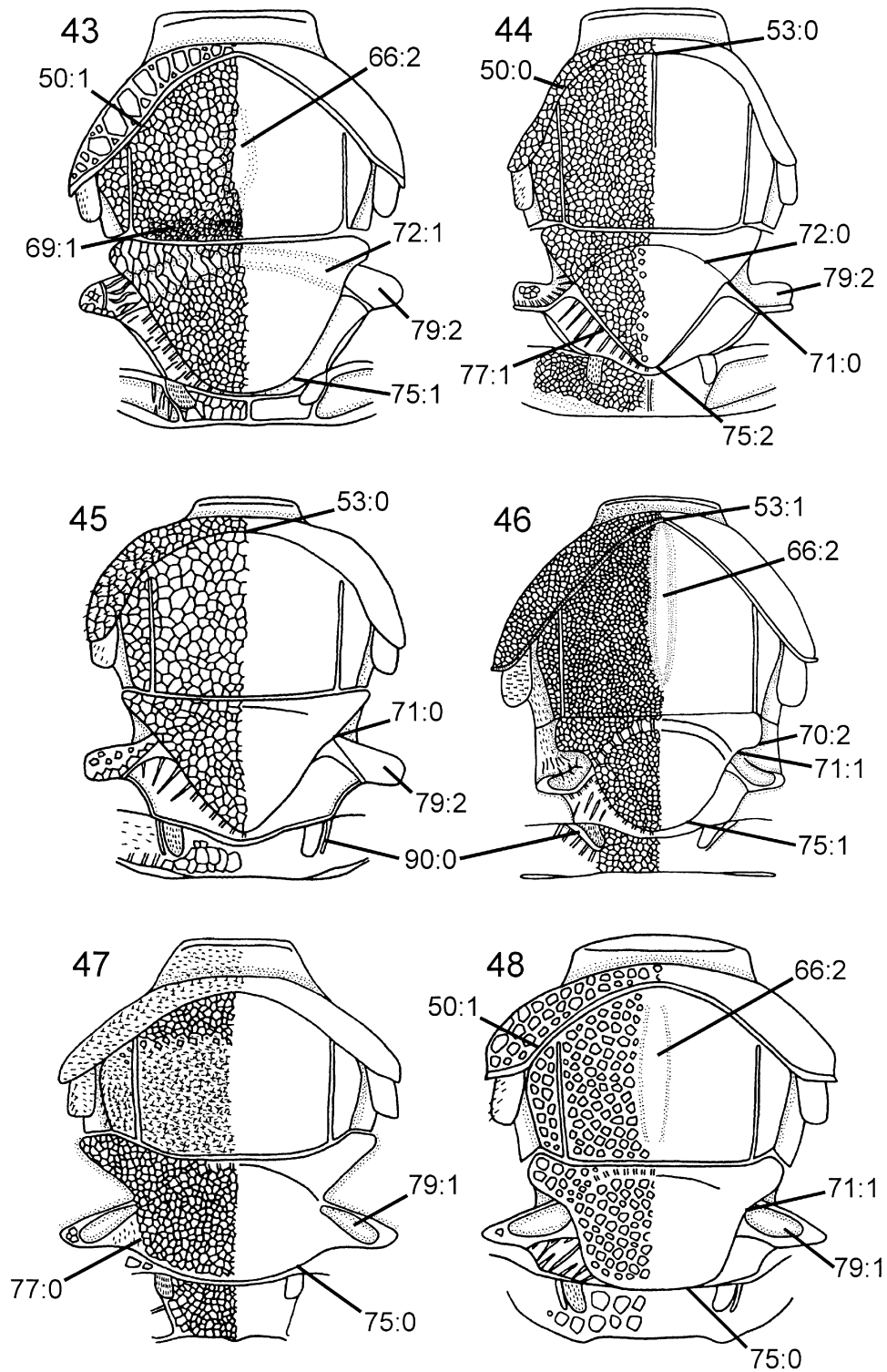
- (45) *Mandible*: broad distally, with at least three teeth = 0; narrowed distally, with at most two teeth (see Benson, 1935a: fig. 10b, c) = 1. *Unambiguous changes*: 148: 0–1. CI: 1.000, RI: 1.000.
- (46) *Configuration, maxillary palp*: elongate, with five or six segments, visible = 0; shortened, but still visible = 1; very reduced, barely discernible = 2 (ordered). *Unambiguous changes*: 1: 2; 93: 0–2; 110: 1–2; 111: 0–1. CI: 0.333, RI: 0.840. In most Orussidae, the maxillary and labial palps have five and three segments, respectively. The exceptions are: *Chalinus* and *Mocsarya* (maxillary and labial palp have only one segment each), *Kulcania* (maxillary palp have three short segments, labial palp one), and *Pedicrista* (maxillary palps have four segments, labial palps two). *Chalinus*, *Mocsarya* and *Kulcania* were assigned the same state as it was usually not possible to discern between the conditions in these taxa without performing dissections. Illustrations of the states in Orussidae are found in Bischoff (1928: fig. 4, state 0, *Orussus*; fig. 5 state 2, *Kulcania*; fig. 6, state 2, *Chalinus*) and Benson (1935a: fig. 10a, state 1, *Pedicrista*).
- (47) *Ventral sclerite, neck membrane*: absent = 0; present = 1. *Unambiguous changes*: 146: 0–1. CI: 1.000, RI: 1.000.

#### Prothorax

- (48) *Shape, pronotum (dorsal view)*: of about equal length throughout (Figs 37, 39–41) = 0; distinctly longer laterally than medially (Figs 38, 42) = 1. *Unambiguous changes*: 21: 1–0; 59: 0–1; 97: 1–0; 108: 1–0; 131: 1–0; 135: 0–1; 142: 0–1; 150: 1–0. CI: 0.091, RI: 0.600.
- (49) *Pronotum medially*: not subdivided (Fig. 48) = 0; subdivided by narrow longitudinal smooth line or carina continuous with the hindmargin of the pronotum (see Vilhelmsen & Smith, 2002: fig. 18) = 1. *Unambiguous changes*: 89: 0–1. CI: 1.000, RI: 1.000.
- (50) *Posterodorsal margin of pronotum*: sculptured (Figs 38, 44) = 0; glabrous (Figs 43, 48) = 1. *Unambiguous changes*: 11: 0–1; 26: 0–1; 34: 1–0; 37: 1–0; 47: 0–1; 51: 0–1; 70: 0–1; 91: 0–1; 103: 0–1; 122: 0–1; 125: 0–1; 145: 1–0; 150: 0–1. CI: 0.077, RI: 0.556.
- (51) *Pronotum anterolaterally*: evenly sculptured = 0; glabrous area present = 1. *Unambiguous changes*: 4: 1–0; 21: 0–1; 34: 1–0; 56: 1–0; 59: 0–1; 63: 0–1; 69: 0–1; 94: 0–1; 111: 0–1; 118: 0–1; 138: 0–1; 145: 1–0. CI: 0.071, RI: 0.606.
- (52) *Hindmargin, pronotum*: deeply excavated (Figs 37, 39) = 0; shallow, pronotum only slightly curved in dorsal view (Fig. 38) = 1. *Unambiguous changes*: 76: 0–1; 93: 0–1; 140: 0–1. CI: 0.333, RI: 0.667.
- (53) *Notch, pronotum hindmargin*: hindmargin evenly rounded, parabolic (Figs 44, 45) = 0; acute, with distinct 'break' (Fig. 46) = 1. *Unambiguous changes*: 85: 0–1; 89: 0–1; 101: 0–1. CI: 0.333, RI: 0.846.
- (54) *Lateral carina on propleuron*: absent or only slightly developed anteriorly = 0; present, separating dorsal smooth area from rugose lateral area = 1. *Unambiguous changes*: 4: 0–1; 144: 0–1. CI: 0.500, RI: 0.833. A small raised projection is present anterolaterally on the propleura in *Orussonia*. However, this condition was assigned state 0; in the taxa having state 1, a distinct carina is developed for a considerable distance posterolaterally on the propleura.
- (55) *Forecoxa*: not expanded medially, trochanter inserts close to median margin = 0; expanded medially, trochanter inserts some distance from the median margin of the coxa = 1. *Unambiguous changes*: 1: 1; 110: 0–1; 132: 0–1. CI: 0.200, RI: 0.867.
- (56) *Ventral longitudinal carina, forefemur*: absent or inconspicuous = 0; present, distinct = 1. *Unambiguous changes*: 31: 0–1; 59: 1–0; 80: 0–1; 119: 1–0; 132: 0–1. CI: 0.200, RI: 0.667.
- (57) *Configuration, foretibia (♀)*: not conspicuously modified, subcylindrical = 0; swollen distally, subdivided medially by groove shaped like an inverted U (see Vilhelmsen *et al.*, 2001: fig. 2a) = 1. *Unambiguous changes*: 147: 0–1. CI: 1.000, RI: 1.000.
- (58) *Longitudinal carina, foretibia (♂)*: at most low carina present laterodistally on foretibia, not extending further than halfway up the tibia = 0; outer margin of tibia with distinct longitudinal carina extending for most of the length of the tibia = 1. *Unambiguous changes*: 108: 0–1. CI: 1.000, RI: 1.000. A fully developed longitudinal carina is present only in male *Chalinus*, where it might be serrated, but is discernible for most of the length of the foretibia. A weakly developed, discontinuous carina was observed in male *Mocsarya*; this condition was assigned state 0.
- (59) *Hair brush, foretibia*: absent = 0; dense mat of flattened setae present dorsal to apical tibial spur = 1. *Unambiguous changes*: 149: 0–1. CI: 1.000, RI: 1.000.
- (60) *Pegs distally on foretibia*: at most weakly developed = 0; males with row of distinct pegs laterally, females with a couple of pegs accommodating socketed hairs distally of transverse tibial furrow = 1. *Unambiguous changes*: 83: 0–1. CI: 1.000, RI: 1.000.



**Figures 37–42.** Thorax, dorsal view. 37. *Orussonia depressa* Riek; 38. *Orussobaius minutus* Benson; 39. *Orussella dentifrons* (Philippi); 40. *Leptorussus kwazuluensis* Vilhelmsen **sp. nov.**; 41. *Chalinus braunsi* (Enslin); 42. *Pedicrista hyalina* Benson. Not to scale. axf, axillar flange; ce, cenchrus; msa, mesoscutellar arm; N1, pronotum; N2, mesoscutum; N3, metanotum; Sc2, mesoscutellum.



**Figures 43–48.** Thorax, dorsal view. 43. *Orussus schoutedeni* Guiglia; 44. *Orussus occidentalis* Cresson; 45. *Pseudoryssus henschii* (Mocsáry); 46. *Guiglia sericata* (Mocsáry); 47. *Ophrella lingulata* Middlekauff; 48. *Ophrynopus plaumanni* Smith. Not to scale.



- (61) *Basitarsal spur* (♀): absent = 0; forebasitarsomere with distal part overlapping next tarsomere, overlapping part with hyaline pad distally (see Vilhelmsen *et al.*, 2001: fig. 3c, f) = 1. *Unambiguous changes*: 147: 0–1. CI: 1.000, RI: 1.000. Female *Schlettererius* (Stephanidae) has the penultimate tarsomere on all legs overlapping the apical tarsomere, but there is apparently no separate, hyaline pad on the overlapping part; hence, *Schlettererius* was scored as having state 0.
- (62) *Probasitarsal notch/comb*: absent = 0; present (see Basibuyuk & Quicke, 1995: fig. 1c) = 1. *Unambiguous changes*: 150: 0–1. CI: 1.000, RI: 1.000.
- (63) *Markings on legs*: entirely absent = 0; white markings of various extend present on at least some of the legs = 1. *Unambiguous changes*: 3: 0–1; 16: 0–1; 74: 0–1; 132: 0–1. CI: 0.250, RI: 0.880. The extent of markings on the hindtibia within *Orussus* is further subdivided in character 111.

#### Mesothorax

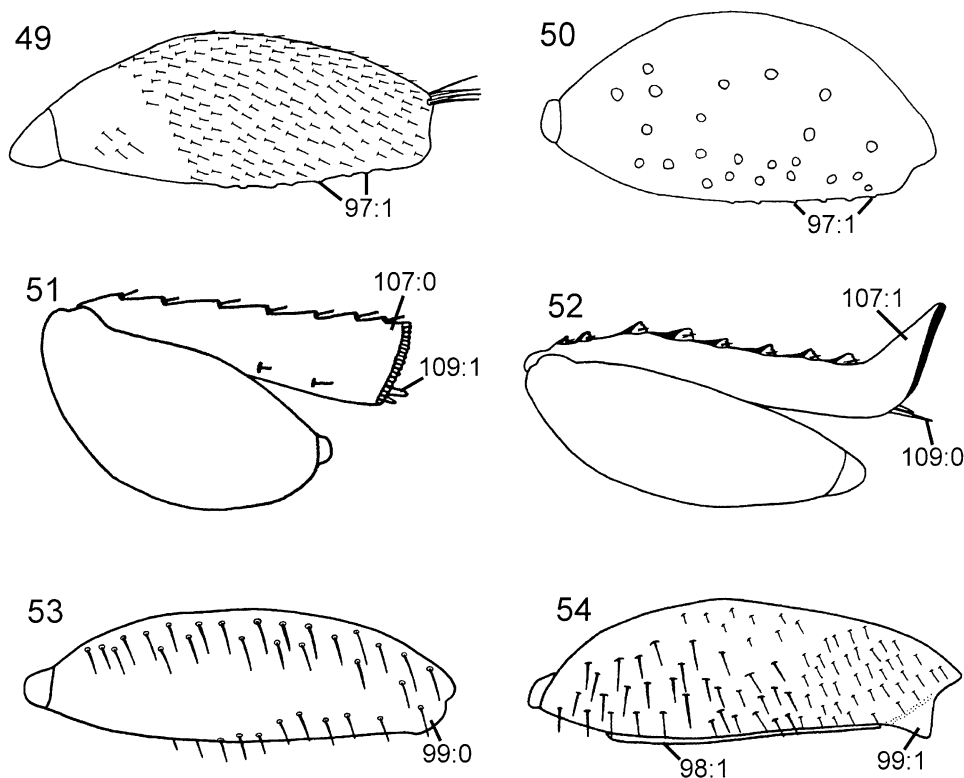
- (64) *Length/width ratio of mesoscutum*: length/width more than 0.6 (Figs 37, 39, 41) = 0; length/width equals or less than 0.6 (Figs 38, 40) = 1. *Unambiguous changes*: 34: 0–1; 80: 0–1. CI: 0.143, RI: 0.538. The length was measured medially from the posterior margin of the pronotum to the transscutal fissure; the width was measured as the longest transverse distance perpendicular to the length, usually between the tegulae.
- (65) *Median mesoscutal sulcus*: absent (Figs 40–42) = 0; present (Fig. 39) = 1. *Unambiguous changes*: None. CI: 0.333, RI: 0.000. Only present within the Orussidae in some *Orussella dentifrons* specimens.
- (66) *Longitudinal carina, mesoscutum*: absent (Figs 38, 40, 44, 45, 47) = 0; present as low swelling/ridge (Figs 37, 41) = 1; present as arched ridge, well developed (Figs 43, 46, 48) = 2 (ordered). *Unambiguous changes*: 41: 0–1/2; 49: 0–1; 100: 1–2; 125: 0–2. CI: 0.182, RI: 0.809. Usually present only in the females, where it corresponds to an internal groove as observed in *Guiglia schauinslandi* (Vilhelmsen *et al.*, 2001) that probably serves to accommodate the coiled ovipositor in the resting position. However, a very distinct carina or tubercle is also present in male *Orussus schoutedeni* (Fig. 43) and *O. scutator*. These taxa and *O. spinifer* (male unknown, female with carina/tubercle) were all scored as state 2. As material was not available for dissection, it was not possible to determine the possible homology of the condition in these *Orussus* spp. and *G. schauinslandi*; the presence of the carina/tubercle in the male as well as female *Orussus* spp. indicates that it could be an entirely external structure and hence not homologous with the carina observed in the females of other Orussidae.
- (67) *Lateral ridge, mesoscutum*: absent or weakly developed = 0; present, distinct at least on the posterior part of the mesoscutum = 1. *Unambiguous changes*: 18: 0–1; 19: 0–1; 43: 0–1; 45: 0–1; 85: 1–0; 90: 0–1; 125: 1–0. CI: 0.062, RI: 0.483.
- (68) *Sculpture, mesoscutum*: horizontal part of mesoscutum does not have coarser sculpture than the adjoining vertical parts of the mesoscutum = 0; horizontal part of mesoscutum distinctly more coarsely sculptured than vertical parts = 1. *Unambiguous changes*: 41: 1–0; 50: 1–0. CI: 0.250, RI: 0.000.
- (69) *Hairs on mesoscutum*: at most a few scattered hairs present (Fig. 44) = 0; dense tufts of hairs present (Fig. 43) = 1. *Unambiguous changes*: 1: 1; 54: 0–1; 59: 0–1; 65: 0–1; 70: 0–1; 83: 0–1; 90: 1–0; 94: 0–1. CI: 0.125, RI: 0.462.
- (70) *Axillar flange*: absent or weakly developed, margins of parascutellar areas rounded = 0; distinct flanges situated anterolaterally of mesoscutellum present = 1; distinct, rectangular flanges present (Fig. 46) = 2 (ordered). *Unambiguous changes*: 28: 1–0; 34: 1–2; 64: 1–0; 98: 1–2; 107: 1–0; 138: 1–0; 145: 0–1. CI: 0.286, RI: 0.750.
- (71) *Angle between axilla and mesoscutellum*: lateral margin of axilla parallel and continuous with lateral margin of mesoscutellum (Figs 44, 45) = 0; distinct 'break' present between lateral margins of axilla and mesoscutellum, margins not parallel (Figs 46, 48) = 1. *Unambiguous changes*: 1: 0; 28: 1–0; 107: 1–0. CI: 0.143, RI: 0.824.
- (72) *Mesoscutellar sulcus*: absent or only weakly developed (Figs 42, 44) = 0; present, distinct, deep (Figs 40, 43) = 1. *Unambiguous changes*: 19: 0–1; 92: 0–1; 97: 0–1; 136: 0–1; 147: 1–0. CI: 0.091, RI: 0.697.
- (73) *Configuration, mesoscutellar sulcus*: continuous anteriorly of scutellum, with crenulation medially (Fig. 41) = 0; subdivided by anterior margin of scutellum, crenulation absent medially = 1. *Unambiguous changes*: 103: 0–1. CI: 1.000, RI: 1.000. Inapplicable when the mesoscutellar sulcus is absent.
- (74) *Sculpture, mesoscutellum*: sparsely sculptured, punctures rounded, extensive smooth interspaces (Figs 37, 41, 42) = 0; densely sculptured, punctures intermingling, hexagonal (Figs 38, 40) = 1. *Unambiguous changes*: 2: 0–1; 33: 1–0; 47: 1–0; 89: 1–0; 111: 1–0; 120: 1–0; 145: 0–1. CI: 0.143, RI: 0.739.

- (75) *Shape, mesoscutellum*: rounded posteriorly, lying parallel to the anterior margin of metanotum for a considerable distance (Figs 47, 48) = 0; rounded posteriorly, at most touching anterior margin of metanotum medially (Figs 40, 43, 46) = 1; acute, triangular (Figs 39, 44) = 2 (ordered). *Unambiguous changes*: 1: 2; 27: 1–2; 41: 1–2; 91: 1–0; 125: 2–1; 132: 1–2. CI: 0.333, RI: 0.886.
- (76) *Posterior extent, mesoscutellum*: posterior margin at most just barely reaches cenchrus (Fig. 42) = 0; posterior margin reaches posterior part of cenchrus (Fig. 41) = 1. *Unambiguous changes*: 1: 1; 15: 1–0; 110: 0–1. CI: 0.333, RI: 0.778.
- (77) *Lateral margin, mesoscutellum*: indistinct, mesoscutellum merges with surrounding sclerites (Figs 41, 47) = 0; distinct, mesoscutellum raised and separated from surrounding sclerites by areas of smooth sculpture (Figs 39, 44) = 1; mesoscutellum with distinct carinated lateral margin = 2 (ordered). *Unambiguous changes*: 53: 1–2; 92: 1–0; 102: 2–1; 108: 2–0; 125: 1–2; 131: 2–1. CI: 0.250, RI: 0.846.
- (78) *Position, mesoscutellar arm*: arises from the posterolateral corners of the mesoscutellum = 0; arises from the anterolateral corners of the mesoscutellum, closer to the anterior than the posterior margin of the mesoscutellum (Figs 37–39, 41, 42–48) = 1. *Unambiguous changes*: 147: 0–1. CI: 1.000, RI: 1.000.
- (79) *Configuration, mesoscutellar arm*: area anterior to mesoscutellar arm without discrete pit and not raised to same level as arms (Figs 37, 39) = 0; with deep pit delimited anteriorly by distinct septum present just anterior to mesoscutellar arm (Figs 38, 47, 48) = 1; curved posteriorly, area anteriorly raised to level of scutellar arms (Figs 4, 43–45) = 2 (unordered). *Unambiguous changes*: 110: 1–2; 134: 1–2; 142: 1–2; 144: 0–1. CI: 0.500, RI: 0.951.
- (80) *Carina on posterior margin of mesoscutellar arm*: not fully developed, missing from basal part = 0; carina extends all the way to the lateral margin of the mesoscutellum = 1. *Unambiguous changes*: 19: 0–1; 56: 1–0; 57: 1–0; 91: 1–0; 101: 1–0; 108: 1–0; 125: 1–0. CI: 0.125, RI: 0.759.
- (81) *Mesoscutellar arm, distally*: does not extend laterally above posterior notal wing process = 0; distal end of mesoscutellar arm overlaps posterior notal wing process dorsally = 1. *Unambiguous changes*: 150: 0–1. CI: 1.000, RI: 1.000.
- (82) *Posterior margin, mesonotum*: continuous medially (Figs 37, 39) = 0; separated medially by mesoscutellum, the latter reaching the hindmargin of the mesonotum (Fig. 38) = 1. *Unambiguous changes*: 25: 0–1; 74: 0–1; 124: 0–1; 143: 0–1. CI: 0.250, RI: 0.700. Inapplicable for taxa with the posterior margins of mesoscutellum and mesopostnotum fused (77: 0), and for taxa with the mesoscutellar arms arising posteriorly on the mesoscutellum (78: 0).
- (83) *Size, mesothoracic basalare*: small, does not extend posterior to anterior thoracic spiracles = 0; large, extends posterior to anterior thoracic spiracles = 1. *Unambiguous changes*: 148: 0–1. CI: 1.000, RI: 1.000.
- (84) *Mesosubalar carina*: not distinctly demarcated = 0; forming distinct smooth area overhanging dorsal part of mesepisternum = 1. *Unambiguous changes*: 2: 0–1; 110: 1–0; 147: 0–1. CI: 0.333, RI: 0.833.
- (85) *Mesepisternal carina*: absent or weakly developed = 0; vertical carina well developed anterolaterally on mesepisternum, separates smooth anteromedian part from sculptured posterolateral part = 1. *Unambiguous changes*: 68: 0–1; 75: 0–1; 87: 0–1; 93: 0–1. CI: 0.200, RI: 0.692.
- (86) *Mesocoxa*: not subdivided medially = 0; subdivided medially (see Johnson, 1988: figs 11,12) = 1. *Unambiguous changes*: 150: 0–1. CI: 1.000, RI: 1.000.
- (87) *Lateral carina on mesocoxa*: entirely absent = 0; present, weakly developed, blunt swelling = 1; present, distinct carina (see Johnson, 1988: figs 11, 12) = 2 (ordered). *Unambiguous changes*: 18: 2–1; 45: 2–1; 144: 1–2; 147: 0–1. CI: 0.500, RI: 0.846.

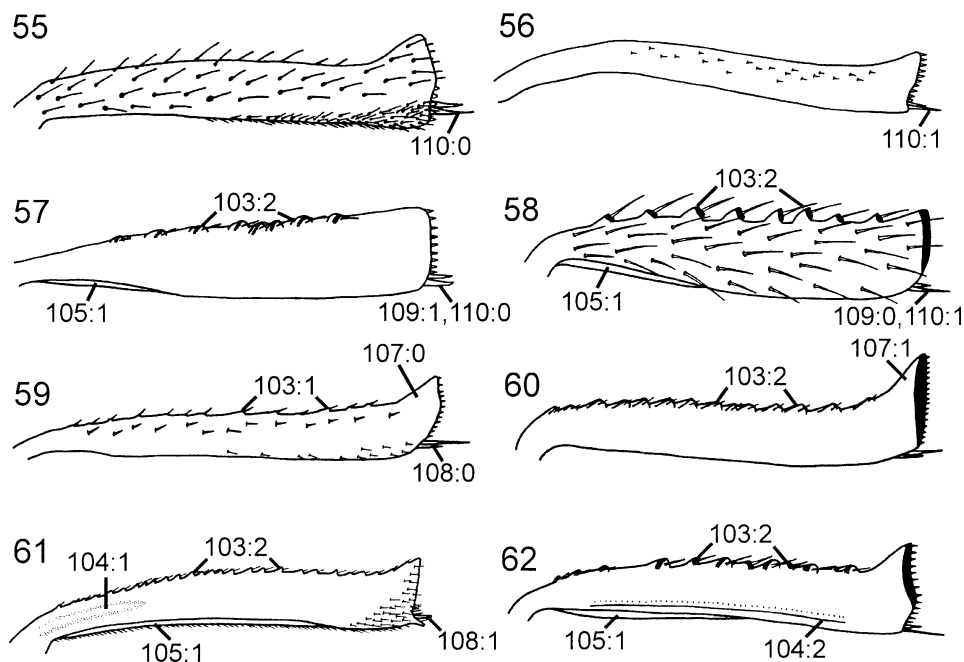
#### *Metathorax*

- (88) *Metascutellum*: weakly developed, confluent with surrounding sclerites (Figs 37, 38, 40) = 0; well developed, delimited by distinct sculpture (Fig. 39) = 1. *Unambiguous changes*: 41: 0–1; 148: 1–0. CI: 0.500, RI: 0.750. In some *Orussonia* specimens, vestiges of a metascutellum is apparent (Fig. 37). However, *Orussella* consistently has the metascutellum developed as a raised, finely sculptured area connected to the hindmargin of the metanotum by slender metascutellar arms (Fig. 39); consequently, it was the only orussid taxon assigned state 1.
- (89) *Median metanotal carina*: absent or incomplete = 0 (Figs 45–48); longitudinal carina fully developed, reaching posterior margin of metanotum (Figs 38, 40) = 1. *Unambiguous changes*: 34: 0–1; 45: 1–0; 64: 0–1; 82: 0–1; 112: 1–0; 121: 1–0. CI: 0.125, RI: 0.708. This and the following character are inapplicable for taxa with a fully developed metascutellum (see preceding character) with the exception of *Orussella*, where the longitudinal median carinae are closely associated with the metascutellum. Indeed, the median longitudinal carina in other Orussidae is probably derived from the metascutellum.

- (90) *Lateral metanotal carina*: absent or incomplete (Figs 45, 46) = 0; fully developed, reaching posterior margin of metanotum (Fig. 40) = 1. *Unambiguous changes*: 19: 0–1; 47: 1–0; 61: 1–0; 68: 1–0; 76: 1–0; 102: 1–0; 108: 1–0. CI: 0.100, RI: 0.654.
- (91) *Cenchrus*: absent = 0; present (Figs 37–48) = 1. *Unambiguous changes*: 147: 0–1; 150: 1–0. CI: 0.500, RI: 0.500.
- (92) *Metepimera-T1 connection*: separate (see Vilhelmsen, 2000a: fig. 5f) = 0; fused = 1. *Unambiguous changes*: 147: 1–0; 150: 0–1. CI: 0.500, RI: 0.500.
- (93) *Metepisternal sculpture*: lateral part of mesepisternum with sculpture covering more than half its surface (see Vilhelmsen, 2000a: fig. 5f) = 0; predominantly glabrous = 1. *Unambiguous changes*: 5: 0–1; 26: 0–1; 138: 0–1. CI: 0.143, RI: 0.400.
- (94) *Hairs, hindcoxa*: only relatively few, short, scattered hairs present = 0; dense pilosity of elongate, shiny hairs present laterally = 1. *Unambiguous changes*: 47: 1–0; 85: 1–0; 92: 0–1; 100: 0–1; 135: 1–0; 147: 0–1. CI: 0.100, RI: 0.719.
- (95) *Posterolateral carina on hindcoxa*: absent or weakly developed = 0; well developed = 1. *Unambiguous changes*: 34: 0–1; 147: 0–1. CI: 0.250, RI: 0.903.
- (96) *Medioventral margins, hindcoxa*: rounded, smooth = 0; distinctly angled, but without ridge = 1; distinctly angled and with ridge (sometimes accompanied by groove) = 2 (ordered). *Unambiguous changes*: 4: 0–1; 19: 1–2; 80: 1–2; 87: 1–2; 112: 2–1; 121: 2–1; 144: 0–2. CI: 0.250, RI: 0.824.
- (97) *Denticles, hindfemur*: ventral part of hindfemora smooth (Figs 51–54) = 0; with small denticles (Figs 49, 50) = 1. *Unambiguous changes*: 87: 0–1; 103: 0–1; 141: 0–1. CI: 0.167, RI: 0.737.
- (98) *Ventral ridge, hindfemur*: absent (Figs 49–52) = 0; present (Fig. 54) = 1. *Unambiguous changes*: 17: 0–1; 74: 0–1; 77: 0–1; 86: 0–1. CI: 0.167, RI: 0.615.
- (99) *Posteroventral corners, hindfemur*: rounded, not protruding (Fig. 53) = 0; triangular, protruding (Fig. 54) = 1. *Unambiguous changes*: 93: 1–0; 102: 0–1. CI: 0.500, RI: 0.955.
- (100) *Predominant colour, hindfemur* (♀): dark brown or black = 0; light brown or red = 1; metallic = 2 (unordered). *Unambiguous changes*: 1: 0; 6: 0–1; 14: 2–1; 27: 0–1; 57: 0–1; 79: 1–0; 84: 1–0; 90: 0–1; 97: 0–1; 108: 0–2; 128: 0–1; 148: 1–0. CI: 0.143, RI: 0.478.



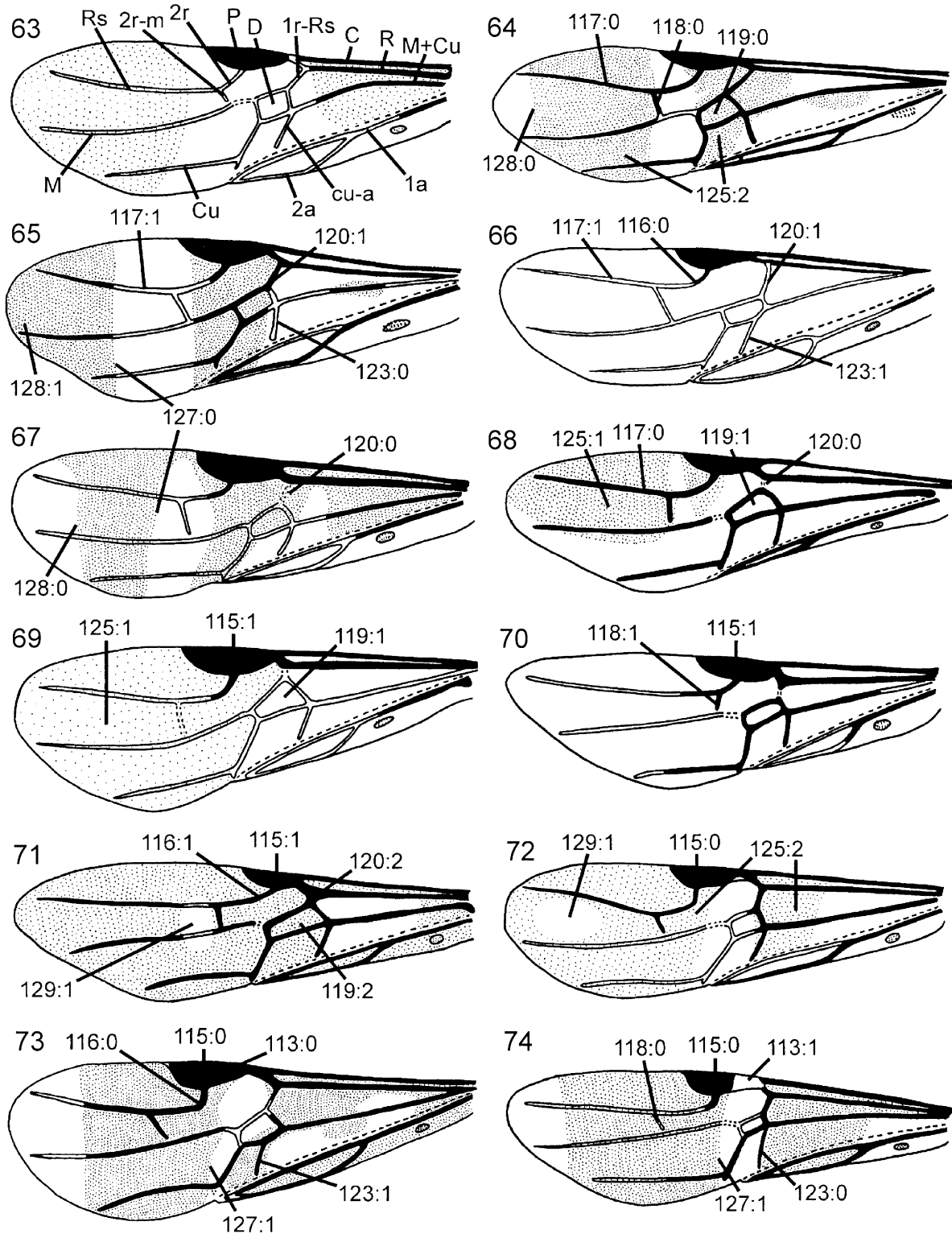
**Figures 49–54.** Hindfemur (49–50, 53–54) or hindleg (51–52), lateral view. 49. *Orussonia depressa* Riek; 50. *Orussobaius minutus* Benson; 51. *Leptorussus kwazuluensis* Vilhelmsen **sp. nov.**; 52. *Orussus schoutedeni* Guiglia; 53. *Pedricista hyalina* Benson; 54. *Stirocorsia kohli* Konow. Not to scale.



**Figures 55–62.** Hindtibia, lateral view. 55. *Orussonia depressa* Riek; 56. *Orussella dentifrons* (Philippi); 57. *Orussobaius minutus* Benson; 58. *Pedicrista hyalina* Benson; 59. *Orussus occidentalis* Cresson; 60. *Orussus tessmanni* Enslin; 61. *Chalinus haugi* du Buysson; 62. *Stirocorsia kohli* Konow. Not to scale.

- (101) *Predominant colour, hindfemur* ( $\sigma$ ): dark brown or black = 0; light brown or red = 1; metallic = 2 (unordered). *Unambiguous changes*: 1: 0; 14: 2–1; 19: 0–1; 20: 0–1; 27: 0–1; 108: 0–2; 147: 1–0. CI: 0.154, RI: 0.389.
- (102) *Silvery hairs on hindfemur*: absent = 0; hindfemur laterally densely covered by broad, silvery hairs (see Vilhelmsen & Smith, 2002: fig. 21) = 1. *Unambiguous changes*: 76: 0–1; 80: 0–1. CI: 0.500, RI: 0.500.
- (103) *Pegs, hindtibia*: entirely absent (Figs 55, 56) = 0; weakly developed, inconspicuous, sockets for hairs (Fig. 59) = 1; distinct pegs accommodating stout spines present (Figs 57, 58, 60–62) = 2 (ordered). *Unambiguous changes*: 118: 2–1; 144: 0–2. CI: 0.500, RI: 0.920.
- (104) *Lateral longitudinal carina, hindtibia*: absent or at most weakly developed proximally (Figs 55–60) = 0; carina developed only on proximal half of tibia (Fig. 61) = 1; carina extending towards the apex of tibia (Fig. 62) = 2 (ordered). *Unambiguous changes*: 77: 0–2; 87: 0–2; 103: 0–1. CI: 0.400, RI: 0.850.
- (105) *Ventral longitudinal carina, hindtibia*: absent (Figs 55, 56, 59, 60) = 0; carina developed at least proximally on hindtibia present (Figs 57, 58, 61, 62) = 1. *Unambiguous changes*: 3: 0–1; 109: 1–0; 112: 0–1; 143: 0–1. CI: 0.250, RI: 0.903.
- (106) *Brush, hindtibia*: absent = 0; brush of dense hairs situated on median part of hindtibia, present = 1. *Unambiguous changes*: 150: 0–1. CI: 1.000, RI: 1.000. Shaw (1988; character 10) commented on the presence of this ‘preening brush’ in Megalyridae, Orussidae and Stephanidae, suggesting that it is a ground plan feature of parasitic Hymenoptera (i.e. Orussidae + Apocrita). Indeed, the distribution of this feature is an autapomorphy for the latter clade in the present analysis. The brush apparently functions in wing grooming (see Basibuyuk & Quicke, 1999), perhaps in conjunction with the ventral longitudinal carina on the hindtibia (see previous character).
- (107) *Apical flanges, hindtibia*: distal width of tibia less than twice the width of the tibia subapically (Figs 51, 59) = 0; distal width of tibia at least twice the width of the tibia subapically (Figs 52, 60) = 1. *Unambiguous changes*: 127: 0–1. CI: 1.000, RI: 1.000. The apical width of the tibia for this character was measured from the insertion point(s) of the tibial spur(s) to the apex of the dorsal projection or flange, the subapical width as the shortest transverse distance across the tibia just prior to the point of origin of the apical flange.
- (108) *Number of apical spurs, hindtibia*: two (Fig. 59) = 0; one (Fig. 61) = 1. *Unambiguous changes*: 103: 0–1. CI: 1.000, RI: 1.000.

- (109) *Length of apical spurs, hindtibia*: elongate, at least as long as half the apical width of the tibia (Figs 52, 58) = 0; short, less than half of the distal width of the tibia (Figs 51, 57) = 1. *Unambiguous changes*: 3: 0–1; 136: 0–1; 141: 0–1. CI: 0.200, RI: 0.333. The apical width of the tibia was measured as in character 107. *Orussus* spp. with the apical flange very distinct (107: 1) were assigned state 0 as estimated from other *Orussus* spp. with the apical flange less developed.
- (110) *Relative length of apical spurs, hindtibia*: of about equal length (Figs 55, 57) = 0; of unequal length, one at least twice as long as the other (Figs 56, 58) = 1. *Unambiguous changes*: 57: 1–0; 60: 1–0; 61: 1–0; 110: 1–0; 122: 1–0. CI: 0.100, RI: 0.550.
- (111) *White mark, hindtibia*: absent = 0; present, does not extend more than a third from the base of the tibia = 1; present, extends at least halfway down the tibia = 2 (ordered). *Unambiguous changes*: 3: 0–1; 16: 0–1; 55: 1–2; 59: 1–2; 74: 0–1; 121: 1–2; 123: 1–0; 124: 1–0; 132: 0–1. CI: 0.222, RI: 0.774.
- Forewing*
- (112) *Vein 1r*: absent (Figs 63–74) = 0; present (see Vilhelmsen, 2001a: fig. 4) = 1. *Unambiguous changes*: 150: 1–0. CI: 1.000, RI: 1.000.
- (113) *Colour of pterostigma* (♀): predominantly piceous/dark (Fig. 73) = 0; basal half of pterostigma white (Fig. 74) = 1; more than half the stigma white (see Vilhelmsen & Smith, 2002: figs 24, 28) = 2 (ordered). *Unambiguous changes*: 3: 0–1; 7: 0–1; 31: 0–1; 79: 0–2; 82: 1–2; 97: 0–2. CI: 0.200, RI: 0.619. The occurrence and extent of white markings on the pterostigma varies between the sexes in *Argentophrynopus*, *Ophrynon* and *Ophrynopos*. Therefore, the sexes were scored separately for this condition.
- (114) *Colour of pterostigma* (♂): predominantly piceous/dark = 0; basal half of pterostigma white = 1; more than half the pterostigma white = 2 (ordered). *Unambiguous changes*: 36: 1–2; 79: 0–2; 86: 0–1. CI: 0.333, RI: 0.692.
- (115) *Position, vein 2r*: arising more than 0.6 the total length of the pterostigma from the proximal part of the latter (Figs 72–74) = 0; arising equal to or less than 0.6 the total length of the pterostigma from the proximal part of the latter (Figs 69–71) = 1. *Unambiguous changes*: 2: 1–0; 3: 1–0; 102: 1–0. CI: 0.333, RI: 0.926. The width of pterostigma was measured from the distal end of the costal cell to the apex of the pterostigma, the point of insertion of vein 2r was measured from the distal end of the coxal cell to the distal margin of 2r.
- (116) *Angle between veins 2r and Rs*: both veins distinct, usually separated by angle where they join (Figs 66, 73) = 0; smooth transition between veins (Fig. 71) = 1. *Unambiguous changes*: 3: 0–1; 110: 0–1. CI: 0.500, RI: 0.900.
- (117) *Colour of vein Rs*: coloured at least until junction with 2r-m (Figs 64, 68) = 0; at most coloured for a short distance distally of 2r (Figs 65, 66) = 1. *Unambiguous changes*: 19: 0–1; 31: 0–1; 76: 1–0; 112: 1–0; 142: 1–0; 147: 0–1. CI: 0.143, RI: 0.760.
- (118) *Position, vein 2r-m*: at least anterior end situated distal to apex of pterostigma (Figs 64, 74) = 0; entire vein situated proximal to apex of pterostigma (Fig. 70) = 1. *Unambiguous changes*: 53: 0–1; 66: 0–1; 74: 0–1; 76: 0–1; 139: 0–1; 145: 1–0. CI: 0.167, RI: 0.545.
- (119) *Configuration, discal cell*: rectangular, basal part not broader than distal part (Fig. 64) = 0; rhomboid, basal part broader than distal part, not reaching R anteriorly (Figs 68, 69) = 1; rhomboid, basal part broader than distal part, reaching R anteriorly (Fig. 71) = 2 (ordered). *Unambiguous changes*: 2: 1–0; 67: 1–0; 110: 0–2; 134: 0–1; 148: 1–0. CI: 0.333, RI: 0.911.
- (120) *Vein 1r-Rs*: spectral (Figs 67, 68) = 0; present, elongate (Figs 65, 66) = 1; present, but very shortened (Fig. 71) = 2 (unordered). *Unambiguous changes*: None. CI: 0.667, RI: 0.969.
- (121) *Vein 3r-m*: absent (Figs 63–74) = 0; present (see Vilhelmsen, 2001a: fig. 4) = 1. *Unambiguous changes*: 149: 1–0. CI: 1.000, RI: 1.000.
- (122) *Vein 2 m-cu*: absent (Figs 63–74) = 0; present (see Vilhelmsen, 2001a: fig. 4) = 1. *Unambiguous changes*: 149: 1–0. CI: 1.000, RI: 1.000.
- (123) *Vein cu-a insertion*: inserts on Cu1 at most slightly distal to M (Figs 65, 74) = 0; inserts on Cu1 more distally, close to the middle of the discal cell (Figs 66, 73) = 1. *Unambiguous changes*: 1: 1; 26: 0–1; 81: 0–1. CI: 0.333, RI: 0.333.
- (124) *Anal vein configuration*: posterior anal veins fully developed, extending to base of wing (see Vilhelmsen, 2001a: fig. 4) = 0; absent proximally (Figs 63–74) = 1; entirely absent = 2 (ordered). *Unambiguous changes*: 147: 2–1; 150: 0–2. CI: 0.667, RI: 0.667.
- (125) *Infuscation* (♀): forewings almost entirely hyaline (Figs 66, 70) = 0; with one large infuscated area distal to pterostigma (Figs 68, 69) = 1; with at least two large infuscated areas distal and proximal to pterostigma, respectively (Figs 64, 72) = 2; entirely infuscated = 3 (ordered). *Unambiguous changes*: 24: 1–0; 44: 2–1; 45: 2–1; 60: 1–2; 68: 1–0; 74: 1–0; 79: 2–1; 103: 1–2; 148: 1–2; 149: 0–1. CI: 0.150, RI: 0.452.
- (126) *Infuscation* (♂): forewings almost entirely hyaline = 0; infuscated for considerable area distal



**Figures 63–74.** Forewing. 63. *Orussonia depressa* Riek; 64. *Orussella dentifrons* (Philippi); 65. *Orussobaius minutus* Benson; 66. *Leptorussus kwazuluensis* Vilhelmsen **sp. nov.**; 67. *Orussus schoutedeni* Guiglia; 68. *Orussus occidentalis* Cresson; 69. *Pseudoryssus henschii* (Mocsáry); 70. *Pedicrista hyalina* Benson; 71. *Chalinus berlandi* Guiglia; 72. *Argentophrynopus gauldi* Vilhelmsen & Smith (♂); 73. *Ophrella lingulata* Middlekauff; 74. *Ophrynopus plaumanni* Smith. Not to scale. D, discal cell; P, pterostigma.

to pterostigma = 1; with broad infuscated areas both distal and proximal to pterostigma = 2; entirely infuscated = 3 (ordered). *Unambiguous changes*: 17: 1–2; 19: 1–2; 24: 1–0; 31: 1–0; 74: 1–0; 92: 1–2; 105: 1–3; 141: 1–0. CI: 0.150, RI: 0.452.

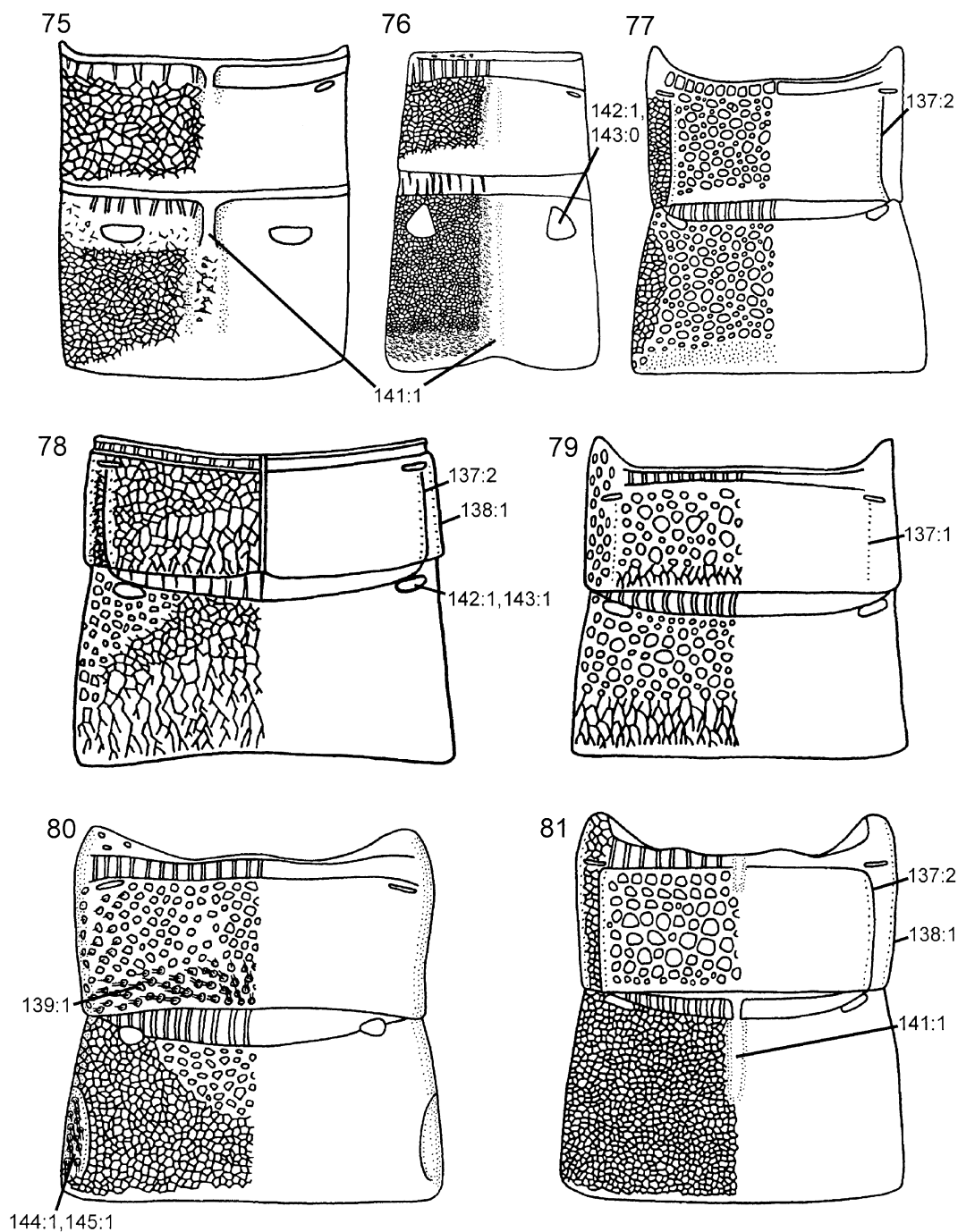
- (127) *Proximal extent, distal infuscated area*: terminates distal to pterostigma (Figs 65, 67) = 0; at least partially overlapping pterostigma (Figs 73, 74) = 1. *Unambiguous changes*: 27: 0–1; 60: 1–0; 75: 0–1; 102: 0–1; 147: 1–0. CI: 0.111, RI: 0.652. This and the following character were treated as inapplicable when the forewing is either entirely hyaline (125–126: 0) or entirely infuscated (125–126: 3).
- (128) *Distal extent, distal infuscated area*: terminates proximal to apex, apex hyaline (Figs 64, 67) = 0; extends to apex, apex infuscated (Fig. 65) = 1. *Unambiguous changes*: 24: 1–0; 56: 0–1; 62: 0–1; 68: 0–1; 74: 1–0; 76: 1–0; 91: 1–0; 117: 1–0; 139: 1–0; 148: 0–1. CI: 0.077, RI: 0.667.
- (129) *Distal hyaline spot*: absent (Figs 73, 74) = 0; forewing with hyaline spot distally of 2r-m, between Rs and M (Figs 71, 72) = 1. *Unambiguous changes*: 80: 0–1; 103: 0–1. CI: 0.500, RI: 0.667. This character was treated as inapplicable when the forewing is entirely hyaline (125 & 126: 0).
- (130) *Density of hairs*: hairs scattered on the wing surface, distance between them at least as long as the length of the hairs = 0; large dense patches of hairs present, at least proximal to pterostigma, distance between hairs less than the length of hairs = 1. *Unambiguous changes*: 21: 1–0; 34: 1–0; 39: 1–0; 40: 1–0; 41: 0–1; 42: 0–1; 48: 0–1; 79: 1–0; 92: 0–1; 101: 0–1; 103: 0–1; 105: 0–1; 129: 0–1. CI: 0.077, RI: 0.636.

#### Hindwing

- (131) *Costa*: absent = 0; present (see Vilhelmsen, 2001a: fig. 4) = 1. *Unambiguous changes*: 150: 1–0. CI: 1.000, RI: 1.000.
- (132) *Vein 1r-m*: absent or at most spectral = 0; present, well developed (see Vilhelmsen, 2001a: fig. 4) = 1. *Unambiguous changes*: 41: 0–1; 58: 0–1; 150: 1–0. CI: 0.333, RI: 0.333. Many Orussidae have a faint spectral 1r-m vein in the hindwing; however, only in *Orussella dentifrons* and *Orussus japonicus* is it sufficiently developed to be scored as state 1.
- (133) *Vein 3r-m*: absent = 0; present (see Vilhelmsen, 2001a: fig. 4) = 1. *Unambiguous changes*: 150: 1–0. CI: 1.000, RI: 1.000.
- (134) *Vein m-cu*: absent = 0; present (see Vilhelmsen, 2001a: fig. 4) = 1. *Unambiguous changes*: None. CI: 1.000, RI: 1.000.
- (135) *Vein 1a*: absent = 0; present (see Vilhelmsen, 2001a: fig. 4) = 1. *Unambiguous changes*: None. CI: 0.500, RI: 0.000.

#### Abdomen

- (136) *Configuration, T1*: longitudinally subdivided (see Vilhelmsen, 2000a: fig. 2c–e) = 0; fused medially (Figs 75–81) = 1. *Unambiguous changes*: 150: 0–1. CI: 1.000, RI: 1.000.
- (137) *Postspiracular carina, T1*: entirely absent = 0 (Figs 75, 80); faint longitudinal swelling extends between spiracle and posterior margin of 1st tergum (Fig. 79) = 1; distinct carina having depression ventrally present (Figs 77, 78, 81) = 2 (ordered). *Unambiguous changes*: 45: 2–1; 59: 2–1; 69: 1–2; 92: 0–2; 100: 1–2; 129: 1–2; 143: 1–2. CI: 0.167, RI: 0.811.
- (138) *Subspiracular carina, T1*: absent or weakly developed (Figs 75, 76, 79, 80) = 0; distinct longitudinal carina extending along lateral margin of 1st terga ventral to spiracle present (Figs 78, 81) = 1. *Unambiguous changes*: 24: 0–1; 45: 1–0; 54: 0–1; 68: 0–1; 90: 0–1; 143: 1–2. CI: 0.167, RI: 0.750.
- (139) *Posterior hair fringe, T1*: absent (Figs 75–79, 81) = 0; dense transverse band of hairs present along posterior margin of 1st tergum (Fig. 80) = 1. *Unambiguous changes*: 93: 0–1. CI: 1.000, RI: 1.000.
- (140) *Constriction between 1st and 2nd abdominal segments*: absent (Figs 75–81) = 0; present = 1. *Unambiguous changes*: 147: 1–0; 150: 0–1. CI: 0.500, RI: 0.500.
- (141) *Median carina, T2* (♀): with at most weakly developed median longitudinal carina (Figs 77–80) = 0; with distinct longitudinal carina developed anteromedially (Figs 75, 76, 81) = 1. *Unambiguous changes*: 17: 0–1; 22: 0–1; 32: 1–0. CI: 0.167, RI: 0.286.
- (142) *Smooth areas laterally on T2*: absent = 0; paired areas with much smoother sculpture than adjacent cuticle present anterolaterally on 2nd tergum (Figs 76, 78) = 1. *Unambiguous changes*: 2: 0–1; 147: 0–1. CI: 0.500, RI: 0.667. Apart from Orussidae, *Xiphydria* (Xiphydriidae) was also observed to have somewhat smooth areas adjacent to the antecostal sulcus; however, these are not as well developed as in the Orussidae.
- (143) *Configuration, smooth areas*: rounded or triangular, at most narrowly touching antecosta (Fig. 76) = 0; somewhat rectangular, anterior margin touching antecosta for almost entire width of area (Fig. 78) = 1. *Unambiguous changes*: 41: 1–0; 110: 1–0. CI: 0.500, RI: 0.900. Inapplicable when the smooth areas are absent.

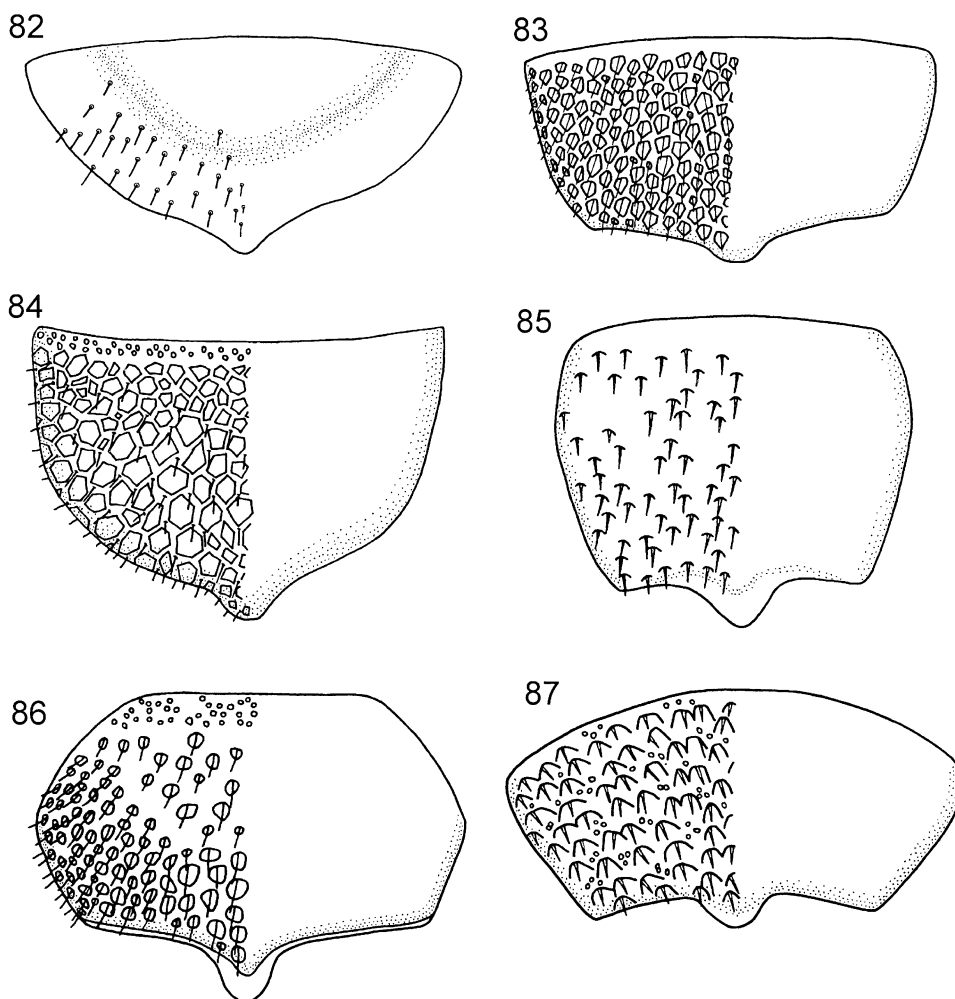


**Figures 75–81.** First and second abdominal terga, dorsal view. 75. *Orussonia depressa* Riek; 76. *Orussella dentifrons* (Philippi); 77. *Orussus schoutedeni* Guiglia; 78. *Orussobaius minutus* Benson; 79. *Pseudoryssus henschii* (Mocsáry); 80. *Kulcania mexicana* (Cresson); 81. *Ophrynopus plaumanni* Smith. Not to scale.

(144) *Lateral swellings, abdominal terga:* absent (Figs 75–79) = 0; several terga, starting from the 2nd, with distinct longitudinal raised area laterally (Fig. 80) = 1. *Unambiguous changes:* 67: 0–1; 93: 0–1. CI: 0.500, RI: 0.500.

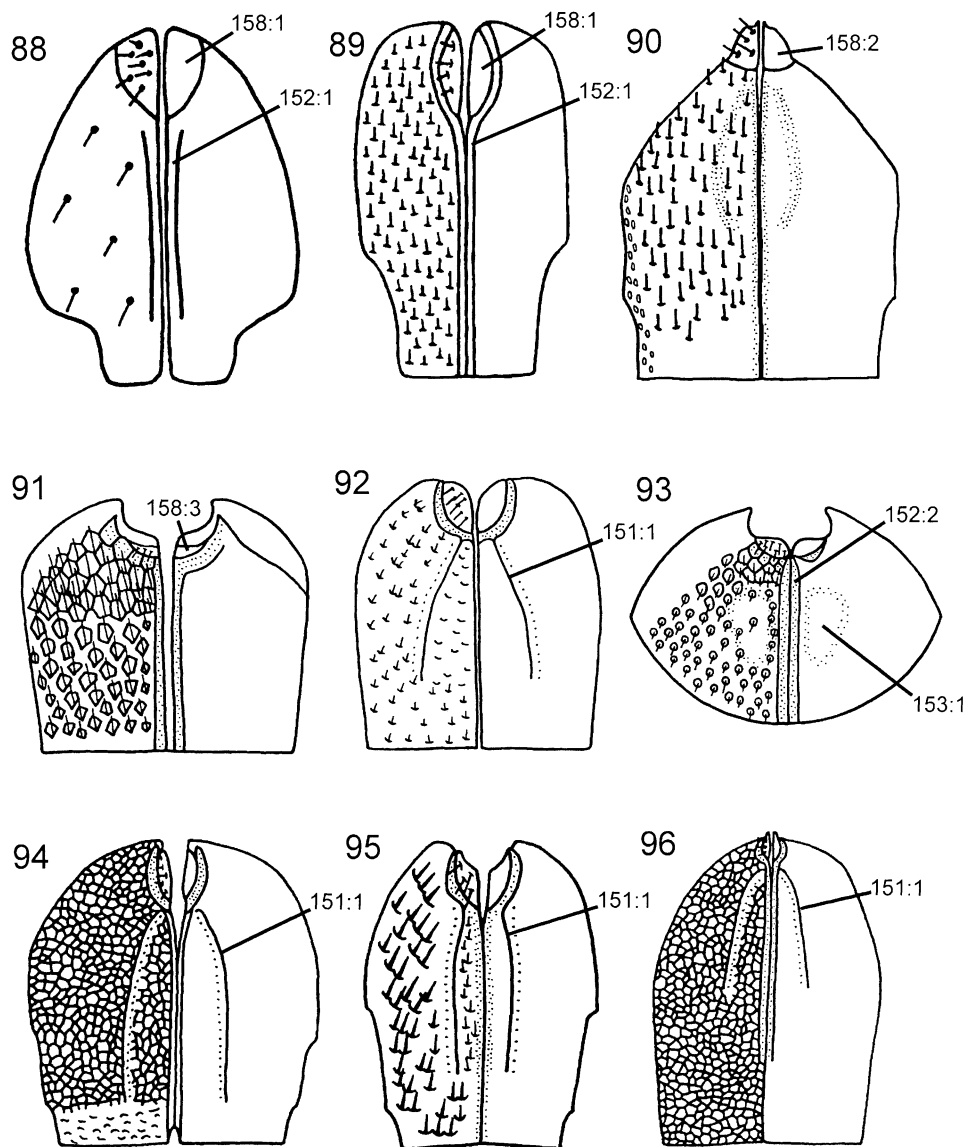
(145) *Lateral hair patches, abdominal terga (♀):* absent (Figs 75–79) = 0; several terga, starting from the 2nd, with distinct hair patch laterally (Fig. 80) = 1. *Unambiguous changes:* 83: 0–1. CI: 0.200, RI: 0.556.





**Figures 82–87.** Eighth female abdominal tergum, dorsal view. 82. *Orussonia depressa* Riek; 83. *Pseudoryssus henschii* (Mocsáry); 84. *Orussobaius minutus* Benson; 85. *Kulcania mexicana* (Cresson); 86. *Stirocorsia kohli* Konow; 87. *Ophrynopus plaumanni* Smith. Not to scale.

- (146) *Abdominal spiracles* (♀): fully developed on 1st to 8th terga = 0; fully developed on 1st and 8th terga, vestigial on remaining terga = 1; fully developed only on 1st tergum, vestigial on remaining terga = 2 (ordered). *Unambiguous changes*: 5: 1–2; 150: 0–1. CI: 1.000, RI: 1.000.
- (147) *Abdominal spiracles* (♂): fully developed on 1st to 8th terga = 0; fully developed on 1st and 8th terga, vestigial on remaining terga = 1; fully developed only on 1st tergum, vestigial on remaining terga = 2 (ordered). *Unambiguous changes*: 150: 0–1/2. CI: 0.667, RI: 0.667.
- (148) *Configuration, S7* (♀): unmodified or with simple median projection = 0; with median projection delimited laterally by weakly sclerotized lines which extend along entire visible part of S7 = 1. *Unambiguous changes*: 147: 0–1. CI: 1.000, RI: 1.000.
- (149) *Configuration, T8* (♀): without posterior projection, hindmargin straight (see Vilhelmsen, 2001b: fig. 22) = 0; with small projection, hindmargin sinuous (Figs 82–87) = 1; strongly developed, swollen projection (see Vilhelmsen, 2001b: fig. 23) = 2 (ordered). *Unambiguous changes*: 59: 1–2; 68: 1–2; 103: 1–2; 107: 1–0; 147: 0–1. CI: 0.400, RI: 0.750.
- (150) *Longitudinal stripe, T8* (♂): absent = 0; white stripe/mark present medially = 1. *Unambiguous changes*: 115: 0–1. CI: 1.000, RI: 1.000.
- (151) *Longitudinal carina, T9* (♀): absent (Figs 88–91, 93) = 0; distinct longitudinal carina present posterolaterally on 9th tergum (Figs 92, 94–96) = 1. *Unambiguous changes*: 102: 0–1; 131: 0–1. CI: 0.333, RI: 0.929.
- (152) *Medioventral groove, T9* (♀): without groove parallel to the median margin = 0; with shallow



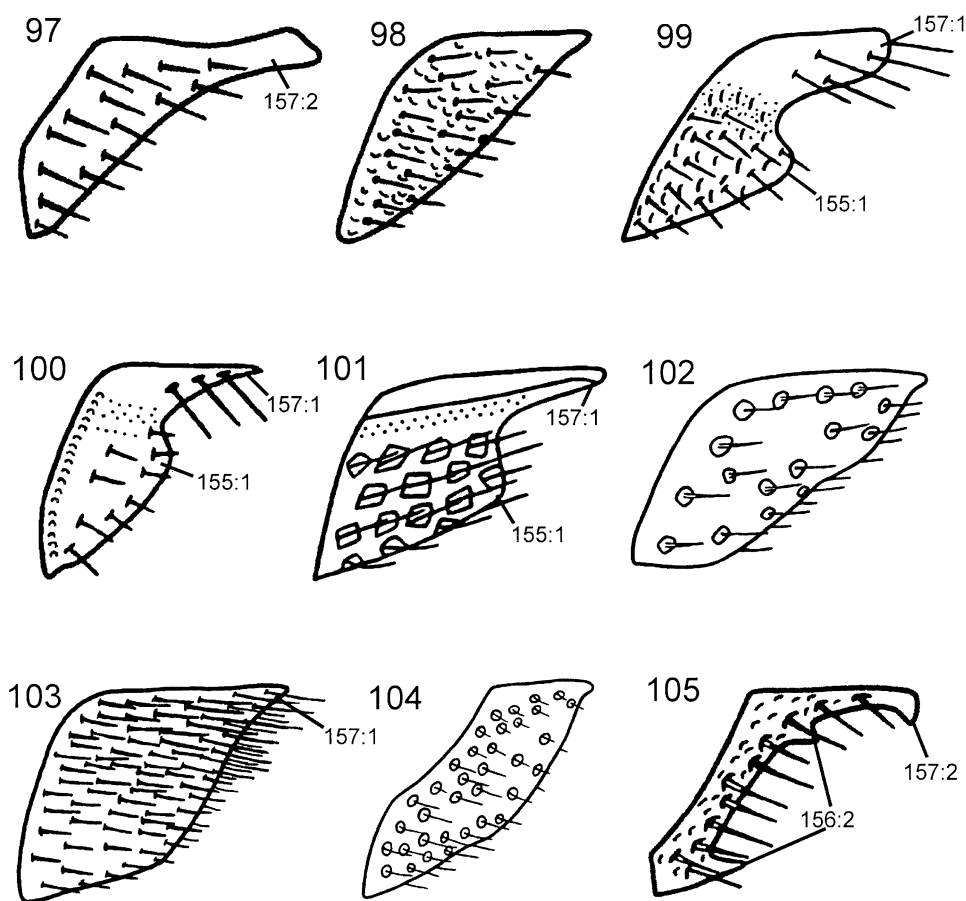
**Figures 88–96.** Ninth female abdominal tergum, ventral view. 88. *Orussonia depressa* Riek; 89. *Orussella dentifrons* (Philippi); 90. *Orussobaius minutus* Benson; 91. *Pseudoryssus henschii* (Mocsáry); 92. *Orussus occidentalis* Cresson; 93. *Chalinus braunsi* (Enslin); 94. *Guiglia sericata* (Mocsáry); 95. *Kulcania mexicana* (Cresson); 96. *Ophrynon levigatus* Middlekauff. Not to scale.

groove parallel to the median margin (Figs 88, 89) = 1; groove deep, but narrow (Fig. 93) = 2 (ordered). *Unambiguous changes*: 110: 1–2; 147: 0–1. CI: 1.000, RI: 1.000.

(153) *Smooth area, T9* (♀): absent (Figs 88–92, 94–96) = 0; raised areas with sparse punctation present posterolaterally on 9th tergum (Fig. 93) = 1. *Unambiguous changes*: 107: 0–1. CI: 1.000, RI: 1.000.

(154) *3rd valvulae*: exposed, projecting posterior to T9, medioventral margins of the latter do not abut = 0; hidden, do not project posterior to T9, medio-

ventral margins of the latter abut ventral to the 3rd valvulae for their entire length (Figs 88–96; see also Vilhelmsen *et al.*, 2001: figs 9a, 10d) = 1. *Unambiguous changes*: 147: 0–1. CI: 1.000, RI: 1.000. *Orthogonalys* (Trigonaliidae) has the 3rd valvulae hidden above the 7th sternum and the medioventral margins of the 9th tergum widely separate. Concealment in this taxon is caused by a general reduction in size of the ovipositor apparatus and should therefore not be regarded as homologous with the condition in Orussidae; therefore *Orthogonalys* was scored as state 0.



**Figures 97–105.** Ninth male abdominal sternum, lateral view. 97. *Orussonia depressa* Riek; 98. *Orussella dentifrons* (Philippi); 99. *Orussobaius minutus* Benson; 100. *Leptorussus kwazuluensis* Vilhelmsen **sp. nov.**; 101. *Pseudoryssus henschii* (Mocsáry); 102. *Pedicrista hyalina* Benson; 103. *Orussus occidentalis* Cresson; 104. *Chalinus braunsi* (Enslin); 105. *Ophrynopus plaumanni* Smith. Not to scale.

The 3rd valvulae can be seen protruding from between the margins of the 9th tergum in some pinned Orussidae specimens, but this is clearly an artefact.

- (155) *S9* (♂): without distinct swelling in the middle, but a spine might be present (Figs 97, 98, 102, 103–105) = 0; with distinct median transverse swelling (Figs 99–101) = 1. *Unambiguous changes*: 96: 0–1; 112: 1–0; 144: 0–1. CI: 0.167, RI: 0.500.
- (156) *Tubercles on S9* (♂): absent (Figs 97–104) = 0; one anteromedian and two posterolateral blunt tubercles present on 9th sternum (see Vilhelmsen & Smith, 2002: figs 31, 33, 34) = 1; distinct pointed tubercles present (Fig. 105) = 2 (ordered). *Unambiguous changes*: 17: 1–2; 38: 2–1; 102: 0–1. CI: 0.333, RI: 0.852.
- (157) *Hindmargin of S9* (♂): straight, without any projections (Figs 102, 104) = 0; with distinct, tongue-like rim (Figs 99–101, 103) = 1; with

stubby, truncated projection (Figs 97, 105) = 2 (ordered). *Unambiguous changes*: 1: 2; 111: 1–0; 147: 0–1. CI: 0.250, RI: 0.778.

- (158) *T10/cercus* (♀): 10th tergum continuous medially, variable in shape, cercus separate cylindrical structure = 0; 10th tergum discontinuous medially, cercus not separate, composite structure triangular, flat = 1 (Figs 88, 89); 10th tergum discontinuous medially, cercus not separate, composite structure swollen in the middle (Fig. 90; see also Schmidt & Vilhelmsen, 2002: fig. 12) = 2; 10th tergum discontinuous medially, cercus not separate, composite structure reduced, rectangular, flat (Fig. 91) = 3 (unordered). *Unambiguous changes*: 133: 1–3; 143: 1–2; 147: 0–1. CI: 0.250, RI: 0.909.
- (159) *Male genitalia and cercus* (♂): at least partly exposed, not enclosed by the 8th tergum and 9th sternum = 0; genitalia concealed between 8th tergum and 9th sternum, which fit closely

together, but cerci tubular, protruding between the former sclerites = 1; cerci flattened; both these and genitalia concealed when at rest, entirely enclosed by 8th tergum and 9th sternum, which fit closely together (see Snodgrass, 1941: plt. 4f, g) = 2 (ordered). *Unambiguous changes*: 147: 0/1–2. CI: 0.667, RI: 0.857. The cerci and genitalia might be partially exposed in some pinned Orussidae specimens, but this is obviously an artefact.

- (160) *Abdominal tergal colour* (♀): change in tergal colour gradual, if discernible at all = 0; 5th/6th to 8th terga reddish brown, contrasting with black 1st to 4/5th terga = 1; 3rd to 8th terga reddish brown, contrasting with black or metallic 1st and 2nd terga = 2 (ordered). *Unambiguous changes*: 28: 0–1; 70: 0–1; 113: 0–2. CI: 0.500, RI: 0.500.
- (161) *Abdominal tergal colour* (♂): change in tergal colour gradual, if discernible at all = 0; 3rd to 8th terga reddish brown, contrasting with black or metallic 1st and 2nd terga = 1. *Unambiguous changes*: 28: 0–1; 113: 0–1. CI: 0.500, RI: 0.500.
- (162) *Golden hairs, posterior abdomen*: absent = 0; golden pilosity of various density and extent present on 6th/7th to 8th terga = 1. *Unambiguous changes*: 98: 0–1. CI: 1.000, RI: 1.000.
- (163) *Body shape*: subcylindrical, not flattened = 0; distinctly flattened (see Riek, 1955: plt. II.2) = 1. *Unambiguous changes*: 146: 0–1. CI: 1.000, RI: 1.000.

#### PHYLOGENETIC ANALYSIS

The matrix was constructed in MacClade 3.08a (Maddison & Maddison, 1999). Analyses were run in PAUP\* 4.0b5 for MacIntosh (Swofford, 2001), NONA 2.0 (Goloboff, 1993a), and Pee-Wee 2.1 (Goloboff, 1993b). In PAUP\*, analyses were run with TBR branch swapping, random addition sequences. Settings of amb0, amb =, and amb- were implemented in turn; amb- was run with 100 replications, the others with 20. NONA and Pee-Wee were run with the following settings: hold50000; hold/5000; amb =; mult\*50 or amb-; mult\*100. All analyses were run with some characters ordered, as indicated in the list of characters. Since NONA and Pee-Wee treat multistate characters as ordered by default (Goloboff, 1993b), characters 14, 79, 100, 101, 120, 158 were set to unordered by entering the command cc-[character number] for each.

A broad range of weighting conditions was implemented. Analyses in PAUP\* and NONA were initially run with equal weights. Successive weighting was implemented in PAUP\* by reweighting characters according to the consistency index (CI), rescaled consistency index (RC), or retention index (RI). For each round of reweighting, 20 replications were run. This

was done until the length of the resulting trees remained stable. Implied weights analyses were run in PAUP\* with the concavity constant  $k$  set to all values from 1 to 20 in turn. Similar analyses were run in Pee-Wee with the concavity constant conc set from 1 through 6 (the entire range allowed by Pee-Wee) in turn. Note that conc-values in Pee-Wee =  $k + 1$ -values in PAUP\* (e.g. conc3 equals  $k = 2$ , the default settings in Pee-Wee and PAUP\*, respectively). After the initial searches, the discovered shortest/most fit trees were filtered to remove topologies with polytomies that were also represented by more resolved trees; in Pee-Wee, this was done by implementing the command 'best'.

Thirteen multistate characters, 11 of which are set as additive/ordered, contain partial polymorphisms. This causes differences between the results obtained by Pee-Wee/NONA and PAUP\* respectively. First, characters containing polymorphisms are considered nonadditive by Pee-Wee and NONA (Goloboff, 1993b); second, if such characters are made additive, they allow the polymorphic taxa to assume all possible states in the character (e.g. 0 & 1, 0 & 2, and 1 & 2 partial polymorphisms would all be treated as having 0 & 1 & 2 polymorphism). For this reason, I abstained from changing multistate polymorphic characters from nonadditive to additive. However, this means that the NONA/Pee-Wee and PAUP\* equal and implied weights analyses are not strictly comparable.

The results are summarized in Table 4. A strict consensus of the equal weights trees retrieved by PAUP\* is displayed in Figure 106. Condensed versions of some of the alternative topologies for the generic relationships and the phylogeny of *Orussus* are displayed in Figures 109–115 and 116–119, respectively. The higher the  $k$ -value, the more the resulting trees resembles those produced by the equal weights analyses, until at  $k = 19 +$ , they are a subset of the equal weights trees. Settings of amb0, amb =, and amb- produced trees of equal length/fit, the analyses differing only in the number of trees discovered. Amb0 produced the largest number of trees, amb- the smallest. This is because zero-length branches, i.e. branches not unambiguously supported by the data (Coddington & Scharff, 1994), are collapsed under amb-. Most amb- analyses in PAUP\* produced only two trees; these differ in the internal phylogeny of *Chalinus* spp., one (Fig. 107) having *C. braunsi*, *C. orientalis* and *C. somalicus* as a clade, the other having *C. braunsi* + *C. orientalis*, *C. imperialis* + *C. purpureiventris*, and *C. somalicus* in an unresolved trichotomy. In the Pee-Wee analyses with settings conc3–4, amb =, it was impossible to carry out all the attempted 50 replications because of memory overflow after 30 replications. In these cases, additional swapping was carried out by implementing the command max\*; this resulted in trees with the same fit as the searches done with conc3–4, amb-.

**Table 4.** Results of cladistical analyses under different weighting conditions

Weighting between genera conditions vary	No. of trees (amb-; filtered)	Length/Fit	Illustration	Comments regarding relationships Internal relationships of genera may vary
e.w., PAUP*	540	744/-	Fig. 106	
e.w., NONA	720	726/-	-	As k = 13-18, except <i>Guiglia</i> resolved slightly differently
CI, PAUP*	4	747/-	Fig. 109	As RC
RC, PAUP*	2	748/-	Fig. 109	As CI
RI, PAUP*	2	744/-	Fig. 110	Subset of e.w.; as CI/RC, except <i>Guiglia</i> polyphyletic
conc1	24	-/806,0	Figs 111, 116	
conc2	3	-/942,4	-	As conc1, except <i>Ophrella</i> is sister to <i>Ophrynopus</i>
conc3	6	-/1035,3	Fig. 112	As k = 3
conc4	36	-/1103,0	-	As k = 4-5, except <i>Ophrynon</i> sister to <i>Argentophrynopus</i> + <i>Kulcania</i>
conc5	6	-/1154,6	-	As conc6; as CI, RI, except <i>Leptorussus</i> and <i>Orussus</i> + <i>Pseudoryssus</i> have switched places
conc6	3	-/1197,8	Fig. 117	As conc5
k = 1	2	-/-94,31430	Figs 113, 118	
k = 2	2	-/-103,42111	Fig. 119	As k = 1, except for <i>Leptorussus</i> + ( <i>Pedicrista</i> + 'ophrinopine' clade)
k = 3	2	-/-110,13236	Fig. 112	As conc3
k = 4-5	2	-/(-115,34080)- (-119,56697)	Fig. 114	
k = 6	2	-/-123,05155	-	As k = 7-12, except <i>Ophrynon</i> sister to <i>Kulcania</i>
k = 7-9	2	-/(-125,98765)- (-130,67481)	Fig. 107	Preferred topology; as k = 10-12
k = 10-12	2	-/(-132,57954)- (-135,78613)	Fig. 107	As k = 7-9
k = 13-18	2	-/(-137,11825)- (-142,22999)	Fig. 115	<i>Guiglia</i> paraphyletic; as k = 19 +
k = 19 +	2	-/(-143,01602)-	Fig. 115	Subset of e.w. trees; as k = 13-18

Abbreviations: CI, successive weighting using the consistency index; conc[1-6], implied weights analysis carried out in Pee-Wee with concavity constant value as indicated; e.w., equal weights; k = [1-19 +], implied weights analysis carried out in PAUP\* with *k*-value as indicated; RC, successive weighting using the rescaled consistency index; RI, successive weighting using the retention index.

Bremer support values were computed in PAUP\* for all nodes present in the consensus tree of the equal weights analysis (Fig. 106). This was done by constructing constrained trees in MacClade and running analyses in PAUP\* constrained not to retrieve the appropriate node in turn. Fifty-seven such analyses were run, each with 20 replications and amb- implemented. The Bremer support value for a node was calculated as the length difference between the shortest trees in the equal weights analysis and the shortest trees not containing the node.

The tree displayed in Figure 107 was chosen for mapping of character evolution (Table 5) and computation of character CI and RI values (see character analysis section above). It is one of two produced by

implementing k = 7-9 in PAUP\*; it differs from k = 10-12 only in the internal phylogeny of *Orussus*. Most nodes retrieved in the majority of the analyses are represented in this tree. Exploration of character evolution and support for alternative topologies was carried out in MacClade. A strict consensus tree for all weighting conditions is shown in Figure 108; it was derived by assembling all trees derived from the different weighting conditions in a single treefile and computing the consensus in PAUP\*.

Many of the character states listed in the following (in parentheses) are marked with a superscript; this indicates that the character subsequently changes (other than reversal) within the clade (c), has evolved

**Table 5.** Unambiguous character state changes by branch, as optimized in Fig. 107. Unique apomorphies shown in bold. Changes on the root, *Urocerus* (SIR), are shown as undirected

- 1 *Urocerus gigas* (SIR). 26: 0; 46: 2; 55: 1; 69: 1; 71: 0; 75: 2; 76: 1; 100: 0; 101: 0; 123: 1; 157: 2.
- 2 *Xiphydria camelus* (XIP). 74: 0–1; 84: 0–1; 115: 1–0; 119: 1–0; 142: 0–1.
- 3 *Schlettererius cinctipes* (STE). 17: 0–1; 63: 0–1; 105: 0–1; 109: 0–1; 111: 0–1; 113: 0–1; 115: 1–0; 116: 0–1.
- 4 *Megalyra fasciipennis* (MEG). 31: 0–2; 51: 1–0; 54: 0–1; 96: 0–1.
- 5 *Orthogonalys pulchella* (TRI). 16: 0–1; 17: 0–1; 19: 0–1; 43: 0–1; 93: 0–1; **146**: 1–2.
- 6 *Argentophrynopus enigmus*. 21: 0–1; 24: 2–1; 100: 0–1
- 7 *A. gauldi*. 113: 0–1.
- 8 *Chalinus berlandi*. No unambiguous changes.
- 9 *C. braunsi*. No unambiguous changes.
- 10 *C. haugi*. No unambiguous changes.
- 11 *C. imperialis*. 50: 0–1
- 12 *C. orientalis*. No unambiguous changes.
- 13 *C. purpureiventris*. No unambiguous changes.
- 14 *C. somalicus*. 100: 2–1; 101: 2–1.
- 15 *C. timnaensis*. 76: 1–0.
- 16 *Guiglia bombycinis*. 63: 0–1; 111: 0–1.
- 17 *G. chiliensis*. 4: 0–1; 98: 0–1; 126: 1–2; 141: 0–1; 156: 1–2.
- 18 *G. coracina*. 9: 0–1; 67: 0–1; 87: 2–1.
- 19 *G. rubicunda*. 12: 2–0; 22: 1–0; 28: 0–1; 67: 0–1; 72: 0–1; 80: 0–1; 90: 0–1; 96: 1–2; 101: 0–1; 117: 0–1; 126: 1–2.
- 20 *G. rubricata*. 101: 0–1.
- 21 *G. schauinslandi*. 21: 1–0; 48: 1–0; 51: 0–1; 130: 1–0.
- 22 *G. sericata*. 6: 1–0; 141: 0–1.
- 23 *Kulcania mexicana*. No unambiguous changes.
- 24 *K. tomentosa*. 125: 1–0; 126: 1–0; 128: 1–0; 138: 0–1.
- 25 *Leptorussus africanus*. 82: 0–1.
- 26 *L. kwazuluensis*. 50: 0–1; 93: 0–1; 123: 0–1.
- 27 *Mocsarya metallicus*. 75: 1–2; 100: 0–1; 101: 0–1; 127: 0–1.
- 28 *M. syriaca*. 7: 0–1; 21: 0–1; 70: 1–0; 71: 1–0; 160: 0–1; 161: 0–1.
- 29 *Ophrella amazonica*. No unambiguous changes.
- 30 *O. lingulata*. No unambiguous changes.
- 31 *Ophrynon levigatus*. 56: 0–1; 113: 0–2; 117: 0–1; 126: 1–0.
- 32 *Ophrynopus andrei*. 141: 1–0.
- 33 *O. batesianus*. 22: 0–1; 74: 1–0.
- 34 *O. carinatus*. 23: 1–0; 50: 1–0; 51: 1–0; 64: 0–1; 70: 0–2; 89: 0–1; 95: 0–1; 130: 1–0.
- 35 *O. depressatus*. No unambiguous changes.
- 36 *O. fulvostigmus*. No unambiguous changes.
- 37 *O. hansonii*. 50: 1–0.
- 38 *O. nigricans*. 156: 2–1.
- 39 *O. plaumanni*. 130: 1–0.
- 40 *O. wagneri*. 130: 1–0.
- 41 *Orussella dentifrons*. 66: 0–1/2; 68: 1–0; 75: 1–2; 88: 0–1; 130: 0–1; 132: 0–1; 143: 1–0.
- 42 *Orussobaius badius*. 130: 0–1.
- 43 *O. caligneus*. 67: 0–1.
- 44 *O. mesembrinus*. 125: 2–1.
- 45 *O. minutissimus*. 67: 0–1; 87: 2–1; 89: 1–0; 125: 2–1; 137: 2–1; 138: 1–0.
- 46 *O. minutus*. 5: 1–0.
- 47 *O. paniculus*. 43: 0–1; 50: 0–1; 74: 1–0; 90: 1–0; 94: 1–0.
- 48 *O. wilsoni*. 23: 0–1; 130: 0–1.
- 49 *Orussonia depressa*. 66: 0–1.
- 50 *O. ruficaudata*. 68: 1–0.
- 51 *Orussus abietinus*. 22: 0–1; 26: 0–1; 50: 0–1.
- 52 *O. afer*. No unambiguous changes.
- 53 *O. bensonii*. 43: 0–1; 77: 1–2; 118: 0–1.
- 54 *O. boninensis*. 23: 0–1; 69: 0–1; 138: 0–1.
- 55 *O. brunneus*. 111: 1–2.

Table 5. Continued

- 56 *O. coreanus*. 51: 1–0; 80: 1–0; 128: 0–1.  
57 *O. decoomani*. 22: 0–1; 80: 1–0; 100: 0–1; 110: 1–0.  
58 *O. japonicus*. 22: 0–1; 26: 0–1; 43: 1–0; 132: 0–1.  
59 *O. loriae*. 21: 1–0; 48: 0–1; 51: 0–1; 56: 1–0; 69: 0–1; 111: 1–2; 137: 2–1; 149: 1–2.  
60 *O. minutus*. 4: 1–0; 16: 1–0; 23: 1–0; 110: 1–0; 125: 1–2; 127: 1–0.  
61 *O. moroi*. 90: 1–0; 110: 1–0.  
62 *O. occidentalis*. 16: 1–0; 23: 1–0; 128: 0–1.  
63 *O. rufipes*. 5: 1–0; 23: 0–1; 51: 0–1.  
64 *O. sayii*. 21: 1–0; 70: 1–0; 89: 0–1.  
65 *O. schoutedeni*. 22: 0–1; 69: 0–1.  
66 *O. scutator*. 118: 0–1.  
67 *O. spinifer*. 119: 1–0; 144: 0–1.  
68 *O. striatus*. 85: 0–1; 90: 1–0; 125: 1/2–0; 128: 1–0; 138: 1–0; 149: 1–2.  
69 *O. taorminensis*. 51: 0–1; 137: 1–2.  
70 *O. terminalis*. 24: 2–0; 50: 0–1; 69: 0–1; **160**: 0–1.  
71 *O. tessmanni*. No unambiguous changes.  
72 *O. thoracicus*. No unambiguous changes.  
73 *O. unicolor*. No unambiguous changes.  
74 *Pedicrista hyalina*. 2: 1–0; 31: 2–1; 38: 1–0; 63: 0–1; 82: 0–1; 98: 0–1; 111: 0–1; 118: 0–1; 125: 1–0; 126: 1–0; 128: 1–0.  
75 *Pseudoryssus henschii*. 22: 1–0; 85: 0–1; 127: 0–1.  
76 *P. niehuisorum*. 2: 1–0; 5: 1–0; 52: 0–1; 90: 1–0; 102: 0–1; 117: 1–0; 118: 0–1; 128: 1–0.  
77 *Stirocorsia kohli*. 98: 0–1; 104: 0–2.  
78 *S. maculipennis*. No unambiguous changes.  
79 *S. tosensis*. 100: 1–0; 113: 0–2; 114: 0–2; 125: 2–1; 130: 1–0.  
80 *Argentophrynopus*. 56: 0–1; 64: 0–1; 96: 1–2; 102: 0–1; 129: 0–1.  
81 *Ophrella*. 7: 0–1; **15**: 0–1; 123: 0–1.  
82 *Ophrynopus andrei* + *O. fulvostigmus* + *O. hansonii*. 2: 1–0; 89: 0–1; 113: 1–2.  
83 *Ophrynopus andrei* + *O. batesianus* + *O. fulvostigmus* + *O. hansonii*. 60: 0–1; 69: 0–1; 145: 0–1.  
84 *Ophrynopus depressatus* + *O. nigricans* + *O. plaumanni*. 2: 1–0.  
85 *Ophrynopus depressatus* + *O. nigricans* + *O. plaumanni* + *O. wagneri*. 53: 0–1; 67: 1–0; 94: 1–0.  
86 *Ophrynopus* except *O. carinatus*. **14**: 0–1; 98: 0–1; **114**: 0–1.  
87 *Ophrynopus*. 85: 0–1; 96: 1–2; 97: 0–1; 104: 0–2.  
88 *Stirocorsia kohli* + *S. tosensis*. 13: 1–0.  
89 *Stirocorsia*. 8: 0–1; **49**: 0–1; 53: 0–1; 74: 1–0.  
90 *Ophrynopus* + *Stirocorsia*. 4: 0–1; 6: 1–0; 67: 0–1; 69: 1–0; 100: 0–1; 138: 0–1.  
91 *Ophrella* + *Ophrynopus* + *Stirocorsia*. 50: 0–1; 75: 1–0; 80: 1–0; 128: 1–0.  
92 *Argentophrynopus* + *Ophrella* + *Ophrynopus* + *Stirocorsia*. 8: 1–0; 12: 2–1; 72: 0–1; 77: 1–0; 94: 0–1; 126: 1–2; 130: 0–1; 137: 0/1–2.  
93 *Kulcania*. 4: 0–1; 13: 1–0; 24: 2–1; 46: 0–2; 52: 0–1; 85: 0–1; 99: 1–0; 125: 2–1; 139: 0–1; 144: 0–1.  
94 Ophrynopine clade except *Guiglia*, *Ophrynon*. 51: 0–1; 69: 0–1.  
95 Ophrynopine clade except *Guiglia*. 38: 1–0; 39: 0–1.  
96 *Guiglia bombycinis* + *G. rubricata*. 155: 0–1.  
97 *Guiglia bombycinis* + *G. rubricata* + *G. sericata*. 48: 1–0; 72: 0–1; 100: 0–1; 113: 0–2.  
98 *Guiglia bombycinis* + *G. coracina* + *G. rubricata* + *G. sericata*. 25: 0–1; 70: 1–2; 162: 0–1.  
99 *Guiglia rubicunda* + *G. schauinslandi*. 8: 1–0.  
100 *Guiglia* except *G. chiliensis*. 66: 1–2; 94: 0–1; 137: 1–2.  
101 *Guiglia*. 53: 0–1; 80: 1–0; 130: 0–1.  
102 Ophrynopine clade. 8: 0–1; 12: 0–2; 77: 2–12; 90: 1–0; 99: 0–1; 115: 1–0; 127: 0–1; 151: 0–1; **156**: 0–1.  
103 *Chalinus berlandi* + *C. haugi*. **36**: 0–1; 50: 0–1; **73**: 0–1; 97: 0–1; **104**: 0–1; **108**: 0–1; 125: 1–2; 129: 0–1; 130: 0–1; 149: 1–2.  
104 *Chalinus berlandi* + *C. orientalis* + *C. somalicus*. 11: 0–1.  
105 *Chalinus imperialis* + *C. purpureiventris*. 23: 1–0; 24: 2–0; **35**: 1–2; **126**: 1–3; 130: 0–1.  
106 *Chalinus berlandi* + *C. imperialis* + *C. orientalis* + *C. purpureiventris* + *C. somalicus*. **20**: 0–1; **35**: 0–1.  
107 *Chalinus* except *C. berlandi*, *C. haugi*. **34**: 0–2; 39: 0–1; **42**: 0–1; 70: 1–0; 71: 1–0; 149: 1–0; **153**: 0–1.  
108 *Chalinus*. 6: 1–0; 22: 1–0; **32**: 0–1; 48: 1–0; **58**: 0–1; 77: 2–0; 80: 1–0; 90: 1–0; 100: 0–2; 101: 0–2.  
109 *Mocsarya*. **10**: 1–0; 12: 0–2; 24: 2–1; 105: 1–0.  
110 *Chalinus* + *Mocsarya*. 14: 0–2; 37: 0–1; 46: 1–2; 55: 0–1; 76: 0–1; 79: 1–2; 84: 1–0; 110: 1–0; 116: 0–1; **119**: 0–2; 143: 1–0; **152**: 1–2.

**Table 5.** *Continued*


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111	<i>Chalinus</i> + <i>Mocsarya</i> + <i>Pedicrista</i> . 9: 0–1; <b>46</b> : 0–1; 51: 0–1; 74: 1–0; 157: 1–0.
112	<i>Chalinus</i> + <i>Mocsarya</i> + <i>Pedicrista</i> + ophrynopine' clade. 4: 1–0; 89: 1–0; 96: 2–1; 105: 0–1; 117: 1–0; 155: 1–0.
113	<i>Orussus abietinus</i> + <i>O. occidentalis</i> . 160: 0–2; 161: 0–1.
114	<i>Orussus coreanus</i> + <i>O. minutus</i> . 24: 2–0.
115	<i>Orussus abietinus</i> + <i>O. coreanus</i> + <i>O. japonicus</i> + <i>O. minutus</i> + <i>O. occidentalis</i> + <i>O. sayii</i> . 150: 0–1.
116	<i>Orussus abietinus</i> + <i>O. coreanus</i> + <i>O. japonicus</i> + <i>O. minutus</i> + <i>O. occidentalis</i> + <i>O. sayii</i> + <i>O. unicolor</i> . 16: 0–1; 17: 0–1.
117	<i>Orussus abietinus</i> + <i>O. coreanus</i> + <i>O. japonicus</i> + <i>O. minutus</i> + <i>O. occidentalis</i> + <i>O. sayii</i> + <i>O. terminalis</i> + <i>O. unicolor</i> . 23: 0–1; 128: 1–0.
118	<i>Orussus abietinus</i> + <i>O. coreanus</i> + <i>O. japonicus</i> + <i>O. minutus</i> + <i>O. occidentalis</i> + <i>O. sayii</i> + <i>O. terminalis</i> + <i>O. thoracicus</i> + <i>O. unicolor</i> . 51: 0–1; 103: 2–1.
119	<i>Orussus abietinus</i> + <i>O. coreanus</i> + <i>O. decoomani</i> + <i>O. japonicus</i> + <i>O. minutus</i> + <i>O. occidentalis</i> + <i>O. sayii</i> + <i>O. terminalis</i> + <i>O. thoracicus</i> + <i>O. unicolor</i> . 43: 0–1; 56: 1–0.
120	<i>Orussus moroi</i> + <i>O. taorminensis</i> . 38: 1–0; 74: 1–0.
121	<i>Orussus abietinus</i> + <i>O. coreanus</i> + <i>O. decoomani</i> + <i>O. japonicus</i> + <i>O. minutus</i> + <i>O. moroi</i> + <i>O. occidentalis</i> + <i>O. sayii</i> + <i>O. taorminensis</i> + <i>O. terminalis</i> + <i>O. thoracicus</i> + <i>O. unicolor</i> . 89: 1–0; 96: 2–1; 111: 1–2.
122	<i>Orussus afer</i> + <i>O. tessmanni</i> . 2: 1–0; 22: 0–1; 50: 0–1; 110: 1–0.
123	<i>Orussus afer</i> + <i>O. bensoni</i> + <i>O. tessmanni</i> . 111: 1–0.
124	<i>Orussus schoutedeni</i> + <i>O. scutator</i> . 82: 0–1; 111: 1–0.
125	<i>Orussus schoutedeni</i> + <i>O. scutator</i> + <i>O. spinifer</i> . 50: 0–1; 66: 0–2; 67: 1–0; 75: 2–1; 77: 1–2; 80: 1–0.
126	<i>Orussus lorae</i> + <i>O. schoutedeni</i> + <i>O. scutator</i> + <i>O. spinifer</i> . 5: 1–0; 6: 1–0.
127	<i>Orussus afer</i> + <i>O. bensoni</i> + <i>O. lorae</i> + <i>O. schoutedeni</i> + <i>O. scutator</i> + <i>O. spinifer</i> + <i>O. tessmanni</i> . <b>107</b> : 0–1.
128	<i>Orussus boninensis</i> + <i>O. brunneus</i> . 2: 1–0; 21: 1–0; 38: 1–0; 100: 0–1.
129	<i>Orussus afer</i> + <i>O. bensoni</i> + <i>O. boninensis</i> + <i>O. brunneus</i> + <i>O. lorae</i> + <i>O. schoutedeni</i> + <i>O. scutator</i> + <i>O. spinifer</i> + <i>O. tessmanni</i> . 130: 0–1; 137: 1–2.
130	<i>Orussus</i> except <i>O. rufipes</i> , <i>O. striatus</i> . 22: 1–0.
131	<i>Orussus</i> except <i>O. striatus</i> . 48: 1–0; 77: 2–1; 151: 0–1.
132	<i>Orussus</i> . 37: 0–1; 55: 0–1; 56: 0–1; 63: 0–1; 75: 1–2; 111: 0–1.
133	<i>Pseudoryssus</i> . 158: 1–3.
134	<i>Orussus</i> + <i>Pseudoryssus</i> . 79: 1–2; 119: 0–1.
135	Orussidae except <i>Leptorussus</i> , <i>Orussella</i> , <i>Orussobaius</i> , <i>Orussonia</i> . 22: 0–1; 24: 0–2; 31: 0/1–2; 48: 0–1; 94: 1–0.
136	<i>Leptorussus</i> . <b>18</b> : 0–1; 72: 0–1; 109: 0–1.
137	Orussidae except <i>Orussella</i> , <i>Orussobaius</i> , <i>Orussonia</i> . 3: 0–1; <b>19</b> : 1–3.
138	<i>Orussobaius badius</i> + <i>O. minutissimus</i> . 51: 0–1; 70: 1–0; 93: 0–1.
139	<i>Orussobaius badius</i> + <i>O. minutissimus</i> + <i>O. paniculus</i> . 118: 0–1; 128: 1–0.
140	<i>Orussobaius badius</i> + <i>O. minutissimus</i> + <i>O. minutus</i> + <i>O. paniculus</i> . 52: 0–1.
141	<i>Orussobaius</i> except <i>O. caligneus</i> , <i>O. mesembrinus</i> . <b>30</b> : 0–1; 97: 0–1; 109: 0–1; 126: 1–0.
142	<i>Orussobaius</i> + <i>O. mesembrinus</i> . 48: 0–1; 79: 1–2; 117: 1–0.
143	<i>Orussobaius</i> . 82: 0–1; 105: 0–1; 137: 0/1–2; 138: 0–1; <b>158</b> : 1–2.
144	Orussidae except <i>Orussella</i> , <i>Orussonia</i> . 54: 0–1; 79: 0–1; 87: 0–2; 96: 0–1/2; 103: 0–2; 155: 0–1.
145	Orussidae except <i>Orussonia</i> . 5: 0–1; 50: 1–0; 51: 1–0; 70: 0–1; 74: 0–1; 118: 1–0.
146	<i>Orussonia</i> . <b>19</b> : 1–2; <b>29</b> : 0–1; <b>33</b> : 0–1; 34: 0–1; <b>47</b> : 0–1; <b>163</b> : 0–1.
147	Orussidae. <b>19</b> : 0–1; 26: 1–0; <b>40</b> : 0–1; <b>57</b> : 0–1; <b>61</b> : 0–1; 72: 1–0; <b>78</b> : 0–1; 84: 0–1; 87: 0–1; 91: 0–1; 92: 1–0; 94: 0–1; 95: 0–1; 101: 1–0; 117: 0–1; <b>124</b> : 2–1; 127: 1–0; 140: 1–0; 142: 0–1; <b>148</b> : 0–1; 149: 0–1; <b>152</b> : 0–1; <b>154</b> : 0–1; 157: 0–1; <b>158</b> : 0–1; <b>159</b> : 0/1–2.
148	Orussidae + <i>Schlettererius</i> (STE). <b>1</b> : 0–1; <b>44</b> : 0–1; <b>45</b> : 0–1; <b>83</b> : 0–1; 100: 1–0; 119: 1–0; 125: 1–2; 128: 0–1.
149	Orussidae + <i>Schlettererius</i> (STE) + <i>Megalyra</i> (MEG). <b>59</b> : 0–1; <b>121</b> : 1–0; <b>122</b> : 1–0; 125: 0–1.
150	Orussidae + Apocrita. 34: 1–0; 48: 1–0; 50: 0–1; <b>62</b> : 0–1; <b>81</b> : 0–1; <b>86</b> : 0–1; 91: 1–0; 92: 0–1; <b>106</b> : 0–1; <b>112</b> : 1–0; 124: 0–2; <b>131</b> : 1–0; 132: 1–0; <b>133</b> : 1–0; <b>136</b> : 0–1; 140: 0–1; <b>146</b> : 0–1; 147: 0–1/2.

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independently in another clade/taxon (i), and/or undergoes reversal within the clade (r).

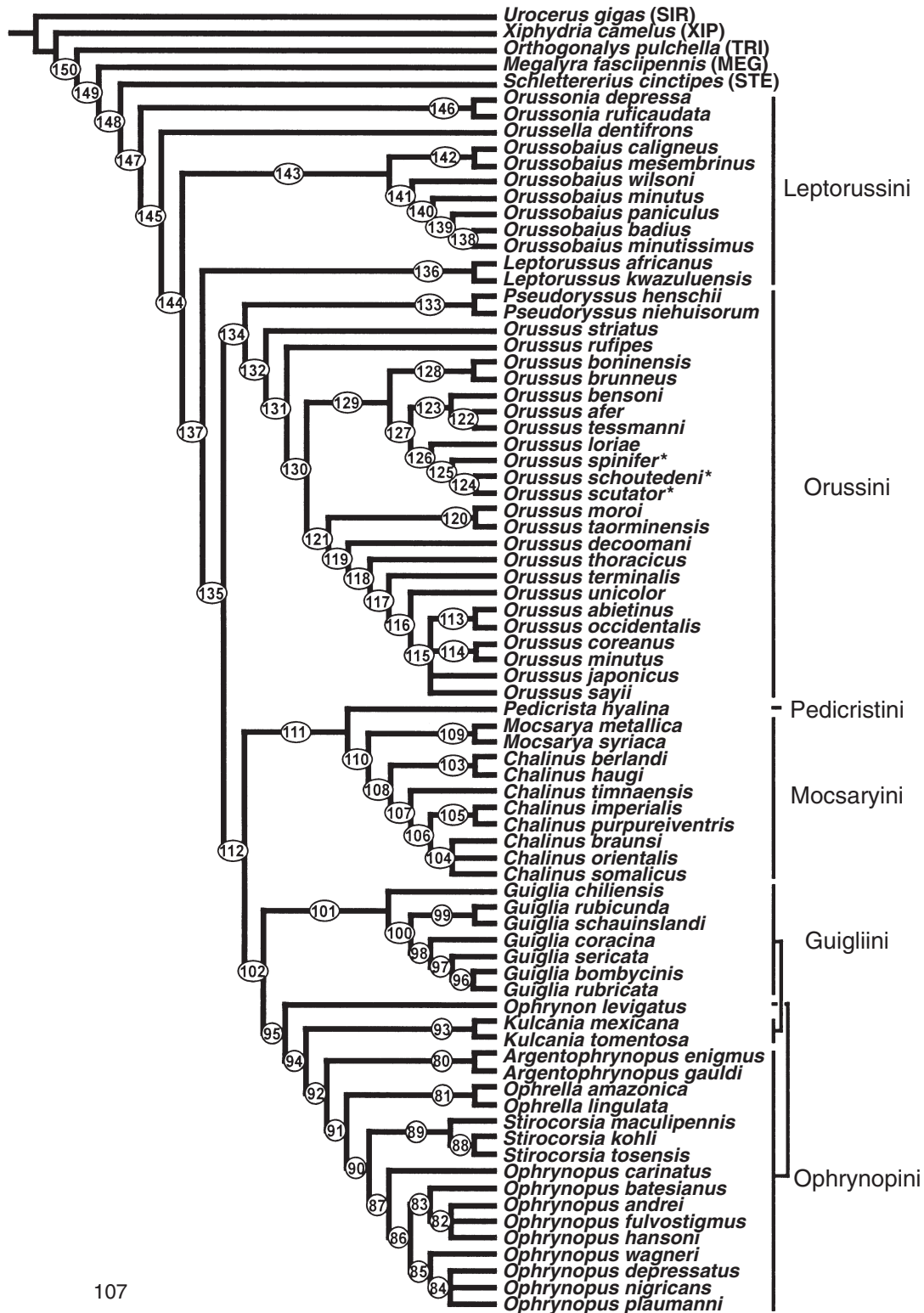
#### MONOPHYLY OF ORUSSIDAE

A number of autapomorphies can be identified for the Orussidae, many of which are correlated with the

echolocation system in the females (antenna (40: 1) and foreleg (57: 1, 61: 1) configuration) and the concealed ovipositor apparatus (female S7 (148: 1) and T9 (154: 1) configuration, hidden 3rd valvulae (Vilhelmsen *et al.*, 2001). The presence of an at least partly developed ventral transverse frontal carina (19: 1<sup>c</sup>), the reduced number of antennomeres in both females

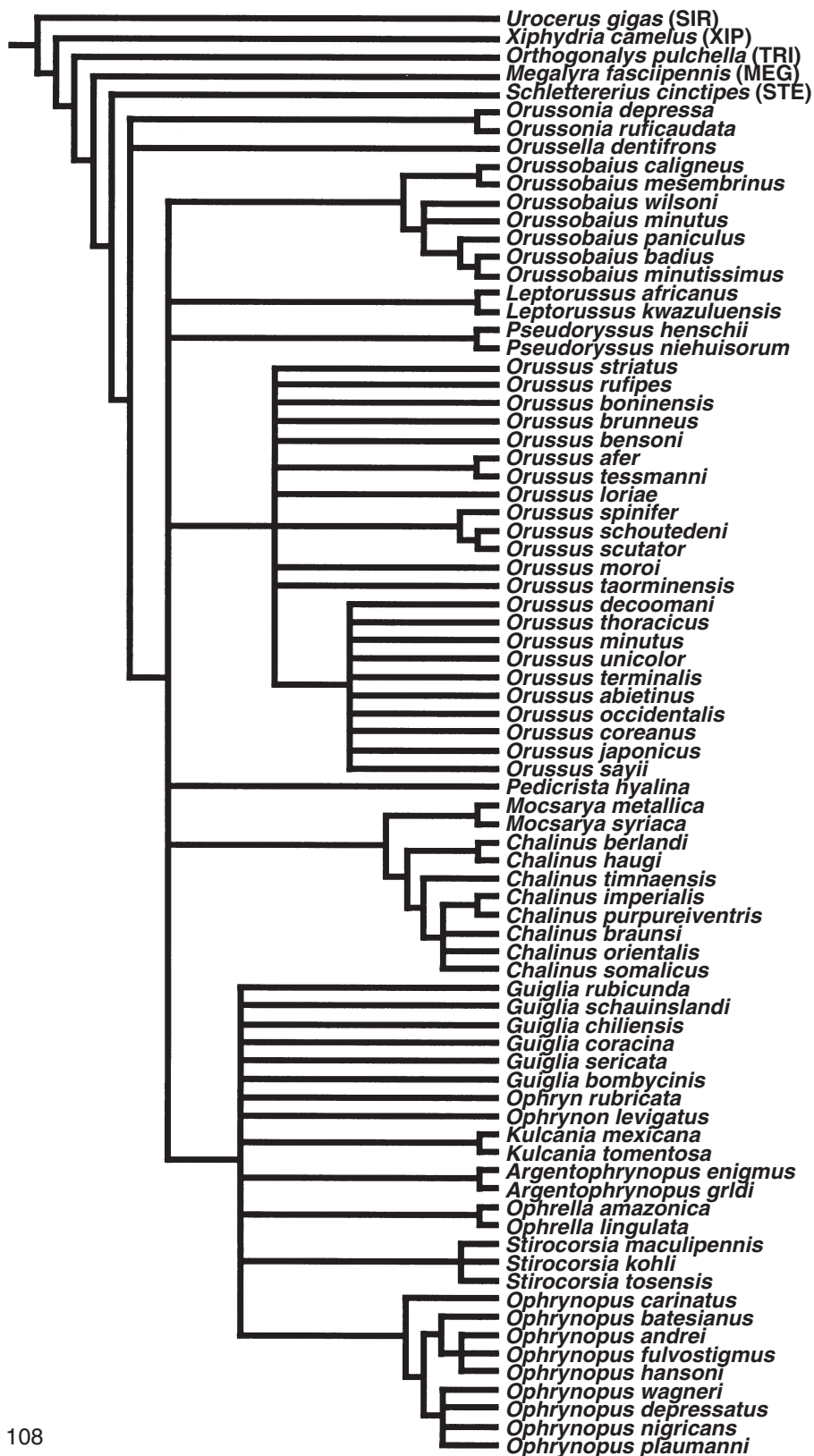






107

**Figure 107.** Preferred topology, used for mapping character evolution. One of two trees derived by implied weights analysis in PAUP\*,  $k = 7-9$ , amb-. The tribal classification of Benson (1955a)/Guiglia (1965) is superimposed on the right. Taxa formerly placed in *Heliorussus* are indicated with asterisks.



108

**Figure 108.** Strict consensus tree computed from all trees derived under every weighting condition implemented in PAUP\* and Pee-Wee.

(10) and males (11; see Vilhelmsen, in press), the anterior position of the base of the mesoscutellar arm (78: 1), the presence of a lateral carina on the mesocoxa (87: 1<sup>c</sup>), the fusion of the female T10/cercus (158: 1<sup>c</sup>), and the concealed male genitalia and cercus (159: 2) are additional autapomorphies for the family (the cercus is reduced or absent in many apocritans [Gibson, 1986: character 18b], but not in any of the outgroup taxa in the present analysis). Gibson (1985) observed that the tergo-pleural muscles are absent from the mesothorax in *Orussus sayii* and that the tergo-trochanteral muscles are enlarged and apparently replace the tergo-pleurals as the primary dorsoventral indirect flight muscles. This is also the case in *Orussobaius minutus* and *Guiglia schauinslandi* (Vilhelmsen, in press), making it likely that the absence of tergo-pleural muscles in the mesothorax is an additional autapomorphy of the Orussidae. Furthermore, the corresponding muscles are absent from the metathorax of *Orussus* spp. (Vilhelmsen, 2000a). The monophyly of the Orussidae is obviously strongly supported.

In the present analyses, the Stephanidae consistently comes out as the sistergroup of the Orussidae. The Orussidae share a number of features with this basal apocritan family (see also Vilhelmsen, 1996, 1997a, 2001a): the presence of the ocellar corona (1: 1), the configuration of the labrum (44: 1) and the mandibles (45: 1), and the presence of a large mesothoracic basalare (83: 1). It is unclear whether these traits are independently derived or shared symplesiomorphies. The absence of the ocellar corona in the fossil Paroryssidae, putatively the extinct sister or stemgroup of the Orussidae (see below), implies that this feature is a parallelism. The monophyly of the Orussidae–Apocrita clade is established beyond any reasonable doubt (Vilhelmsen, 1997a, 2001a). The Orussidae are unique among the parasitic Hymenoptera in not having the 1st abdominal tergum incorporated in the thorax as the propodeum (92: 1<sup>r</sup>) and lacking the constriction between the 1st and 2nd abdominal segments (140: 1<sup>r</sup>), the defining features of the Apocrita. Further plesiomorphies retained by the Orussidae are the presence of the cenchrus (91: 0<sup>i</sup>) and part of the posterior anal vein in the forewing (124: 1<sup>i</sup>).

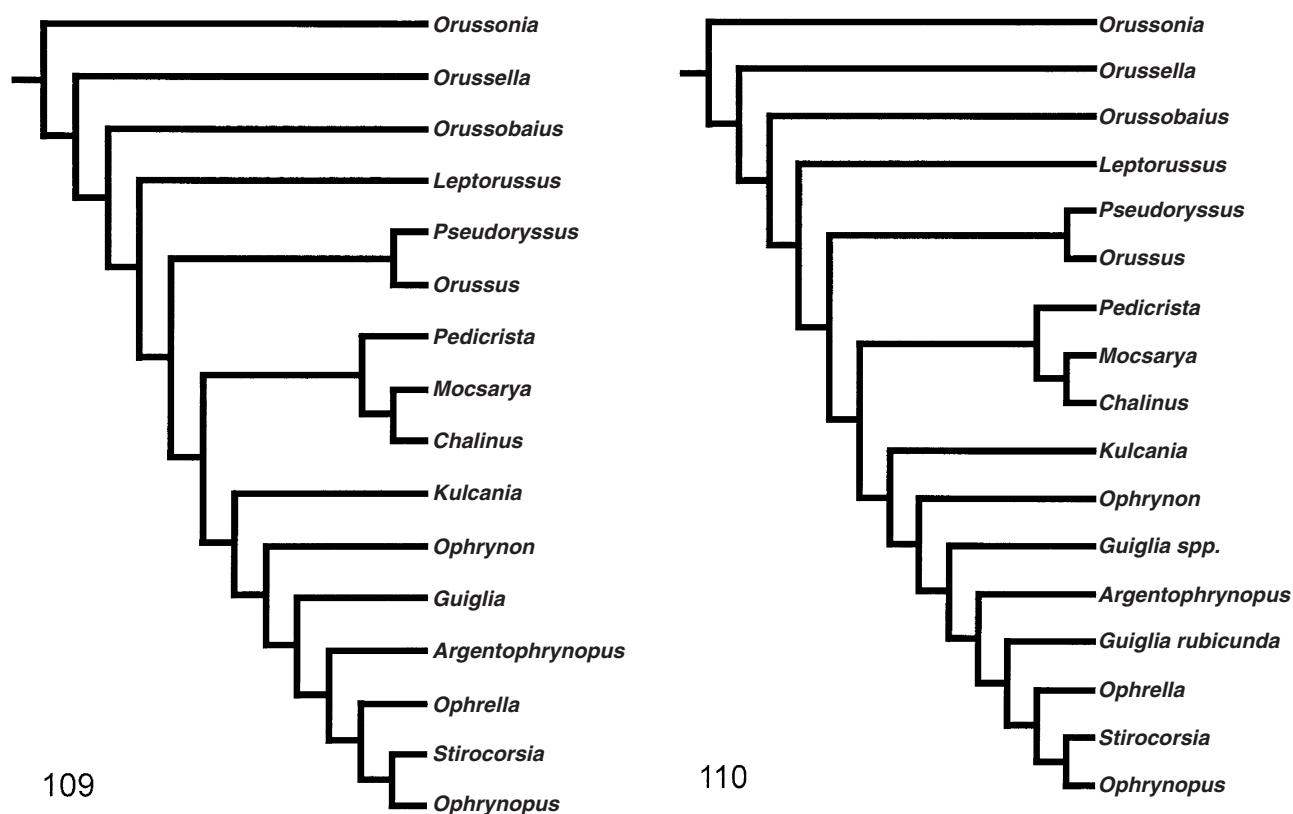
The monophyly of the Apocrita is fairly well supported in the analyses of Ronquist *et al.* (1999) and Vilhelmsen (2001a). The failure to retrieve this clade in the present study can perhaps be ascribed to the very limited apocritan taxon sample and the exclusion of characters requiring the examination of internal morphological features. Additional putative autapomorphies of the Apocrita are (character numbers refer to Vilhelmsen, 2001a): the presence in the mouthparts of a hypopharyngeal lobe (28: 1) and hypopharyngeal pectens (30: 1), the retracted cervical

prominences (44: 2), and the incorporation of the prospinasternum in the mesothorax (65: 2). The retracted cervical prominences is part of a tight articulation between the postocciput and the cervical prominences (Vilhelmsen, 2000b), forming a close connection between the head and thorax. It is not so well developed in *Orussus* spp., the only representatives of the Orussidae examined by Vilhelmsen (2000b, 2001a). However, other members of the family (*Guiglia schauinslandi*, *Orussobaius minutus*, *Orussonia depressa*; Vilhelmsen, in press) have a condition more resembling that of the Apocrita, making it more likely that it evolved in the common ancestor of Orussidae and Apocrita; the condition observed in *Orussus* spp. apparently is a reversal.

#### INTERGENERIC RELATIONSHIPS

The basal branching pattern within the Orussidae is identical under almost all weighting schemes: *Orussonia* + (*Orussella* + (*Orussobaius* + remaining Orussidae) (Figs 106, 107, 109, 110, 112–115). The most convincing support for the Orussidae exclusive of *Orussonia* is provided by the development of the axillar flanges (70: 1<sup>cr</sup>), the presence of dense sculpture on the mesoscutellum (74: 1<sup>ir</sup>), and the forewing vein 2r-m being positioned distally of the pterostigma (118: 0<sup>r</sup>). However, *Orussonia* + *Orussella* occasionally come out as sister taxa (concl-2; Fig. 111). This is supported by the absence of the ventral coronal tooth (3: 0<sup>i</sup>), the absence of the occipital carina (26: 0<sup>i</sup>), the presence of dense pilosity (94: 1<sup>i</sup>) and a well developed carina laterally on the hindcoxa (95: 1<sup>i</sup>), and the presence of a longitudinal carina medially on the 2nd abdominal tergum (141: 1<sup>i</sup>); all but the last of these traits are interpreted as plesiomorphic for the Orussidae in the preferred topology. The clade comprising all genera except *Orussonia* and *Orussella* is retrieved under all weighting schemes (Fig. 108) and is well supported by the presence of a lateral carina on the propleuron (54: 1<sup>i</sup>), the presence of a distinct pit anteriorly of the mesoscutellar arm (79: 1<sup>c</sup>), the presence of a carina laterally on the midcoxa (87: 1<sup>c</sup>), and the presence of pegs dorsally on the hindtibia (103: 1/2). *Orussobaius* is the sistergroup of all genera except *Orussonia* and *Orussella* in most of the analyses, but can also be placed with *Leptorussus* + *Pseudoryssus* (concl-2; Fig. 111). The latter topology is supported by the presence of a carina on the medioventral margin of the hindcoxa (96: 2<sup>i</sup>) and the presence of a transverse swelling on the male 9th abdominal sternum (155: 1<sup>i</sup>).

*Leptorussus* is the sistergroup of all Orussidae except the three basalmost genera under most weighting conditions (Figs 106, 107, 109, 110, 114, 115). This is only supported by the presence of the ventral coronal tooth (3: 1<sup>ir</sup>) and a fully developed ventral transverse frontal



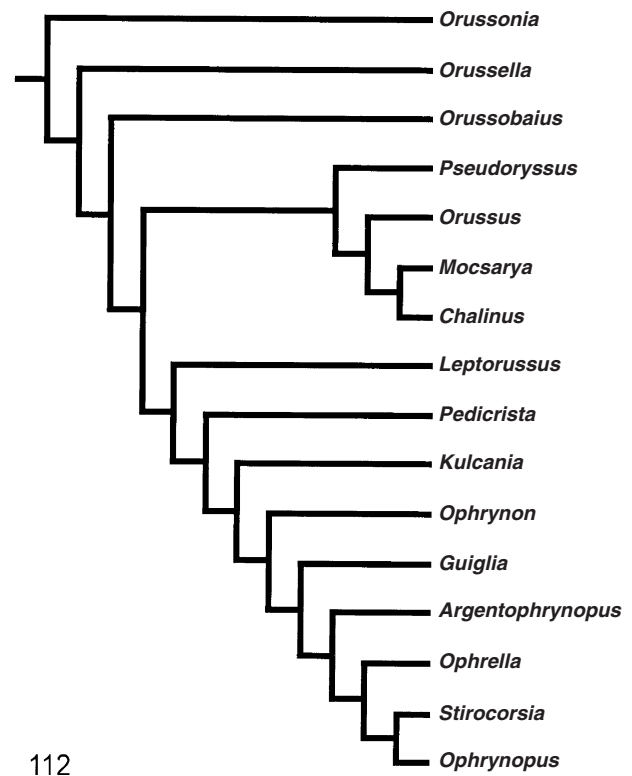
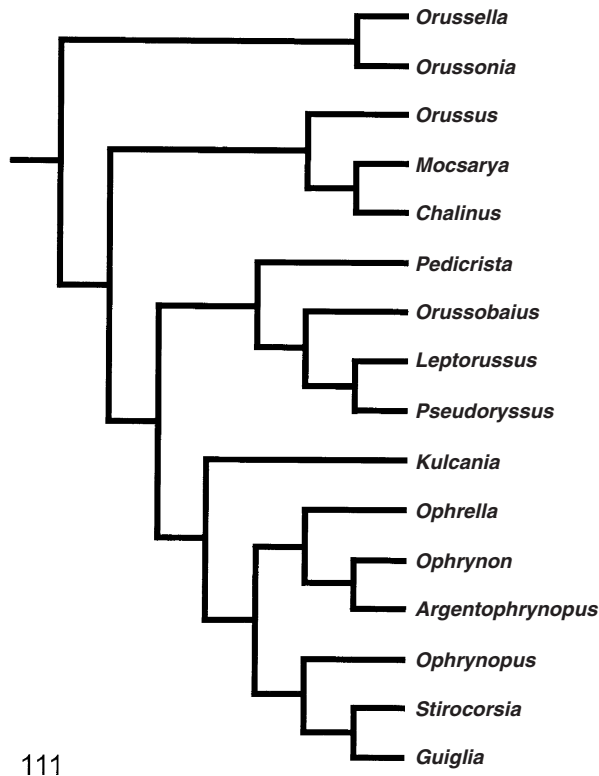
Figures 109–110. Topology of genera of Orussidae, from successive weightings in PAUP\* with 109.CI and 110.RI.

carina (19: 3); however, these characters are very strong, exhibiting few changes over the entire tree. Alternative positions of *Leptorussus* nonetheless occur: sistergroup of *Pseudoryssus* (conc1–2; Fig. 111), of *Pedicrista* + ‘ophrynopine’ genera (conc3; Fig. 112), of (*Pedicrista* + (*Chalinus* + *Mocsarya*)) + ‘ophrynopine’ genera (conc5–6;  $k = 2–3$ ), and of *Pedicrista* + (*Pseudoryssus* + (*Orussus* + (*Chalinus* + *Mocsarya*))) ( $k = 1$ ; Fig. 113). These are mostly weakly corroborated, the presence of a distally swollen 9th female antennomere (38: 0<sup>tr</sup>) and the absence of the posterolateral carina on the hindcoxa (95: 0<sup>tr</sup>) lending some support to the *Leptorussus* + (*Pedicrista* + ‘ophrynopine’ genera) and *Leptorussus* + ((*Pedicrista* + (*Chalinus* + *Mocsarya*)) + ‘ophrynopine’ genera) topologies.

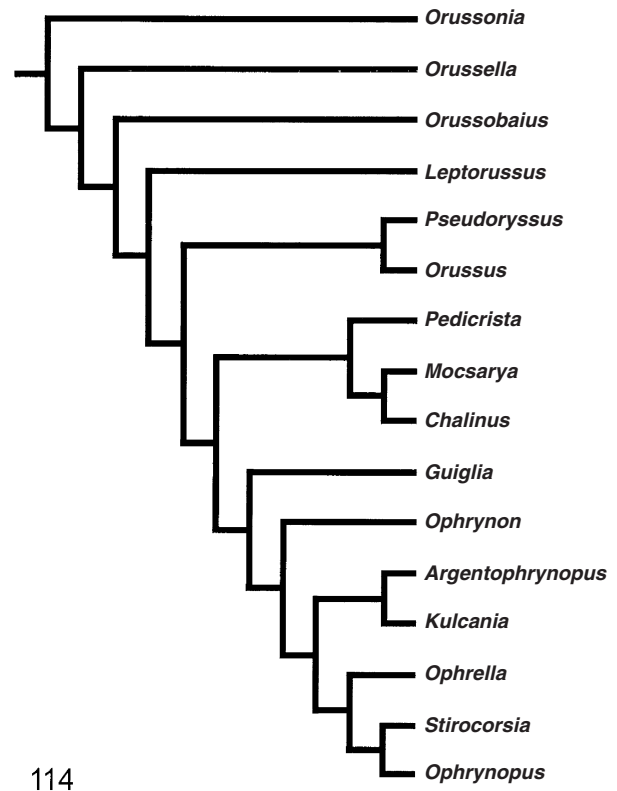
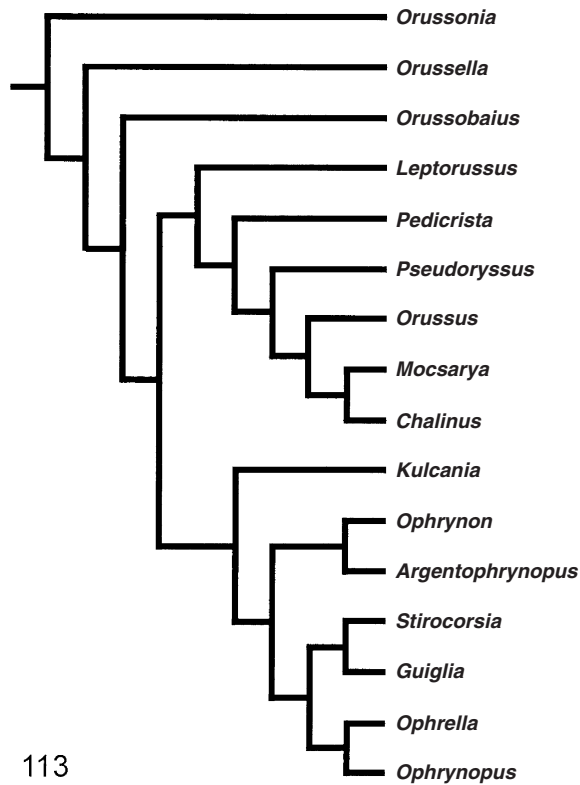
*Chalinus* + *Mocsarya* is the most well supported intergeneric relationship in the entire Orussidae. Prominent synapomorphies, several of which are unique, are the metallic body colour, including the frons (14: 2), the very reduced maxillary and labial palps (46: 2<sup>i</sup>), the posterior margin of the mesoscutellum reaching posterior to the cenchrus (76: 1<sup>r</sup>), the absence of a distinct mesosubar carina (84: 0<sup>i</sup>), the absence of a distinct angle between forewing veins 2r and Rs (116: 1<sup>i</sup>), the forewing discal cell reaching vein R anteriorly (119: 2), the smooth area laterally on the

2nd abdominal tergum being triangular (143: 0<sup>i</sup>), and the presence of a deep, narrow groove medioventrally on the female 9th abdominal tergum (152: 2). The sistergroup of *Chalinus* + *Mocsarya* is usually *Pedicrista* (Figs 106, 107, 109, 110, 114, 115); this is corroborated by the presence of a median longitudinal frontal carina (9: 1<sup>tr</sup>), the presence of maxillary and labial palps with four and two segments, respectively (46: 1<sup>c</sup>; assuming that this condition evolved prior to the more reduced condition in *Chalinus* and *Mocsarya*), having only sparse sculpture on the mesoscutellum (74: 0<sup>i</sup>), and the presence of a straight, nonprotruding posterior margin on the male 9th abdominal sternum (157: 0<sup>i</sup>). However, *Chalinus* + *Mocsarya* occasionally comes out as the sistergroup of *Orussus* (conc1–3;  $k = 1–3$  (Figs 111–113)). This is supported by the presence of shortened antennomeres 4–5 in the female antenna (37: 1) and having the forecoxa expanded medially (55: 1i); these traits only change a few times over the whole tree and the topology they support must be considered a serious alternative.

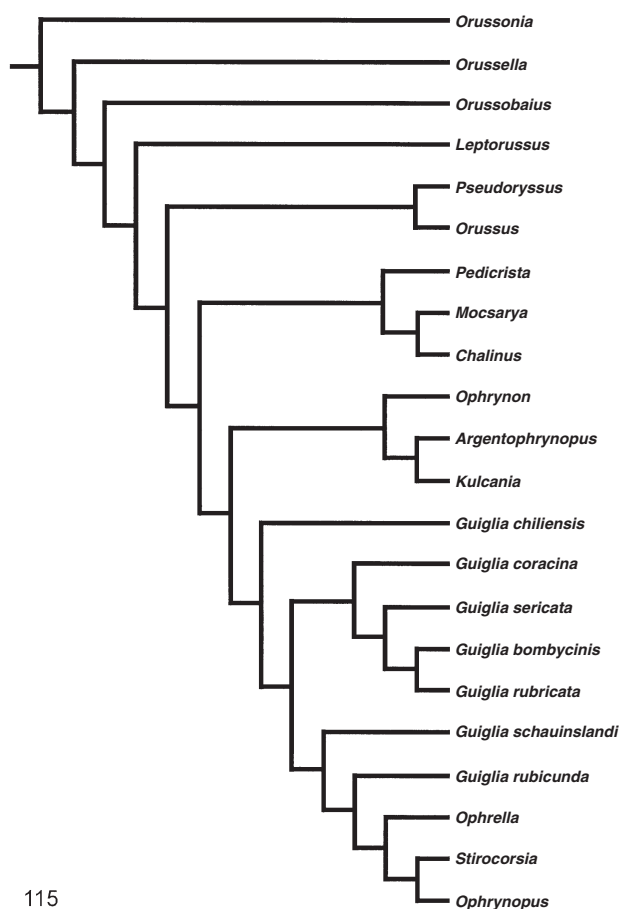
*Pedicrista* may occupy several different positions in addition to the one just discussed: sistergroup of (*Leptorussus* + *Pseudoryssus*) + *Orussobaius* (conc1–2; Fig. 111), supported by the wide mesonotum (64: 1<sup>tr</sup>) and the presence of distinctly carinate lateral



Figures 111–112. Topology of genera of Orussidae, from Pee-Wee with concavity constant 111. conc1, and 112. conc3.



Figures 113–114. Topology of genera of Orussidae, from PAUP\* with settings 113. k = 1, 114. k = 4–5.



**Figure 115.** Topology of genera of Orussidae, from PAUP\* with settings  $k = 13$ – $18$ . Note that *Guiglia* is paraphyletic.

margins of the mesoscutellum (77: 2<sup>i</sup>); sistergroup of the ‘ophrynopine’ genera (conc3;  $k = 2$ – $3$  (Fig. 112), supported by the presence of a ventral carina on the hindtibia (105: 1<sup>i</sup>); sistergroup of (*Orussus* + (*Chalinus* + *Mocsarya*)) + *Pseudoryssus* ( $k = 1$ ; Fig. 113), supported by the forewing vein 1r-Rs being spectral (120: 0<sup>e</sup>). None of these alternatives seem well corroborated in comparison with the preferred topology.

*Pseudoryssus* is usually placed as the sistergroup of *Orussus* (Figs 106, 107, 109, 110, 114, 115). The support is rather weak, putative synapomorphies being the mesoscutellar arm having a raised area without a pit anteriorly (79: 2<sup>i</sup>), the forewing discal cell being rhomboid (119: 1<sup>c,i,r</sup>), and, under some weighting schemes (conc5–6), the forewing vein 1r-Rs being spectral (120: 0<sup>i</sup>). *Pseudoryssus* rarely comes out as the sistergroup of *Leptorussus* (conc1–2; Fig. 111, see also above), but occasionally as sistergroup to (*Chalinus* + *Mocsarya*) + *Orussus* (conc3;  $k = 1$ – $3$  (Figs 112, 113). The latter topology is supported by the same characters as the preferred one, the differences being caused by the conflict between the characters supporting (*Chali-*

*nus* + *Mocsarya*) + *Orussus* (see above) and ((*Chalinus* + *Mocsarya*) + *Pedicrista*) + ‘ophrynopine’ genera.

The ‘ophrynopine’ genera (*Argentophrynopus*, *Guiglia*, *Kulcania*, *Ophrella*, *Ophrynon*, *Ophrynopus* and *Stirocorsia*) constitute a clade that is retrieved under all weighting conditions (Fig. 108). The most convincing synapomorphies are the distal position of the forewing vein 2r relative to the pterostigma (115: 0<sup>i</sup>), the presence of a longitudinal carina laterally on the female 9th abdominal tergum (151: 1<sup>i</sup>), and the presence of tubercles on the male 9th abdominal sternum (156: 1<sup>c,i</sup>). The sistergroup of the ‘ophrynopine’ genera usually is (*Chalinus* + *Mocsarya*) + *Pedicrista* (Figs 106, 107, 109, 110, 114, 115); this topology is rather weakly supported, the strongest support coming from having a carina developed ventrally on the hindtibia (105: 1<sup>i,r</sup>) and having a transverse swelling absent from the male 9th abdominal sternum (155: 0<sup>i,r</sup>). Rarely occurring alternative sistergroups to the ‘ophrynopine’ genera are all other genera except *Orussonia*, *Orussella* and *Orussobaius* ( $k = 1$ ; Fig. 113), being supported by the characters mentioned above for the clade comprising all genera of Orussidae except the three latter, and ((*Leptorussus* + *Pseudoryssus*) + *Orussobaius*) + *Pedicrista* (conc1–2; Fig. 111), a relationship supported mainly by the presence of a carina ventrally on the hindtibia (105: 1<sup>i,r</sup>). The support for *Pedicrista* alone as the sistergroup of the ‘ophrynopine’ genera (conc3;  $k = 2$ – $3$  (Fig. 112) has already been discussed.

The relationships between the ‘ophrynopine’ genera are weakly supported and changes substantially depend on which weighting scheme is implemented. *Guiglia* is placed as sistergroup of the remaining genera under many weighting conditions, including the preferred topology (conc = 4;  $k = 4$ – $12$  (Figs 107, 114). The ‘ophrynopine’ genera excluding *Guiglia* are supported by having the 9th female antennomere swollen subapically (38: 0<sup>i</sup>) and a carina present laterally (39: 1<sup>i</sup>). An alternative topology (CI; RC; RI; conc1–3, 5–6;  $k = 1$ – $3$  (Figs 109–113) has *Kulcania* as the basalmost ‘ophrynopine’ genus; the other genera are supported by the presence of a distinct triangular projection on the posteroventral corner of the hindfemur (99: 1). A third possibility is (*Argentophrynopus* + *Kulcania*) + *Ophrynon* ( $k = 13$  +; Fig. 115) as the sistergroup of the remaining ‘ophrynopine’ genera; the former clade is supported by the antennal characters listed above as support for the ‘ophrynopine’ genera exclusive of *Guiglia*, the latter clade by the absence of a distinct carina posteriorly on the mesoscutellar arm (80: 0<sup>r</sup>).

*Argentophrynopus* is the most recently described genus in the Orussidae (Vilhelmsen & Smith, 2002). A survey of its changing position within the ‘ophrynopine’ clade under different weighting conditions corroborates that it should not be merged with any of the other genera. *Argentophrynopus* turns up as

the sistergroup of ((*Ophrynopus* + *Stirocorsia*) + *Ophrella*) + *Guiglia rubicunda* (RI; Fig. 110), of (*Ophrynopus* + *Stirocorsia*) + *Ophrella* (CI, RC; conc3, 5–6; k = 3, 6–12 (Figs 107, 109, 112), of *Ophrynon* (conc1–2; k = 1–2 (Figs 111, 113), and of *Kulcania* (conc4; k = 4–5, 13 + (Figs 114, 115). The topology ((*Ophrynopus* + *Stirocorsia*) + *Ophrella*) + *Argentophrynopus* occurs in the preferred tree (Fig. 107) and is supported by the presence of an indistinct lateral margin on the mesoscutellum (77: 0<sup>i</sup>); the sistergroup relationship between *Argentophrynopus* and *Ophrynon* is supported by the presence of a carina ventrally on the forefemur (56: 1<sup>i</sup>). Additional support for these and for the other possible placements of *Argentophrynopus* is weak, being provided by characters that are highly variable even within the 'ophrynopine' clade.

*Guiglia* is the only genus in the Orussidae that is not retrieved under all weighting conditions. In most cases (CI; RC; conc1–6; k = 1–12 (Figs 107, 109, 111–114) the monophyly of the genus is corroborated, although the internal relationships vary; however, *Guiglia* occasionally comes out as paraphyletic relative to (*Ophrynopus* + *Stirocorsia*) + *Ophrella* (k = 13 +; Fig. 115) or rarely as polyphyletic (RI), displaying the topology (((*Ophrynopus* + *Stirocorsia*) + *Ophrella*) + *G. rubicunda*) + *Argentophrynopus*) + remaining *Guiglia* spp. (Fig. 110). Character support for the monophyly of *Guiglia* is weak, but so are the characters that corroborate the para- and polyphyletic topologies. I consider it most prudent to retain *Guiglia* as a valid genus until more evidence can be acquired. The problems with retrieving *Guiglia* as monophyletic may be caused by missing data for *G. rubicunda*. This species is only known from a single male specimen, and thus it could not be scored for the characters specific for the female sex. The examination of female *G. rubicunda* specimens might provide additional support for the inclusion of this species in *Guiglia* and perhaps strengthen the case for the monophyly of the genus.

The clade (*Ophrynopus* + *Stirocorsia*) + *Ophrella* is retrieved under most weighting conditions (Figs 106, 107, 109, 110, 112, 114, 115); it is supported by the unique trait of having the mesoscutellum rounded posteriorly and lying parallel with the anterior margin of the metanotum (75: 0). The sistergroup relationship between *Ophrynopus* and *Stirocorsia* also comes out in most of the analyses; this is supported by the dorsally extended ocellar corona (6: 0<sup>i</sup>) and by the presence of a well developed subspiracular carina (138: 1<sup>i</sup>). An additional putative synapomorphy for these two genera is the presence of an occipital concavity dorsally on the head (28: 1<sup>i</sup>); however, this trait is absent from *Ophrynopus carinatus*. In a few instances, *Stirocorsia* is the sistergroup of *Guiglia* (conc1–2; k = 1–2), in which case *Ophrynopus* is either most closely related to the former two genera

combined (conc1; Fig. 111) or to *Ophrella* (conc2; k = 1–2 (Fig. 113). The *Ophrynopus* + *Ophrella* clade is corroborated by the presence of a lateral metanotal carina (90: 1<sup>i</sup>), but otherwise support for these relationships is weak.

#### CONSEQUENCES FOR CLASSIFICATION

In summary, all but one genus (*Guiglia*) are always retrieved as monophyletic (Fig. 108). The most well supported of the nonmonotypic genera are *Argentophrynopus*, *Chalinus*, *Kulcania*, *Mocsarya*, *Ophrella* and *Orussonia*, all having Bremer support values of three or more (Fig. 106). In contrast, only three nodes within the Orussidae connecting two or more genera are present in all trees, the intergeneric relationships being weakly corroborated in general. The high degree of homoplasy in the dataset might be caused by the extensive timespan it has to bridge. The basal branching events within the family possibly took place as early as the late Jurassic (150 Mya; Vilhelmsen, in press), whereas some of the present day sibling species might have separated only a few Mya. Characters supporting distal nodes in the phylogeny are often highly variable when viewed over the entire tree. Implied weighting is apparently helpful in sorting characters that are informative at different levels, but the noise caused by homoplasious characters at the deeper level might still interfere with the signal provided by the characters that are useful for resolving the basal splitting events. It is possible that the separation of the present day genera occurred in a few rapid radiations with little time for morphological traits linking the genera to evolve, interrupted by long periods with little speciation where autapomorphies of the individual genera accumulated.

The unstable intergeneric relationships of the Orussidae have substantial implications for the higher-level classification of the family. The state-of-the-art classification of the Orussidae (Benson, 1955a; Guiglia, 1965) comprises two subfamilies and six tribes (Table 1). Of the subfamilies, Ophrynopinae is monophyletic and well supported, whereas Orussinae is paraphyletic under all circumstances. When superimposed upon the preferred topology (Fig. 107), the tribal classification is not corroborated either: Orussini, Mocsaryini, and the monotypic Pedicristini are monophyletic, but Leptorussini and Ophrynopini are paraphyletic and Guigliini polyphyletic. Ophrynopini and Guigliini can both be rendered monophyletic by transferring *Kulcania* from the latter to the former. However, no such convenient solution offers itself for the Leptorussini, which comprises the four basalmost genera within the Orussidae.

A proper systematic classification should be both cladistically stringent (i.e. only monophyletic groups



should be formally recognized) and useful (i.e. the hierarchies in the classification should facilitate organizing information about the group, allowing easy recognition and assignment of new species to their proper subgroups). To meet the first criteria, the number of subfamilies and tribes within the Orussidae would have to be increased drastically, or other major changes introduced. The four genera (*Orussonia*, *Orussella*, *Orussobaius*, *Leptorussus*) now comprising the 'Leptorussini' would have to be assigned a separate subfamily and tribe each. An additional three subfamilies would be needed to accommodate the remaining genera: (1) the Ophrynopinae; (2) *Orussus*, *Pseudoryssus*; (3) *Chalinus*, *Mocsarya*, *Pedicrista*. It might be considered appropriate to merge the latter with the Ophrynopinae, but the relationship between these two clades is weakly supported, and it would violate the longstanding and well corroborated definition of the Ophrynopinae. At the tribal level, one might uphold the Pedicristini and the revised Guigliini, but they would comprise only *Pedicrista hyalina* and *Guiglia*, respectively.

The classification outlined above, revised according to the analyses undertaken in the present study, would comprise seven subfamilies and nine tribes. I abstain from proposing this rearrangement for two reasons: (1) the revised groups are either highly redundant (four subfamilies and six tribes comprising single genera, two of which are monotypic) or weakly corroborated (the remaining groups) and hence difficult to identify; (2) it runs contrary to the utility criteria outlined above because it enforces a cumbersome, largely redundant and hence more or less superfluous higher level classification. The systematic information on the Orussidae accumulated here is adequately conveyed by the revised generic

**Table 6.** Genera in Orussidae recognized in the present study (number of valid species in brackets)

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<i>Argentophrynopus</i> (2)
<i>Chalinus</i> (8)
<i>Guiglia</i> (7)
<i>Kulcania</i> (2)
<i>Leptorussus</i> (2)
<i>Mocsarya</i> (2)
<i>Ophrella</i> (2)
<i>Ophrynon</i> (1)
<i>Ophrynopus</i> (9)
<i>Orussella</i> (1)
<i>Orussobaius</i> (7)
<i>Orussonia</i> (2)
<i>Orussus</i> (23)
<i>Pedicrista</i> (1)
<i>Pseudoryssus</i> (2)
<i>Stirocorsia</i> (4)

---

classification (Table 6), as most genera are well defined and easily recognized. Therefore, I propose abandoning recognition of formal taxa above the genus within the Orussidae.

#### FAMILY DIAGNOSIS

##### Head

Cuticular teeth around median ocellus present, number variable. Antenna inserted below ventral margin of eye, torulus overlapped dorsally by distinct carina. Female antenna with ten segments, male antenna with 11. Female 10th antennomere reduced in size, rectangular in lateral view and with thickened apex. Labrum narrow, comma-shaped and with dense tuft of elongate hairs distally. Mandible blunt, chisel-like, without differentiated teeth. Labiomaxillary complex in ground plan with elongate maxillary palp having five segments and short labial palp having three segments.

##### Thorax

Female foretibia swollen and subdivided by inverted U-shaped furrow. Foretibial anterior apical spur developed into calcar, forebasitarsus proximally with notch. Five foretarsomeres present in male, three in female; female forebasitarsus elongate, distally with spur overlapping 2nd tarsomere. Mesoscutum with well-developed parapsidal signa and transscutal fissure. Mesoscutellum with lateral arm arising from anterolateral corner. Mesothoracic basalare large, postspiracular sclerite absent, anterior thoracic spiracle and prepectus concealed beneath posterolateral margin of pronotum. Mesocoxa subdivided by transverse groove, delimited by lateral carina. Cenchrus present. Metapleuron reduced posterodorsally, not fused with lateral margin of 1st abdominal tergum. Hindtibia with dense pilosity of short hairs medially. Preapical tibial spurs absent from all legs.

##### Wings

Forewing veins 1r, 3r-m and 2 m-cu absent; posterior anal vein of forewing reduced proximally. Hindwing costa, veins 3r-m and m-cu absent; vein 1a present.

##### Abdomen

First tergum continuous medially. No constriction between 1st and 2nd segment. 2nd tergum laterally with smooth area. Female with functional spiracles on 1st and 8th terga, male only on 1st. Female 7th sternum with narrow median part delimited by grooves, median part continuous with distinct projection posteromedially. Female 9th tergum deeply cleft medially, dorsally overlapped by 8th. Medioventral margins of 9th tergum closely abutting and enclosing 3rd valvulae ventrally; remaining parts of ovipositor apparatus also concealed. Female 10th tergum subdivided

medially, with cercus incorporated. Male cercus well developed, flattened, concealed between 8th tergum and 9th sternum together with male genitalia.

#### DESCRIPTIONS OF GENERA

Genus *Argentophrynopus* Vilhelmsen & Smith, 2002 (Figs 23, 36, 72)

*Argentophrynopus* Vilhelmsen & Smith [2002: 11]. Type species *Argentophrynopus gauldi* Vilhelmsen & Smith, 2002, by original designation.

*Description.* Head and body almost entirely dark brown to black, median part of female S7 light brown. Antenna predominantly dark brown, in female some basal antennomeres light brown. Legs variously coloured. Forewing pterostigma usually dark, remaining venation dark brown, except in median hyaline area; two infusate areas present, proximal one extending from just distally of bifurcation of anal veins to base of pterostigma, distal one from distal part of pterostigma to apex (Fig. 72); hyaline area situated subapically between veins Rs and M. Hindwing with transparent venation, except for basal part of vein R slightly infuscated distally. Following areas in female densely covered by short, broad silvery hairs: occiput and gena (but not area between eye and postocular carina; Fig. 23), posterodorsal part of pronotum, mesoscutellar sulcus, dorsal part of mesepisternum, lateral parts of hindcoxa and femur, and lateral parts of T2–8; lateral hair patches of abdominal terga progressively broader posteriorly. Silvery pilosity less developed in male, absent from abdominal terga.

*Head.* Ocellar corona narrow, ventral tooth present; dorsal transverse and median longitudinal frontal carinae absent, lateral longitudinal frontal carina only weakly developed and not reaching well-developed ventral transverse frontal carina; only scattered hairs present posterior to eye; postocular and occipital carinae well developed (Fig. 23), no dorsal concavity on latter observed; subantennal groove well developed; frons and vertex with areolate sculpture, overlain by microimbricate pattern. Female antenna with combined length of A4 + 5 longer than A6; A9 expanded distally (Fig. 36) and with carina laterally. Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

*Thorax.* Pronotum deeply curved posteriorly and without notch medially in hindmargin; dorsal part broader laterally than medially. Forecoxa not expanded medially. Forefemur with distinct longitudinal carina ventrally. Female mesoscutum without longitudinal carina medially; mesoscutellar sulcus distinct. Mesoscutellum rounded posteriorly, not broadly contiguous with hindmargin of mesonotum; lateral margin of mesoscutellum indistinct, merging with surrounding areas;

mesoscutellum not projecting posterior to cenchrus; mesoscutellar arm pointed laterally and with deep pit anteriorly. Mesopleuron with mesosubar carina present, mesepisternal carina absent. Metascutellum not developed. Pronotum, mesonotum, and metanotum areolate-punctulate, dorsal part of mesepisternum rugose-punctulate, mesepimeron imbricate with scattered punctures. Hindcoxa with lateral pilosity well developed. Hindfemur without denticles ventrally, short longitudinal carina present distally, posteroventral corner triangular and projecting. Hindtibia with one irregular row of distinct pegs dorsally, weakly developed longitudinal carina ventrally. Hindtibial apical spurs differ considerably in length.

*Wings.* Forewing vein 2r arising from pterostigma about 2/3rds from base of latter; distinct angle where 2r joins vein Rs (Fig. 72); discal cell of about equal length proximally and distally; vein 1r-Rs distinct and of considerable length; cu-a inserts proximal to discal cell, opposite vein M.

*Abdomen.* T1 postspiracular carina well developed. T2 with smooth lateral area rectangular and continuous with antecostal sulcus anteriorly. Female T8 with well-developed projection posteromedially. Female T9 with distinct longitudinal carina delimiting concave area medially. Male S9 obliquely sloping in lateral view, with extended posterior margin; tubercles well developed. T1 areolate-punctulate; T2–8 and sterna punctate-imbricate; female T9 rugose-imbricate; male S9 imbricate proximally, rugose in middle, with glabrous area posteriorly.

*Discussion.* *Argentophrynopus* was erected by Vilhelmsen & Smith (2002) for two species previously placed provisionally in *Ophrynopus* (see Smith, 1995: fig. 7.01). Putative autapomorphies includes the presence of white silvery hairs on large parts of the body, including the hindfemur (102: 1<sup>i</sup>) and the presence of a hyaline spot in the distal infuscated area of the forewing (129: 1<sup>i</sup>), both unique features within the 'ophrynopine' clade (see discussion of generic relationships above). The 'ophrynopine' affinity of the genus is confirmed by the presence of a distally inserted 2r in the forewing (115: 0<sup>i</sup>) and the presence of tubercles on the male 9th abdominal sternum (156: 2<sup>i</sup>), as well as several conditions occurring only among some of the other ophrynopine genera: female A9 swollen distally (38: 0<sup>i</sup>) and with lateral carina (39: 1<sup>i</sup>), lateral margin of mesoscutellum indistinct, merging with surrounding areas (77: 0<sup>i</sup>), and hindfemur with posteroventral corner triangular (99: 1).

#### Valid species

*Argentophrynopus enigmus* Vilhelmsen & Smith, 2002: 12. Holotype female (NMNH).

## KEY TO GENERA

- 1** Head with cirlet of cuticular teeth (ocellar corona) around median ocellus (Figs 1–12) and 1st and 2nd abdominal segments broadly contiguous, no constriction between them (Figs 75–81) ..... 2 (Orussidae)
- Ocellar corona absent and/or distinct constriction between 1st and 2nd abdominal segments present ..... (other Hymenoptera)
- 2** (1) Head with ventral transverse frontal carina at most weakly developed medially (Fig. 1) or present only above toruli (Figs 2, 3); ventralmost coronal tooth at about same level as median ocellus (Figs 1–3), median longitudinal frontal carina always absent ..... 3
- Ventral transverse frontal carina complete and distinct along entire width of frons (Figs 4–12); ventralmost coronal tooth usually situated well below level of median ocellus (Figs 4, 6–12); if teeth at level with ocellus, then median longitudinal frontal carina present (Fig. 5) ..... 5
- 3** (2) Body conspicuously dorsoventrally compressed ..... *Orussonia* Riek (2 species)
- Body cylindrical ..... 4
- 4** (3) Thorax with mesoscutellum triangular posteriorly and mesopostnotum continuous medially (Fig. 39); metascutellum developed, with distinct scutellar arms delimiting depression posteromedially ..... *Orussella* Benson (1 species)
- Mesoscutellum rounded posteriorly, separating the two halves of the mesopostnotum entirely (Fig. 38); metascutellum reduced, at most a median longitudinal ridge present ..... *Orussobaius* Benson (7 species)
- 5** (2) Head with distinct transverse frontal furrow ventrally (Fig. 15); subantennal groove weakly developed; postocular carina absent ..... *Leptorussus* Benson (2 species)
- Transverse frontal furrow absent (Figs 16–18); subantennal groove usually well developed (Figs 7, 8); if weakly developed, then median longitudinal frontal carina present (Fig. 5); postocular carina usually present (Figs 16–18) ..... 6
- 6** (5) Forewing vein 2r arising from pterostigma about 2/3rds from base of latter (Figs 72–74); hindfemur with laterodistal corner having distinct, triangular projection (Fig. 54) or T1 with distinct dense transverse fringe of hairs on hindmargin (Fig. 80); male S9 with three tubercles or spines variously developed (Fig. 105) ..... 7
- Forewing 2r arising from middle of pterostigma (Figs 63–71); hindfemur with laterodistal corner rounded (Figs 52, 53) and T1 hindmargin at most with scattered hairs (Fig. 79); male S9 entirely devoid of spines and tubercles (Figs 97–104) ..... 13
- 7** (6) Head with postocular carina distinct but present only ventrally, not extending much above lower margin of eye (Fig. 20); labiomaxillary complex reduced, maxillary palp very short, three-segmented, indiscernible. Hindfemur with laterodistal corner rounded (e.g. Figs 49–53). 1st abdominal tergum with distinct transverse fringe of hairs along hindmargin (Fig. 80) ..... *Kulcania* Benson (2 species)
- Postocular carina usually extending for a considerable length posterior to eye (Figs 19, 21–24); labiomaxillary complex well developed, maxillary palp elongate, five-segmented. Hindfemur with laterodistal corner having distinct, triangular projections (Fig. 54). T1 hindmargin at most with scattered hairs (Figs 75–79, 81) ..... 8
- 8** (7) Frons with broadly expanded and flattened setae; posterior coronal teeth separated by narrow longitudinal furrow. Forewing cu-a inserts on Cu1 distally of M, in middle of discal cell (Fig. 73) ..... *Ophrella* Middlekauff (2 species)
- Frons devoid of broadly expanded or flattened setae; posterior coronal teeth not separated by narrow longitudinal furrow. Forewing cu-a inserts on Cu1 opposite or at most slightly distally of M (Figs 72, 74) ..... 9
- 9** (8) Hindfemur laterally and several areas on thorax (posterodorsal part of pronotum, mesoscutellar sulcus, anterolateral parts of mesopleuron) covered with distinct broad, silvery hairs. Forewing always infuscated all the way to apex but with subapical hyaline spot between veins Rs and M, distally of vein 2r-m (Fig. 72) ..... *Argentophrynopus* Vilhelmsen & Smith (2 species)
- Haircover on hindfemur less dense and/or not silvery, distribution and colour of hairs on thorax not as above. Forewing, if densely infuscated, usually with hyaline apex and never with hyaline spot subapically (Figs 73, 74) ..... 10
- 10** (9) Thorax with mesoscutellum having distinct lateral margin, raised relative to adjacent sclerite, posterior part of mesoscutellum rounded and at most touches metanotum for short distance medially (Fig. 46) ..... 11

–	Mesocutellum with lateral margin indistinct, not raised relative to adjacent sclerite, posterior part of mesocutellum parallel with and closely abutting metanotum for a considerable distance (Figs 47,48).....	12
<b>11 (10)</b>	Head with frons having only scattered punctation, separated by large smooth spaces; female antenna with 9th antennomere swollen distally (Fig. 35) and having carina laterally. Forefemur with longitudinal carina ventrally.....	<i>Ophrynon</i> Middlekauff (1 species)
–	Head with frons densely sculptured (Fig. 10); female antenna with A9 not swollen distally (e.g. Fig. 30) and without carina laterally. Forefemur without carina ventrally.....	<i>Guiglia</i> Benson (7 species)
<b>12 (10)</b>	Thorax with pronotum having short longitudinal carina/smooth line medially; mesopleuron anteriorly without vertical carina (mesepisternal carina). Hindfemur without denticles ventrally (e.g. Figs 51–54).....	<i>Stirocorsia</i> Konow (4 species)
–	Pronotum without short longitudinal carina medially (Fig. 48); mesopleuron with vertical carina. Hindfemur with denticles ventrally (e.g. Figs 49, 50).....	<i>Ophrynopus</i> Konow (9 species)
<b>13 (6)</b>	Body colour predominantly blue-green metallic. Maxillary palp very shortened, one-segmented, hardly visible. Forewing with vein 1r-Rs very reduced, so discal cell touches vein R anteriorly (Fig. 71).....	14
–	Body colour not blue-green metallic. Labiomaxillary complex at most slightly reduced, maxillary palps visible, four or five-segmented. Forewing with vein 1r-Rs variously developed, but discal cell always well separated from vein R (Figs 67–70).....	15
<b>14 (13)</b>	Head with lateral and usually also median longitudinal and dorsal transverse frontal carinae present; median longitudinal carinae do not converge ventrally when present. Thorax with lateral margins of mesoscutellum always distinct.....	<i>Mocsarya</i> Konow (2 species)
–	At most, median longitudinal carina present, lateral longitudinal and dorsal transverse carinae on frons always absent; median longitudinal carinae converge ventrally when present (Fig. 6). Lateral margins of the mesoscutellum usually smooth (Fig. 41).....	<i>Chalinus</i> Konow (8 species)
<b>15 (13)</b>	Head with ventrally converging median longitudinal frontal carinae well developed (Fig. 5), frons distinctly concave; maxillary palp shortened, four-segmented.....	<i>Pedicrista</i> Benson (1 species)
–	Median longitudinal frontal carina absent (Figs 8, 9), frons flat; maxillary palp elongate, five-segmented.....	16
<b>16 (15)</b>	Female antenna with A4 + 5 longer than A3 (Fig. 32). Legs without white markings.....	<i>Pseudoryssus</i> Guiglia (2 species)
–	Female antennae with A4 + 5 equal in length or shorter than A3 (Fig. 33). One or more legs with distinct white markings.....	<i>Orussus</i> (23 species)

*Distribution:* Costa Rica (Vilhelmsen & Smith, 2002: fig. 39).

*Argentophrynopus gauldi* Vilhelmsen & Smith, 2002: 13. Holotype female (NHML).

*Distribution:* Uncertain, probably Mexico (see Vilhelmsen & Smith, 2002).

*Biology.* Unknown.

Genus *Chalinus* Konow, 1897 (Figs 6, 34, 41, 61, 71, 93, 104)

*Chalinus* Konow (1897a): 605. Type species *Orussus plumicornis* Guérin-Menneville, 1848 by designation of Rohwer (1911).

*Description.* Body predominantly bright green or blue/green metallic; appendages of various colours. Forewings variously infuscated; veins and pterostigma dark brown.

*Head.* Ocellar corona wide, ventral coronal tooth situated well below median ocellus (Fig. 6); dorsal transverse and lateral longitudinal frontal carinae absent, median longitudinal frontal carina usually present, ventral frontal transverse carina always present; median longitudinal frontal carinae, when fully developed, extending from ventral coronal tooth and converge medially towards ventral transverse frontal carina, which they sometimes reach; pilosity posterior to eye usually dense; postocular carina usually present for entire height of eye; occipital carina present; subantennal groove well developed; posteroventral margins of head converge sharply in ventral view, forming V-shaped depression medially; frons and vertex areolate to reticulate or reticulate to punctate, occiput and gena reticulate to punctate. Antenna with shape of scapus and shape and pilosity of the remaining antennomeres variable; female A4 + 5 equal in length or shorter than A6 (Fig. 34). Labiomaxillary

complex very reduced, maxillary and labial palps with one segment each.

*Thorax.* Pronotum with posterior margin deeply curved, dorsal part equally long throughout (Fig. 41). Forecoxa expanded medial to trochanteral insertions; male foretibia with distinct, often serrated carina laterally. Mesoscutum with shallow longitudinal carina medially in female, carina delimited by shallow troughs submedially; mesoscutellar sulcus variable. Mesoscutellum with lateral margin usually indistinct (Fig. 41), usually merging with surrounding areas; mesoscutellum projects posteriorly beyond cenchrus; mesoscutellar arm distinct and rectangular, without pit anteriorly. Mesopleuron with mesosubalar carina absent. Metascutellum not developed. Dorsal part of pronotum and mesoscutum punctate, reticulate, or areolate, mesoscutum usually most densely sculptured; mesoscutellum sparsely punctate and with glabrous lateral margins. Mesopleuron usually punctate or reticulate laterally, rarely areolate, and often with predominantly glabrous area posterodorsally. Hindcoxa with lateral pilosity variously developed. Hindfemur with denticles present or absent ventrally, longitudinal carina always absent, laterodistal corner rounded. Hindtibia with dorsal pegs well developed, ventral carina present, one (Fig. 61) or two apical spurs present, spurs subequal in length when two present.

*Wings.* Forewing with vein 2r arising from middle of pterostigma and curving gently into vein Rs, without distinct break where veins join; discal cell longer proximally than distally, its anteromedian corner reaching vein R and obliterating 1r-Rs (Fig. 71); vein 2r-m situated distally of or at level of distal end of pterostigma.

*Abdomen.* T1 with postspiracular carina entirely absent. T2 with lateral smooth area rounded or triangular in shape and barely touching antecostal sulcus anteriorly. Female T8 with distinct median projection on hindmargin present or absent. Female T9 with narrow longitudinal depression medially (Fig. 93), but without longitudinal carina posterolaterally. Male S9 flat and without tubercles (Fig. 104). T1 reticulate or punctulate, T2 areolate or reticulate, subsequent terga progressively less sculptured, ranging from reticulate to punctulate/variolate with imbricate interspaces; female T9 usually rugose-punctate, sometimes with raised glabrous area posteriorly. Abdominal sterna punctate with imbricate interspaces; male S9 punctulate.

*Discussion.* Vilhelmsen (2001b) revised this genus, synonymizing several of the names suggested by Guiglia (1936a, b, 1937c). The monophyly of *Chalinus* is well supported by the following putative autapomor-

phies: the presence of a suboccipital trough (32: 1), distinct longitudinal keel on the male foretibia (58: 1), and bluegreen metallic hindfemora in both sexes (100: 2<sup>c</sup>; 101: 2<sup>c</sup>). The basal splitting event in the genus is between *C. berlandi* + *C. haugi* and the remaining species. The former are held together by the antennomeres being constricted basally (36: 1), the mesoscutellar sulcus being discontinuous medially (73: 1), plus the presence of the following: denticles ventrally on the hindfemur (97: 1<sup>i</sup>), a short lateral longitudinal ridge proximally on the hindtibia (104: 1), just one apical spur on the hindtibia (108: 1), a distal hyaline spot in the forewing (129: 1<sup>i</sup>) and a swollen projection posteromedially on the female T8 (149: 2<sup>i</sup>). The monophyly of the remaining *Chalinus* spp. is also well supported by the scapus being flattened and curved (34: 2), the female A9 having a distinct carina laterally (39: 1<sup>i</sup>), the presence of distinct hairs ventrally on the female antenna (42: 1), the female T8 being entirely without a posteromedian projection (149: 0<sup>i</sup>), and the female T9 having a raised, smooth area posterolaterally (153: 1). Most nodes within the larger clade are weakly corroborated, except for the sistergroup relationship between *C. imperialis* and *C. purpureiventris*, which is supported by the absence of the postocular carina (23: 0<sup>i</sup>), the presence of a distinct carina ventrally along the entire length of the scapus (35: 2), and the forewings being entirely infuscated (126: 3).

#### *Valid species*

*C. berlandi* Guiglia, 1935a. Holotype female (MNHN).

= *C. balianii* Guiglia, 1937c. Holotype male (MRAC). Synonymized by Vilhelmsen (2001b).

*Distribution:* Democratic Republic of the Congo (Vilhelmsen, 2001b: fig. 25).

*C. braunsi* (Enslin, 1911). Holotype male (TMSA).

= *C. schulthessi* Guiglia, 1936a. Holotype female (ZSMC). Synonymized by Vilhelmsen (2001b).

*Distribution:* Botswana, Mozambique, South Africa, Zimbabwe (Vilhelmsen, 2001b: fig. 25).

*C. haugi* du Buysson, 1902. Holotype female (MNHN).

*Distribution:* Gabon (Vilhelmsen, 2001b: fig. 25).

*C. imperialis* (Westwood, 1874). Holotype female (OXUM).

= *C. congoensis* Guiglia, 1936b; Guiglia, 1954b. Holotype female (MNHN). Synonymy reestablished by Vilhelmsen (2001b).

*Distribution:* Democratic Republic of the Congo, Ghana, Nigeria, Tanzania (Vilhelmsen, 2001b: fig. 25).

*C. orientalis* Guiglia, 1937a. Holotype female (ZMHB).

*Distribution:* Tanzania (Vilhelmsen, 2001b: fig. 25).

*C. purpureiventris* Cameron, 1912. Holotype male (MRAC).

*Distribution*: Democratic Republic of the Congo (Vilhelmsen, 2001b: fig. 25).

*C. somalicus* Guiglia, 1935b. Holotype male (MCSN).

*Distribution*: Kenya, Somalia (Vilhelmsen, 2001b: fig. 25).

*C. timnaensis* Kraus, 1998. Holotype female (ZSMC).

*Distribution*: Central African Republic, Côte D'Ivoire, Israel, Liberia, Nigeria (Vilhelmsen, 2001b: fig. 25).

*Biology*. The only biological information associated with any *Chalinus* species comes from a specimen of *C. somalicus* which was reared from *Rinorea convallariiflora* (Violaceae) infested by Cerambycidae (Vilhelmsen, 2001b).

Genus *Guiglia* Benson, 1938

(Figs 10, 19, 27, 46, 94)

*Guiglia* Benson, 1938b: 11. Type species *Guiglia bombycinis* Benson, 1938b by original designation.

*Description*. Body of various colour, often predominantly dark brown to black, but sometimes with large reddish-brown areas. Appendages variable, from dark brown to reddish brown. Forewing with several strongly infuscated bands of varying extent; pterostigma and venation usually dark brown.

*Head*. Ocellar corona variable in size, ventral coronal tooth present (Fig. 10); ventral transverse frontal carina always present, dorsal transverse frontal and lateral frontal carinae usually present, median frontal carina usually absent; in most species only few hairs posterior to eyes, postocular carina well developed (Fig. 19); occipital carina usually distinct, displaced medially when present, being considerably removed from lateral margin of head (Fig. 27); subantennal groove well developed; frons and vertex areolate-rugulose, occiput and gena punctulate with scattered short rows of variolate impressions. Female antenna with combined length of A4 + 5 longer than A6, A9 not expanded distally and with lateral margin rounded. Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

*Thorax*. Pronotum deeply curved posteriorly and with notch medially in hindmargin (Fig. 46), relative length medially and laterally of dorsal parts varies. Forecoxa not expanded medially. Female mesoscutum with distinct longitudinal carina medially; mesoscutellar sulcus variously developed. Mesoscutellum rounded posteriorly, not broadly contiguous with hindmargin of mesonotum (Fig. 46); lateral margin of mesoscutellum distinct, well set off from surrounding area; mesoscutellum not projecting posterior to cenchrus; mesoscutellar arm pointed laterally and with deep pit

anteriorly. Mesopleuron with mesosubalar carina present. Metascutellum not developed. Dorsal parts of pronotum and mesonotum reticulate or areolate, posterior margin of mesoscutellum and mesoscutellar arms imbricate or glabrous, mesopleuron reticulate to punctate, metanotum reticulate to areolate. Hindcoxa usually with dense pilosity laterally. Hindfemur usually without longitudinal carina or denticles ventrally, posteroventral corner triangular. Hindtibia with one or two rows of distinct pegs dorsally and longitudinal carina ventrally. Hindtibial apical spurs differ considerably in length.

*Wings*. Forewing vein 2r arising from forewing pterostigma about 2/3rds from base of latter, distinct angle where 2r joins vein Rs; forewing discal cell of equal length proximally and distally; vein 1r-Rs distinct and of considerable length; 2r-m bent proximally and does not reach vein M in most species; cu-a inserts proximal to discal cell, opposite vein M.

*Abdomen*. T1 postspiracular carina usually distinct. T2 with smooth lateral area rectangular and continuous with antecostal sulcus anteriorly. Female T8 with projection posteromedially. Female T9 with distinct longitudinal carina, delimiting concave area medially (Fig. 94). Male S9 obliquely sloping in lateral view, with extended posterior margin and tubercles variously developed. Abdominal tergal sculpture less dense posteriorly, ranging from areolate to reticulate on T1-2 to punctate/punctulate with imbricate interspaces on T8; female T9 weakly rugose. Abdominal sterna usually punctate/punctulate with imbricate interspaces, male S9 rugose with glabrous area posteromedially.

*Discussion*. The monophyly of *Guiglia* is weakly corroborated, and the genus is indeed not retrieved in all the analyses (see discussion of generic relationships above). The median position of the occipital carina (27: 1) is unique to the genus, but cannot be ascribed to the ground plan with certainty, as the occipital carina is entirely absent (26: 0<sup>i</sup>) in *G. chiliensis*, the taxon most often placed as the sistergroup of the remaining *Guiglia* spp. The basalmost relationships within the genus are also weakly supported and vary according to the weighting conditions. However, the Australian species (*G. bombycinis*, *G. coracina*, *G. rubricata*, *G. sericata*) almost always come out together, as supported by the presence of a longitudinal line medially on the occiput (25: 1<sup>r</sup>), the presence of rectangular axillar flanges on the mesoscutum (70: 2<sup>i</sup>), and the presence of golden pilosity of various extent on the abdominal terga (162: 1). In most analyses, *G. bombycinis*, *G. coracina* and *G. rubricata* constitute a clade, corroborated by having the female hindfemur reddish brown (100: 1<sup>i</sup>) and the female forewing pterostigma predominantly white (113: 2<sup>i</sup>). Alternatively (concl-3; k = 1-6), *G.*

*coracina* is more closely related to *G. bombycinis* and *G. rubricata* than *G. sericata*; however, this is only supported by having the ocellar corona reduced in size (5: 1').

#### Valid species

*G. bombycinis* Benson, 1938b. Holotype female (NHML).

*Distribution*: Australia (Vilhelmsen & Smith, 2002: fig. 37).

*G. chiliensis* Benson, 1955b. Holotype female (depository uncertain, in 'In Buenos Aires Mus.[MACN] according to Benson, 1955b).

*Distribution*: Chile (Vilhelmsen & Smith, 2002: fig. 38).

*G. coracina* Benson, 1955a. Holotype female (ANIC).

*Distribution*: Australia (Vilhelmsen & Smith, 2002: fig. 37).

*G. rubicunda* Schmidt, 2002 in Vilhelmsen & Smith (2002). Holotype male (CNCI).

*Distribution*: Fiji Islands (Vilhelmsen & Smith, 2002: fig. 37).

*G. rubricata* Riek, 1955. Holotype female (ANIC).

*Distribution*: Australia (Vilhelmsen & Smith, 2002: fig. 37).

*G. schauinslandi* (Ashmead, 1903). Holotype male (according to Ashmead, 1903; in UMBB, depository confirmed by P.-R. Becker).

*Distribution*: New Zealand (Vilhelmsen & Smith, 2002: fig. 37).

*G. sericata* (Mocsáry, 1900). Lectotype female (HNHM).

= *O. queenslandensis* Turner, 1900. Holotype female (NHML). Synonymized by Benson (1938b).

= *G. queenslandensis coronata* Rayment (1951). Holotype female (ANIC). Synonymized by Vilhelmsen & Smith (2002).

*Distribution*: Australia (Vilhelmsen & Smith, 2002: fig. 37).

*Biology*. *Guiglia chiliensis* was observed by Smith & Béêche (1999) to emerge from *Baccharis linearis* (Ruiz & Pavon) (Compositae) infested by *Trigonogenium bifforme* Cobos (Buprestidae). A *Guiglia sericata* specimen was labelled as reared from beetle larva (Vilhelmsen & Smith, 2002); Rayment (1951) reported other specimens taken from a fallen *Angophora lanceolata* Cav. (Myrtaceae), and a female was observed ovipositing in hard, dry wood. *Guiglia schauinslandi* has been reared from *Sirex noctilio* (Fabricius) (Siricidae) in New Zealand (Gourlay, 1951; Rawlings, 1957; Morgan & Stewart, 1966; Zondag, 1969); the relationship is not a natural one as the host is introduced to New Zealand. *Guiglia schauinslandi* apparently is an ectoparasite, only feeding inside the host to extract edible remains in the later stages of its development (Nutall, 1980).

Genus *Kulcania* Benson, 1935

(Figs 11, 20, 80, 85, 95)

*Kulcania* Benson, 1935a: 5. Type species *Orussus costaricensis* Bischoff, 1928, by original designation.

*Description*. Body predominantly dark brown to black. Appendages predominantly dark brown, tarsi reddish brown to light brown. Forewing at most with weakly infuscated area distally of pterostigma; pterostigma and venation dark brown.

*Head*. Ocellar corona narrow, ventral coronal tooth present; dorsal and ventral transverse and lateral longitudinal frontal carinae well developed, median frontal carina absent (Fig. 11); area delimited by frontal carinae slightly concave and densely sculptured and setose; dense pilosity present posterior to eye; postocular carina developed only ventrally, terminating at level with ventral margin of eye (Fig. 20); occipital carina distinct, being discontinuous for only short distance dorsally; subantennal groove well developed; frons and vertex is areolate to reticulate, occiput and gena coarsely punctate. Female antenna with combined length of A4 + 5 longer than A6; A9 usually expanded distally and with carina laterally. Labiomaxillary complex reduced, maxillary and labial palps with three and two segments, respectively.

*Thorax*. Pronotum only slightly curved posteriorly and without notch medially in hindmargin; dorsal part somewhat longer laterally than medially, densely covered with hairs. Forecoxa not expanded medially. Mesoscutum with weakly developed longitudinal carina medially; mesoscutellar sulcus weakly developed. Mesoscutellum rounded posteriorly, not broadly contiguous with hindmargin of mesonotum; lateral margin of mesoscutellum distinct; mesoscutellum not projecting posterior to cenchrus; mesoscutellar arm pointed laterally and with deep pit anteriorly. Mesopleuron with mesosubalar carina and distinct mesepisternal carina. Metascutellum not developed. Dorsal parts of thorax variously sculptured, from areolate over reticulate to punctate; mesopleuron predominantly punctate, with large glabrous/imbricate area posteriorly. Hindcoxa usually with only few hairs laterally. Hindfemur with distinct longitudinal carina ventrally, denticles absent; laterodistal corner rounded and not projecting. Hindtibia with two parallel rows of distinct pegs dorsally and a distinct longitudinal carina ventrally. Hindtibial apical spurs differ considerably in length.

*Wings*. Forewing vein 2r arises from pterostigma about 2/3rds from base of latter; distinct angle present where 2r joins vein Rs; discal cell of equal length proximally and distally; vein 1r-Rs distinct and of consid-

erable length; cu-a inserts proximal to discal cell, opposite vein M.

**Abdomen.** T1 postspiracular carina weakly developed; dense fringe of hairs extends along posterior margin (Fig. 80). T2 with smooth lateral area rectangular and continuous with antecostal sulcus anteriorly. T2–5 with longitudinal swellings laterally and distinct hair patches above them. Female T8 with well-developed projection posteromedially (Fig. 85). Female T9 with distinct longitudinal carina, delimiting concave area between them (Fig. 95). Male S9 obliquely sloping in lateral view, with extended posterior margin; tubercles well developed and pointed, area delimited by them depressed and glabrous. Abdominal terga reticulate anteriorly (T1–2), punctate or variolate posteriorly; female T9 punctate-rugose or variolate. Abdominal sterna punctate.

**Discussion.** The monophyly of *Kulcania* is strongly supported by the following characters: the postocular carina is only developed ventral to the eye (24: 1<sup>1</sup>), the pronotum has a shallow posterior margin (52: 1<sup>1</sup>), the presence of a mesepisternal carina (85: 1<sup>1</sup>), a transverse fringe of hairs posteriorly on T1 (139: 1), and lateral swellings on some of the abdominal terga (144: 1<sup>1</sup>). The highly reduced maxillary and labial palps (46: 2<sup>1</sup>) are also observed in *Chalinus* and *Mocsarya*, being a putative synapomorphy for these two genera. They and *Kulcania* have been scored the same state for practical reasons (see character analysis), but they actually differ: *Chalinus* and *Mocsarya* have both the maxillary and labial palps reduced to one segment each, whereas in *Kulcania* they have three and two segments, respectively (Bischoff, 1928). These differences as well as the distribution of the states within the Orussidae (see also discussion under *Pedicrista*) indicates that the condition in *Kulcania* is independently derived.

*Kulcania* was earlier conflated with *Ophrynopus* and the genus *Ophrynella* Ross, 1937 by workers only dealing with the North American orussid fauna (Ross, 1937; Middlekauff, 1983). Smith (1979) clarified matters by treating *Ophrynella* as a synonym of *Ophrynopus*. The appropriateness of this act is evident when comparing the type species of the three genera; this was not done by Ross and Middlekauff (see Vilhelmsen & Smith, 2002 for further discussion). As presently defined, *Kulcania* is a very distinct genus.

#### Valid species

*K. mexicana* (Cresson, 1879). Holotype female (ANSP).

= *O. costaricensis* Bischoff, 1928. Lectotype female (ZMHB). Synonymized by Smith (1988).

**Distribution:** Colombia, Costa Rica, Mexico, USA (Vilhelmsen & Smith, 2002: fig. 39).

*K. tomentosa* (Middlekauff, 1983). Holotype female (AMNH).

**Distribution:** USA (Vilhelmsen & Smith, 2002: fig. 39).

**Biology.** An adult *K. mexicana* has been collected or reared from *Cyrilla racemiflora* Linnaeus (Cyrillaceae) in Floridae according to Middlekauff (1983) and specimen label data.

Genus *Leptorussus* Benson, 1955

(Figs 4, 15, 40, 51, 66, 100)

*Leptorussus* Benson, 1955a: 19. Type species *Leptorussus africanus* Benson, 1955a by original designation.

**Description.** Body, hindfemur and larger part of hindtibia dark brown to black; remaining appendages, including distal part of hindtibia and hindtarsus lighter brown (*L. africanus* colours, see Benson, 1955a). Fore- and hindwings predominantly hyaline (*L. kwazuluensis* sp. nov.) or with two weakly infuscate bands (*L. africanus*); forewing pterostigma, costal vein, vein R, vein 2r, and proximal part of anal vein dark brown, remaining venation hyaline.

**Head.** Ocellar corona narrow, ventral coronal tooth present. Dorsal transverse and median and lateral longitudinal frontal carinae absent (Fig. 4), ventral transverse frontal carina well developed and continuous medially. Transverse frontal furrow present dorsal to ventral transverse frontal carina (Fig. 15); pilosity posterior to eye absent, postocular and occipital carinae absent; subantennal groove only weakly developed, delimited laterally by at most short carina. Head sculpture highly variable (see description of *L. kwazuluensis* sp. nov.). Female antenna with combined length of A4 + 5 longer than A6; A9 expanded distally, with lateral margin rounded. Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

**Thorax.** Pronotum deeply curved posteriorly, without notch in posterior margin; dorsal part of equal length throughout (Fig. 40). Forecoxa not expanded medially. Mesoscutellar sulcus distinct. Mesoscutellum rounded posteriorly, not broadly contiguous with hindmargin of mesonotum, lateral margin distinct, well set off from surrounding sclerites; mesoscutellum not reaching posterior to cenchrus. Mesoscutellar arm with deep pit anteriorly. Mesosubar carina present. Metascutellum not developed. Dorsal parts of thorax areolate to reticulate; mesopleuron with areas of reticulate sculpture interspaced with glabrous areas, posterior part entirely glabrous. Hindcoxa with dense pilosity laterally. Hindfemur without longitudinal ridge or denticles ventrally, posteroventral corner rounded (Fig. 51).



Hindtibia with one row of distinct pegs dorsally, no longitudinal ridge ventrally. Hindtibial apical spurs very short (Fig. 51), one twice as long as the other.

*Wings.* Forewing vein 2r arises from middle of pterostigma (Fig. 66); distinct angle present where 2r joins vein Rs; forewing discal cell of equal length proximally and distally; vein 1r-Rs distinct and of considerable length; vein cu-a inserts opposite vein M in *L. africanus*, some distance distally of vein M, towards middle of discal cell in *L. kwazuluensis* sp. nov. (Fig. 66).

*Abdomen.* T1 with postspiracular carina absent. T2 with smooth area laterally rectangular and continuous with antecostal sulcus anteriorly. Female T8 with a distinct projection posteromedially; T9 without longitudinal carinae. Male S9 with distinct transverse swelling in lateral view and extended posterior margin (Fig. 100); tubercles absent. Female T10/cercus reduced distally, rectangular in outline. Abdominal terga areolate anteriorly (T1–2) to imbricate with scattered variolate depressions posteriorly (T7–8 (*L. africanus*); female T9 slightly rugose. Abdominal sculpture in *L. kwazuluensis* sp. nov. less developed (see description).

*Discussion.* The monophyly of *Leptorussus* is supported by the presence of a transverse frontal furrow (18: 1) and the very short apical spurs on the hindtibia (109: 1<sup>1</sup>). The presence of only a weakly developed antennal groove (31: 1<sup>1</sup> (at least in *L. africanus*) and of a distally swollen A9 in the females (38: 0<sup>1</sup>), as well as the exclusively southern African distribution might suggest that *Leptorussus* is close to *Pedicrista*, but they never come out together in the analyses and usually are only distantly related within the Orussidae. Furthermore, they can be separated easily from each other by their respective autapomorphies.

#### *Valid species*

*L. africanus* Benson, 1955a. Holotype female (NHML).

*Distribution:* Zimbabwe.

*L. kwazuluensis* Vilhelmsen sp. nov. Holotype male (CNCI).

*Distribution:* South Africa.

*Biology.* Unknown.

#### ***Leptorussus kwazuluensis* Vilhelmsen sp. nov.**

(Figs 4, 15, 40, 51, 66, 100)

Holotype male. S[outh] Africa: [KwaZulu-] Natal, Nkandla, Umfolozi Game Reserve, 10.–30.xi.1978, D.J. Brothers M[alaise] T[rap] (CNCI).

*Female:* Unknown.

*Male.* Body length 2.6 mm. Body, basal part of antenna, mandible, all coxae, hindfemur, and larger part of hindtibia entirely dark brown to black, larger part of antenna, labrum, maxillary palp, fore- and midfemur and tibia medium brown, distal part of hindtibia and all tarsi light brown. Forewing hyaline, pterostigma, costa, vein R, and basal part of anal vein dark brown, remaining venation hyaline; hindwing could not be observed properly.

Head with three pairs of medially separate coronal teeth, transverse frontal furrow very deep (Fig. 15), frons raised just dorsal to furrow; subantennal groove not delimited laterally by carina. Frons and vertex predominantly glabrous, with scattered punctures, raised area dorsal to transverse furrow transversely strigate (Fig. 4); dorsal part of gena and occiput lacunose-areolate. Thorax with posterior margin of mesonotum continuous medially, not separated by posterior margin of mesoscutellum (Fig. 40); dorsal parts reticulate-areolate, mesopleuron predominantly glabrous, with areolate area anterolaterally, metepisternum predominantly glabrous. Forewing vein cu-a arising in discal cell distally of vein M (Fig. 66). Abdomen with transverse row of variolate punctures anteriorly on terga, otherwise predominantly glabrous with scattered punctures, number of punctures smaller on posterior terga; sterna with transverse row of variolate punctures anteriorly, otherwise almost entirely glabrous.

*Etymology.* The sole known specimen comes from the KwaZulu-Natal Province in South Africa.

*Discussion.* Remarkable differences between this species and *L. africanus* are the very distinct transverse frontal furrow (less developed in *L. africanus*), the absence of a carina laterally of the subantennal groove (a short carina is present in *L. africanus*), the posterior margin of the mesonotum being continuous medially (the posterior margin of the mesoscutellum reaches the hindmargin of the mesonotum in *L. africanus*), the forewing vein cu-a arising close to the middle of the discal cell (much closer to vein M in *L. africanus*), the forewing being entirely hyaline (with two weakly developed infuscate bands in *L. africanus*), and the much less densely sculptured body surface (*L. africanus* has areolate sculpture on the head, dorsal parts of the thorax and anterior abdominal terga, and is more densely sculptured on the metepisternum). One might argue that these could represent sex differences (the sole known *L. africanus* specimen is a female), but the differences listed here go far beyond intraspecific sexual variation in other Orussidae. The type localities are also widely separated, *L. africanus* being collected from Bulawayo, Zimbabwe.

Genus *Mocsarya* Konow, 1897

(Not illustrated; see Vilhelmsen, 2001b: figs 3, 4, 13, 17, 19, 24)

*Mocsarya* Konow, 1897a: 608. Type species *Orussus metallicus* Mocsáry, 1896, by monotypy.

*Description.* Body predominantly blue/green metallic, posterior part of abdomen same colour or reddish brown. Appendages variable in colour. Forewing predominantly hyaline, apical third slightly infuscated; veins and pterostigma dark brown.

*Head.* Ocellar corona wide, ventral coronal tooth absent; dorsal transverse and median longitudinal frontal carinae often present, lateral longitudinal frontal and ventral transverse carinae always present; median longitudinal frontal carinae, when present, not converging medially; pilosity posterior to eye variable; postocular carina developed only ventrally; occipital carina present or absent; subantennal groove well developed; head in ventral view with posteroventral margin gently curved, with only shallow depression medially; frons and vertex areolate/reticulate-rugose, occiput and gena reticulate to punctate. Antenna with scapus short, subcylindrical and only slightly curved; remaining antennomeres not flattened and with only slender, scattered hairs; female A4 + 5 distinctly shorter than A6. Labiomaxillary complex very reduced, maxillary and labial palps with one segment each.

*Thorax.* Pronotum with posterior margin deeply curved, dorsal part longer laterally than medially. Forecoxa expanded medial to trochanteral insertion. Male foretibia with at most low carina laterodistally. Female mesoscutum with shallow longitudinal carina delimited by shallow troughs medially; mesoscutellar sulcus well developed. Mesoscutellum with distinct lateral margin, projecting posteriorly beyond cenchrus on metanotum, overlapping median incurvation in latter; mesoscutellar arm distinct and rectangular, but without pit anteriorly. Mesopleuron with mesosubalar carina absent. Metascutellum not developed. Pronotum dorsally and mesoscutum reticulate to areolate, mesoscutellum punctate; mesopleuron predominantly punctate to reticulate, usually with distinct glabrous area posterodorsally. Hindcoxa with only scattered hairs laterally. Hindfemur ventrally without denticles and longitudinal carina, laterodistal corner rounded. Hindtibia with dorsal pegs well developed, ventral carina absent; two apical spurs of subequal length present.

*Wings.* Forewing with vein 2r arising from middle of pterostigma and curving gently into vein Rs, without distinct break where veins join; discal cell longer proximally than distally, its antero-

median corner reaching vein R and obliterating 1r-Rs; vein 2r-m situated distally of distal end of pterostigma.

*Abdomen.* T1 with postspiracular carina entirely absent. T2 with smooth lateral area rounded or triangular in shape and barely touching antecostal sulcus anteriorly. Female T8 sometimes with small median projection on hindmargin. Female T9 without longitudinal carina posterolaterally, narrow longitudinal depression present medially, evenly sculptured posterolaterally. Male S9 flat and without tubercles. T1–2 areolate to reticulate, T3–8 ranges from reticulate on anterior terga to punctate with imbricate interspaces on posterior terga; Female T9 punctate-rugose. Abdominal sterna, including male S9, punctate with imbricate interspaces.

*Discussion.* The monophyly of *Mocsarya* is well established by the median longitudinal frontal carinae (when present) not converging medially (10: 1), the presence of a fully developed lateral longitudinal frontal carina (12: 2<sup>i</sup>), the postocular carina being developed only ventrally (24: 1<sup>i</sup>) and the absence of a ventral longitudinal carina from the hindtibia (105: 0<sup>i</sup>). These features distinguish it from its sister group, *Chalinus* (see below).

*Valid species*

*M. metallica* (Mocsáry, 1896). Holotype female (HNHM).

*Distribution:* Indonesia, Sri Lanka (Vilhelmsen, 2001b: fig. 26).

*M. syriaca* Benson, 1936. Holotype female (NHMW).

*Distribution:* Greece, Syria, Turkey (Vilhelmsen, 2001b: fig. 27).

*Biology.* Unknown.

Genus *Ophrella* Middlekauff, 1985

(Figs 22, 47, 73)

*Ophrella* Middlekauff, 1985a: 184. Type species *Ophrella lingulata* Middlekauff, 1985a, by original designation.

*Description:* Body and appendages predominantly dark brown to black; female 10th antennomere and forebasitarsus reddish brown. Forewing heavily infuscated (Fig. 73) and with dense setation on anterior half proximal to discal cell and in area from pterostigma to subapically on wing, latter area traversing wing entirely; venation predominantly dark brown.

*Head.* Ocellar corona narrow, ventral coronal tooth present; posterodorsal coronal teeth separated by dis-

tinct longitudinal groove; ventral transverse frontal carina present, other carinae absent; dense pilosity present posterior to eye; postocular and occipital carinae well developed (Fig. 22); the latter discontinuous dorsally, separated by small notch medially; subantennal groove well developed; frons punctate, each puncture accommodating a distinct, distally expanded hair, areas between punctures imbricate; occiput punctulate, gena punctulate or weakly rugose. Female antenna with combined length of A4 + 5 longer than A6; A9 expanded distally and with carina laterally. Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

*Thorax.* Pronotum deeply curved posteriorly, without notch medially in hindmargin (Fig. 47); dorsal part equally long throughout. Forecoxa not expanded medially. Mesoscutum without distinct longitudinal carina medially; mesoscutellar sulcus well developed. Mesoscutellum rounded posteriorly, broadly contiguous with hindmargin of mesonotum (Fig. 47); lateral margin of mesoscutellum indistinct, merging with surrounding sclerites; mesoscutellum not projecting posterior to cenchrus; mesoscutellar arm pointed laterally and with deep pit anteriorly. Mesopleuron with mesosubalar carina present. Metascutellum not developed. Pronotum and mesonotum reticulate; axillae, mesoscutellum and metanotum scabriculous; posterior margin of mesoscutellum and mesoscutellar arms imbricate; anterior part of mesopleuron reticulate-rugose, posterior part imbricate. Hindcoxa with lateral pilosity well developed. Hindfemur with neither longitudinal carina nor denticles ventrally, posteroventral corner triangular. Hindtibia with two parallel rows of distinct pegs dorsally and distinct longitudinal carina ventrally. Hindtibial apical spurs short, but differ considerably in length.

*Wings.* Forewing vein 2r arises from pterostigma about 2/3rds from base of latter; distinct angle present where 2r joins vein Rs; discal cell slightly longer proximally than distally; vein 1r-Rs distinct and of considerable length; cu-a inserts in middle of discal cell, well distally of vein M (Fig. 73).

*Abdomen.* T1 postspiracular carina well developed. T2 with smooth lateral area rectangular and continuous with antecostal sulcus anteriorly. Female T8 with small, distinct projection posteromedially. Female T9 with well-developed longitudinal carina, delimiting concave area medially. Male S9 unknown. Abdominal terga reticulate anteriorly (T1–2), punctulate with short rows of variolate depressions posteriorly (including female T9). Abdominal sterna punctulate with imbricate interspaces.

*Discussion.* The monophyly of *Ophrella* is corroborated by the presence of a median furrow separating the posterodorsal coronal teeth (7: 1<sup>1</sup>), the presence of distinctly flattened hairs on the frons (15: 1), and having the forewing vein cu-a inserted in the middle of the discal cell (123: 1<sup>1</sup>). *Ophrella* is a distinct taxon with well established 'ophryonine' affinities (see discussion of generic relationships above).

#### *Valid species*

*O. amazonica* (Westwood, 1874). Holotype female (OXUM).

*Distribution:* Brazil (Vilhelmsen & Smith, 2002: fig. 39).

*O. lingulata* Middlekauff (1985a). Holotype female (CASC).

*Distribution:* Panama (Vilhelmsen & Smith, 2002: fig. 39).

*Biology.* Unknown.

Genus *Ophrynon* Middlekauff, 1983

(Figs 21, 35, 96)

*Ophrynon* Middlekauff, 1983: 28. Type species *Ophrynon levigatus* Middlekauff, 1983 by original designation.

*Description.* Body dark brown to black, appendages variable in colour, dark brown to light brown. Forewing only weakly infuscated on proximal half and in band distal to pterostigma; pterostigma variable in colour, almost entirely dark brown or with posterodistal part white; remaining venation dark brown proximally, hyaline distally. Hindwing venation hyaline, except for basal part of vein R.

*Head.* Ocellar corona narrow, ventral coronal tooth present, dorsal transverse frontal carina weakly developed, lateral longitudinal and ventral transverse frontal carinae distinct, median frontal carina absent; pilosity posterior to eye absent; postocular carina distinct (Fig. 21), occipital carina absent; subantennal groove well developed; frons glabrous with scattered fovea each accommodating a hair; vertex and occiput areolate/reticulate, gena foveate. Female antenna with combined length of A4 + 5 longer than A6; A9 expanded distally and with carina laterally (Fig. 35). Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

*Thorax.* Pronotum deeply curved posteriorly, without notch medially in hindmargin; dorsal part somewhat longer laterally than medially. Forecoxa not expanded medially. Forefemur with longitudinal carina ventrally. Mesoscutum without distinct longitudinal carina medially, faint median line present in female;

mesoscutellar sulcus weakly developed. Mesoscutellum rounded posteriorly, not broadly contiguous with hindmargin of mesonotum; lateral margin of mesoscutellum distinct, separate from surrounding areas; mesoscutellum not projecting posterior to cenchrus; mesoscutellar arm pointed laterally and with deep pit anteriorly. Mesopleuron with mesosubar carina. Metascutellum not developed. Dorsal parts of thorax areolate to reticulate, mesopleuron predominantly punctate, with distinct glabrous areas posteriorly. Hindcoxa with only few hairs laterally. Hindfemur with neither longitudinal carina nor denticles ventrally, posteroventral corner triangular. Hindtibia with distinct pegs in irregular row dorsally and distinct longitudinal carina ventrally. Hindtibial apical spurs differ considerably in length.

*Wings.* Forewing with vein 2r arising from pterostigma about 2/3rds from base of latter, distinct angle present where 2r joins vein Rs; discal cell of equal length proximally and distally; cu-a inserts proximal to discal cell, opposite vein M.

*Abdomen.* T1 with postspiracular carina weakly developed. T2 with smooth lateral area rectangular and continuous with antecostal sulcus anteriorly. Female T8 with small projection posteromedially. Female T9 with low, distinct longitudinal carina, delimiting concave area medially (Fig. 96). Male S9 rounded in lateral view, with extended posterior margin; weakly developed tubercles present ventromedially and dorsolaterally. Abdominal terga reticulate anteriorly, punctate with imbricate interspaces posteriorly; female T9 punctate-rugose. Abdominal sterna (including male S9) punctate.

*Discussion.* *Ophrynon* is monotypic and was originally described from a single female (Middlekauff, 1983); Middlekauff (1985b) provided a description of the male. *Ophrynon* is a distinct taxon having a unique character combination within the 'ophrynopine' clade; it always comes out distinct from other genera and rarely as the sistergroup of just one other genus, corroborating its recognition as a separate genus. Putative autapomorphies are the absence of an occipital carina (26: 0<sup>i</sup>), the forewing vein R being hyaline distally (117: 1<sup>i</sup>), and the male forewing being almost entirely hyaline (126: 0<sup>i</sup>). Another feature which distinguishes *Ophrynon* from most other Orussidae (including all 'ophrynopine' taxa) is the sparse sculpture on the frons, separated by large smooth interspaces (see Middlekauff, 1983: fig. 54, and Vilhelmsen & Smith, 2002: fig. 2).

#### *Valid species*

*O. levigatus* Middlekauff, 1983. Holotype female (CASC).

*Distribution:* USA (Vilhelmsen & Smith, 2002: fig. 39).

*Biology.* Unknown.

Genus *Ophrynopus* Konow, 1897

(Figs 12, 28, 48, 74, 81, 87, 105)

*Ophrynopus* Konow, 1897a: 605. Type species: *Ophrynopus andrei* Konow, 1897a, designated by Rohwer (1911).

*Ophrynella* Ross, 1937: 113. Type species: *Oryssus nigricans* Cameron, 1883 by original designation.

*Description.* Body dark brown to black. Appendages variously coloured, at least some femora and tibiae usually reddish brown. Forewing usually with several strongly infuscated bands of various extent (Fig. 74); pterostigma often partially light coloured, venation usually dark brown. Hindwing venation predominantly hyaline.

*Head.* Ocellar corona usually wide, ventral coronal tooth present; dorsal transverse frontal carina present or absent, ventral transverse frontal carina always present (Fig. 12); lateral longitudinal frontal carina at most discernible dorsally, sometimes entirely absent, median longitudinal frontal carina always absent; pilosity posterior to eye usually dense; postocular and occipital carinae fully developed; occiput usually with distinct concavity dorsally (Fig. 28); subantennal groove well developed; frons and vertex areolate or reticulate, occiput and gena usually reticulate. Female antenna with combined length of A4 + 5 longer than A6; A9 expanded distally and with carina laterally. Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

*Thorax.* Pronotum deeply curved posteriorly and sometimes with notch medially in hindmargin; relative length of dorsal parts medially and laterally variable. Forecoxa not expanded medially. Female mesoscutum medially with longitudinal carina variously developed (Fig. 48); mesoscutellar sulcus distinct. Mesoscutellum rounded posteriorly, broadly contiguous with hindmargin of mesonotum; lateral margin of mesoscutellum indistinct, merging with surrounding areas; mesoscutellum not projecting posterior to cenchrus; mesoscutellar arm pointed laterally and with deep pit anteriorly. Mesopleuron with mesosubar and mesepisternal carinae present. Metascutellum not developed. Dorsal parts of pronotum, mesoscutum, and metanotum areolate to reticulate, mesoscutellum reticulate or punctate, mesopleuron reticulate or punctate anteriorly, predominantly imbricate posteriorly. Hindcoxa with lateral pilosity variously developed. Hindfemur with denticles and

longitudinal carina ventrally, laterodistal corner triangular. Hindtibia with two parallel rows of distinct pegs dorsally and longitudinal carinae laterally and ventrally. Hindtibial apical spurs differ considerably in length.

*Wings.* Forewing vein 2r arising from pterostigma about 2/3rds from base of latter, with distinct angle present where it joins vein Rs (Fig. 74); discal cell of equal length proximally and distally; cu-a inserts proximal to discal cell, opposite vein M.

*Abdomen.* T1 postspiracular carina well developed (Fig. 81). T2 smooth lateral area rectangular and continuous with antecostal sulcus anteriorly. Female T8 with well developed projection posteromedially (Fig. 87). Female T9 with distinct longitudinal carina, delimiting concave area medially. Male S9 obliquely sloping in lateral view, with extended posterior margin terminating in distinct, stubby projection (Fig. 105); tubercles variously developed. Abdominal terga areolate or reticulate anteriorly (T1–2), punctate with imbricate interspaces in middle (T3–6), and with transverse rows of variolate depressions (sometimes also with punctures) with imbricate interspaces posteriorly (T7–8); female T9 rugose. Abdominal sterna punctate or punctulate with imbricate interspaces. Male S9 may be slightly rugose or predominantly glabrous.

*Discussion.* *Ophrynopus* comes out as monophyletic in all analyses, being supported by the presence of a mesepisternal carina (85: 1<sup>i</sup>) and the presence of denticles ventrally on the hindfemur (97: 1<sup>i</sup>). A lateral longitudinal carina extending along the entire length of the hindtibia (104: 2<sup>i</sup>) is present in all *Ophrynopus* spp., but also in *Stirocorsia kohli*; since *Stirocorsia* usually is the sister taxon of *Ophrynopus*, this character is doubtful as an autapomorphy of the latter. Within *Ophrynopus*, *O. carinatus* consistently comes out as the sistergroup of the remaining *Ophrynopus* spp.; the best putative synapomorphy for the latter is the frons being coloured dark green with a faint metallic luster (14: 1), but having the pterostigma coloured white for areas of various extent (114: 1<sup>ic</sup>) also provides support. Two species groups can be recognized within *Ophrynopus* s.s., one consisting of *O. andrei*, *O. batesianus*, *O. fulvostigmus*, and *O. hansonii*, the other of *O. depressatus*, *O. nigricans*, *O. plaumanni*, and *O. wagneri*. The former is supported by the presence of distinct pegs accommodating sensillar hairs distally on the foretibia (60: 1) and the presence of hair patches on the mesoscutum (69: 1<sup>i</sup>) and laterally on some of the abdominal terga (145: 1<sup>i</sup>), the latter by the absence of hairs laterally on the hindcoxae (94: 0<sup>i</sup>).

#### *Valid species*

*O. andrei* Konow, 1897a. Holotype female (DEIE).

*Distribution:* Brazil (Vilhelmsen & Smith, 2002: fig. 40).

*O. batesianus* (Westwood, 1874). Holotype female (NHML).

*Distribution:* Brazil (Vilhelmsen & Smith, 2002: fig. 40).

*O. carinatus* Vilhelmsen & Smith, 2002. Holotype male (INPA).

*Distribution:* Brazil (Vilhelmsen & Smith, 2002: fig. 40).

*O. depressatus* Smith, 1988. Holotype female (NMNH).

*Distribution:* Argentina, Brazil (Vilhelmsen & Smith, 2002: fig. 40).

*O. fulvostigmus* (Westwood, 1874). Lectotype female (OXUM).

*Distribution:* Brazil (Vilhelmsen & Smith, 2002: fig. 40).

*O. hansonii* Vilhelmsen & Smith, 2002. Holotype female (CNCI).

*Distribution:* Costa Rica, Trinidad (Vilhelmsen & Smith, 2002: fig. 40).

*O. nigricans* (Cameron, 1883). Holotype female (NHML).

*Distribution:* Costa Rica, Ecuador, Guatemala, Mexico, Panama (Vilhelmsen & Smith, 2002: fig. 40).

*O. plaumanni* Smith, 1988. Holotype female (NMNH).

*Distribution:* Brazil, Paraguay (Vilhelmsen & Smith, 2002: fig. 40).

*O. wagneri* (du Buysson, 1910). Holotype female (MNHN).

*Distribution:* Argentina (Vilhelmsen & Smith, 2002: fig. 40).

*Biology.* An *Ophrynopus depressatus* specimen was reared from *Araucaria angustifolia* (Bert.) (Araucariaceae), together with a *Derecyrtia* sp. (Xiphydriidae) (Vilhelmsen & Smith, 2002); it was not determined if the former actually is parasitic on the latter. *Ophrynopus nigricans* was reared from *Agave nelsonii* (Agavaceae) stalks containing *Agavenema pallida* Davis (Incurvariidae) (Middlekauff, 1983).

#### Genus *Orussella* Benson, 1935

(Figs 2, 26, 30, 39, 56, 64, 76, 89, 98)

*Orussella* Benson, 1935a: 7. Type species *Orussella dentifrons* Philippi, 1873 by original designation (Benson, 1935a).

*Description.* Slender with elongate legs. Body and appendages black to dark brown. Forewing with extensive infuscated areas (Fig. 64): small area close to wing base, larger one extending proximally from vein 2r towards anal vein bifurcation, largest extend-

ing distally from vein 2r-m, may reach tip of wing distally. Hindwing almost entirely hyaline. Pterostigma and veins dark brown, except for proximal part of vein M and occasionally distal parts of veins R and M.

*Head.* Ocellar corona narrow, ventral coronal teeth absent (Fig. 2). Dorsal transverse and lateral and median longitudinal carinae absent, ventral transverse frontal carina incomplete, developed only above toruli. No dense pilosity posterior to eye; postocular and occipital carinae absent (Fig. 26). Subantennal groove only weakly developed, not delimited laterally by distinct carina. Frons and vertex finely areolate, occiput and gena finely areolate to reticulate. Scapus variable in shape. Female antenna with combined length of A4 + 5 longer than A6; A9 not expanded distally and with lateral margin rounded (Fig. 30). Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

*Thorax.* Pronotum deeply curved posteriorly and without notch in posterior margin; dorsal part is of about equal length throughout (Fig. 39). Forecoxa not expanded medially. Mesoscutum with median sulcus and notauli sometimes developed in female as short longitudinal lines, longitudinal ridge variously developed. Mesoscutellar sulcus weakly developed. Mesoscutellum triangular and raised relative to surrounding sclerites (Fig. 39), with distinct lateral margin and not reaching posterior margin of mesopostnotum. Mesoscutellar arm straight and raised relative to adjacent sclerites, without pit delimited by distinct carina anteriorly. Mesopleuron with mesosubar carina present. Metascutellum somewhat reduced, short metascutellar arm delimiting rounded depression posteriorly discernible. Dorsal parts of thorax finely areolate/rugulose with scattered punctures or variolate impressions. Mesopleuron finely reticulate-rugulose. Lateral part of hindcoxa covered with elongate, golden hairs. Hindfemur devoid of longitudinal ridge and denticles ventrally, its posterolateral corners rounded. Hindtibia without pegs dorsally or longitudinal ridge ventrally (Fig. 56). Apical hindtibial spurs unequal in length, one twice as long as the other.

*Wings.* Vein 2r arises from middle of forewing pterostigma, with distinct angle where it joins vein Rs (Fig. 64). Forewing discal cell of equal length proximally and distally. Vein 1r-Rs distinct and of considerable length, continuous with vein Rs without a break. Forewing cu-a inserts proximal to discal cell, opposite vein M.

*Abdomen.* Postspiracular carina weakly developed. Smooth area laterally on T2 triangular in outline and

situated short distance posterior to antecostal sulcus (Fig. 76). Female T8 with projection posteromedially. Female T9 without longitudinal carina and depression, narrow longitudinal groove along median margin present (Fig. 89). Male S9 rounded in lateral view, devoid of tubercles but with posterior margin somewhat extended (Fig. 98). Anterior abdominal terga (T1–2) finely reticulate-rugulose, posterior finely reticulate (anteriormost) to imbricate with scattered punctures or variolate impressions (posteriormost, including female T9). Abdominal sterna (including male S9) predominantly imbricate, females in addition having scattered punctures or variolate impressions.

*Discussion.* The sole species in this genus, *Orussella dentifrons*, was originally described from an incomplete female specimen (Philippi, 1873; see also Introduction); Rohwer (1925) reexamined the holotype and redescribed the species. Smith (1988) at first was unable to locate the type, but subsequently managed to examine it from the MNNC (Smith & Beéche, 1999). F. Rojas confirmed that it is in the MNNC, but not in condition to be sent on loan.

*Orussella* is a quite distinct taxon. The absence of the ventral coronal tooth (3: 0<sup>i</sup>) and of a complete ventral transverse frontal carina (19: 1<sup>i</sup>) are plesiomorphic features shared with other basal orussid genera (*Orussonia* and *Orussobaius*). *Orussella* can be distinguished from these by the triangular mesoscutellum (75: 2<sup>i</sup>), which is distinctly raised above the surrounding sclerites, and the triangular shape of the smooth area laterally on T2 (143: 0<sup>i</sup>); these are autapomorphies for the genus. The comparatively fine sculpture on head and thorax is also unusual. The comparatively well-developed metascutellum (88: 1<sup>i</sup>) and the presence of a distinct vein 1r-m in the hindwing (132: 0<sup>i</sup>) are more likely to be plesiomorphies. *Orussella* probably retains more basal traits than any other members of the Orussidae.

#### *Valid species*

*O. dentifrons* (Philippi, 1873). *Orussus dentifrons* Philippi, 1873. Combination by Benson (1935a). Holotype female (MNNC; depository confirmed by F. Rojas). Collection data (from Philippi, 1873): CHILE, Valdivia, Los Ulmos [No date], H. Krause leg.

*Distribution.* Southern South America, previously only reported from Chile. The following specimens were examined by me: ARGENTINA: ♀, Río Negro, El Bolsón, Topál, 7.xi.1961 [no collector] (HNHM). CHILE: ♀, Los Muermos, 19.i.1951, Ross & Michelbacher leg. (EMEC); ♂, Chillan, Trancas, Ñuble, 6.xii.1984–19.ii.1985, S. & J. Peck (CNCI); ♀, ♂, Valparaiso, Los Vázquez, 25.vii.1989, J.E. Barriga leg. (MNNC).

*Biology.* The two specimens from Los Vázquez are labelled 'ex. *Oectropsis latifrons* [Blanchard in Gay] (Cerambycidae)'. These must be the specimens referred to by Barriga (1990) as 'Orussidae sp.' (see also Smith & Beéche, 1999). The specimen from Ñuble was collected on *Nothofagus* (Fagaceae).

Genus *Orussobaius* Benson, 1938

(Figs 3, 14, 31, 38, 50, 57, 65, 78, 84, 90, 99)

*Orussobaius* Benson, 1938b: 8–9. Type species *Orussobaius mesembrinus* Benson, 1938b by original designation.

*Description.* Body predominantly black to dark brown; appendages of various colours. Forewing variously infuscated; pterostigma dark brown, veins variously coloured.

*Head.* Size of ocellar corona variable, ventral coronal teeth absent. Dorsal transverse and longitudinal carinae absent, ventral transverse carinae incomplete, only developed dorsal to toruli (Fig. 3). Usually no dense pilosity posterior to eye, postocular and occipital carinae absent (Fig. 14). Subantennal groove only weakly developed. Frons and vertex usually areolate or reticulate, occiput and gena usually areolate or reticulate, occasionally foveate or punctate. Female antenna with scapus short and subcylindrical, combined length of A4 + 5 longer than A6 (Fig. 31); A9 not expanded distally and with rounded lateral margin. Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

*Thorax.* Pronotum variously curved posteriorly and without notch medially in the hindmargin; relative length medially and laterally of dorsal part variable. Forecoxa not expanded medially. Mesoscutum in females without longitudinal ridge medially. Mesoscutellar sulcus variously developed. Mesoscutellum rounded posteriorly, not broadly contiguous with hindmargin of mesonotum, lateral margin distinct, well set off from surrounding sclerites. The mesoscutellum reaches the posterior margin of the mesopostnotum, separating the latter medially (Fig. 38), not projecting posterior to cenchrus. Mesoscutellar arm pointed laterally and usually with deep pit anteriorly. Mesopleuron with mesosubalar carina present. Metascutellum not developed. Dorsal part of thorax usually areolate or reticulate, rarely punctate; mesopleuron areolate, reticulate, or punctate, often with considerable glabrous area posterodorsally. Hindcoxa usually with dense pilosity laterally. Hindfemur usually without longitudinal ridge ventrally, denticles variously developed, posteroventral corner rounded (Fig. 50). Hindtibia usually with one or two rows of distinct pegs dorsally and a longitudinal ridge ventrally (Fig. 57).

Hindtibial apical spurs usually short and subequal in length.

*Wings.* Vein 2r arises from middle of forewing pterostigma, distinct angle where it joins vein Rs. Forewing discal cell of equal length proximally and distally; vein 1r-Rs distinct and of considerable length (Fig. 65). Forewing cu-a inserts proximal to discal cell, opposite vein M.

*Abdomen.* Postspiracular carina usually distinct laterally on T1. Smooth area laterally on T2 rectangular and continuous with antecostal sulcus anteriorly (Fig. 78). Female T8 with projection posteromedially (Fig. 84). Female T9 slightly depressed medially, without longitudinal carina (Fig. 90). Male S9 with distinct swelling in lateral view (Fig. 99); extended posterior margin variously developed; tubercles absent. Female T10/cercus swollen (Fig. 90). Sculpture of the abdominal terga highly variable; most species with T1–2 areolate to reticulate, some with following terga punctate and T8–9 punctate-rugose; several species with substrigulate sculpture on some terga, especially on posterior part. Abdominal sterna (including male S9) punctate-rugose with imbricate interspaces.

*Discussion.* The monophyly of *Orussobaius* is supported by the median subdivision of the mesopostnotum by the posterior margin of the mesoscutellum (82: 1<sup>i</sup>), the presence of a carina ventrally on the hindtibia (105: 1<sup>i</sup>), the well-developed subspiracular carina (138: 1<sup>ix</sup>), and the swollen T10/cerci in the females (158: 2). The basal split within the genus is between *Orussobaius caligneus* + *O. mesembrinus* and the remaining species. Synapomorphies for the former clade are the mesoscutellar arms being raised and without a pit anteriorly (79: 2<sup>i</sup>) and the forewing vein Rs being coloured distally (117: 0<sup>i</sup>); synapomorphies for the remaining *Orussobaius* spp. are the presence of a malar groove (30: 1) and denticles ventrally on the hindfemur (97: 1<sup>i</sup>). The sistergroup relationship between *O. badius* and *O. minutissimus* is supported by the presence of a glabrous area laterally on the pronotum (51: 1<sup>i</sup>), the reduced axillar flange (70: 0<sup>i</sup>), and the mostly glabrous metepisternum (93: 1<sup>i</sup>); the sister to these two species is *O. paniculus*, based on having the forewing vein 2r-m situated proximal to the distal end of the pterostigma (118: 1<sup>i</sup>) and having the forewing apex hyaline (128: 0<sup>i</sup>).

#### *Valid species*

*O. badius* Schmidt & Vilhelmsen, 2002. Holotype female (QMBA).

*Distribution:* Australia (Schmidt & Vilhelmsen, 2002: fig. 14a).

*O. caligneus* Schmidt & Vilhelmsen, 2002. Holotype female (WAMP).

*Distribution*: Australia (Schmidt & Vilhelmsen, 2002: fig. 14a).

*O. mesembrinus* Benson, 1938b. Holotype female (MVMA).

*Distribution*: Australia (Schmidt & Vilhelmsen, 2002: fig. 14a).

*O. minutissimus* Schmidt & Vilhelmsen, 2002. Holotype female (ANIC).

*Distribution*: Australia (Schmidt & Vilhelmsen, 2002: fig. 14b).

*O. minutus* Benson, 1938b. Holotype female (MVMA). = *O. normani* Rayment, 1951. Holotype female (QMBA). Synonymized by Schmidt & Vilhelmsen (2002).

*Distribution*: Australia (Schmidt & Vilhelmsen, 2002: fig. 14d).

*O. paniculus* Schmidt & Vilhelmsen, 2002. Holotype male (ANIC).

*Distribution*: Papua New Guinea (Schmidt & Vilhelmsen, 2002: fig. 14e).

*O. wilsoni* Benson, 1938b. Holotype female (MVMA).

*Distribution*: Australia (Schmidt & Vilhelmsen, 2002: fig. 14c).

*Biology*. The sole known specimen of *O. caligneus* was reared from a larva of Buprestidae. Specimens of *O. mesembrinus* were collected on *Acacia pendula* Boree (Mimosaceae), *O. minutissimus* on *Eucalyptus* sp. (Myrtaceae). *Orussobaius minutus* has been reared from *Saccolaemus* sp. (Curculionidae) on silver wattle (*Acacia dealbata* Link (Mimosaceae), possibly from *Melobasis purpurascens* (Fabricius) (Buprestidae; see Schmidt & Vilhelmsen, 2002) and from trunks of *Acacia cunninghamii* Hook (Mimosaceae), citrus, and introduced *Pinus radiata* Don (Pinaceae). All biological data are from Schmidt & Vilhelmsen (2002) and references therein.

Genus *Orussonia* Riek, 1955

(Figs 1, 13, 25, 29, 37, 49, 55, 63, 75, 82, 88, 97)

*Orussonia* Riek, 1955: 104. Type species *Orussonia depressa* Riek, 1955 by original designation.

*Description*. Entire body conspicuously dorsoventrally flattened, head usually held in prognathous position. Body and appendages predominantly dark brown, proximal part of antenna and distal parts of legs (tarsi, sometimes also tibiae) lighter brown. Forewing distally of pterostigma at most slightly infuscated; pterostigma and veins subcosta and R dark brown, remaining forewing venation hyaline (Fig. 63). Hindwing entirely hyaline, venation also predominantly so, except for brown proximal parts of R and anal veins.

*Head*. Ocellar corona broad, ventral coronal teeth absent. Dorsal transverse and median and lateral longitudinal frontal carinae absent (Fig. 1). Ventral

transverse frontal carina mostly developed above toruli, being continuous medially through narrow ridge. Only scattered hairs present posterior to eye. Postocular and occipital carinae absent (Fig. 13). Subantennal groove indistinct, not delimited laterally. Head flattened posteriorly, except for distinct notch dorsomedially and narrow groove ventromedially (Fig. 25); foramen magnum displaced dorsally, situated about one third of height of head from dorsal margin of head. Frons foveate or reticulate, vertex, occiput, and gena areolate to reticulate. Scapus elongate, cylindrical and slightly curved. Female antenna with A4 + 5 longer than A6, A9 extended distally and with rounded lateral margin; A10 inserted close to middle of median margin of A9 (Fig. 29). Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively. Distinct transverse sclerite present in ventral part of neck membrane.

*Thorax*. Pronotum deeply curved posteriorly, without notch in posterior margin, dorsal part of equal length throughout (Fig. 37). Forecoxa expanded medially. Female mesoscutum with median longitudinal ridge variously developed; mesoscutellar sulcus weakly developed, median longitudinal ridge extends from transscutal fissure to anterior margin of mesoscutellum. Mesoscutellum rounded posteriorly, but not broadly contiguous with the hindmargin of the mesonotum (Fig. 37), with lateral margin distinct, well set off from surrounding sclerites. Mesoscutellar arm rounded posteriorly and raised relative to surroundings, without pit delimited by distinct carina anteriorly. Mesopleuron with mesosubalar carina distinct. Metascutellum reduced, short metascutellar arms delimiting a pair of rounded depressions posteriorly weakly developed. Pronotum dorsally carinate, mesoscutum areolate/reticulate-rugose with glabrous areas especially in female, mesoscutellum and mesoscutellar arms glabrous except for scattered punctures on former. Mesopleuron rugose-reticulate anteriorly, predominantly glabrous posteriorly, with a punctulate area having hairs posterolaterally. Hindcoxa laterally covered with elongate, shiny hairs. Hindfemur without longitudinal ridge, with small denticles ventrally (Fig. 49) and posterolateral corner rounded. Hindtibia without dorsal pegs and ventral longitudinal ridge (Fig. 55). Hindtibial spurs elongate and subequal in length.

*Wings*. Vein 2r arises from middle of forewing pterostigma, distinct angle where it joins vein Rs (Fig. 63). Forewing discal cell not longer proximally than distally; vein 1r-Rs elongate and distinct. Forewing vein cu-a inserts proximal to discal cell, opposite vein M.



*Abdomen.* T1 with postspiracular carina absent. T2 with smooth areas laterally rounded to rectangular in outline, anteriorly more or less continuous with antecostal sulcus (Fig. 75). Female T8 with distinct projection posteromedially (Fig. 82). Female T9 without longitudinal carina laterally (Fig. 88), narrow groove situated along median margin. Male S9 with distinct projection posteromedially (Fig. 97), without tubercles. T1–2 rugulose-reticulate, remaining abdominal terga predominantly imbricate, some with transverse row of irregular punctures; female T9 imbricate with scattered punctures. Abdominal sterna (including male S9) imbricate with scattered punctures.

*Discussion.* The dorsoventrally flattened body (163: 1) makes *Orussonia* the most easily recognized orussid genus, and its monophyly is strongly supported by several additional unique autapomorphies: the presence of a narrow ventral transverse frontal carina (19: 2), the occipital foramen being situated dorsally on the occiput (29: 1), the presence of a suboccipital groove (33: 1), and of a ventral neck sclerite (47: 1). Most of these characters (e.g. 29, 33, 47) are probably correlated with the body shape. An additional putative autapomorphy is the female A10 being inserted on the median margin of A9 (41: 1); this feature is unique for *Orussonia*, but its polarization is ambiguous when the genus comes out as the sistergroup of all other Orussidae (this is usually the case), since the character cannot be scored for the outgroup taxa (see character analysis).

#### *Valid species*

*O. depressa* Riek, 1955. Holotype male (ANIC).

*Distribution:* Australia (Schmidt & Gibson, 2001).

*O. ruficaudata* Schmidt & Gibson, 2001. Holotype female (ANIC).

*Distribution:* Australia (Schmidt & Gibson, 2001).

*Biology.* Unknown. Schmidt & Gibson (2001) suggested that the flattened body would allow *Orussonia* spp. to venture under bark. This may be in order to expand their host search range, or to hide; however, this is entirely conjectural. Other Orussidae are apparently limited to ovipositing in bark-free wood in order to be able to employ their echolocation system (Vilhelmsen *et al.*, 2001). The unique insertion of the distal (10th) female antennomere might allow the female to tap the wood by sweeping the antennae in a horizontal rather than in a vertical plane, as observed in other Orussidae; this would facilitate echolocating while moving under bark.

Genus *Orussus* Latreille, 1796

(Figs 7, 8, 18, 33, 43, 44, 52, 59, 60, 67, 68, 77, 92, 103)

*Orussus* Latreille, 1796: 111. Type species *Oryssus coronatus* Fabricius, 1798, designated by Latreille (1811).

*Heliorussus* Benson, 1955: 16. **syn. nov.** Type species *Heliorussus scutator* Benson, 1955 by original designation.

*Description.* Body and appendages variously coloured, legs with white markings in various patterns. Forewing usually with extensive infuscated areas (Figs 67, 68), hindwing hyaline. Forewing pterostigma usually dark brown, remaining venation variable in colour.

*Head.* Ocellar corona usually narrow, ventral coronal tooth present. Dorsal transverse and longitudinal frontal carinae absent (Figs 7, 8), ventral transverse frontal carina complete. Pilosity posterior to eye variously developed; postocular carina usually present (Fig. 18), occipital carina variously developed. Subantennal groove distinct. Sculpture on different parts of head variable. Scapus short and subcylindrical. Female antenna with A4 + 5 at most equal in length to A6 (Fig. 33), A9 usually not expanded distally and with lateral margin rounded. Labiomaxillary complex fully developed, maxillar and labial palps with five and three segments, respectively.

*Thorax.* Pronotum deeply curved posteriorly and usually without notch in posterior margin, dorsal part usually of equal length throughout (Fig. 44). Forecoxa expanded medially. Mesoscutum usually without median longitudinal ridge, mesoscutellar sulcus usually indistinct (but see Fig. 43). Mesoscutellum usually triangular (Fig. 44), rarely rounded (Fig. 43) and broadly contiguous with posterior margin of mesonotum; lateral margin of mesoscutellum distinct, well set off from surrounding areas. Mesoscutellar arm distinct and rectangular, without pit anteriorly. Mesopleuron with mesosubar carina well developed. Metascutellum reduced. Sculpture on different parts of thorax variable. Hindcoxa with pilosity laterally usually weakly developed. Hindfemur without denticles and longitudinal ridge ventrally, posteroventral corner rounded (Fig. 52). Hindtibia with dorsal pegs weakly (Fig. 59) or fully (Figs 52, 60) developed, when fully developed, only one row present; longitudinal ridge ventrally on hindtibia usually not developed, posterodorsal margin sometimes extended into distinct apical flange (Figs 52, 60). Hindtibial apical spurs unequal in length, one twice as long as the other.

*Wing.* Vein 2r arises from middle of forewing pterostigma, joins vein Rs in distinct angle. Forewing discal cell longer proximally than distally, not touching vein R anteriorly (Figs 67, 68); vein 1r-Rs short and spectral. Forewing vein cu-a inserts proximal to discal cell, opposite vein M.

*Abdomen.* T1 with postspiracular carina variously developed. T2 with smooth area laterally rectangular and broadly contiguous with antecostal sulcus (Fig. 77). Female T8 with projection posteromedially. Female T9 usually with distinct longitudinal carina laterally delimiting concave area medially (Fig. 92). Male S9 with posterior rim variously developed, transverse swelling and tubercles absent (Fig. 103). Sculpture on different parts of abdomen variable.

*Discussion.* With 23 species recognized, *Orussus* is the largest genus in Orussidae by far. Despite its size, *Orussus* as defined here (see below) always comes out monophyletic, being fairly well supported. The most convincing autapomorphies for *Orussus* are the white markings on the legs (63: 1<sup>i</sup>; 111: 1<sup>c,i,r</sup>) and the triangular shape of the mesoscutellum (75: 2<sup>i,r</sup>; reversed in a few species, see below). The shortened A4 + A5 in the female antenna (37: 1<sup>i</sup>) and the medially expanded forecoxa (55: 1<sup>i</sup>) are also found in *Chalinus* + *Mocsarya*, which in some analyses comes out as the sistergroup of *Orussus*, and the ventral longitudinal carina on the forefemur (56: 1<sup>i,r</sup>) is not present in all *Orussus* spp.

Relationships within *Orussus* are generally weakly corroborated (Fig. 106), and the topology varies considerably according to the weighting conditions (Figs 116–119). However, a few nodes are usually retrieved. A large clade comprising *Orussus abietinus*, *O. coreanus*, *O. japonicus*, *O. minutus*, *O. occidentalis*, *O. sayii*, *O. terminalis*, *O. thoracicus* and *O. unicolor* is supported by the reduction of the dorsal pegs on the hindtibia (103: 1<sup>i</sup>). The sistergroup to this clade is *Orussus decoomani*, supported by the presence of white spots on the antenna (43: 1<sup>i,r</sup>) and the absence of a carina ventrally on the forefemur (56: 0<sup>i</sup>). *Orussus abietinus* and *O. occidentalis* are usually sister taxa, putative synapomorphies being the predominantly red abdominal colour in both sexes (160: 2<sup>i</sup>; 161: 1<sup>i</sup>).

*Orussus scutator* and *O. spinifer* were described and placed in a new genus, *Heliorussus*, by Benson (1955a); he also included *O. schoutedeni*. Indeed, the three species are very similar, and their monophyly is well corroborated by the presence of a well developed longitudinal carina on the mesoscutum (66: 2<sup>i</sup>), having the posterior margin of the mesoscutellum rounded posteriorly (75: 1<sup>i</sup>), and having the carina posteriorly on the mesoscutellar arm weakly developed (80: 0<sup>i</sup>). However, it is obvious that this clade is nested deeply within the larger genus *Orussus* (Figs 116–119). The sistergroup to '*Heliorussus*' spp. is usually *Orussus loriae*, supported by the enlarged and dorsally expanded ocellar corona (5: 0<sup>i</sup>; 6: 0<sup>i</sup>). Recognizing *Heliorussus* as a separate genus would require further extensive subdivision of *Orussus s.l.*, if only strictly monophyletic taxa are to be formally recognized. If such a subdivision was to be based on the preferred

topology, this would entail the erection of half a dozen additional genera, most of which would be small (1–2 species), weakly supported and difficult to recognize. A much more appealing alternative is to incorporate *Heliorussus* into *Orussus*. This does not require extensive changes in the classification, and *Orussus s.l.* is well corroborated and comparatively easily recognized. Even if *Orussus* encompasses almost a third of the known species of Orussidae, it is only large compared with other genera within the family. *Heliorussus* is therefore abandoned as a formal taxon.

*Orussus afer* and *O. tessmanni* always comes out as sister taxa, being supported by having the hindtibial spurs of about equal length (110: 0<sup>i</sup>); indeed, these two species resembles each other in most features, being separated only by slight differences in the coloration of the antenna (see Appendix). *Orussus moroi* and *O. taorminensis* are usually placed as sister taxa; this is supported by the sparse sculpture on the mesoscutellum (74: 0<sup>i</sup>). These two species together are often the sistergroup of the *Orussus decoomani*–*O. unicolor* clade (Figs 107, 117), but this is weakly corroborated. *O. boninensis* and *O. brunneus* usually come out together, being supported by having the hindfemur reddish brown (100: 1<sup>i</sup>). These two species are occasionally (conc3; k = 1–3) the sistergroup of *Orussus moroi* + *O. taorminensis* (Figs 118, 119), a clade corroborated by having the 9th female antennomere swollen distally (38: 0<sup>i</sup>).

*Orussus striatus* is usually (all conditions except conc1–4; k = 1) the sistergroup of all other *Orussus* spp. (Figs 106, 107, 117, 119), the latter being supported by the dorsal part of the pronotum being of about equal length throughout (48: 0<sup>i,r</sup>) and the presence of a longitudinal carina laterally on the female 9th abdominal tergum (151: 1<sup>i,r</sup>). *Orussus rufipes* is often (CI, RC, and RI; k = 4 +) the next species to branch off from *Orussus* spp., but this is weakly corroborated.

An annotated key to the world species of *Orussus* spp. is provided in the Appendix.

#### Valid species

*O. abietinus* (Scopoli, 1763). Holotype destroyed.

= *O. albo-punctatus* Gimmerthal, 1836. Type depository unknown.

= *O. coronatus* Fabricius, 1798. Holotype male (ZMUC).

= *O. vespertilio* (Fabricius, 1793). *Sirex vespertilio* Fabricius, 1793. Type depository unknown. Synonymized by Latreille (1811).

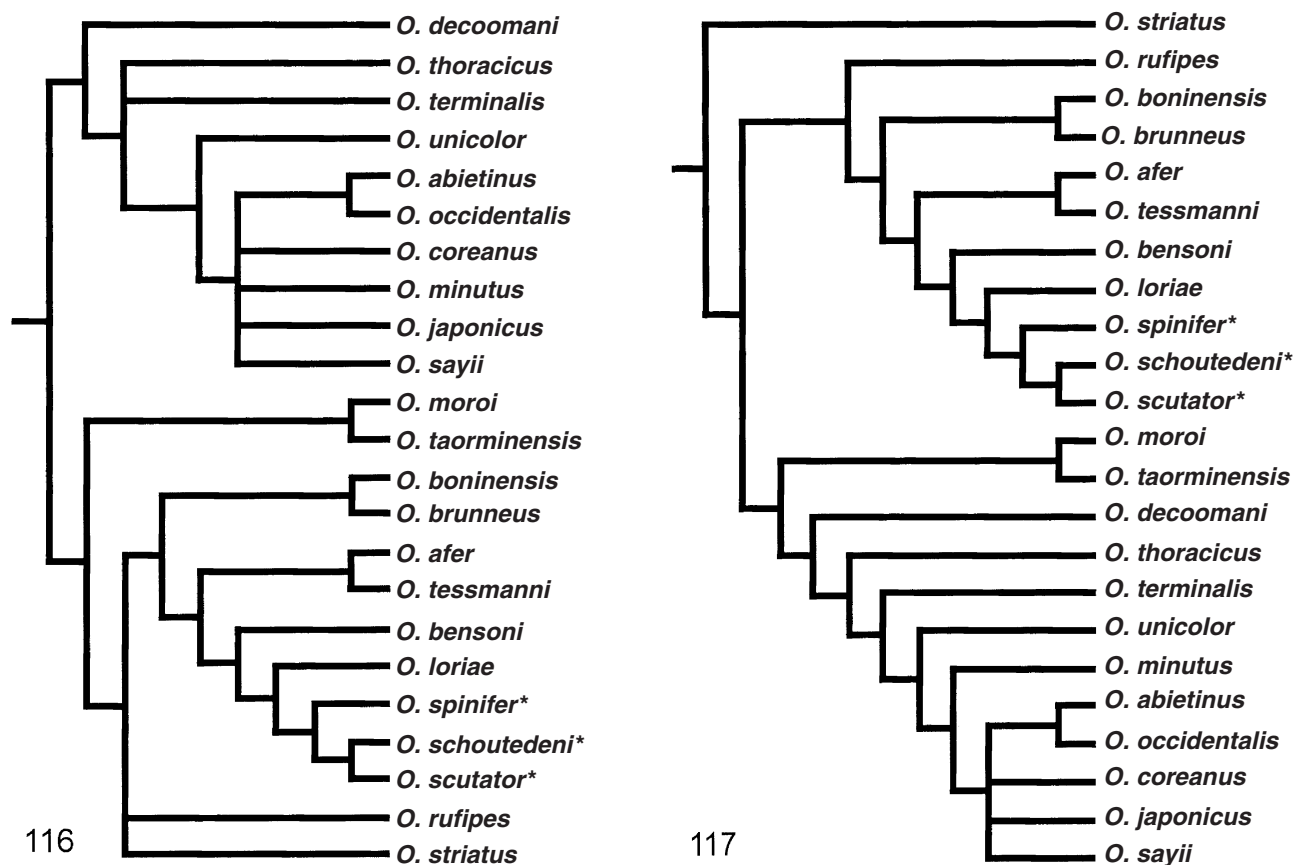
= *Sphex abietina* Scopoli, 1763. Holotype destroyed.

= *Tenthredo degener* Christ, 1791. Holotype destroyed. Synonymized by Latreille (1811).

*O. afer* Guiglia, 1937b. Holotype female (MRAC).

*O. bensoni* Guiglia, 1937d. Holotype male (EITH).

*O. boninensis* Yasumatsu, 1954. Holotype female (KUEC).



**Figures 116–117.** Topology of *Orussus* spp., from Pee-Wee with settings 116. conc1, 117. conc6. Taxa formerly placed in *Heliorussus* are indicated with asterisks.

*O. brunneus* Shinohara & Smith in Shinohara (1983). Holotype female (BPBM).

*O. coreanus* Takeuchi, 1938. Holotype female (UOPJ).

*O. decoomani* Maa, 1950. Holotype male (IEAS; depository not confirmed).

*O. japonicus* Tosawa, 1930. Holotype male (depository unknown according to Guiglia, 1965).

*O. loriae* Mantero, 1899. Holotype female (MCSN).

*O. minutus* Middlekauff, 1983. Holotype female (NMNH).

*O. moroi* Guiglia, 1954a. Holotype female (MCSN).

*O. occidentalis* Cresson, 1879. Lectotype female (ANSP).  
= *O. abietes* Rohwer, 1912. Holotype female (NMNH). Synonymized by Ross (1951).

= *O. hopkinsi* Rohwer, 1912. Holotype male (NMNH). Synonymized by Ross (1951).

= *O. modestus* Rohwer, 1912. Holotype female (NMNH). Synonymized by Ross (1951).

= *O. pini* Rohwer, 1912. Holotype female (NMNH). Synonymized by Ross (1951).

= *O. relativus* Rohwer, 1912. Holotype female (NMNH). Synonymized by Ross (1951).

*O. rufipes* Tsuneki, 1963. Holotype male (BLFU, according to Guiglia, 1965; depository not confirmed).

*O. sayii* Westwood, 1830. Holotype female (OXUM).

= *O. maurus* Harris, 1841. Holotype female (MCZH). Synonymized by Bradley (1901).

*O. schoutedeni* Guiglia, 1937b **status reestablished**. Holotype female (MRAC).

*O. scutator* (Benson, 1955a) **comb. nov.** *Heliorussus scutator* Benson, 1955a. Holotype male (NHML).

*O. spinifer* (Benson, 1955a) **comb. nov.** *Heliorussus spinifer* Benson, 1955a. Holotype female (NHML).

*O. striatus* Maa, 1950. Holotype female (TARI; depository not confirmed).

*O. taorminensis* Trautmann, 1922. Holotype female (EITH).

*O. terminalis* Newman, 1838. Holotype female (lost).

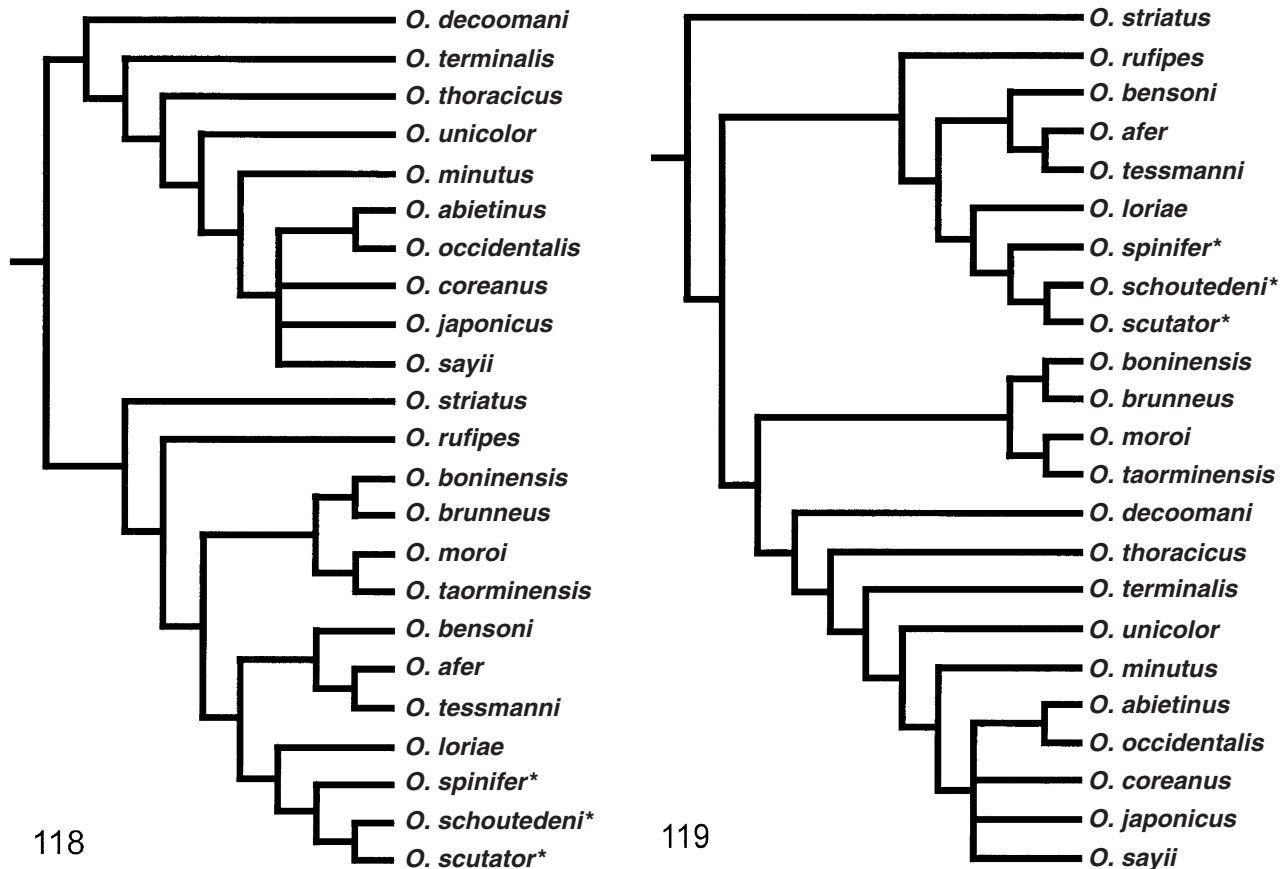
= *O. affinis* Harris, 1841. Holotype male (MCZH). Synonymized by Ross (1951).

= *O. haemorrhoidalis* Harris, 1841. Holotype female (MCZH). Synonymized by Bradley (1901).

*O. tessmanni* Enslin, 1913. Holotype female (ZMHB).

*O. thoracicus* Ashmead, 1898. Holotype female (NMNH).

*O. unicolor* Latreille, 1811. Holotype female (perhaps in ZMHB, according to Guiglia, 1965).



**Figures 118–119.** Topology of *Orussus* spp., from PAUP\* with settings 118.  $k = 1$ , 119.  $k = 2$ . Taxa formerly placed in *Heliorussus* are indicated with asterisks.

**Distribution.** *Orussus* is the largest and most widespread genus of Orussidae. Most known species are found in the northern hemisphere (Palearctic: 8; Nearctic: 5; Oriental: 4), including the most widely distributed species of all, *O. abietinus*, which ranges throughout most of the Palearctic from Europe to eastern Asia. However, there is also a handful of species in the Afrotropics (5). A single species, *O. loriae*, is known from New Guinea, but the genus is otherwise absent from the Australian and Neotropical regions. For more detailed distribution data of individual species, see Appendix.

**Biology.** Most current knowledge about orussid biology has been obtained by studying a few of the comparatively common Nearctic (*O. occidentalis*, *O. sayii*) and Palearctic (*O. abietinus*) species. Extensive reviews of the biology and behaviour of *Orussus* spp. are found in Cooper (1953), Middlekauff (1983), Ahnlund & Ronquist (2001), and Vilhelmsen *et al.* (2001). In summary, *Orussus* spp. appear to be ectoparasites of woodboring insect larvae, preferably Buprestidae (Coleoptera). Echolocation is apparently

paramount for host detection (see Vilhelmsen *et al.*, 2001) and restricts the female wasps to oviposit in dry, barkfree wood (see however, discussion under *Orusso-nia*). The biology of *Orussus* spp. seems to be representative for the family as a whole, judging from the scarce information available for other species of Orussidae.

Genus *Pedicrista* Benson, 1935  
(Figs 5, 16, 42, 53, 58, 70, 102)

Benson, 1935a: 6. Type species *Pedicrista hyalina* Benson, 1935a by original designation.

**Description.** Body and appendages predominantly dark brown, tarsi light brown; light brown markings on femora and proximally on tibiae. Elongate hairs on frons, gena (Fig. 16), dorsal part of pronotum, lateral part of mesopleuron, femora (Fig. 53), tibiae (Fig. 58), and abdomen. Forewing predominantly hyaline (Fig. 70), at most weakly infuscated posterior to pterostigma; pterostigma, veins C and R, and proximal part of vein dark brown,

remainder of forewing venation light brown or uncoloured.

*Head.* Three pairs of coronal teeth present, dorsal-most pair fused medially; ventral coronal teeth absent (Fig. 5). Lateral ocellus situated well posterior to ocellar corona, separated from median margin of eye by distance equal to its own diameter. Dorsal transverse and lateral longitudinal frontal carinae absent, median longitudinal frontal carinae extend from ventral coronal teeth, converge medially and join ventral transverse frontal carina (Fig. 5); area between median longitudinal frontal carinae distinctly concave. Ventral transverse frontal carina with distinctly upturned lateral ends. Dense pilosity posterior to eye absent, postocular carina well developed, occipital carina absent (Fig. 16). Subantennal groove only weakly developed, delimited laterally by short, low carina. Frons and vertex areolate, occiput reticulate, gena predominantly foveate. Scapus short and subcylindrical. Female antenna with A4 + 5 longer than A6, A9 expanded distally with lateral margin rounded. Labiomaxillary complex reduced, maxillary and labial palps with four and two segments, respectively.

*Thorax.* Pronotum deeply curved posteriorly, dorsal part longer laterally than medially (Fig. 42). Forecoxa not expanded medially. Mesoscutum in female with slightly raised area medially, mesoscutellar sulcus absent. Mesoscutellum rounded posteriorly, fused with posterior margin of mesonotum, subdividing mesopostnotum medially (Fig. 42). Mesoscutellum not projecting beyond cenchrus, with lateral margin distinct. Mesoscutellar arm distinct and pointed, with shallow depression anteriorly. Mesopleuron with mesosubar carina well developed. Metascutellum reduced. Dorsal part of pronotum and mesoscutum reticulate to foveate, mesoscutellum foveate with large glabrous interspaces. Mesopleuron reticulate to foveate anterolaterally, glabrous posteriorly and ventrally. Hindcoxa with only scattered hairs laterally. Hindfemur with denticles absent, longitudinal ridge present ventrally, posteroventral corner rounded (Fig. 53). Hindtibia with dorsal pegs well developed, ventral ridge present (Fig. 58). Two apical spurs present on hindtibia, one more than twice as long as the other.

*Wings.* Vein 2r arises from middle of forewing pterostigma, curving to join vein Rs where 2r-m issues from latter, proximal to distal end of pterostigma (Fig. 70); transition between Rs and 2r distinct. Forewing discal cell of equal length proximally and distally, well separated from vein R. Vein 1r-Rs weakly developed, spectral.

*Abdomen.* Postspiracular carina on T1 not observed with certainty. T2 with smooth area laterally rectangular and broadly contiguous with antecostal sulcus. Female T8 with small projection posteromedially. Female T9 with longitudinal carina absent, shallow groove along median margin present. Male S9 flat and without cuticular projections (Fig. 102). Anterior abdominal terga (T1–3) areolate to articulate, posterior ones punctate with large glabrous interspaces, with depressed glabrous hindmargins. Abdominal sterna, including male S9, punctate with large glabrous interspaces.

*Discussion.* *Pedicrista* is a very distinct taxon; unique features are the position of the lateral ocelli relative to the ocellar corona and the eyes, the frons being concave between the median longitudinal frontal carinae, and the presence of elongate hairs on various body parts (see description). Additional putative autapomorphies are the presence of white markings on the legs (63: 1<sup>i</sup>; 111: 1<sup>i</sup>), the median subdivision of the mesopostnotum by the posterior margin of the mesoscutellum (82: 1<sup>i</sup>), the position of the forewing 2r-m proximal to the distal end of the pterostigma (118: 1<sup>i</sup>), and the forewing being almost entirely hyaline in both sexes (125: 0<sup>i</sup>; 126: 0<sup>i</sup>). The presence of maxillary and labial palps with four and two segments (46: 1), respectively, is unique within the Orussidae; however, it might be regarded as an intermediate step in a transformation series leading to the even further reduced labiomaxillary complex of *Chalinus* + *Mocsarya*, which is probably the sistergroup of *Pedicrista*. Some features can be interpreted as autapomorphies of *Pedicrista* in this case also: the absence of an occipital carina (26: 0<sup>i</sup>), the subantennal groove with only a weakly developed carina laterally (31: 1<sup>i</sup>), and the presence of a distally swollen A9 in the female antenna (38: 0<sup>i</sup>). The first two of these traits are reversals, and all of them could be interpreted as indicating a sistergroup relationship between *Pedicrista* and *Leptorussus*; however, these two genera do not come out together in any of the analyses.

#### *Valid species*

*Pedicrista hyalina* Benson, 1935a. Holotype female (NHML).

*Distribution:* Malawi, South Africa, Zimbabwe.

*Biology.* Unknown.

Genus *Pseudoryssus* Guiglia, 1954

(Figs 9, 17, 32, 45, 69, 79, 83, 91, 101)

*Pseudoryssus* Guiglia, 1954a: 16. Type species *Orussus henshii* Mocsáry, 1910 by original designation (Guiglia, 1954a).

*Description.* Body dark brown to black. Appendages mainly dark brown, tarsi light brown. Forewing weakly infuscated from base of pterostigma to apex of wing (Fig. 69); hindwing entirely hyaline. Forewing pterostigma, costal vein, vein R, vein 2r, and proximal part of anal vein dark brown, remaining venation hyaline. Hindwing venation hyaline except for base of subcostal and anal veins.

*Head.* Ocellar corona variable in size, ventral coronal tooth present. Dorsal transverse and longitudinal frontal carinae absent (Fig. 9), ventral transverse frontal carina complete and with notch medially. Pilosity posterior to eye absent, postocular and occipital carinae well developed (Fig. 17). Subantennal groove distinct. Frons and vertex areolate, occiput and gena areolate to reticulate (difficult to see sculpture on *P. niehuisorum* due to dense pilosity). Scapus short and subcylindrical. Female antenna with A4 + 5 longer than A3 (Fig. 32), A9 not expanded distally and with lateral margin rounded. Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

*Thorax.* Pronotum variously curved posteriorly and without notch medially in posterior margin, dorsal part longer laterally than medially (Fig. 45). Forecoxa not expanded medially. Mesoscutum in female without median longitudinal ridge, mesoscutellar sulcus indistinct. Mesoscutellum rounded posteriorly, not broadly contiguous with hindmargin of mesonotum, with lateral margin distinct. Mesoscutellar arm distinct and rectangular, without a pit anteriorly (Fig. 45). Mesopleuron with mesosubalar carina well developed. Metascutellum reduced. Dorsal part of pronotum and mesoscutum areolate, mesoscutellum reticulate, mesopleuron reticulate or areolate. Hindcoxa without dense pilosity laterally. Hindfemur without denticles and longitudinal ridge ventrally, posteroventral corner rounded. Hindtibia with one row of distinct pegs dorsally, no longitudinal ridge ventrally. Hindtibial apical spurs unequal in length, one twice as long as the other.

*Wings.* Vein 2r arises from middle of forewing pterostigma, with distinct angle where it joins vein Rs. Forewing discal cell longer proximally than distally, not touching vein R anteriorly (Fig. 69); vein 1r-Rs short and spectral. Forewing vein cu-a inserts proximal to discal cell, opposite vein M.

*Abdomen.* T1 with postspiracular carina weakly developed (Fig. 79). T2 with smooth area laterally rectangular and broadly contiguous with antecostal sulcus. Female T8 with small projection posteromedially (Fig. 83). Female T9 with longitudinal carina absent, distinct groove along median margin present (Fig. 91). Male S9 with posterior margin extended

into distinct, tonguelike rim (Fig. 101), without transverse swelling or tubercles. Female T10/cercus rectangular in outline (Fig. 91). Abdominal terga, including female T9, areolate/reticulate-rugose with imbricate interspaces. Abdominal sterna, including male S9, reticulate/punctate-rugose with imbricate interspaces.

*Discussion.* The monophyly of *Pseudoryssus* is weakly corroborated, the only putative autapomorphy being the reduced and rectangular female T10/cercus (158:3<sup>3</sup>). Despite this, I consider it preferable to retain it as a separate genus rather than include it in *Orussus*, which usually comes out as its sistergroup. *Pseudoryssus* lacks a number of the features present in the ground plan of *Orussus* (see discussion of that genus), and merging these two genera would weaken the definition of *Orussus*, as the node connecting them is weakly supported.

Guiglia (1956) described the species *P. emanuelis* from a single female specimen from Cassanola Spinola, Piemonte, Northern Italy. She separated it from the very similar *P. henschii* by slight differences in the configuration of the 'anterior margin of the clypeus' (= ventral transverse frontal carina), the colour, relative size and proportions of the antennal segments, and the shape of the forebasitarsus. No additional specimens have been assigned to *P. emanuelis* (Kraus, 1998). The holotype of *P. emanuelis* has been compared with that of *P. henschii* and other specimens of this species. I consider the differences listed by Guiglia (1956) between the two nominal taxa insufficient to warrant species status for *P. emanuelis*, and hence regard it as a junior synonym of *P. henschii*.

#### *Valid species*

*P. henschii* (Mocsáry, 1910). *Orussus henschii* Mocsáry, 1910. Holotype female (HNHM).

= *P. emanuelis* Guiglia, 1956. **syn. nov.**

*Distribution:* Bulgaria, Croatia, Germany, Greece, Iraq, Italy, Morocco, Turkey.

*P. niehuisorum* Kraus, 1998. Holotype female (ZSMC).

*Distribution:* Israel.

*Additional material.* In addition to the material listed by Kraus (1998: fig. 18) I have seen *P. henschii* from the following localities: IRAQ, Mosul 1978, C.I.E. leg., 1♀, 2, 'On Pistacia' (NHML); MOROCCO, Moyen Atlas, Aguelman, Sidi Ali, [no date], S. Benhalima leg., 3♀♀, 1♂, 's/[ur] Cèdres' (MNHN).

*Biology.* The type material was collected from pine wood (Mocsáry, 1910). Rose (1998) reared *P. henschii* from a branch of *Pyrus communis* L. (Rosaceae) infested by *Clytus arietis* (L.) (Cerambycidae); he also

listed a number of emergence records from different tree species.

Genus *Stirocorsia* Konow, 1897  
(Figs 24, 54, 62, 86)

*Stirocorsia* Konow, 1897b: 372. Type species *Stirocorsia kohli* Konow, 1897b, by monotypy.

**Description.** Body dark brown to black. Appendages variously coloured, at least some femora and tibiae usually reddish brown. Forewing with one or two infuscated bands of various extent; forewing pterostigma usually dark brown, venation predominantly dark brown.

**Head.** Ocellar corona wide, ventral coronal tooth present; dorsal and ventral transverse frontal carina always present, lateral longitudinal frontal carina usually present, median longitudinal frontal carina always absent; dense pilosity present posterior to eye, postocular and occipital carinae fully developed (Fig. 24); occiput with distinct concavity dorsally; sub-antennal groove well developed; frons and vertex reticulate to foveate, occiput and gena foveate. Female antenna with combined length of A4 + 5 longer than A6; A9 expanded distally and with carina laterally. Labiomaxillary complex fully developed, maxillary and labial palps with five and three segments, respectively.

**Thorax.** Pronotum deeply curved posteriorly and with notch medially in hindmargin, dorsal part of pronotum broader laterally than medially; short longitudinal carina present medially on pronotum. Forecoxa not expanded medially. Female mesoscutum medially with well-developed longitudinal carina; mesoscutellar sulcus distinct. Mesoscutellum rounded posteriorly, broadly contiguous with hindmargin of mesonotum; lateral margin of mesoscutellum indistinct, merging with surrounding areas; mesoscutellum not projecting posterior to cenchrus; mesoscutellar arm pointed laterally and with deep pit anteriorly. Mesopleuron with mesosubalar carina present, mesepisternal carina absent. Metascutellum not developed. Pronotum, mesonotum and mesopleuron foveate, metanotum reticulate. Hindcoxa with pilosity laterally well developed. Hindfemur without denticles and usually without longitudinal carina, laterodistal corner triangular (Fig. 54). Hindtibia with two parallel rows (sometimes only developed distally) of distinct pegs dorsally and longitudinal carina ventrally (Fig. 62). Hindtibial apical spurs differ considerably in length.

**Wings.** Forewing with vein 2r arises from pterostigma about 2/3rds from base of latter, distinct angle present where 2r joins Rs; discal cell of equal length proxi-

mally and distally; cu-a inserts proximal to discal cell, opposite vein M.

**Abdomen.** T1 with postspiracular carina well developed. T2 with smooth lateral area rectangular and continuous with antecostal sulcus anteriorly. Female T8 with well-developed projection posteromedially (Fig. 86). Female T9 with distinct longitudinal carina, delimiting concave area medially. Male S9 obliquely sloping in lateral view, with extended posterior margin terminating in distinct, stubby projection; tubercles small, but distinct. Abdominal tergal sculpture variable, usually reticulate to foveate on anterior terga (T1–2), foveate to punctate on posterior terga (T3–8); female T9 rugose-reticulate. Abdominal sterna foveate to punctate, male S9 reticulate-rugose.

**Discussion.** The monophyly of *Stirocorsia* is rather weakly supported, the only good autapomorphy being the presence of a short longitudinal carina medially on the dorsal part of the pronotum (49: 1; see Vilhelmsen & Smith, 2002: fig. 18); this is a unique feature, but still has to be confirmed for *S. apicalis*, which was not available for study. Benson (1935a) regarded *Stirocorsia* as a synonym of *Ophrynopus*; however, Benson (1938b) reestablished *Stirocorsia* after revising which species should be included. Benson (1938b) has been followed here because even though *Stirocorsia* resembles *Ophrynopus* in many traits, it does not come out as the sistergroup of the latter in all analyses (see discussion of generic relationships below).

#### Valid species

*S. apicalis* Togashi, 2000. Holotype male (NSMT).

**Distribution:** Japan (Vilhelmsen & Smith, 2002: fig. 42).

*S. kohli* Konow, 1897b. Holotype female (NHMW).

= *S. cariniceps* Cameron, 1905. Holotype female (NHML). Synonymized by Benson (1935b).

= *O. philippinensis* Guiglia, 1937e. Holotype female (EITH). Synonymized by Vilhelmsen & Smith (2002).

**Distribution:** Indonesia, Laos, Malaysia, Philippines (Vilhelmsen & Smith, 2002: fig. 41).

*S. maculipennis* (Smith, 1859). Holotype female (OXUM).

= *O. trifasciata* Cameron, 1906. Holotype female (ZOMU). Synonymy reestablished by Vilhelmsen & Smith (2002).

= *O. rossi* Yasumatsu, 1952. Holotype female (KUEC). Synonymized by Vilhelmsen & Smith (2002).

**Distribution:** Indonesia, Papua New Guinea (Vilhelmsen & Smith, 2002: fig. 41).

*S. tosenis* (Tosawa & Sugihara, 1934). Holotype female, depository unknown; according to Guiglia

(1966) 'Tipo in Coll. Tosawa (Osaka) [private collection]'.  
*Distribution*: Japan (Vilhelmsen & Smith, 2002: fig. 42).

*Biology*. *S. tosensis* has been collected from dead wood of *Quercus* (Fagaceae (Guiglia, 1966).

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## APPENDIX

ANNOTATED KEY TO THE WORLD SPECIES OF *ORUSSUS*  
LATREILLE, 1796

An exhaustive revision of the genus *Orussus* is beyond the scope of the present study. The comparatively common species in the Nearctic and Palearctic regions are treated in the regional surveys of Middlekauff (1983) and Kraus (1998), respectively. In addition, Takeuchi (1938) deals with some *Orussus* spp. in the eastern Palearctic. The majority of the remaining species are known only from very few specimens each, eight only from the holotype. I have examined holotypes of most species. If more material is accumulated, it may be possible to merge some of the species currently considered valid, as the diversity of putatively more inclusive species is sampled more densely. However, given the limited material available at present, I consider it more prudent to retain the species currently recognized. The key provided below is the first attempt at circumscribing the entire genus at the global level. The keys in the above-mentioned regional surveys should also be consulted to cross-check identifications.

The present key relies heavily on the distribution of white marks on the body and appendages (characters 16: 1; 17: 1; 43: 1; 63: 1; 111: 1–2; 150: 1). Extensive white markings are found only in *Orussus*, except for a few other species of Orussidae having limited white markings on some of the appendages. Observations of behavioural interactions in *O. abietinus* (Ahnlund & Ronquist, 2001) indicate that the markings play a prominent role in threat and courtship displays. The different patterns seem to be species-specific and perhaps allows the individual wasp to recognize conspecifics from closely related species. They might hence serve as a precopulatory reproductive isolation mechanism. In other words, the pattern of white markings might be as useful for the wasps as for the systematist when attempting to identify *Orussus* spp.

KEY TO *ORUSSUS* SPP.

- 1** At least some of the legs with white markings and head with frons devoid of longitudinal carinae..... 2 (*Orussus*)  
 – White markings absent from all legs; if present, then either median or lateral longitudinal frontal carina also present ..... (other Orussidae)
- 2** (1) Forewing entirely hyaline; mesopleuron with vertical carina anterolaterally. Hainan (China), Ryukyu Islands (Japan)..... *O. striatus* Maa, 1950  
 – Forewing with at least one infuscated transverse band; mesepisternal carina absent..... 3
- 3** (2) T2 with large yellowish white spot anterolaterally. Japan ..... *O. japonicus* Tosawa, 1930  
 – T2 without yellowish white spot ..... 4
- 4** (3) Antenna with several of the middle antennomeres (3–8) having large white spots ..... 5  
 – Antennomeres without white spots..... 23
- 5** (4) Female ..... 6  
 – Male ..... 14
- 6** (5) Hindtibia with dorsal pegs well developed. India (but see comments) and Vietnam ..... *O. decoomani* Maa, 1950 (♀)  
 – Hindtibia with dorsal pegs weakly developed..... 7
- 7** (6) Head with white markings present on frons (inconspicuous in *O. coreanus*)..... 8  
 – White markings entirely absent from frons ..... 11
- 8** (7) Head with frons having dorsoventrally elongate white spots lying close to inner margin of eye for a considerable distance ..... 9  
 – White spots circular or transversely elongate, situated on lower part of frons, at most touching inner margin of eye for a short distance ..... 10
- 9** (8) Abdomen with T3–7 and usually also T8 reddish brown, contrasting significantly with the black T1–2 and dark brown/black T9 (T8 rarely partly dark brown as well). Palearctic..... *O. abietinus* (Scopoli, 1763) (♀)  
 – Abdomen with T3–7 slightly lighter coloured than, but not contrasting remarkably with remaining terga. North & South Korea ..... *O. coreanus* Takeuchi, 1938 (♀)
- 10** (8) Head with frons having white spots transversely elongate, lying close to eyes (separated from inner margin of eye by a distance less than its own breadth), not touching medially; forewing with only one distinct transverse infusate band, lying distally of pterostigma. Eastern North America..... *O. sayii* Westwood, 1830 (♀)  
 – White spots on frons subcircular (separate from the inner margins of the eye by a distance at least their own breadth), abutting or even continuous medially; forewing with two distinct transverse infusate bands, a proximal one reaching the base of pterostigma in addition to distal one. Central & Western Europe, Mediterranean region..... *O. unicolor* Latreille, 1811 (♀)
- 11** (7) Abdomen with at least T6–8 reddish brown ..... 12  
 – Abdominal terga uniformly black or dark brown ..... 13
- 12** (11) Abdomen with at least T1–4 black to dark brown, at most T5–8 reddish brown. Eastern North America..... *O. terminalis* Newman, 1838 (♀)  
 – Only T1–2 black, T3–8 reddish brown. Western North America ..... *O. occidentalis* Cresson, 1879 (♀)
- 13** (11) Head with postocular carina usually well developed; midtibia with distinct white spot of various extend proximally; mesoscutum with distinct carina laterally on axilla. Western North America ..... *O. thoracicus* Ashmead, 1898 (♀)  
 – Postocular carina absent; midtibia black or dark brown, except for at most very small white spot proximally; axilla with lateral carina at most weakly developed. Eastern North America ..... *O. minutus* Middlekauff, 1983 (♀)
- 14** (5) Hindtibia with dorsal pegs well developed (e.g. Fig. 60) ..... 15  
 – Hindtibia with dorsal pegs weakly developed (Fig. 59) ..... 16
- 15** (14) Mesonotum with mesoscutellar sulcus weakly developed; hindtibia with extensive white area dorsally. India (but see comments) and Vietnam ..... *O. decoomani* Maa, 1950 (♂)  
 – Mesoscutellar sulcus distinct; hindtibia without white area dorsally. Philippines ..... *O. bensoni* Guiglia, 1937d (♂)
- 16** (14) Abdomen with T1–T2 black, T3–8 reddish brown (except for white mark on T8) ..... 17  
 – All abdominal terga dark brown or black (except for white mark on T8) ..... 18
- 17** (16) Pronotum with white dorsolateral corners; abdomen with S9 distinctly darker than other sterna, usually predominantly dark brown. Palearctic..... *O. abietinus* (Scopoli, 1763) (♂)

- Pronotum all black; S9 same colour as other sterna, usually reddish brown.  
Western North America..... *O. occidentalis* Cresson, 1879 (♂)
- 18** (16) Abdomen with T8 usually without white marking; if present (some *O. thoracicus*),  
then small and does not traverse entire length of T8 ..... 19
- T8 with white median longitudinal stripe of various width traversing entire length of T8..... 21
- 19** (18) Head with frons having distinct white markings ventrally, abutting or even continuous  
medially. Central & Western Europe, Mediterranean region..... *O. unicolor* Latreille, 1811 (♂)
- Frons without white markings ..... 20
- 20** (19) Mesoscutum with only scattered, evenly spaced hairs; forefemur brown to reddish brown.  
Western North America..... *O. thoracicus* Ashmead, 1898 (♂)
- Mesoscutum with white hairs situated in a pair of sublateral longitudinal bands;  
forefemur dark brown to black. Eastern North America..... *O. terminalis* Newman, 1838 (♂)
- 21** (18) Head with white spots on frons always present, dorsoventrally elongate, lying close  
to inner margin of eye for a considerable distance; abdomen faintly girdled, T4–5/6 being  
slightly lighter in colour dorsally than remaining abdominal terga. North &  
South Korea ..... *O. coreanus* Takeuchi, 1938 (♂)
- White spots on frons present or absent, when present subcircular or transversely  
elongate, at most touching inner margin of eye for short distance; abdominal terga of  
same colour throughout (dark brown to black) ..... 22
- 22** (21) Head with frons having transversely elongate white spot lying close to inner margin of  
eye, separated from latter by distance less than its own breadth, not touching medially;  
ventral transverse frontal carina straight or with small projection medially.  
Eastern North America ..... *O. sayii* Westwood, 1830 (♂)
- White spots on frons usually absent, when present separate from the inner margins  
of the eyes by a distance at least their own breadth, abutting or continuous medially;  
ventral transverse frontal carina with small notch medially. Eastern North  
America..... *O. minutus* Middlekauff, 1983 (♂)
- 23** (4) Head with ocellar corona wide, distance between median ocellus and lateralmost  
coronal tooth more than twice diameter of former (Fig. 7), dorsalmost coronal teeth  
situated dorsal to lateral ocellus; mesoscutum with distinct raised tubercle or carina  
medially, posterior margin of mesoscutellum rounded (Fig. 43) ..... 24
- Ocellar corona narrow, distance between median ocellus and lateralmost coronal tooth  
at most equals 1.5× the diameter of former (Fig. 8), dorsalmost coronal tooth situated  
at level with lateral ocellus; mesoscutum without tubercle medially, mesoscutellum  
triangular, angled posteriorly (Fig. 44)..... 26
- 24** (23) Mesoscutellum with hindmargin not reaching anterior margin of metanotum,  
mesopostnotum continuous posteriorly; hindtibia with white spot proximally.  
Zimbabwe ..... *O. spinifer* (Benson, 1955a)
- Mesoscutellum with hindmargin reaching anterior margin of metanotum,  
subdividing mesopostnotum; hindtibia without white spot proximally ..... 25
- 25** (24) Mesoscutum with highly raised tubercle medially; abdominal tergal sculpture  
weakly developed beyond T3. Sierra Leone ..... *O. scutator* (Benson, 1955a)
- Mesoscutum with low, but distinct median longitudinal carina; abdominal tergal  
sculpture coarser, punctures discernible on T4. Angola, Democratic Republic  
of the Congo, Nigeria..... *O. schoutedeni* Guiglia, 1937b
- 26** (23) Hindtibia without dorsal white spot proximally ..... 27
- Hindtibia with dorsal white spot proximally ..... 28
- 27** (26) Antenna with A1–2 reddish brown, distinctly lighter coloured than remaining  
antennomeres (except A10). Democratic Republic of the Congo ..... *O. afer* Guiglia, 1937b
- A1–2 dark brown, same colour as remaining antennomeres.  
Equatorial Guinea ..... *O. tessmanni* Enslin, 1913
- 28** (26) Hindtibia with only small dorsal white spot proximally, extending less than half length of tibia ..... 29
- Hindtibia with large dorsal white spot, extending at least half length of tibia ..... 30
- 29** (28) Female antenna with A9 swollen distally, broadest close to apex; mesoscutum  
covered with conspicuous golden hairs. Bonin Islands (Japan)..... *O. boninensis* Yasumatsu, 1954
- Female A9 not swollen distally, broadest medially; pilosity on mesoscutum sparse  
and not golden. Japan ..... *O. rufipes* Tsuneki, 1963
- 30** (28) Mesoscutellum sparsely punctured, with large shining interspaces ..... 31

–	Mesoscutellum densely sculptured .....	32
<b>31</b> (30)	Female with pronotum, mesonotum, and anterodorsal part of mesopleuron reddish brown, contrasting with colour of other body parts. Male with cenchri black. France, Italy .....	<i>O. taorminensis</i> Trautmann, 1922
–	Both sexes with thorax brown or black, not differently coloured from other body parts. Male with cenchri pale brown. Bulgaria, Canary Islands (Spain), Greece, Italy, Morocco.....	<i>O. moroi</i> Guiglia, 1954a
<b>32</b> (30)	Distal part of hindfemur entirely white laterally, hindtibia with dorsal white spot extending to apex; abdomen with female T8 having swollen posterior projection. Papua New Guinea .....	<i>O. lorae</i> Mantero, 1899
–	Hindfemur with distal white spot not covering entire lateral surface, hindtibia with dorsal white spot extending only halfway to apex; female T8 with posterior projection inconspicuous. Taiwan .....	<i>O. brunneus</i> Shinohara & Smith, 1983

## COMMENTS

*Orussus abietinus* (Scopoli, 1763). Holotype destroyed according to Guiglia (1965).

*Additional records.* Kraus (1998) lists extensive collection records from Europe, as well as biological information. I have knowledge of the following specimens from outside Europe: ALGERIA: ♂, Ras el Ma [No date, no collector] (ANIC). KAZAKHSTAN: 2♀♀, 1♂, S. Kirgyzsay, Ketmen Mt. 1800 m, 43°17'N, 79°31'E, 1–3.vi.2001, M. Hauser leg. (DEIE; record after S. Blank, unpubl. data). NORTH KOREA: ♀, Musan Mts., 22.iii.1911, J. C. Thompson leg. (EMEC; misidentified as *O. coreanus*). RUSSIA: ♀, Primorskii kraj, Ussurijskij Res., 24.v.1994, A. Lelej leg. (NSMT); ♀, Khabarovskij kraj, Bol'shekhokhtsirskij Res., Sosninskij River, 14.vi.1994, A. Shinohara leg. (NSMT). TURKEY: ♂, Marmoris, 14.iv.1964, F. Ressi leg. (NHMW); ♀, Namrun, 16.vi.–2.vii.1979, Holzschuh & Ressel leg. (OLML).

*Remarks.* This is the most common Palearctic species and the most widespread of all species of Orussidae. *O. abietinus* mostly resembles *O. occidentalis* among other *Orussus* spp., both species having the abdomen predominantly reddish brown in both sexes. The species differ in *O. abietinus* females having white markings on the frons and the 9th abdominal tergum considerably darker than the adjacent sclerites; the same is the case for the male 9th abdominal sternum. In addition, male *O. abietinus* have the dorsolateral corners of the pronotum white. All these features except the white markings on the frons are unique to the species.

*Orussus afer* Guiglia, 1937b. Holotype ♀. DEMOCRATIC REPUBLIC OF THE CONGO: Mayumbe, Bemba, ix.1926, A. Collart leg. (MRAC). Examined.

*Remarks.* Male unknown. *O. afer* closely resembles *O. tessmanni*, from which it can be recognized by the coloration of the antenna (see above).

*Orussus bensoni* Guiglia, 1937d. Holotype ♂. PHILIPPINES: Panaon, xii.1915, Böttcher leg. (EITH). Examined.

*Remarks.* Female unknown.

*Orussus boninensis* Yasumatsu, 1954. Holotype ♀. JAPAN: Bonin Islands, Hahajima, 27.vi.1932, E. Asahina leg. (KUEC). Examined.

*Remarks.* Male unknown. Resembles *O. brunneus* in a number of features, but differs in having more extensive pilosity on the gena and dorsal parts of the thorax. In addition, the white spot on the hindtibia is developed only proximally, whereas it extends at least halfway to the apex in *O. brunneus*.

*Orussus brunneus* Shinohara & Smith in Shinohara (1983). Holotype ♀. TAIWAN: Kuraru 5.v.1934, J. L. Gressitt leg. (BPBM). Examined.

*Remarks.* Male unknown. Shinohara (1983) commented on the similarity between *O. brunneus*, *O. decoomani* (see also below), and *O. rufipes* and speculated that some of them might eventually have to be synonymized. I consider that they should all be recognized as separate species, given the limited material currently available for study; the examination of additional specimens might disprove that the species boundaries are sufficiently distinct as presently defined.

*Orussus coreanus* Takeuchi, 1938. Holotype ♀. NORTH KOREA: Nanseturei, 12.vi.1936, K. Takeuchi leg. (UOPJ). Examined.

*Additional records.* NORTH KOREA: ♂, paratype, identical data with holotype. SOUTH KOREA: Kangwondo, Mirugam (Pugdaesa) 1300 m, Mt. Odaesan, 29.v.–1.vi.1996, A. Shinohara leg. (NSMT).

*Remarks.* Takeuchi (1938) in his key separated *O. coreanus* from *O. abietinus* by the presence of three notches in the ventral transverse frontal carina and the infusate area in the forewing extending to the

apex in the former; these characters are highly variable within *Orussus* spp. in general. However, the differences in the coloration of the abdomen and the absence of white marks on the ♂ pronotum indicate that *O. coreanus* should be recognized as a separate species. *O. coreanus* has the middle abdominal terga (♀: T3–7; ♂: T4–5/6) discernibly lighter coloured than the remaining terga, but never as red as *O. abietinus*; the 8th abdominal tergum of *O. coreanus* is always entirely black, whereas female *O. abietinus* at most has the posterior margin of T8 black (specimens from eastern Asia), in addition to T9. The frons in *O. coreanus* has dorsoventrally elongate light marks along the inner margins of the eyes, though they are more darkened than in *O. abietinus*.

*Orussus decoomani* Maa, 1950. Holotype ♂. VIETNAM: Tonkin, Hoa-Binh, vii.1940, A. de Cooman leg. (IEAS according to Maa, 1950; depository not confirmed). Not examined.

*Additional records.* INDIA: ♀, ♂, Punjab, Koti-Kula, iv.1964; ♀, ♂, Himachal Pradesh, Dalhousie, Ahla (H. P), vi.1964; 3♀♀ (same locality as previous), vii.1964 (all NHML).

*Remarks.* Benson (1965) identified the first four specimens listed above as *O. decoomani*. The three additional female specimens were found among the unidentified Orussidae in NHML; these are obviously conspecific with the specimens Benson identified. Benson (1965) remarked that the specimens in the NHML differ from the description of Maa (1950), as also noticed by Shinohara (1983). These specimens have extensive white markings on the antenna, tibiae, and tarsi, whereas Maa (1950) states that in the holotype of *O. decoomani* only the 'knees [are] whitish', 'all tarsi brownish black', and that it differs from *O. unicolor* in that in the latter the '4th antennal segment and dorsal surfaces of the tibiae are whitish'. Furthermore, according to Maa (1950), the forewing has both 'a trans-stigmal and an apical infuscated fascia' (e.g. Fig. 67), whereas Benson (1965) states that in the specimens examined by him the 'infuscate stigmal transverse band is reduced to a small spot' (e.g. Fig. 68). Considering these differences and their distribution across *Orussus* spp., it is very likely that the NHML specimens from India represent a new, unnamed species. However, this is impossible to confirm without examining the holotype of *O. decoomani*, which unfortunately was not available for study.

*Orussus japonicus* Tosawa, 1930. Holotype ♂. JAPAN: Osaka pref., Chihaya, Nara (according to Tosawa, 1930; type depository unknown according to Guiglia, 1965). Not examined.

*Additional records.* JAPAN: ♂, Kawachi, Kongosan, 3.v.1931, N. Tosawa leg. (UOPJ); ♂, Kasuga, Nara,

30.iv.1940, N. Tosawa leg.; ♀, Honshu, Wakayama Pref., Mt. Koyasan, 10.vi.1940, J. Yoshioka leg. (both NSMT); ♂, Shikoku, Mt. Iwaya, 15.v.1948, T. Kobayashi leg. (UOPJ); ♀, ♂, [locality data in Japanese], 20.vi.1946; ♂, [locality data in Japanese], 21.vi.1946; 3♀, 2♂, Hokkaido, Jōzankei, [no date]; ♂, Hokkaido, Sapporo, [no date]; ♀, Hokkaido, Sounkyo, [no date]; all K. Tsuneki leg. (all NMNH).

*Remarks.* This species is easily recognized by both sexes having a large whitish spot laterally on the 2nd abdominal tergum. The body and appendages are otherwise predominantly dark brown to black.

*Orussus lorae* Mantero, 1899. Holotype ♀. PAPUA NEW GUINEA: Hughibagu, v.–ix.1891, L. Loria leg. (MCSN). Examined.

*Remarks.* Male unknown. The only *Orussus* sp. recorded from New Guinea and the Australian region as a whole; as such, easily recognizable from other Orussidae occurring in that region.

*Orussus minutus* Middlekauff, 1983. Holotype ♀. USA: Maryland, Cabin John, along river, 17.iv.1965, D. R. Smith leg. (NMNH; depository confirmed by D. R. Smith). Not examined (but paratypes with same data as holotype and compared with holotype studied).

*Additional records.* Middlekauff (1983) lists a number of additional records and some biological information.

*Remarks.* Closely resembles *O. thoracicus* in a number of features, but can be separated from the latter by the absence of the postocular carina and the carina laterally on the axilla as well as the entirely dark midtibia.

*Orussus moroi* Guiglia, 1954a. Holotype ♀. ITALY: Piemonte, Cassano Spinola, 21–31.vii.1946, G. B. Moro leg. (MCSN). Examined.

*Additional records.* Kraus (1998) lists a number of occurrences and a few host tree records from around the Mediterranean and the Canary Islands.

*Remarks.* The female mostly resembles *O. unicolor* among the other European species, but it can be separated from the latter by the absence of white spots on the antenna and the presence of a distinct ventral carina on the forefemur. The male resembles *O. taorminensis* (see below), from which it can be discerned by the colour of the cenchri (see key).

*Orussus occidentalis* Cresson, 1879. Lectotype ♀. USA: Colorado [no other data, according to Middlekauff, 1983] (ANSP, according to Middlekauff, 1983; depository confirmed by D. R. Smith). Not examined.

*Additional records.* Numerous records and host and host tree records are provided by Middlekauff (1983).

*Remarks.* *O. occidentalis* is the most common western North American species. It can be separated from



*O. abietinus* by the features mentioned in the key. It can be discerned from other Nearctic *Orussus* spp. by the predominantly red abdomen. However, according to Middlekauff (1983), about 10% of the females of *O. occidentalis* are melanic; *O. abietis* Rohwer and *O. hopkinsi* Rohwer were described from melanic specimens of *O. occidentalis*. Furthermore, female *O. sayii* might have the abdomen predominantly red; however, such aberrant specimens can be identified by the frons having transverse whitish spots not lying adjacent to the inner margins of the eyes for more than a short distance, whereas the frons of female *O. occidentalis* is entirely dark.

*Orussus rufipes* Tsuneki, 1963. Holotype ♂. JAPAN: Aomori Pref., Towada, 16.vii.1961, K. Shimoyama leg. (BLFU, according to Guiglia, 1965; depository not confirmed). Not examined.

*Additional records.* JAPAN: ♀, ♂, Hokkaido, Tokachi, Horoka, 27.vii.1974, A. Shinohara leg.; 2♀♀, Honshu, Kyoto Pref., Ashiu, 21.vi. & 17.vii.1975, K. Mizuno leg.; ♀, Honshu, Fukushima, Tateiwa, Masuzawa, 3–5.vi.1994 (all NSMT).

*Remarks.* Distinguished from *O. japonicus*, the other species of *Orussus* occurring in mainland Japan, by the absence of a white spot laterally on the 2nd abdominal tergum and the limited extent of the white mark on the hindtibia (present only proximally).

*Orussus sayii* Westwood, 1830. Holotype ♀. USA: Indiana, New Harmony (according to Westwood, 1830), G. B. Sowerby leg. (OXUM). Examined (lost according to Middlekauff, 1983).

*Additional records.* Middlekauff (1983) lists a number of occurrences from North America.

*Remarks.* Middlekauff (1983) was unable to locate the holotype in OXUM, but studied three other female specimens there. I examined a female specimen from OXUM, which is labelled 'GB. Sowerby N Amer', and on another handwritten label 'sayii Westw. 29i.' These label data do not match any of the specimens examined by Middlekauff (1983), but agree with Westwood (1830), who states that 'Dom. G. B. Sowerby communicavit'. The specimen bears several printed labels which states that this is the type of *O. sayii*; I concur with this. *O. sayii* can be separated from the closely related North American species *O. occidentalis* and *O. terminalis* by the presence of transversely elongate white spots situated low on the frons; furthermore, the female abdomen is usually entirely dark brown to black, only rarely reddish brown posteriorly.

*Orussus schoutedeni* Guiglia, 1937b **validity reestablished.** Holotype ♀. DEMOCRATIC REPUBLIC OF THE CONGO: Haut Uele, Moto, iv.v.1923, L. Burgeon leg. (MRAC). Examined.

*Additional records.* ANGOLA: ♀, Vila Salazar, 8.ix.1949, B. Malkin leg. (EMEC; misidentified as *Lep-torussus africanus*); NIGERIA: ♂, Ibadan, Olokemeji [no collection date, but identified by H. K. Townes in 1948], Bridwell leg. (?) (NMNH).

*Remarks.* For reasons for including this and the two following species in *Orussus* instead of placing them in a separate genus *Heliorussus*, see discussion of internal relationships of *Orussus* under the genus description above. The differences between these species, especially between *O. schoutedeni* and *O. scutator* are not great, and they might have to be merged, pending the study of additional material.

*Orussus scutator* (Benson, 1955a) **comb. nov.** Holotype ♂. SIERRA LEONE: Movabha, 16.ii.1925, E. Hargreaves leg. (NHML). Examined.

*Remarks.* Female unknown. The sole known specimen is distinguished by the very well developed tubercle in the middle of the mesoscutum.

*Orussus spinifer* (Benson, 1955a) **comb. nov.** Holotype ♀. ZIMBABWE: Melsetter, 18.x.1950, G. Arnold leg. (NHML). Examined.

*Remarks.* Male unknown. This species can be distinguished from its close relatives *O. schoutedeni* and *O. scutator* by the presence of a distinct white spot proximally on the hindtibia (absent from the two other species), and by having the posterior margin of the mesonotum continuous (separated medially by the mesoscutellum in the other two species).

*Orussus striatus* Maa, 1950. Holotype ♀. JAPAN: Ryukyu Islands, Iriomote, 6.vi.1932, S. Hirayama leg. (TARI; depository not confirmed). Not examined.

*Additional records.* Paratype ♀, same data and depository as holotype. CHINA: ♀, Hainan, Ta Hian, 15.vi.1935 (no collector) (UOPJ).

*Remarks.* Male unknown. The female from Hainan agrees very well with the description of Maa (1950) in the coloration of the legs and wings. *O. striatus* can be distinguished from all other *Orussus* spp. by the entirely hyaline forewings and the presence of a mesepisternal carina.

*Orussus taorminensis* Trautmann, 1922. Holotype ♀. ITALY: Sicily, Fontana Vecchia, Taormina, 18.v.1922, W. Trautmann leg. (EITH). Examined.

*Additional records.* Kraus (1998) lists several additional records from southern France and Italy; Bella & Turrisi (1998) and Pesarini & Turrisi (2001) list additional records from Sicily, with some possible hosts (*Trichoferus holosericeum* (Rossi, 1790) and *T. fasciculatus* (Faldermann, 1837), both Ceramby-

cidae (Coleoptera)) and host tree (*Pistachia terebinthus* (Anacardiaceae)) records.

*Remarks.* The female of *O. taorminensis* is easily distinguished from all other *Orussus* spp. by the extensive red coloration of the thorax, contrasting starkly with the darker remaining body parts. According to Trautmann (1922), the collection date for the holotype is 19.v.1922, but the label clearly reads '18.v.22'. The male does not have red markings on the thorax. Bella & Turrisi (1998) provided the first description of the male of *O. taorminensis* and list a number of differences between it and that of *O. moroi*; their list was based on comparison of the original description of *O. moroi* (Guiglia, 1954a), supplemented by information from Schedl (1985; especially Fig. 1), since no males of the latter were available for them to study. I have had the opportunity to examine alleged males of both species and found it difficult to substantiate most of the differences listed by Bella & Turrisi (1998), with the exception of the differences in the colour of the cenchri (see key).

*Orussus terminalis* Newman, 1838. Holotype ♀. USA: New Hampshire, Trenton Falls, Doubleday leg. (lost according to Middlekauff, 1983).

*Additional records.* Middlekauff (1983) provides numerous collection records from eastern North America, as well as some host and host tree information.

*Remarks.* Female *O. terminalis* can be distinguished from *O. occidentalis* and *O. sayii* by having at most T5–8 reddish brown (T3–8 reddish brown in *O. occidentalis*, all terga dark brown to black in *O. sayii*); furthermore, they differ from *O. sayii* in having no white markings on the frons. The male *O. terminalis* can likewise be discerned from the other two species by the absence of white markings on the frons, and from *O. occidentalis* by the predominantly dark brown or black abdomen.

*Orussus tessmanni* Enslin, 1913. Holotype female. EQUATORIAL GUINEA: Nkolentangan, xi.1907–v.1908, G. Tessmann leg. (ZMHB). Examined.

*Remarks.* Male unknown. *O. tessmanni* is very closely related to *O. afer*, from which it can be distinguished by the coloration of the antenna (entirely dark brown in *O. tessmanni*, with A1–2 light brown in *O. afer*).

*Orussus thoracicus* Ashmead, 1898. Holotype ♀. USA: California, Santa Cruz Mts. (no collection date), W. H. Ashmead. (NMNH). Examined.

*Additional records.* Middlekauff (1983) provides numerous collection records from North America, as well as some host and host tree information.

*Remarks.* Ashmead (1898) erroneously described the holotype as a male. *O. thoracicus* resembles *O. minutus* most among the North American *Orussus* spp., but can be distinguished from the latter by having well developed postocular and lateral axillar carinae, as well as having a distinct white spot dorsally on the midtibia. Furthermore, the 8th abdominal tergum in male *O. minutus* always has a well developed longitudinal white stripe; this is at most weakly developed in male *O. thoracicus* and usually entirely absent.

*Orussus unicolor* Latreille, 1811. Holotype ♀. FRANCE: Paris, Bois de Boulogne (no collection date?), P. A. Latreille leg. (perhaps in ZMHB, according to Guiglia, 1965; depository not confirmed). Not examined.

*Additional records.* Kraus (1998) lists numerous records from Europe & Algeria. Merz (2000) provided the first record from Switzerland and some behavioural information. I have seen the following material. FRANCE: ♀, Savoie, Moutiers, O. Sichel leg.?; ♀, Oise?, O. Sichel leg.?; ♂, Sicile, O. Sichel leg.?; ♀, [no data] O. Sichel leg.?; ♂, Fontainebleau 1909, Bourgoin leg.; 2♀, Seine-et-Oise, Maisons-Lafitte 1919, J. de Gaulle leg.; ♂, Paris, Mont de Masson, F. Picard leg.? (all MNHN). GERMANY: ♀, ♂, Herkulesbad, 27.v.1931 (collector not listed) (ZMHB); ♂, Herkulesbad, Banat, M. Herting leg. (ZMHB); ♀, ♂, Rheinland-Pfalz, Gernersheim, Bienwald, 7.vi.1996, F. Brechtel leg. (SBPC). SLOVAKIA: ♂, Zadiel, 15.–18.vi.1980, J. Halada leg. (OLML). SWITZERLAND: ♂, Bernex, Chante-Merle, 16.v.1999, B. Merz leg. (MHNG); 3♂ [same data as previous] (EITH); ♀, 3♂, 23.v.1999, [otherwise as previous] (MHNG).

*Remarks.* *O. unicolor* mostly resembles *O. moroi* among the other European species, but can be separated from the latter by the presence of white spots on the antenna and the frons and the absence of a ventral carina on the forefemur; furthermore, the mesoscutellum is more densely punctured in *O. unicolor*.