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> Abstract

The phylogeny of the parasitic wasp family Orussidae is analyzed with a slightly expanded version of a previously published data set. The basal splitting events in the family between two fossil taxa and the extant members are not unambiguously resolved. Intergeneric relationships in general are poorly supported and change under different analytical conditions. This corroborates earlier findings regarding the phylogeny of the family. A resumé of the evolutionary history of the Orussidae is provided. *Leptorussus madagascarensis* sp.n. is described.

> Key words

Age estimate, body size evolution, fossils, parasitic wasps, zoogeography.

1. Introduction

The Orussidae is a small family of parasitic wasps. They occur worldwide, but are rarely collected. Their biology is incompletely known, but the majority of the evidence bearing on the lifestyle of Orussidae indicates that they are idiobiont ectoparasites of woodboring beetle larvae, primarily Buprestidae (Vilhelmsen 2003a; Vilhelmsen et al. 2001). Striking adaptations to host detection and oviposition are developed in the females, which apparently employ a form of vibrational sounding involving tapping the wood with the modified antennal tips and detecting reflected vibrations with greatly enlarged subgenual organs in the forelegs; the very elongate and thin ovipositor is concealed inside the body of the female when it is not in use, being gradually unrolled during oviposition (Vilhelmsen et al. 2001). These are unique features that strongly support the monophyly of extant Orussidae.

The Orussidae occupy a crucial position within the Hymenoptera, being the only non-apocritan parasitic wasps. They lack the wasp-waist diagnostic of the Apocrita, comprising all other parasitic wasps and their relatives, but otherwise the Orussidae share an overwhelming number of synapomorphies with the Apocrita, both larval (Vilhelmsen 2003b) and adult (Vilhelmsen 2001a). Indeed, recent phylogenetic analyses of the basal hymenopteran lineages have consistently retrieved the Orussidae and Apocrita as sister groups, with substantial support (Vilhelmsen 2001a; Schulmeister 2003). This relationship implies that the parasitic lifestyle in Hymenoptera arose in the common ancestor of these two taxa, and indicates that the Orussidae might have a lifestyle that in some ways is reminiscent of that of the common ancestor of parasitic wasps.

Vilhelmsen (2003a) conducted a phylogenetic revision of the extant Orussidae, based on a comprehensive morphological dataset assembled by examining material of virtually all known species of the family, something that had not been undertaken previously. He revised the generic concepts and abolished the higher-level (subfamily, tribal) classification. Furthermore, Vilhelmsen (2004) included the two undoubted amber fossil members of the family in phylogenetic and biogeographic analyses attempting to unravel the distributional history and estimate the age of the Orussidae. The Paroryssidae is an extinct family of Hymenoptera from the upper Jurassic which have been suggested to be ‘ancestral’ to Orussidae (Rasnitsyn 1969, 1980, 1988, 2002), mainly because of shared reductional characters in the wings. Due to the preservational state of these compression fossils, not enough characters could be scored for them to include them in the analyses of Vilhelmsen (2004), so the Paroryssidae have yet to be demonstrated to be closely related to the Orussidae.

In addition to the phylogenetic generic revision, most genera of the Orussidae have been revised recently (Schmidt & Gibson 2001; Schmidt & Vilhelm-

SEN 2002; VILHELMSEN 2001b; VILHELMSEN & SMITH 2002). These studies form a baseline from which to embark on description of additional taxa in the future. 75 species in 16 genera were recognized by VILHELMSEN (2003a). Since then, two additional species have been described (*Chalinus albitibialis* in VILHELMSEN 2005; *Orussus smithi* in BLANK et al. 2006). With the species described in the present paper (see Appendix), this brings the number of described extant orussid species to 78.

2. Materials and methods

The dataset analyzed in the present paper is a slightly expanded version of that initially presented in VILHELMSEN (2003a). The two fossil species of Orussidae and two additional characters in which they differ from all extant Orussidae are included (see VILHELMSEN 2004), as well as the newly described species *Chalinus albitibialis* (for scorings, see VILHELMSEN 2005). Finally, an undescribed species of *Leptorussus* from Madagascar was scored for the expanded character set (see Appendix). The dataset, including outgroups, comprises 83 taxa and 165 characters; it is available from the author on request. BLANK et al. (2006) scored *Orussus smithi* for all the abovementioned characters and an additional one shared only by it and its putative sister species, *O. abietinus*. This additional information was not included here as I did not have access to any specimens of *O. smithi*.

The dataset was analyzed in TNT (GOLOBOFF et al. 2000) with the following characters treated as additive: 12, 19, 24, 31, 34, 35, 46, 66, 70, 75, 77, 87, 96, 103, 104, 111, 113, 114, 119, 124, 125, 126, 137, 146, 147, 149, 152, 156, 157, 159, 160, and 164. Space for 600,000 trees was reserved in the memory. Traditional searches in equal weights analyses and implied weights analyses with the concavity constant k set in turn to 3, 7, and 10 were run. Analyses were run with collapsing rules set to max. length = 0. For each weighting scheme analyses with the following settings were run: 100 replications/5,000 trees saved pr. replication; 500 replications/1,000 trees saved pr. replication; 1,000 replications/500 trees saved pr. replication. The trees obtained by analyses were filtered to remove any suboptimal trees. The root was *Urocerus gigas* (Linné, 1758) (Siricidae). Bremer support values were calculated in TNT by searching for suboptimal trees using the trees obtained by the equal weights analyses as starting point. Suboptimal trees of up to 20 steps longer than the shortest trees were looked for, the search continuing until the number of trees checked reached 100,000. The Bremer support values were obtained from these suboptimal trees. Absolute jackknifing values were calculated in TNT. Support values are shown in Fig. 1.

3. Results

The equal weights analyses found up to 75,651 trees of 767 steps length; a consensus is shown in Fig. 1. The shortest trees were obtained in approx. 60% of the replications. The k = 3 analyses found up to 2,673 trees of fit 66.5576; the optimal trees were obtained in approx. 40% of the replications. The k = 7 analyses found up to 1,782 trees of fit 43.53326; a consensus is shown in Fig. 2. The optimal trees were obtained in approx. 40% of the replications. The k = 10 analyses found up to 2,430 trees of fit 34.90856. The optimal trees were obtained in approx. 25% of the replications. The different settings of replications vs. number of trees saved found trees of the same length and fitness, and there was little difference in the number of trees found. Filtering did not identify any suboptimal trees in any analyses.

The topology of the trees retrieved by equal weights analyses (Fig. 1) is very similar to those presented in VILHELMSEN (2003a; 2004); differences might be caused by analyzing the data set in TNT, the previous analyses being conducted with NONA (GOLOBOFF 1993a), PeeWee (GOLOBOFF 1993b), and PAUP* (SWOFFORD 2001). Orussidae s.str. (including the fossil taxa *Mesorussus taimyrensis* Rasnitsyn, 1977 and *Minyorussus luzzi* Basibuyuk et al., 2000, see Fig. 2, but excluding members of the Paroryssidae) are always retrieved as monophyletic. In the consensus, there is an unresolved trichotomy at the base of Orussidae s.str. between the two fossil taxa and all extant Orussidae. The latter is always retrieved as monophyletic, and the topology of the extant Orussidae was found not to be influenced by the inclusion of the fossil species (VILHELMSEN 2004). At the base of the extant Orussidae, the topology is *Orussonia* + (*Orussella* + (*Orussobaius* + (*Leptorussus* + other genera))). The clade comprising the majority of the extant species has a dichotomy between *Pseudoryssus* + *Orussus* and the clade (*Pedicrista* + (*Mocsarya* + *Chalinus*)) + ophrynopine genera (Fig. 2). The relationships among the ophrynopine genera are not well resolved, except for a clade comprising *Ophrella* + (*Stirocorsia* + *Ophrynopus*), and *Guiglia* is not retrieved as monophyletic. All non-monotypic genera of Orussidae except *Guiglia* are retrieved as monophyletic, and most are well supported.

All the implied weights analyses retrieved all genera of Orussidae as monophyletic. The relationships among the basalmost extinct and extant genera are similar to the equal weights analyses. In the k = 3 analyses, *Pseudoryssus* + *Orussus* is the sistergroup to *Pedicrista* + (*Mocsarya* + *Chalinus*). The topology of the ophrynopine genera is *Kulcania* + (*Ophrynon* + (*Guiglia* + (*Argentophrynopus* + (*Ophrella* + (*Stirocorsia* + *Ophrynopus*))))). In the k = 7 (Fig. 2) and k = 10 analyses, the ophrynopine genera are the sister-group of *Pedicrista* + (*Mocsarya* + *Chalinus*), as in the equal weights analyses. The topology of the ophrynopine genera is *Guiglia* + ((*Kulcania* + *Ophrynon*) + (*Argentophrynopus* + (*Ophrella* + (*Stirocorsia* + *Ophrynopus*)))).

The new *Leptorussus* sp. consistently comes out as the sister species to *Leptorussus kwazuluensis* Vilhelmsen, 2003. Putative synapomorphies are the predominantly glabrous posterodorsal margin of the pronotum (character 50, state 1) and metepisternum (character 93, state 1).

4. Discussion

The support for both Orussidae s.str. and extant Orussidae is very low compared with the support obtained in Vilhelmsen (2003a). This is caused by the inclusion of the fossils in the present analyses. Most of the putative autapomorphies of the Orussidae are sex specific, many of which are missing from one or the other of the fossil species, which are probably a male and a female, respectively (Vilhelmsen 2004). Furthermore, the putative female *Mesorussus taimyrensis* is missing the posterior part of the body, making it impossible to score characters associated with the ovipositor. The missing data from the fossils prevents unambiguous resolution and optimization of characters at the base of Orussidae s.str., hence the low support.

The intergeneric relationships within the Orussidae were shown in Vilhelmsen (2003a) to be highly unstable under changing analytical conditions. On the other hand, all non-monotypic genera except *Guiglia* were retrieved as monophyletic in all analyses, and even *Guiglia* was monophyletic in most analyses. The analyses carried out here corroborate this. For further discussion of intergeneric and intrageneric relationships in extant Orussidae, see Vilhelmsen (2003a).

Subfamily and tribal classification in Orussidae was introduced and later revised by Benson (1935, 1955). In the final version, he operated with 2 subfamilies, Orussinae and Ophrynopinae, and 6 tribes, one of which was monotypic (Pedicristini). Vilhelmsen (2003a) demonstrated that this classification could not be upheld after a phylogenetic analysis of the family. Only one subfamily, Ophrynopinae, and three tribes, Orussini, Mocsaryini and Pedicristini, were monophyletic (Fig. 2). Especially the tribe Leptorussini was problematic, forming a grade comprising the four basalmost extant genera of Orussidae (*Orussonia*, *Orussella*, *Orussobaius*, and *Leptorussus*). To make the tribal and subfamily classification conform to the phylogeny, it would have been necessary to introduce a number of monotypic and/or redundant taxa at these levels, providing little additional information when compared to the generic classification. This and the weak support for most intergeneric relationships led Vilhelmsen (2003a) to discard the tribal and subfamily classification as superfluous.

The diversity of Orussidae is well reflected by the generic classification, which required only minor modifications to conform to the results of the cladistic analyses by Vilhelmsen (2003a). Vilhelmsen & Smith (2002) sunk the genus *Ophrynella* originally proposed by Ross (1937), finding it to be based on a conflation of *Ophrynopus* and *Kulcania*. On the other hand, they described *Argentophrynopus* as new (Vilhelmsen & Smith 2002). Vilhelmsen (2003a) sunk *Heliorussus* Benson, 1955 into *Orussus*, since its constituent species were always retrieved deeply nested within *Orussus*. With these adjustments, the generic classification of Orussidae is likely to remain stable.

The dataset compiled by Vilhelmsen (2003a) provides a useful embarkation point for describing new taxa in Orussidae. The species that have been described since (Vilhelmsen 2005; Blank et al. 2006; present paper) have all been entered into the dataset and analysed with the already described species of Orussidae or at least some of them (Blank et al. 2006). The dataset provides a standard reference that allows to identify the phylogenetic placement and hence the taxonomic affinity of a putatively new taxon. Generic autapomorphies and possible closest relatives within a genus can be identified, making it possible to narrow down the number of species with which the new species has to be more closely compared.

The phylogeny of Orussidae has also been used to explore evolutionary and biogeographic scenarios for the family. Vilhelmsen (2004) tested a hypothesis initially proposed by Rasnitsyn (1969, 1980) contending that the Orussidae had experienced an episode of substantially reduced body size in their early evolutionary history. This would explain some putatively reductional features in the morphology of Orussidae (see Vilhelmsen 2004). The size variation among extant species is substantial (2–20+ mm), but both fossil species have a body length of around 2 mm. This and the basal placement of the fossils in the phylogeny corroborates that the common ancestor of Orussidae s.str. might have been small (body length < 5 mm). However, since the relationships among the two fossil species and the extant Orussidae are not resolved unequivocally, the results of the body size evolution analysis were ambiguous with regard to the basalmost splitting events in Orussidae s.str. However, it was evident that the common ancestor of extant Orussi-

Fig. 1. Strict consensus of 75,671 trees of length 767 steps derived by equal weights analysis. Numbers below branches are Bremer/Jacknife support values. Only Jacknife supports above 50 are shown.

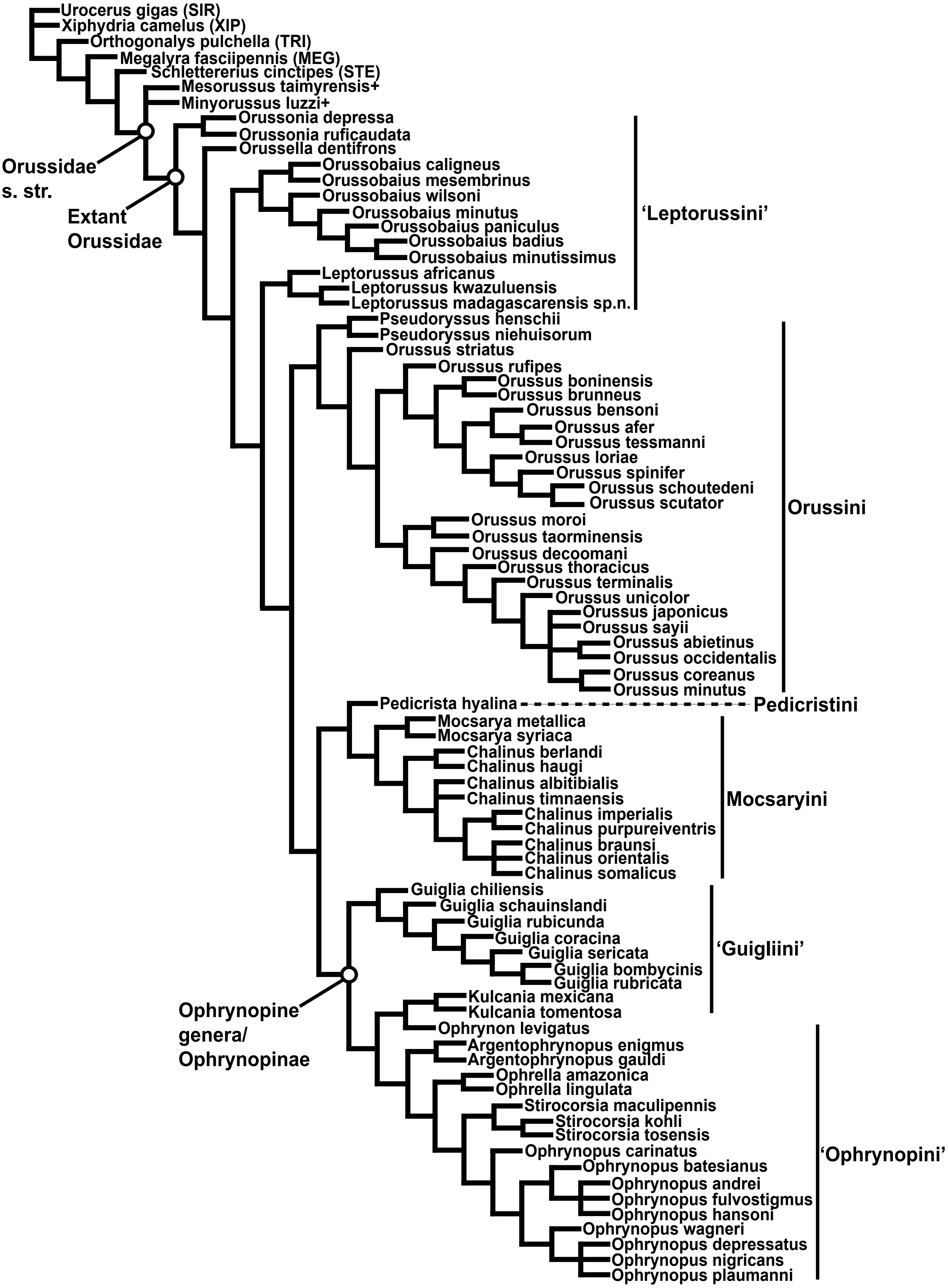

Fig. 2. Strict consensus of 1,782 trees of fit 43.53326 derived by implied weights analysis with k = 7. The tribal classification of Benson (1955) is indicated on the right.

dae was not under 5 mm long, all instances of reduced body size within this clade being secondary (VILHELMSEN 2004).

Biogeographic analyses showed the distributional history of the Orussidae to be highly complex (VILHELMSEN 2004). Furthermore, the analyses are somewhat compromised by the low support for higher-level relationships within the family; phylogenies with only marginally lower support than the one selected for the analyses might generate drastically different biogeographic scenarios. The distributional history of Orussidae is evidently dominated by speciation within the areas delimited for the biogeographic analysis and dispersal events which tend to obscure putative vicariance events. However, some of the vicariance events that could be identified are possibly correlated with tectonic events in the Mesozoic, like the breakup of Pangea (160–180 Mya) and Gondwana (105–135 Mya). This indicates that the common ancestor of Orussidae s.str. was around in the early Mesozoic, much earlier than the minimum age suggested by the fossils, the oldest of which have an age of approx. 95 Myr (VILHELMSEN 2004).

The dataset compiled by VILHELMSEN (2003a) was entirely based on external morphological characters. It would be highly desirable to supplement this by internal morphological and molecular data, especially in view of the weakly supported higher-level relationships within the Orussidae. However, since most species of the family are extremely rarely collected, being known from at most a handful of specimens, it is unlikely that a sufficient taxon sample for such studies can be accumulated within a reasonable time.

5. Acknowledgements

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7. Appendix: Description of a new species of *Leptorussus*

Leptorussus madagascarensis Vilhelmsen sp. nov. (Fig. 3A–F)

Holotype female. MADAGASCAR: Tulear Province, Beza Mahafaly Reserve, Parcel I, 22°41.19’S 44°35.46’E. Malaise in dry gallery forest 165 m. R. Marin ‘Hala’, M.E. Irwin leg. 11.–20.x.2002. Type depository: California Academy of Sciences, San Francisco, USA.

Description female. Body length 4.5 mm. Fore wing length 2.8 mm. Body generally dark brown to black (Fig. 3A), sternum 7 reddish brown apically (Fig. 3F); mouthparts and antennomeres 7–10 dark brown, antennomeres 1–6 and legs mostly reddish brown, two distalmost tarsomeres on all legs darker. Fore wing with two large infuscated areas (Fig. 3D), one extending from halfway along vein C to distal end of pterostigma, the other from much distally of pterostigma to apex of wing. Pterostigma, veins C, R, 2r, and basal part of 1a dark brown, remainder of venation hyaline or light brown (in infuscated areas). Hind wing hyaline, vein R light brown proximally, venation otherwise hyaline (Fig. 3D).

Head with three pairs of medially separate coronal teeth (Fig. 3C), transverse frontal furrow shallow (Fig. 3B), ventral transverse frontal carina well developed (Fig. 3C), all other frontal carinae absent; subantennal groove laterally delimited by short longitudinal carina not extending to postocciput (Fig. 3B); pilosity posterior to eye absent, postocular and postoccipital carinae absent (Fig. 3B). Frons rugose, vertex, gena and occiput punctate. Lateral margin of mesoscutellum not carinate, but well set off from surrounding sclerites, mesocutellum rounded posteriorly, mesonotum continuous behind mesoscutellum (Fig. 3E). Pronotum punctate, posterodorsal margin glabrous (Fig. 3E); mesoscutum, mesoscutellum, and mesopleuron punctate, metepisternum predominantly glabrous. Hind coxa laterally with dense mat of silvery hairs (Fig. 3F); hind femur without longitudinal ridge or denticles ventrally, with rounded posteroventral corners; hind tibia with row of distinct pegs dorsally, ventral longitudinal carina absent, apical spurs very short (Fig. 3F). Vein 2r-m difficult to observe, vein cu-a arises from discal cell opposite vein M (Fig. 3D). Terga 1–2 predominantly foveolate-rugose with glabrous posterior margin, terga 3–6 foveolate-rugose anteriorly, glabrous posteriorly, terga 7–8 punctate; abdominal sterna predominantly punctuate.

Male. Unknown.

Etymology. The only known specimen was collected on Madagascar.

Discussion. This species differs from other *Leptorussus* spp. in having the mesoscutum and mesoscutellum less densely sculptured and the lateral margins of the mesoscutellum not carinate. The differences in sculpture with *L. africanus* Benson, 1955 are especially striking, *L. madagascarensis* being significantly less densely sculptured on the head and thorax. *L. madagascarensis* shares with *L. kwazuluensis* Vilhelmsen, 2003 the features of having the posterior margin of the pronotum glabrous, the posterior margin of the mesonotum continuous posterior to the mesoscutellum, and the metepisternum predominantly glabrous. It differs from *L. kwazuluensis* in having a less developed frontal groove, more developed subantennal groove laterally delimited by a short but distinct carina, proximally inserted cu-a, and the partly infuscate fore wings. These differences might be correlated with the sex of the specimens (*L. kwazuluensis* is only known from a male specimen), but until specimens of both sexes from this genus are found together, it is considered reasonable to regard all the known specimens of *Leptorussus* as separate species.

The only other orussid species ever reported from Madagascar is ?*Chalinus oberthueri* (Saussure, 1890).

VILHELMSEN (2001b) considered this taxon as a *species inquirenda* since no material can be associated with it. There is also no proper description, just some illustrations (SAUSSURE 1890: pl. 20, fig. 5). Until material of this species becomes available, *Leptorussus madagascarensis* sp.n. is the only confirmed record of Orussidae from Madagascar. Given that the other known species of *Leptorussus* have a southern African distribution (*L. africanus*: Zimbabwe; *L. kwazuluensis*: South Africa), its occurrence in Madagascar is not surprising. Other genera with a southern African distribution that could also be expected in Madagascar are *Chalinus*, *Pedicrista*, and *Orussus* (VILHELMSEN 2001b, 2003a, 2004).

Tab. 1. Scorings for *L. madagascarensis* for the data matrix published in VILHELMSEN (2003a) and modified by VILHELMSEN (2004).

Chars 1–20	101111000--0-000?130
Chars 21–40	000000--001000000002
Chars 41–60	000110?001000?001?10
Chars 61–80	11000011010100101111
Chars 81–100	10110120111011020001
Chars 101–120	?020010011000?101001
Chars 121–140	00012?01000000010000
Chars 141–160	011001?11?0101???1?0
Chars 161–165	?002?

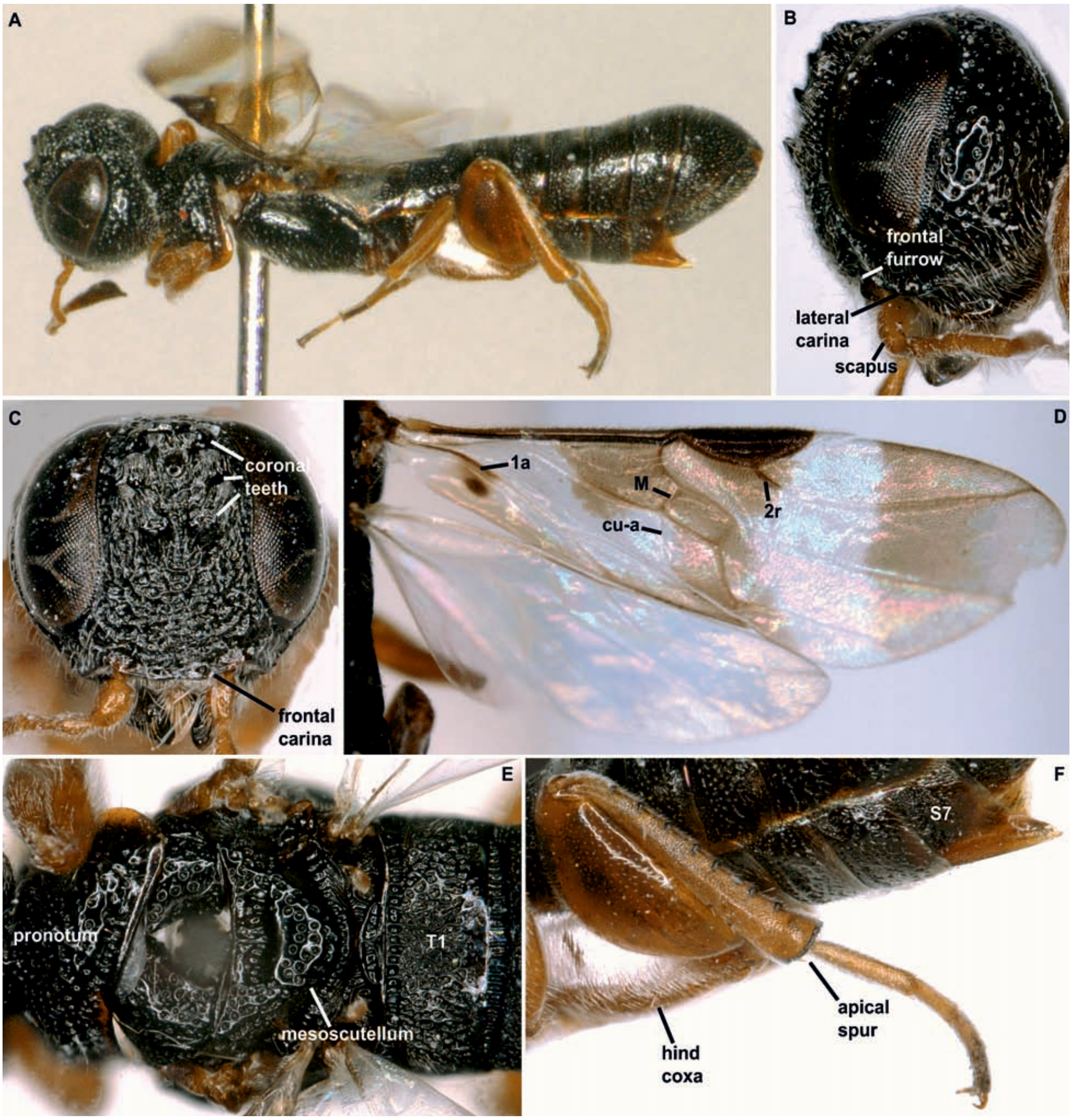

Fig. 3. *Leptorussus madagascarensis* sp.n. **A**: Entire specimen, lateral view. **B**: Head, lateral view. **C**: Head, anterior view. **D**: Wings, dorsal view. **E**: Thorax, dorsal view. **F**: Hind leg, lateral view. Not to scale. S7 = sternum 7; T1 = tergum 1.