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The old wasp and the tree: fossils, phylogeny and biogeography in the Orussidae (Insecta, Hymenoptera)

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The phylogenetic relationships of the fossil orussid taxa *Mesorussus taimyrensis* and *Minyorussus luzzi* are examined by analysing them together with a large data set compiled previously for the extant Orussidae. The fossils are placed in an unresolved trichotomy with the extant Orussidae. The phylogeny is used for evaluating the hypothesis that the ancestors of the family had reduced body size; the results of this analysis are inconclusive. The biogeographical history of the Orussidae is explored. The common ancestor of the family was probably widespread, the initial splitting events taking place prior to or coinciding with the separation of Laurasia from Gondwana. Later putative vicariance events can be correlated with the gradual breakup of Gondwana. However, the biogeographical history of the Orussidae is dominated by speciation within regions and dispersal. The minimum age of the common ancestor of the Orussidae is >180 Myr when estimated from the biogeographical pattern, >95 Myr when estimated from the phylogenetic position of the fossils; the earlier date is considered to be the most likely. © 2004 The Linnean Society of London*, Biological Journal of the Linnean Society*, 2004, **82**, 139–160.

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INTRODUCTION

The Orussidae are a small family of rarely collected parasitic wasps with 75 species worldwide (Vilhelmsen, 2003a). They have the distinction of being the only parasitic wasp taxon not having the wasp-waist so characteristic of the Apocrita, to which all other parasitic wasps and the vast majority of the species in the order Hymenoptera belong. Recent phylogenetic analyses (Ronquist *et al*., 1999; Vilhelmsen, 2001a) strongly corroborate the monophyly of Vespina (= Orussidae + Apocrita); the clade is exceedingly well supported by a host of morphological synapomorphies. The first comprehensive simultaneous analyses (including both morphological and molecular data) of basal hymenopteran relationships also retrieve Vespina, even though the molecular evidence is equivocal (Schulmeister, Wheeler & Carpenter, 2002; Schulmeister, 2003). Biological information for the Orussidae is sparse but the existing evidence (see Vilhelmsen *et al*., 2001 and Vilhelmsen, 2003a) indicates that they have a diet of woodboring insect larvae, primarily Coleoptera [jewel beetles (Buprestidae) and, to a lesser extent, longhorn beetles (Cerambycidae)]. That Orussidae have a parasitoid lifestyle is further corroborated by the anatomy of their larvae, which resemble apocritan larvae in having very reduced mouthparts, sensory, and locomotory apparatus (Vilhelmsen, 2003b). The hosts are located in dead wood with an echolocation mechanism involving the female antennae and fore legs and targeted with a very elongate, but entirely concealed ovipositor (Vilhelmsen *et al*., 2001).

The Orussidae are most diverse in the southern hemisphere, but they are represented in all major biogeographical regions. At least three distinct lineages occur in the Afrotropic (*Chalinus–Pedicrista*; *Leptorussus*; *Orussus*). Mainland Australia has three separate lineages (*Guiglia*; *Orussonia*; *Orussobaius*), with two additional (*Orussus*; *Stirocorsia*) on nearby New Guinea. Tropical South America houses only members of the ophrynopine clade (see Fig. 1) (*Argentophrynopus*; *Kulcania*; *Ophrella*; *Ophrynopus*), but adjacent Chile is occupied by members of two additional genera (*Guiglia*; *Orussella*). The diversity is almost as high in the northern hemisphere. Two sep-

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arate lineages are represented in the Nearctic (ophrynopine clade: *Kulcania–Ophrynon–Ophrynopus*; *Orussus*), and three in the Oriental (*Mocsarya*; *Orussus*; *Stirocorsia*) and Palaearctic (*Mocsarya*; *Orussus–Pseudoryssus*; *Stirocorsia*). The presence in most major biogeographical regions of several independent lineages of Orussidae, some of which are comparatively speciose, indicates that the distributional history of the family is dominated by dispersal and speciation within regions.

The rarity of extant Orussidae is matched by a very limited fossil record. The first fossil to be associated with the family was *Lithoryssus parvus* Brues, 1906, from the Florissant (Oligocene, approx. 34 Mya) in Colorado; it is the only fossil taxon listed in the world catalogues of Guiglia (1943, 1965). The original description only illustrates the wing venation, which does not resemble that of extant Orussidae. Other features listed by Brues (1906) differing from those displayed by extant Orussidae are the number of antennal segments in the female, and the presence of an external ovipositor. Already Rohwer (1912) expressed doubts about the affinities of this fossil. Rasnitsyn (1969: fig. 9) illustrated the entire specimen, considering it to be a member of the Tenthredinoidea (true sawflies). Consequently, *L. parvus* has been excluded from the present study.

The extinct family Paroryssidae comprise nine species in three genera, all from the Upper Jurassic, Southern Kazakhstan (see Table 1). Martynov (1925) described the family; Rasnitsyn (1969) provided illustrations and a key to the species. Paroryssidae are characterized by a number of reductional wing venation traits shared with Orussidae and most extant Apocrita. They differ from extant Orussidae primarily by the absence of an ocellar corona (a circlet of cuticular teeth surrounding the median ocellus) and by having a very long external ovipositor (Rasnitsyn, 1988). Rasnitsyn (1969, 1980, 1988, 2002) considered Paroryssidae to be the ancestors of the Orussidae; he stated that Orussidae ‘appeared not later than the beginning of the late Cretaceous’ (Rasnitsyn, 1980). In the analysis of Ronquist *et al*. (1999), Paroryssidae were included as a single terminal combining information from several of the fossil taxa; they came out as the sistergroup of Orussidae, a relationship that was well supported. However, given the absence of autapomorphies for the Paroryssidae, their relationship to extant Orussidae might not be correctly resolved.

Table 1. Genera and species of extinct Orussidae and Paroryssidae

Orussidae *s. s.* Newman, 1834
Mesorussus Rasnitsyn, 1977
M. taimyrensis Rasnitsyn, 1977*
Minyorussus Basibuyuk *et al*., 2000
M. luzzii Basibuyuk *et al*., 2000*
Paroryssidae Martynov, 1925
Microryssus Rasnitsyn, 1968
M. antennatus Rasnitsyn, 1968
M. brachyurus Rasnitsyn, 1968
M. crassipes Rasnitsyn, 1968
M. minus Rasnitsyn, 1968
M. robustus Rasnitsyn, 1968
M. subtilis Rasnitsyn, 1968
Paroryssus Martynov, 1925
P. extensus Martynov, 1925*
Praeoryssus Rasnitsyn, 1968
P. gracilis Rasnitsyn, 1968
P. venosus Rasnitsyn, 1968*

*Included in the present study

Two amber fossils have been assigned to the Orussidae proper: *Mesorussus taimyrensis* Rasnitsyn, 1977 (probably a female) and *Minyorussus luzzii* Basibuyuk, Quicke & Rasnitsyn, 2000 (probably a male). They both display traits shared only with extant Orussidae (see below). They are from the Upper Cretaceous, *Mesorussus* being from Taimyr, Siberia (age 95 Myr), and *Minyorussus* from New Jersey, North America (age 90 Myr). These two fossils and extant Orussidae together will be referred to as Orussidae *s. s.* in the following.

Rasnitsyn (1969, 1980; see also Basibuyuk, Quicke & Rasnitsyn, 2000) has repeatedly argued that the Orussidae have undergone considerable size reduction at some point in their early evolutionary history; the fairly large size (i.e. body length > 5 mm) of most extant members of the family is inferred to be secondary. Evidence cited in favour of this hypothesis is the low number of antennal segments (Rasnitsyn, 1980), the reduced wing venation, and low number of hindwing hamuli (see Basibuyuk & Quicke, 1997) displayed by extant members of the family. Size reduction has definitely occurred within the Apocrita, with many parasitic microhymenoptera (e.g., Ceraphronoidea, Chalcidoidea, Mymmarommatoidea, Platygastroidea; Sharkey & Roy, 2002) usually having a body length not exceeding 3 mm. Small size in Apocrita is clearly correlated with reduced wing venation. The comparatively small size of Paroryssidae (Rasnitsyn, 1968) and extinct Orussidae (Basibuyuk *et al*., 2000) seems to corroborate the size reduction hypothesis.

The aims of the present paper are threefold: first, to place the fossil taxa of Orussidae *s. s.* within the phylogeny of its extant members; second, to employ the resulting phylogeny in testing the possible influence of size reduction in shaping the anatomy of the family; third, to develop a biogeographical hypothesis for the family using the phylogeny and distribution data. Biogeographical scenarios will be 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).

MATERIAL AND METHODS

Fossil material

The following fossils were available for detailed study: Paroryssidae, *Paroryssus extensus* Martynov, 1925; holotype, spec. 2452/479 Palaeontological Institute, Russian Academy of Sciences (PIRAS); Paroryssidae, *Praeoryssus venosus* Rasnitsyn, 1968; holotype, spec. 2066/3345 (PIRAS); *Mesorussus taimyrensis* Rasnitsyn, 1977; holotype (PIRAS); *Minyorussus luzzi* Basibuyuk *et al*., 2000; holotype (AMNH). The extant taxa of Orussidae and outgroup taxa included are listed in Table 2. For further information about depositories and number of specimens examined, see Vilhelmsen (2003a: table 2).

Fossil study and measurements

The fossils were studied under a dissection microscope. Limestone fossils (Paroryssidae) were wetted with 95% ethanol to enhance clarity of structures and studied with reflected light. The amber fossils were suspended in maple syrup from beneath a coverslip mounted in a piece of wax on a slide and lighted both from above and below.

Measurements were taken with an ocular scale. Body length was measured from the anterior margin of the head capsule (excluding antennal bases and protruding mouthparts) to the tip of the abdomen (excluding ovipositor, if externally visible in the females); in the apocritan representatives, the length of the pro+mesosoma and metasoma were measured separately, as the latter was often angled upwards relative to the former, especially in ethanol preserved specimens. Mean and range of body length measured, estimated or obtained from the literature is given in Table 2.

The body length of *Orussella dentifrons* Phillipi, 1873 (no full body length measurements given in the literature, and no specimens available for study) and *Mesorussus taimyrensis* Rasnitsyn (fossil incomplete, only anteroventral part of head and thorax preserved) was estimated from the ratio between the width of the head (2.25 mm in *O. dentifrons*, see Philippi, 1873; 0.5 mm in *M. taimyrensis*, see Rasnitsyn, 1977) and the full body length. This ratio was obtained from measurements taken from three specimens of *Orussobaius minutus* Benson. *O. minutus* is a fairly basal taxon within extant Orussidae (Vilhelmsen, 2003a), as are *O. dentifrons* and *M. taimyrensis* (see below). Head width was measured as the shortest transverse distance between the lateral margins of the head just posterior to the eyes (where the head is most wide). Body lengths were 2.8, 3.5, and 5.7 mm, head widths 0.8, 1.0, and 1.6 mm, respectively. This gives a body length:head width ratio of roughly 3.5.

No body size information was available for *Orussus decoomani* Maa, 1950. The holotype of this species could not be accessed for study. The specimens examined in Vilhelmsen (2003a) are deposited in the Natural History Museum, London (NHML). They were identified to *O. decoomani* by Benson (1965), who did not provide any measurements. However, the description of *O. decoomani* (Maa, 1950) does not fit the specimens in the NHML, and it is possible that they represent a different, undescribed species (see Vilhelmsen, 2003a for further discussion).

Taxon sampling, character scoring, cladistic analyses, and character evolution

The Orussidae *s. s.* fossils were scored for as many characters as possible from the data set compiled for extant Orussidae in the cladistic analysis of Vilhelmsen (2003a) (see Appendix). This data set includes 74 out of 75 known extant species of Orussidae, as well as five outgroup taxa. The outgroup comprises representatives of the Siricidae and Xiphydriidae, the nonapocritan families that repeatedly come out as the closest relatives of the Orussidae in recent analyses of basal hymenopteran relationships (e.g. Vilhelmsen, 2001a; Schulmeister, 2003). The other outgroup taxa are representatives of the apocritan families Megalyridae, Stephanidae, and Trigonalidae. These families were placed basally in the Apocrita in most of the analyses of Ronquist *et al*. (1999) and Dowton & Austin (2001). The apocritan taxa did not come out as a monophylum in Vilhelmsen (2003a), probably because potential apocritan autapomorphies that required examination of internal anatomy were not included (see Vilhelmsen, 2003a). They were left out because they could not be scored for the vast majority of Orussidae. Additional exemplars might have been chosen to represent the basal Apocrita (e.g. from among the Aculeata, Ichneumonoidea, or Evanoidea). However, the sample included in Vilhelmsen (2003a) and the present paper I consider sufficient to polarize the characters informative within the Orussidae. Unravelling the phylogeny of the basal Apocrita is beyond the scope of the present paper. Furthermore, most of the species of the selected outgroups and many of those belonging to the other basal apocritan taxa are comparatively large (body length > 5 mm); that this is the ground plan state for these taxa is indicated by their comparatively complete wing venation. The apocritan superfamilies (Ceraphronoidea, Chalcidoidea, Mymmarommatoidea, Platygastroidea) whose common ancestors are likely to have had a smaller body size are invariantly

Table 2. Body size and geographical distribution of species of Orussidae *s. s.*, Paroryssidae, and outgroup taxa

Taxon	Author, date	Mean size (mm) (range in parentheses)	Distribution
Urocerus gigas (SIR)	(Linné, 1758)	24.1 (13.8–37.5)[m(6specs)]	EPA, WPA
Xiphydria camelus (XIP)	(Linné, 1758)	12.9 (9.8–15.4)[m(6specs)]	EPA, WPA
Schletterius cinctipes (STE)	(Cresson, 1880)	14.2 (12.0–16.4)[m(2specs)]	NEA
Megalyra fasciipennis (MEG)	Westwood, 1832	9.5 (6.4–12.6)[m(2specs)]	AUS
Orthogonalys pulchella (TRI)	(Cresson, 1867)	8.6 (7.0–10.4)[m(5specs)]	NEA
Argentophrynopus enigmus	Vilhelmsen & Smith, 2002	6.0[1]	NNA (Mexico)
A. gauldi	Vilhelmsen & Smith, 2002	4.4 (3.8–5.0)[1]	NNA (Costa Rica)
Chalinus berlandi	Guiglia, 1935	12.5 (11.0–14.0)[2]	AFR (Democratic Republic of the Congo)
C. braunsi	(Enslin, 1911)	9.0 (8.0–18.0)[2]	AFR (southern Africa)
C. haugi	du Buysson, 1902	19.0[2 (1spec.)]	AFR (Gabon)
C. imperialis	(Westwood, 1874)	17.5 (12.0–23.0)[2]	AFR (central & western Africa)
C. orientalis	Guiglia, 1937	16.0 (15.0–17.0)	AFR (eastern Africa)
C. purpureiventris	Cameron, 1912	11.0[2]	AFR (Democratic Republic of the Congo)
C. somalicus	Guiglia, 1935	11.5 (10.0–13.0)[2]	AFR (eastern Africa)
C. timnaensis	Kraus, 1998	12.0 (9.0–15.0)[2]	AFR (western Africa), WPA (Israel)
Guiglia bombycinis	Benson, 1938	7.25 (5.0–9.5)[3]	AUS (Queensland)
G. chiliensis	Benson, 1955	9.0[4]	SNT (Chile)
G. coracina	Benson, 1955	8.5[5]	AUS (Queensland)
G. rubicunda	Schmidt in Vilhelmsen & Smith, 2002	3.8[1]	OCE (Fiji Islands)
G. rubricata	Riek, 1955	7.9[m,1spec.]	AUS (eastern Australia)
G. schauinslandi	(Ashmead, 1903)	6.6[6]	OCE (Chatham Island, New Zealand)
G. sericata	(Mocsáry, 1900)	8.5 (6.0–11.0)[7]	AUS (eastern Australia)
Kulcania mexicana	(Cresson, 1879)	13.5 (12–15)[8]	NEA (s. USA), NNA (Colombia, Mesoamerica)
K. tomentosa	(Middlekauff, 1983)	13.65 (11.8–15.5)[8]	NEA (south-western USA)
Leptorussus africanus	Benson, 1955	5.0[5]	AFR (Zimbabwe)
L. kwazuluensis	Vilhelmsen, 2003a	2.6[9]	AFR (South Africa)
Mocsarya metallicus	(Mocsáry, 1896)	15.0 (12.0–18.0)[2]	ORI (Indonesia, Sri Lanka)
M. syriaca	Benson, 1936	9.0 (6.0–12.0)[2]	WPA (Levantine region, Minor Asia)
Ophrella amazonica	(Westwood, 1874)	7.0[10]	NNT (Brazil)
O. lingulata	Middlekauff, 1985a	6.5[11]	NNT (Panama)
Ophrynon levigatus	Middlekauff , 1983	5.5 (5.0–6.0)[8,12]	NEA (California)
Ophrynopus andrei	Konow, 1897	9.0[10]	NNS (Brazil)
O. batesianus	(Westwood, 1874)	12.5[10]	NNS (Brazil)
O. carinatus	Vilhelmsen & Smith, 2002	2.8[1]	NNT (Brazil)
O. depressatus	Smith, 1988	7.5 (5.0–10.0)[13]	NNT (Argentina, Brazil)
O. fulvostigmus	(Westwood, 1874)	10.5[10]	NNT (Brazil)
O. hansoni	Vilhelmsen & Smith, 2002	5.9 (4.5–7.3)[1]	NNT (Costa Rica, Trinidad)
O. nigricans	(Cameron, 1883)	7.0 (5.0–9.0)[8]	NEA (s. USA), NNT (Ecuador, Mesomerica)
O. plaumanni	Smith, 1988	6.25 (4.0–8.5)[13]	NNT (Brazil, Paraguay)
O. wagneri	du Buysson, 1910	7.0[14]	NNT (Argentina)
Orussella dentifrons	(Philippi, 1873)	7.9[e]	SNT (Argentina, Chile)
Orussobaius badius	Schmidt & Vilhelmsen, 2002	3.0[15]	AUS (Queensland)
O. caligneus	Schmidt & Vilhelmsen, 2002	11.0[15]	AUS (Western Australia)
O. mesembrinus	Benson, 1938	9.0 (7.0–11.0)[15]	AUS (south-eastern Australia)
O. minutissimus	Schmidt & Vilhelmsen, 2002	2.0[15]	AUS (Queensland)

Table 2. *Continued*

Taxon	Author, date	Mean size (mm) (range in parentheses)	Distribution
O. minutus	Benson, 1938	6.75 (2.8–10.7)[15]	AUS (widespread in mainland Australia)
O. paniculus	Schmidt & Vilhelmsen, 2002	3.0[15]	AUS (New Guinea)
O. wilsoni	Benson, 1938	6.5 (6.0–7.0)[15]	AUS (eastern Australia, New Guinea)
Orussonia depressa	Riek, 1955	5.5 (5.0–6.0)[16]	AUS (south-eastern Australia)
O. ruficaudata	Schmidt & Gibson, 2001	8.5[16]	AUS (Victoria)
Orussus abietinus	(Scopoli, 1763)	11.0 (6.0–16.0)[17]	EPA, WPA (widespread)
O. afer	Guiglia, 1937	8.0[18]	AFR (Democratic Republic of the Congo)
O. bensoni	Guiglia, 1937	6.0[19]	ORI (Philippines)
O. boninensis	Yasumatsu, 1954	7.0[20]	EPA (Bonin Islands)
O. brunneus	Shinohara & Smith in Shinohara, 1983	5.4[21]	ORI (Taiwan)
O. coreanus	Takeuchi, 1938	9.25 (8.5–10.0)[22]	EPA (Korea)
O. decoomani	Maa, 1950	not known[9]	ORI (India?, Vietnam)
O. japonicus	Tosawa, 1930	13.0 (10.0–16.0)[23]	EPA (Japan)
O. loriae	Mantero, 1899	7.5[24]	AUS (New Guinea)
O. minutus	Middlekauff, 1983	6.4 (3.8–9.0)[8]	NEA (eastern USA)
O. moroi	Guiglia, 1954	6.5 (4.0–9.0)[17]	WPA (Canary Islands, Mediterranean region)
O. occidentalis	Cresson, 1879	11.5 (7.0–16.0)[8]	NEA (western Canada & USA)
O. rufipes	Tsuneki, 1963	5.7[25]	EPA (Japan)
O. sayii	Westwood, 1830	13.5 (11.0–16.0)[8]	NEA (eastern Canada & USA)
O. schoutedeni	Guiglia, 1937	7.0[18]	AFR (central & western Africa)
O. scutator	(Benson, 1955)	5.0[5]	AFR (Sierra Leone)
O. spinifer	(Benson, 1955)	7.0[5]	AFR (Zimbabwe)
O. striatus	Maa, 1950	7.5 (7.0–8.0)[26]	ORI (China, Ryukyu Islands)
O. taorminensis	Trautmann, 1922	7.75 (5.5–10)[17,27]	WPA (France & Italy)
O. terminalis	Newman, 1838	11.0 (7.0–15.0)[8]	NEA (eastern Canada & USA)
O. tessmanni	Enslin, 1913	10.0[28]	AFR (Equatorial Guinea)
O. thoracicus	Ashmead, 1898	5.5 (4.0–11.0)[8]	NEA (western USA)
O. unicolor	Latreille, 1811	6.5 (5.0–9.0)[17,29]	WPA (Algeria, Europe)
Pedicrista hyalina	Benson, 1935	8.5 (8.0–9.0)[30]	AFR (southern Africa)
Pseudoryssus henschii	(Mocsáry, 1910)	5.5 (5.0–6.0)[31]	WPA (Europe, Iraq, Morocco, Turkey)
P. niehuisorum	Kraus, 1998	5.0 (4.0–6.0)[17]	WPA (Israel)
Stirocorsia kohli	Konow, 1897	13.0[31]	ORI (Indonesia, Philippines, south-east Asia)
S. maculipennis	(Smith, 1859)	13.0 (11.0–15.0)[10]	AUS (New Guinea)
S. tosensis	(Tosawa & Sugihara, 1934)	10.5 (9.0–12.0)[m,2specs]	EPA (Japan)
Mesorussus taimyrensis +	Rasnitsyn, 1977	1.75[e]	EPA (Russia)
Minyorussus luzzi +	Basibuyuk *et al*., 2000	2.2[32]	NEA (USA)
Paroryssus extensus +	Martynov, 1925	5.7[m,1spec.]	EPA (Kazakhstan)
Praoryssus venosus +	Rasnitsyn, 1968	6.0[m,1spec.]	EPA (Kazakhstan)

Abbreviations: MEG = Megalyridae; SIR = Siricidae; STE = Stephanidae; TRI = Trigonalidae; XIP = Xiphydriidae. AFR = Afrotropic; AUS = Australia (including New Guinea); EPA = eastern Palaearctic; NEA = Nearctic; NNT = northern Neotropic; OCE = Oceania (Fiji and New Zealand); ORI = Oriental; SNT = southern Neotropic; WPA = western Palaearctic. Sources: [1]Vilhelmsen & Smith (2002); [2]Vilhelmsen (2001b); [3]Benson (1938); [4]Benson (1955a); [5]Benson (1955b); [6]Ashmead (1903); [7]Mocsáry (1900); [8]Middlekauff (1983); [9]Vilhelmsen (2003a); [10]Konow (1897a); [11]Middlekauff (1985a); [12]Middlekauff (1985b); [13]Smith (1988); [14]du Buysson (1910); [15]Schmidt & Vilhelmsen (2002); [16]Schmidt & Gibson (2001); [17]Kraus (1998); [18]Guiglia (1937a); [19]Guiglia (1937b); [20]Yasumatsu (1954); [21]Shinohara (1983); [22]Takeuchi (1938); [23]Tosawa (1930); [24]Mantero (1899); [25]Tsuneki (1963); [26]Maa (1950); [27]Bella & Turrisi (1998); [28]Enslin (1913); [29]Merz (2000); [30]Benson (1935); [31]Konow (1897b); [32]Basibuyuk *et al*. (2000); e = estimated, see Material and Methods; m = measured, number after m indicates number of specimens examined.

placed distally in the apocritan phylogeny, usually within the clade Proctotrupomorpha (Dowton & Austin, 2001). Hence, the body size evolution analysis is unlikely to be compromised by the choice of outgroup taxa.

Representatives of the Paroryssidae (*Paroryssus*, *Praeoryssus*) were included in a data set compiled by L. Vilhelmsen, A. P. Rasnitsyn & F. Ronquist (unpubl. data); they scored a number of fossil taxa putatively basal in the Hymenoptera for characters included in the data set published for extant taxa by Vilhelmsen (2001a). Few additional characters could be scored for the Paroryssidae for the data set analysed here, as the fossils are not sufficiently well preserved. Instead, *Paroryssus* and *Praeoryssus* were grafted onto the results of the analyses of the Orussidae *s. s.* according to their positions in the analyses of L. Vilhelmsen, A. P. Rasnitsyn & F. Ronquist (unpubl. data) for the purpose of the evaluation of body size evolution (see below).

The scorings from the fossil Orussidae *s. s.* were entered in the matrix presented in Vilhelmsen (2003a) in MacClade 4.03 (Maddison & Maddison, 2001). Analyses were run in PAUP* 4.0b10 for Macintosh (Swofford, 2002) with TBR branch swapping, random addition sequences, with some characters treated as ordered (see Vilhelmsen, 2003a). Equal weights and implied weights analyses were run. Under implied weights, a concave fitting function defined by the concavity constant k is implemented during analysis; the higher the value of k, the less heavily homoplasious characters are downweighted (Goloboff, 1993). The tree(s) preferred are those having the highest overall fit rather than the shortest. Analyses with k values set to 1, 3, 4, 7, 10, 13, and 20, respectively, were run. These represent the range of values retrieving the entire spectrum of topologies observed in the analyses of Vilhelmsen (2003a). The implied weights analyses were run with 100 replications and the setting amb-. Under amb-, branches having no unambiguous support (zero-length branches) are collapsed (Coddington & Scharff, 1994), which means fewer, less resolved trees are retrieved. An analysis with k = 7 (the setting used to produce the preferred tree) and the setting amb0 was run with 20 replications. Under amb0 ambiguously supported branches are reported; this results in more trees, as alternative solutions to the unsupported branches are counted. After the initial searches, the discovered most fit trees were filtered to remove topologies with polytomies that were also represented by more resolved trees.

Character evolution was traced in McClade 4.03. For body size evolution, 'trace continuous' was used with the option 'minimize sum of absolute values of change (Linear)' implemented; both 'minstate' and 'maxstate' was implemented in turn. This option was preferred over the default ('minimize sum of squared changes') for reasons that are discussed at length in Hormiga, Scharff & Coddington (2000). In brief, linear parsimony is equal to Wagner parsimony and is more conservative, i.e. will propose fewer but larger changes in the parameter being evaluated, whereas squared changes will infer more but smaller changes, distributing the variation more evenly over the cladogram. In order to be able to implement trace continuous in MacClade, all polytomies were arbitrarily resolved, and *Orussus decoomani* (see above) was initially assigned an arbitrary value (10.0 mm) for body length; this was subsequently changed to 7.0 mm, which is the value inferred for the nodes both above and below *O. decoomani* by tracing with 'minstate' implemented (see Fig. 2).

The body size evolution analysis is severely hampered by the limited material available for Orussidae *s. s.* Of the 74 species of extant Orussidae studied by Vilhelmsen (2003a), five or fewer specimens were available for 44 species, only one specimen for 24 species; only one sex was known for 28 species (see Vilhelmsen, 2003a: table 2). The fossils *Mesorussus* and *Minyorussus* are also only known from one specimen each. The few species that are comparatively well represented (by ten or more specimens) display considerable intraspecific size variation, especially between the sexes. Ideally, these variations should have been taken into account, e.g. by analysing the size variation of males and females separately. However, this was not feasible, as the lack of information for species where only one sex is known precluded tracing size variation if the data were partitioned according to sex. Instead, all the data were pooled in one analysis despite the intraspecific variation of the majority of the species not being adequately represented.

BIOGEOGRAPHICAL ANALYSES

Analyses in DIVA 1.2 (Ronquist, 2001a) and TreeFitter (Ronquist, 2001b) were undertaken to elucidate the relative influence of different processes in shaping the biogeographical history of the Orussidae. For both programmes, the preferred tree (see below) was used as the estimate of orussid phylogeny. The Paroryssidae were excluded from the biogeographical analyses because the uncertainty of their position might obscure the distribution patterns basally in the Orussidae *s. s.* The distribution data entered for each species is shown in Table 2. In total, nine different biogeographical regions are recognized: Afrotropic, Australia (including New Guinea), Nearctic, northern Neotropic (including Mesoamerica), southern Neotropic (Chile), Oceania (Fiji and New Zealand), Oriental, eastern Palaearctic, and western Palaearctic.

DIVA was used to identify putative ancestral areas for each node. To be able to estimate these areas for the basalmost nodes in the phylogeny of Orussidae, the outgroup taxa were included in the analyses as well. Despite this, reconstructions are not reliable at the deeper nodes. Furthermore, the outgroup taxa, being exemplars, are not representative of the distribution of their respective families as a whole. Two sets of analyses were run, one with the northern hemisphere areas (Nearctic, Oriental, eastern and western Palaearctic) treated as separate areas, the other lumping them into a single area; distinct hierarchical relationships between northern hemisphere areas have been difficult to correlate with plausible geological area cladograms (Sanmartín, Enghoff & Ronquist, 2001). Maxareas values were set to 2–9 or 2–6, respectively, in turn, delimiting an upper boundary to how many ancestral areas are allowed at each node. None of the Orussidae *s. s.* terminals are present in more than two of the areas included in the analyses; the setting maxareas = 2 makes the assumption that no ancestor was more widespread either. In contrast, maxareas = 9 allows all ancestors to be widespread. The latter setting has the effect that especially the deeper nodes will have most or all areas included as potential ancestral areas. In addition to the DIVA analyses, the distributional data were traced in McClade using Fitch parsimony, in order to identify possible single ancestral areas.

In TreeFitter the interaction between members of two different tree types, e.g. organism phylogenies (P-tree) and area cladograms (H-tree), is analysed. Four different types of events are invoked to explain these interactions: codivergence, corresponding to vicariance events in biogeography; duplication, corresponding to speciation within the regions delimited in the analysis; sorting, corresponding to partial extinction; switching, corresponding to dispersal. Costs are assigned to each of these event types, and optimal reconstructions that minimize the overall cost are computed. For further information about TreeFitter and the rationale behind it, see Ronquist (2001b, 2002).

TreeFitter analyses were executed by fitting the preferred topology to the geological scenario shown in Fig. 4; the latter was compiled from information in Sanmartín *et al.* (2001) and McLoughlin (2001). Again, analyses were run with the northern hemisphere areas (see above) treated either individually or as one area. The preferred topology of Orussidae was designated as the P-tree, the geological scenario as the H-tree. The outgroup taxa were excluded from the TreeFitter analyses, as they do not contribute to the calculation of the number of events within Orussidae. The analyses were carried out using the default cost settings (codivergence = 0.0; duplication = 0.0; sorting = 1.0; switching = 2.0), using the command fit. To test the significance of the reconstructions, 1000 random permutations were carried out (nperm = 1000). Permutations were carried out under different conditions by implementing in turn the commands perm = hterm/pterm/hpterm (permuting only the terminals of the H-tree, P-tree, or both, respectively, while keeping the topologies constant), and htree/ptree/hptree (drawing random topologies for the H-tree, P-tree, or both, from a treespace generated by a random Markov process). In addition, the H-trees (area cladograms) best explaining the distribution data were calculated by an exhaustive search, implemented by using the commands search type = exhaustive.

RESULTS & DISCUSSION

PHYLOGENY OF ORUSSIDAE *S. S.*

The results of the cladistic analyses of Orussidae *s. s.* are summarized in Table 3. Orussidae *s. s.* are consistently retrieved as monophyletic (Fig. 1). *Mesorussus* and *Minyorussus* are placed basally in an unresolved trichotomy with the extant Orussidae, the latter likewise coming out monophyletic under all weighting schemes. The inclusion of *Mesorussus* and *Minyorussus* does not affect the relative positions of the outgroup taxa when compared with the results of Vilhelmsen (2003a). The equal weights analysis produced an identical result with regard to the internal phylogeny of the extant Orussidae when compared to the corresponding analysis in Vilhelmsen (2003a: see fig. 106). The results of the analysis with k = 1 in the present paper were slightly different. The difference concerns the placement of the genus *Leptorussus*, which came out as the sistergroup to all extant Orussidae except *Orussonia*, *Orussella*, and *Orussobaius* (i.e. similar to its placement in Fig. 1); in the analysis including only extant Orussidae, *Leptorussus* was placed as the sistergroup to a clade comprising

Table 3. Results of cladistic analyses under implied weights with different *k*-values

Weighting conditions	No. of trees (amb-; filtered)	Length/Fit
equal	627	754/–
k = 1	2	–/–95,71564
k = 3	2	–/–111,58171
k = 4	2	–/–116,82764
k = 7	2	–/–127,56976
k = 10	2	–/–134,23132
k = 13	2	–/–138,82070
k = 20	2	–/–145,52228

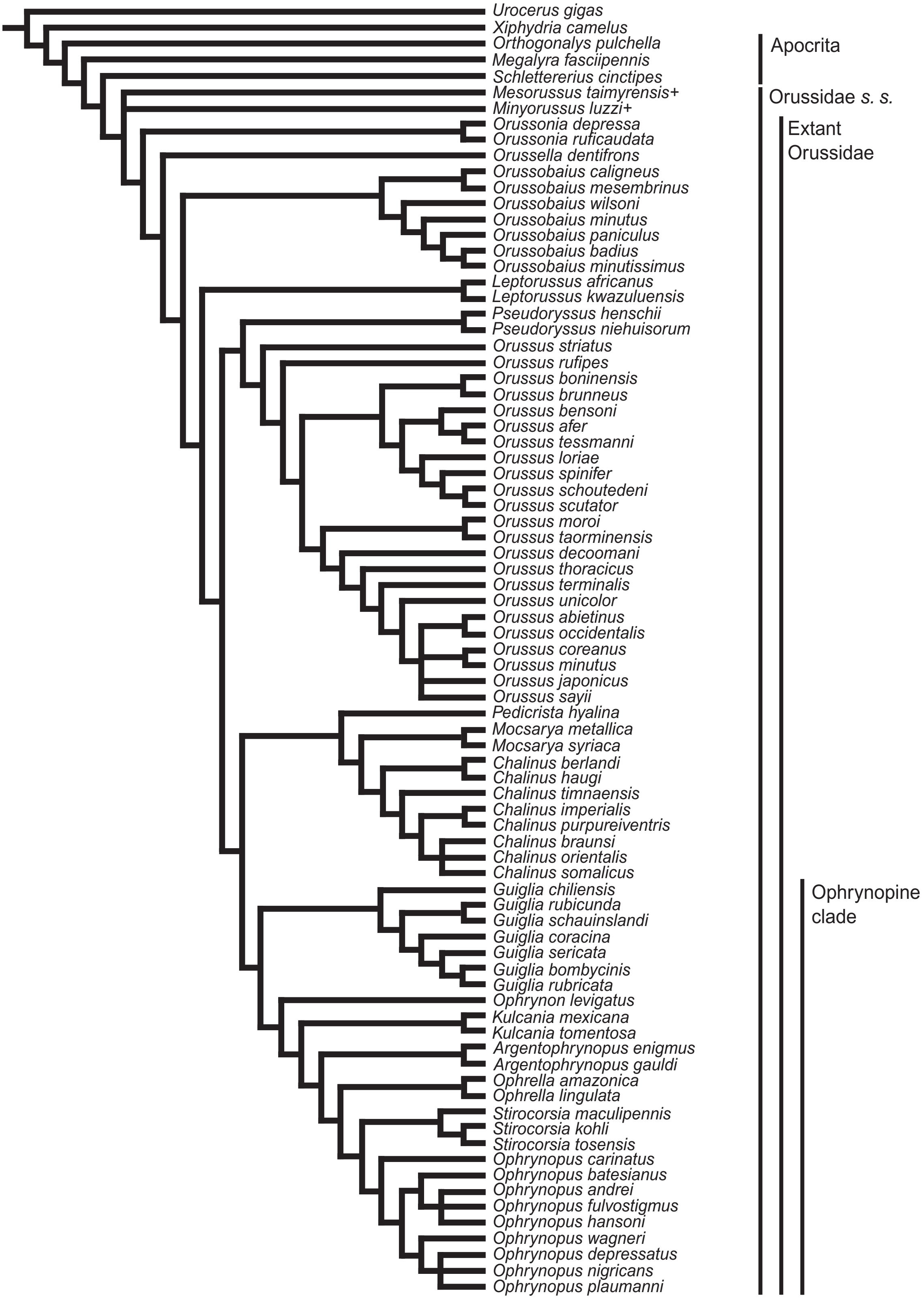

Figure 1. Preferred topology of Orussidae *s. s.*, one of two trees derived by analysis in PAUP* with implied weights, settings constant k = 7, amb- implemented. + indicates extinct taxa.

the genera *Pedicrista*, *Pseudoryssus*, *Orussus*, *Mocsarya*, and *Chalinus* (see Vilhelmsen, 2003a: fig. 113). All the other implied weights analyses produced topologies that were identical with regard to the phylogeny of the extant Orussidae to the ones in Vilhelmsen (2003a) having similar settings. For further discussion of the relationships of extant Orussidae under different weighting conditions, see Vilhelmsen (2003a). The tree chosen for tracing character evolution and exploring biogeography was one of two trees derived by analyses with amb-, k = 7 (Fig. 1); the two trees differ only in the topology within the genus *Chalinus*. The preferred tree of Vilhelmsen (2003a) was produced by the same settings. The trees retrieved with amb- implemented are identical to the consensus of the ones produced with amb0 for k = 7. The topology of the extant taxa in the preferred tree was retrieved over a considerable range of concavity constant settings (k = 7–12) in the analyses of Vilhelmsen (2003a).

The basal trichotomy in the Orussidae *s. s.* is unresolved because of missing data for the fossil taxa, making it impossible to optimize many characters in this part of the tree. This problem is further enhanced by the specimens of *Mesorussus* and *Minyorussus* probably being female and male, respectively. Many of the numerous autapomorphies for extant Orussidae identified by Vilhelmsen (2003a) are sex specific, and hence cannot be optimized unequivocally at the base of the preferred tree. When the basal trichotomy is resolved in the three ways possible, the Orussidae *s. s.* and the extant Orussidae are always supported, but not by the same characters, as the individual characters are optimized differently on the different topologies.

When the Orussidae *s. s.* are resolved as *Mesorussus* + (*Minyorussus* + extant Orussidae), the Orussidae *s. s.* are supported by the presence of an elongate, cylindrical scapus (34 : 1), the configuration of the apical antennomere in the female (40 : 1), and the number of female antennomeres being 12 or less (164 : 1). An elongate, cylindrical scapus is present in *Orussonia* spp. and some specimens of *Orussella dentifrons*, both very basal within extant Orussidae; the presence of this trait in the fossil taxa as well indicates that it is the plesiomorphic condition for Orussidae *s. s.*, but it is not present in any other extant Orussidae. *Mesorussus* was assigned a unique state for the configuration of the apical female antennomere (see Appendix), which was hypothesized to be incipient in the formation of the condition (40 : 2) in extant Orussidae. The basal phylogenetic position of *Mesorussus* supports this hypothesis, although the position is decided very much by the inclusion of this character. The number of antennomeres in the female in *Mesorussus* (12; 164 : 1) is likewise intermediate between outgroup taxa (more than 12) and extant Orussidae (10). In the latter, the penultimate 9th antennomere is about twice as big as the preceding one, whereas in *Mesorussus* the three penultimate (9th – 11th) antennomeres are subequal in size. It is tempting to hypothesize that the penultimate antennomere in extant female Orussidae is really a composite structure consisting of two previously independent segments, explaining in part the discrepancy in number of antennomeres between *Mesorussus* and extant Orussidae. The extant Orussidae are supported only by the absence of the occipital carina (26 : 0). The occipital carina is absent from the extant genera *Orussonia*, *Orussella*, *Orussobaius*, *Leptorussus*, *Pedicrista*, and *Ophrynon* but present in most other extant Orussidae. However, since the first four of the genera just mentioned are the most basal extant Orussidae, the absence of the occipital carina can be inferred to be the ground plan state for this clade. *Minyorussus* + extant Orussidae is not unequivocally supported.

When the Orussidae *s. s.* are resolved as *Minyorussus* + (*Mesorussus* + extant Orussidae), the Orussidae *s. s.* are supported by the shape of the scapus (34 : 1), the presence of a mesosubalar carina (84 : 1), and the presence of only 11 antennomeres in the male antenna (165 : 1). The two latter features are present in most extant Orussidae; however, the mesosubalar carina is also present in *Xiphydria* among the outgroup taxa, so it is doubtful whether it is a genuine autapomorphy of Orussidae *s. s.* This is also the case for the metepimera and abdominal tergum 1 being separate (92 : 0), the absence of the posterior anal vein only proximally (124 : 1), and the absence of a constriction between the first and second abdominal segments (140 : 0); all these characters are reversals of traits characteristic of the Apocrita, a taxon which does not come out monophyletic in the analyses (for further discussion, see below). The monophyly of the extant Orussidae is putatively supported by the presence of a carina above the torulus (incipient ventral transverse frontal carina; 19 : 1), absence of the occipital carina (26 : 0), the configuration of the female apical antennomere (40 : 2), and the presence of ten antennomeres in the female (164 : 2). *Mesorussus* apparently does not have a carina above the torulus (see Appendix) as seen in *Orussella* and *Orussobaius*. The exact condition in *Minyorussus* is uncertain, but a fully developed ventral frontal transverse carina as seen in most extant Orussidae (19 : 3) is apparently absent. The clade *Mesorussus* + extant Orussidae is not unequivocally supported.

When the Orussidae *s. s.* are resolved as (*Minyorussus* + *Mesorussus*) + extant Orussidae, the Orussidae *s. s.* are supported by the same traits as for the topology *Minyorussus* + (*Mesorussus* + extant Orussidae), except for character 34 : 1. Additional features corroborating the Orussidae *s. s.* are those from the female antenna (40 : 1, 164 : 1). The support for extant Orussidae is identical to that for the topology *Minyorussus* + (*Mesorussus* + extant Orussidae). The clade *Mesorussus* + *Minyorussus* is not unequivocally supported.

Minyorussus has some characters in the wing venation [distal placement of the forewing vein 2r (115 : 0); insertion of forewing vein cu-a in the middle of the discal cell (123 : 1)] that indicates a possible affinity with the extant 'ophrynopine' genus *Ophrella*, a fairly derived member of the extant Orussidae (Vilhelmsen, 2003a). This evidence was discussed by Basibuyuk *et al*. (2000). However, they concluded that 'these similarities appear superficial when evaluated in a phylogenetic sense' and that *Minyorussus* should be 'considered as a basal grade [sic] to extant orussids with available evidence at present'. The results of the present analyses corroborate this.

Given the lack of resolution at the base of Orussidae *s. s*., it seems prudent to retain *Mesorussus* and *Minyorussus* as separate genera rather than merge them or include them in any of the extant genera. *Mesorussus* was placed in a separate subfamily (Mesorussinae) by Rasnitsyn (1977). Vilhelmsen (2003a) recommends discarding the tribal and subfamily classification within Orussidae altogether. Accepting this, there is no reason to assign *Mesorussus* and *Minyorussus* to any formal categories between family and genus.

BODY SIZE EVOLUTION

The evolution of body size within the Orussidae *s. s.* was traced on the topologies shown in Figures 2 and 3. They differ from those derived by the cladistic analyses by having the two Paroryssidae taxa (*Praeoryssus venosus* and *Paroryssus extensus*) grafted onto them, the Apocrita (*Schlettererius*, *Megalyra*, *Orthogonalys*) constrained to be monophyletic, and having all polytomies resolved (see Material and methods). The Paroryssidae were included in the analyses of L. Vilhelmsen, A. P. Rasnitsyn & F. Ronquist (unpubl. data), with *Praeoryssus* consistently coming out as the sistergroup to Vespina (including *Paroryssus*), and *Paroryssus* either as sister to Orussidae *s. s.* or to Apocrita (see Fig. 3). Resolving the polytomies within the extant Orussidae does not significantly affect tracing the evolution of body size basally in the Orussidae *s. s*., since all the polytomies are situated fairly distally in the cladograms (deeply within large-sized clades). However, the relative positions of the fossil Orussidae *s. s.* and extant Orussidae are crucial when attempting to infer body size reduction in the early evolutionary history of the family, so all three possible solutions to the trichotomy at the base of Orussidae *s. s.* were evaluated in turn. Furthermore, the effect of placing *Paroryssus* in its two alternate positions was investigated (Figs 2, 3). Apocrita does not come out monophyletic in the results of the cladistic analyses presented here, in contrast with the findings of the more comprehensive treatments by Ronquist *et al*. (1999) and Vilhelmsen (2001a); the reasons for this are discussed above and in Vilhelmsen (2003a). Assuming the Apocrita to be monophyletic (Figs 2, 3) is considered more in accord with current understandings of hymenopteran phylogeny and hence more appropriate for the tracing of body size evolution within the Orussidae. Furthermore, the Apocrita were recovered in the analyses of L. Vilhelmsen, A. P. Rasnitsyn & F. Ronquist (unpubl. data), which served as the basis for the placement of the Paroryssidae.

When either *Mesorussus* (Figs 2, 3F) or *Minyorussus* (Fig. 3B, H) is placed as sistergroup to the remaining Orussidae *s. s.* and the 'minstate' option is implemented, the body size of the common ancestor of both Orussidae *s. s.* and extant Orussidae + either *Mesorussus* or *Minyorussus* is inferred to be 2.20 mm. In contrast, the body size of the common ancestor of Orussidae *s. s.* and its sistergroup (either *Paroryssus* or *Paroryssus* + Apocrita) as well as that of extant Orussidae is above 5 mm (Figs 2, 3). This means that the body size of the grade spanned by the fossil Orussidae *s. s.* approached that of many microhymenoptera (e.g. Ceraphronoidea, Chalcidoidea, Diapriidae, Platygastroidea). These taxa are characterized by substantial reduction in wing venation, even more than observed in extant Orussidae. This result is not influenced by the placement of *Paroryssus* (Figs 2, 3). However, when the 'maxstate' option is implemented (Fig. 3A, C, G, I), the reduced body size of *Mesorussus* and *Minyorussus* is inferred to be independently derived; when these two taxa are sistergroups (Fig. 3D–E, J–K), the reduction in body size is confined to their common ancestor, regardless of whether the 'minstate' or 'maxstate' option is implemented. In either case, no common ancestor on the lineage leading to extant Orussidae was less than 5 mm in body size.

Within extant Orussidae, body length reduction to less than 5 mm is inferred to have occurred four times independently, regardless of the optimization criteria implemented: in *Guiglia rubicunda* (3.8 mm), *Leptorussus kwazuluensis* (2.6 mm), *Ophrynopus carinatus* (2.8 mm), and the common ancestor of *Orussobaius badius*, *O. minutissimus* and *O. paniculus* (3.0 mm). The three first instances are terminal taxa, the fourth also occurs fairly distally in the phylogeny of the extant taxa (Fig. 2). Furthermore, all these taxa except *Orussobaius badius* and *O. minutissimus* are males. Since males of Orussidae are usually considerably smaller than females, it is likely that the females of most of the small extant species are considerable larger, not unlikely to exceed

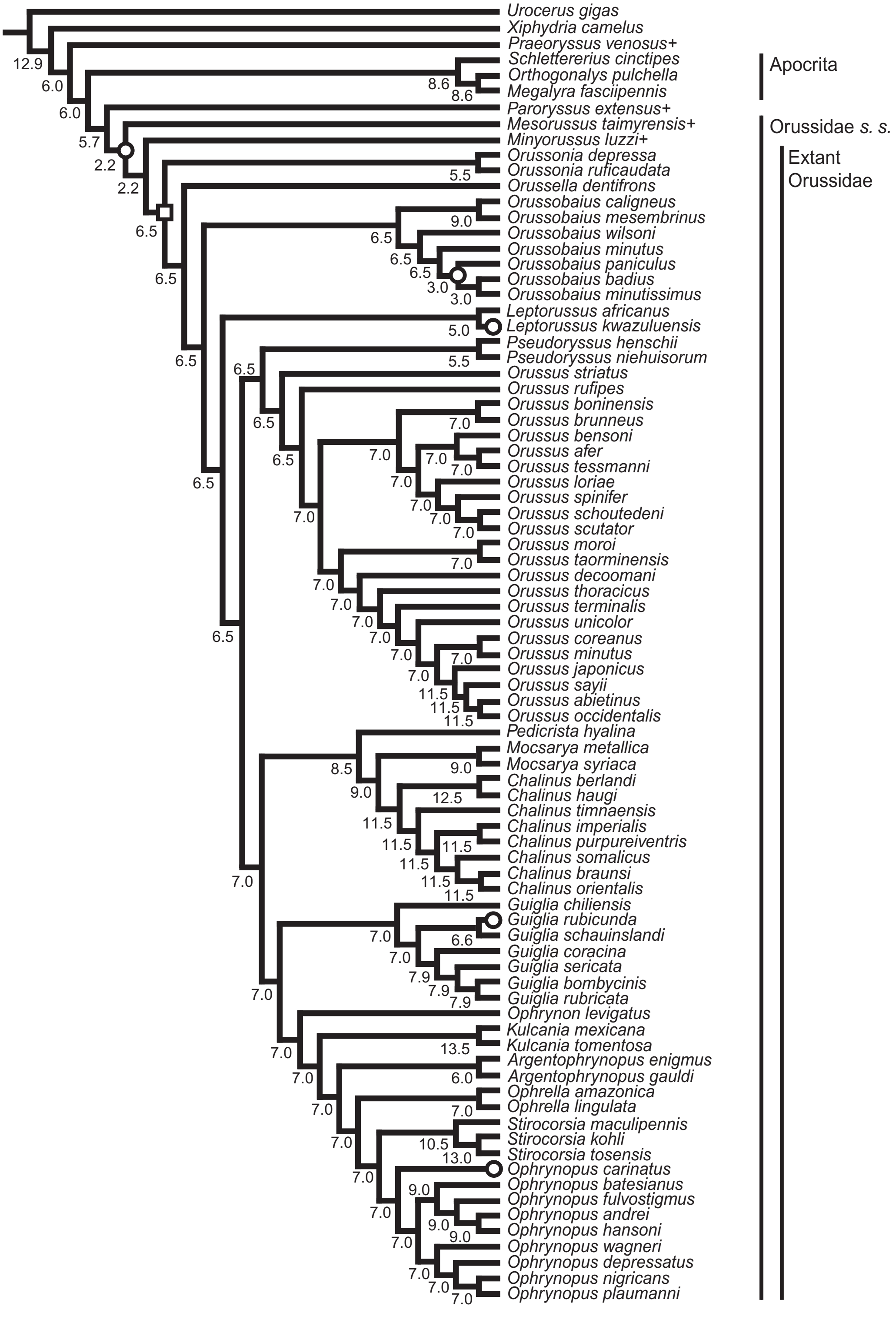

Figure 2. Topology used for tracing body size evolution in Orussidae *s. s.* All polytomies have been resolved, the Apocrita have been constrained to be monophyletic, and two members of the 'Paroryssidae' have been grafted onto the topology. See text for further explanation. +indicate extinct taxa. Numbers below branches indicate body length in mm, as inferred from tracing continuous character in MacClade with the options minimize sum of absolute values of change, minstate implemented. Circles indicate instances of body length reduction to 5.0 mm or shorter, square indicates subsequent reversal to body length longer than 5.0 mm.

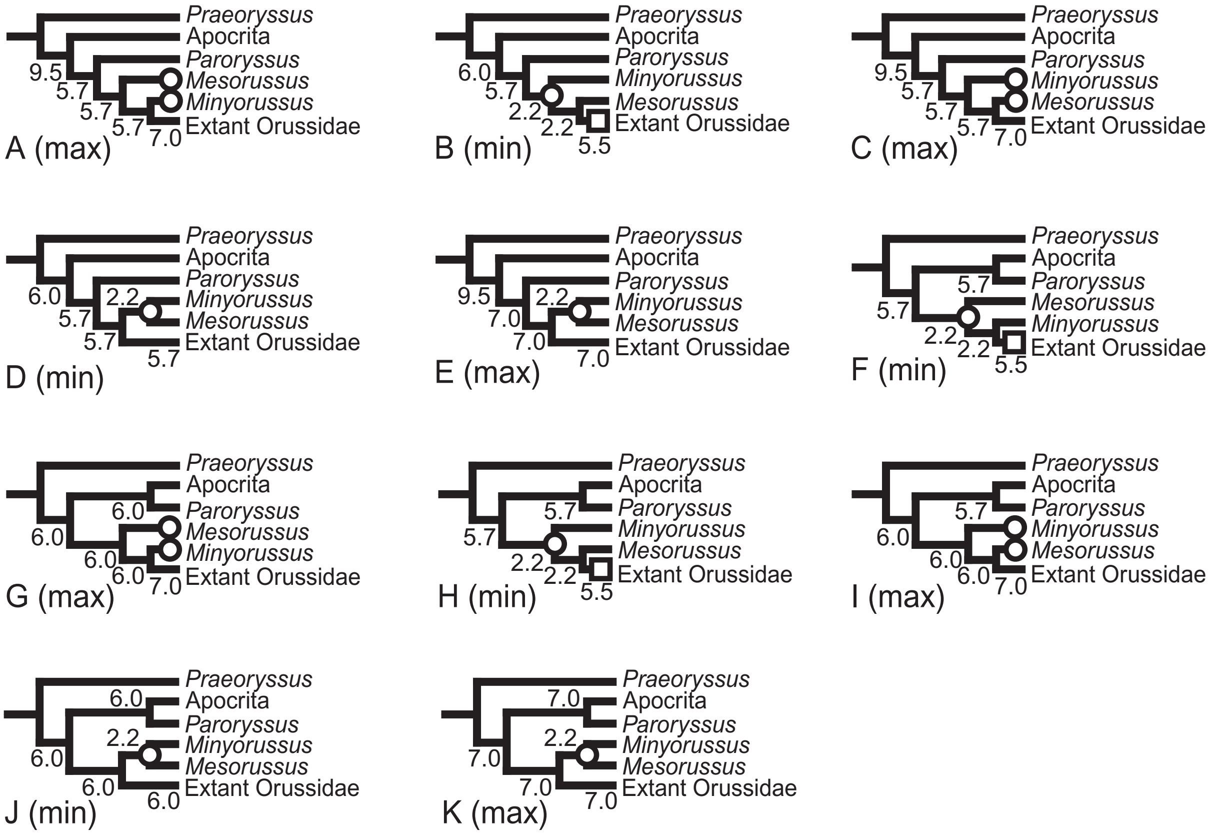

Figure 3. Summary of topologies for basal Orussidae *s. s.*, 'Paroryssidae', and Apocrita, used for tracing body size evolution. Numbers below branches indicate body length in mm, as inferred from tracing continuous character in MacClade with the option minimize sum of absolute values of change, minstate (min)/maxstate (max) implemented. Circles indicate instances of body length reduction to 5.0 mm or shorter, square indicates subsequent reversal to body length longer than 5.0 mm.

5 mm in body length. Only *Orussobaius badius*, *O. minutissimus*, and *Mesorussus taimyrensis* (the smallest of them all, with an estimated body length of 1.75 mm) have observed female body lengths of 3 mm or less.

In summary, the body size variation analysis is inconclusive with regard to the size of the common ancestor of Orussidae *s. s.*, in the sense that substantial body size reduction and subsequent enlargement is only demonstrated under the most favourable optimization criteria and topology ('minstate' optimization, *Mesorussus* and *Minyorussus* placed as successive outgroups to extant Orussidae). If size reduction played a significant role in moulding the body plan of Orussidae, it apparently occurred in the common ancestor of Orussidae *s. s.* Body size increased again prior to the radiation of extant Orussidae. More rigorous testing of this hypothesis has to await the discovery of additional basal orussid taxa, fossil or extant, as well as a better representation of the size variation within all extant Orussidae, sex specific or not. The data accumulated at present are insufficient.

BIOGEOGRAPHY

When discussing the biogeography of the Orussidae, the comparatively weak support for the intergeneric relationships has to be borne in mind (Vilhelmsen, 2003a). Topologies that differ only marginally in support from the one chosen here to map distributional data might corroborate substantially different biogeographical scenarios. In addition, many species and even genera are known from only a few specimens each (e.g. *Leptorussus*, *Ophrynon*, *Ophrella*), making it doubtful that their true distribution ranges have been sufficiently sampled.

The results of the TreeFitter analyses are summarized in Table 4. The optimal reconstructions have a cost of 48.00 (27.00 if the northern hemisphere areas are treated as one); this is significant at the $P < 0.01$ level (i.e. less than 10 random permutations out of

Table 4. Results of TreeFitter 1.0 analyses. Numbers in parentheses are from analyses with the areas eastern Palaearctic, western Palaearctic, Nearctic, and Oriental treated as one

Permutation setting	Random cost ≤ observed	Event	Random ≤ observed	Random ≥ observed
hterm	537 (817)/1000	Vicariance	597 (444)/1000	197 (965)/1000
		Sympatric speciation	341 (1000)/1000	95 (960)/1000
		Partial extinction	811 (685)/1000	142 (938)/1000
		Dispersal	195 (953)/1000	750 (446)/1000
pterm	0** (0**)/1000	Vicariance	31* (110)/1000	977 (1000)/1000
		Sympatric speciation	1000 (1000)/1000	0** (0**)/1000
		Partial extinction	360 (402)/1000	573 (991)/1000
		Dispersal	0** (0**)/1000	1000 (1000)/1000
hpterm	0** (0**)/1000	Vicariance	33* (74)/1000	984 (998)/1000
		Sympatric speciation	1000 (1000)/1000	0** (0**)/1000
		Partial extinction	262 (130)/1000	760 (996)/1000
		Dispersal	0** (0**)/1000	1000 (1000)/1000
htree	497 (838)/1000	Vicariance	680 (395)/1000	156 (979)/1000
		Sympatric speciation	323 (1000)/1000	106 (954)/1000
		Partial extinction	825 (637)/1000	117 (975)/1000
		Dispersal	159 (975)/1000	793 (411)/1000
ptree	0** (0**)/1000	Vicariance	5** (23*)/1000	980 (999)/1000
		Sympatric speciation	1000 (1000)/1000	0** (0**)/1000
		Partial extinction	194 (93)/1000	664 (998)/1000
		Dispersal	0** (3**)/1000	1000 (1000)/1000
hptree	0** (0**)/1000	Vicariance	18* (29*)/1000	981 (999)/1000
		Sympatric speciation	1000 (1000)/1000	0** (0**)/1000
		Partial extinction	169 (47*)/1000	830 (998)/1000
		Dispersal	0** (23*)/1000	1000 (1000)/1000

*: significant at the $P < 0.05$ level. **: significant at the $P < 0.01$ level.

1000 generated reconstructions with a lower cost), except when permutations were carried out with hterm or htree implemented. The optimal reconstructions require (number in brackets are the results of the analyses when the northern hemisphere areas are lumped together): 5–10 (2) vicariance events, 45–50 (60) sympatric speciation events, 4–12 (1) partial extinction events, and 18–22 (13) dispersal events (not counting widespread terminals). Only sympatric speciation events were usually significantly more frequent than expected by chance (see Table 4); both vicariance and dispersal events were usually significantly less frequent than expected. When the northern hemisphere areas are treated as one, the number of sympatric speciation events goes up, whereas all other events becomes less frequent; this is obviously an effect of the lower number of areas. Fourteen different H-tree topologies, corresponding to area cladograms, were retrieved by the exhaustive search (only one when the northern hemisphere areas are treated as one). None are identical to the geological scenario (Fig. 4), further corroborating that vicariance was not a dominant factor in the biogeographical history of Orussidae. The findings of the TreeFitter analyses indicate that the present day distribution of the family is primarily a result of speciation within continents and dispersal between them; even if fewer dispersal events are inferred by the reconstructions than expected, they are still much more frequent than vicariance and partial extinction events. In the DIVA analyses with the northern hemisphere areas treated separately, between 33 (maxareas = 9) and 35 (maxareas = 2) dispersal events were inferred; when the northern hemisphere areas were lumped, 19 dispersal events were inferred under all maxareas settings. The discrepancy between the number of dispersals in TreeFitter and DIVA analyses are caused by the inclusion of outgroup taxa and dispersal in widespread terminals when counting events in the DIVA analyses.

Despite the obvious difficulties in reconstructing biogeography of Orussidae *s. s.*, a correlation with Earth history and dating of certain splitting events in their phylogeny will be attempted. This interpretation is based on the DIVA analyses and the Fitch optimization of ancestral areas shown in Figure 5.

The distribution of the genera *Orussonia*, *Orussella*, *Orussobaius*, and *Leptorussus* is restricted to the

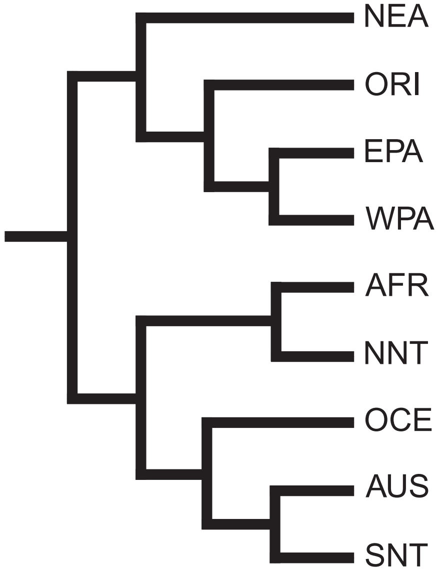

Figure 4. Geological scenario showing relationships of biogeographical regions employed in analysing distributional data of the Orussidae. *Abbreviations:* AFR = Afrotropic, AUS = Australia (including New Guinea), EPA = eastern Palaearctic, NEA = Nearctic, NNT = northern Neotropic, OCE = Oceania (Fiji and New Zealand), ORI = Oriental, SNT = southern Neotropic, WPA = western Palaearctic.

southern hemisphere (Australia, southern South America, South Africa). This indicates that the early radiation of extant Orussidae was restricted to Gondwana, even though this supercontinent might not yet have separated from Laurasia. However, the occurrence of the fossil Orussidae *s. s. Mesorussus* and *Minyorussus* in the northern hemisphere (eastern Palaearctic and Nearctic, respectively) contradicts this, indicating that the common ancestor of Orussidae *s. s.* was widespread, ranging over large parts of Pangaea. Nonetheless, the DIVA analyses with the northern hemisphere areas treated separately and low (2–5) maxareas settings all point to Australia as the ancestral area of the common ancestor of extant Orussidae; this is in accordance with the Fitch optimization (Fig. 5). The split between the extant and extinct Orussidae *s. s.* was possibly concurrent with the initial breakup of Pangaea 180–160 Mya (McLoughlin, 2001), the ancestor of the former being isolated in Gondwana, the latter in Laurasia. Alternatively, this tectonic event is echoed by the separation of the *Orussus–Pseudoryssus* lineage, which has a primarily Holarctic/Oriental distribution, from the *Chalinus–Mocsarya–Pedicrista*–ophrynopine clade lineage, which is represented in virtually all of the former parts of Gondwana.

The DIVA analyses indicate that the common ancestor of *Orussus* was restricted to the Oriental region (or the northern hemisphere in general in the analyses where this area was not subdivided). From there, its members apparently dispersed into the Afrotropic, Australian (New Guinea), Nearctic, and Palaearctic regions. The position of *Orussus loriae*, the only New Guinean representative of the genus, among almost only Afrotropical species is intriguing. However, the placement of this species is weakly supported (Vilhelmsen, 2003a) and does not justify the inference of contrived biogeographical scenarios. Another remarkable feature is the apparent single dispersal to the Nearctic within *Orussus*, with several subsequent dispersals to the Palaearctic. This pattern prevails even under the changing topologies imposed by different weighting conditions. However, given the frequent dispersals in the biogeography by numerous Holarctic animal groups in the Cenozoic (Sanmartín *et al.*, 2001), multiple dispersal events from the Nearctic to the Palaearctic within the Orussidae is quite plausible.

The branching events within the *Chalinus–Mocsarya–Pedicrista*–ophrynopine clade lineage can tentatively be linked with the gradual breakup of Gondwana. The DIVA analyses give combinations of primarily southern hemisphere areas (AFR, AUS, NEA, OCE, SNT) as the most likely ancestral areas for this node. The split between *Chalinus* + *Mocsarya* + *Pedicrista* and the ophrynopine clade (see Fig. 1 for the taxa included in this clade) possibly corresponds to the separation of Africa from the rest of Gondwana; most DIVA analyses indicate that the common ancestor of *Chalinus* + *Mocsarya* + *Pedicrista* was restricted to Africa. The separation of Africa from South America was primarily caused by the opening of the South Atlantic, which started 135 Mya; however, these two continents were probably not well separated before 105 Mya (McLoughlin, 2001). The occurrence of *Mocsarya* in Indonesia, the eastern Mediterranean and Sri Lanka probably has to be explained by dispersal out of Africa, as the separation of the India–Madagascar block took place prior to the separation between Africa and northern South America.

Within the ophrynopine clade, *Guiglia* has a southern temperate distribution. The basal dichotomy within the genus is between the Chilean *G. chiliensis* and the remaining species in Australia, Fiji, and New Zealand. This splitting event probably corresponds to the termination of the connection (via Antarctica) between Australia and southern South America no later than 35 Myr and perhaps as early as 50 Mya (McLoughlin, 2001). The occurrence of *G. rubicunda* on Fiji and *G. schauinslandi* in New Zealand, respectively, was probably caused by dispersal from Australia, as New Zealand separated from Gondwana around

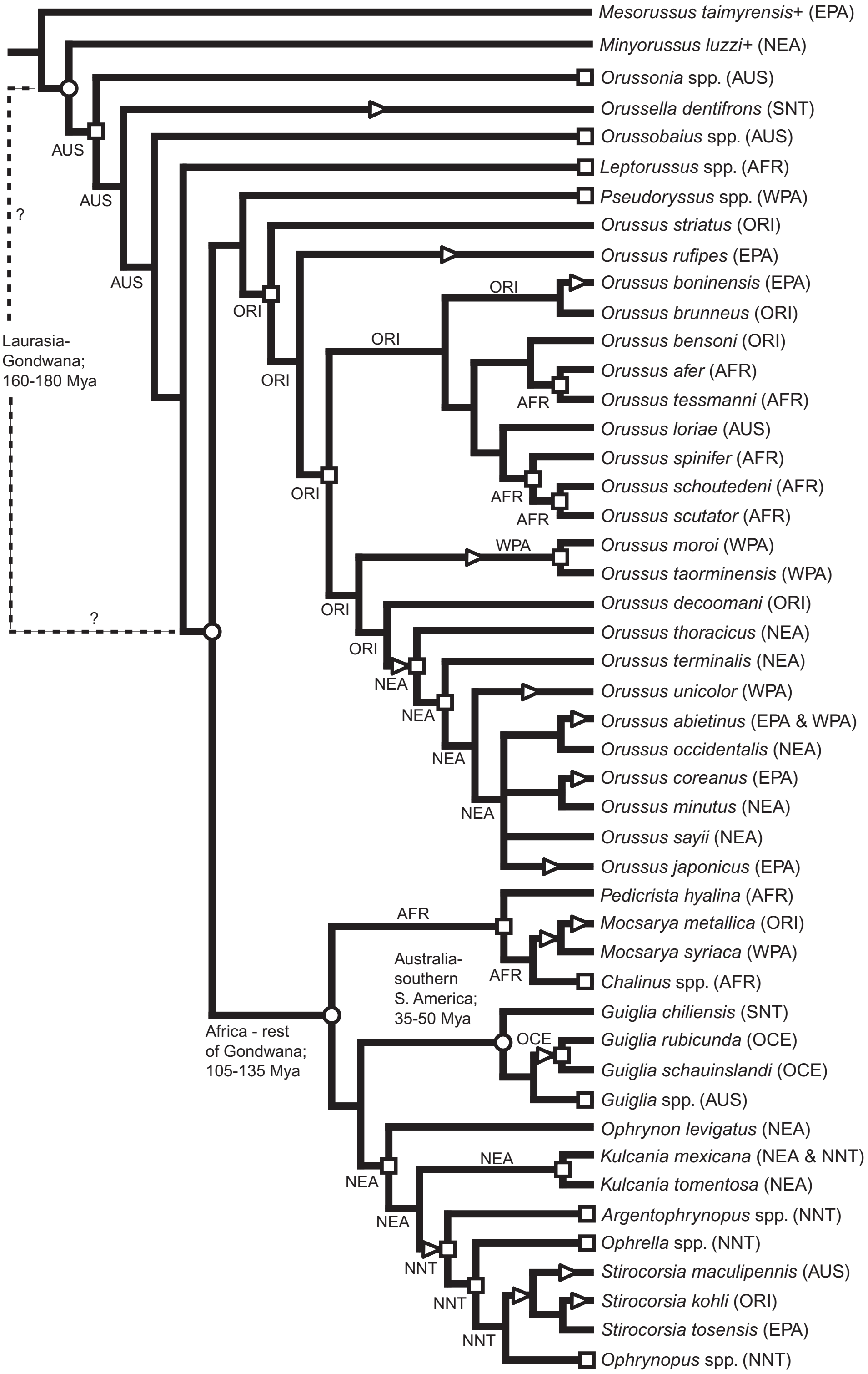

Figure 5. Biogeographical scenario for the Orussidae *s. s.* Distributions of terminals are shown in parentheses. Clades outside *Orussus* comprising taxa with identical distributions have been merged to single terminals. Putative single ancestral areas (according to Fitch optimization) are indicated for selected branches. Putative events are indicated as follows: circle = vicariance; square = speciation within one area; triangle = dispersal. Possible geological cause and approximate age is indicated for the vicariance events. See text for further discussion. Abbreviations as in Fig. 4. + indicate extinct taxa.

84 Mya (McLoughlin, 2001), well before the separation of Australia and South America.

The biogeography of the remainder of the ophrynopine clade is more difficult to explain. *Ophrynon* and *Kulcania tomentosa* are only found in the Nearctic; DIVA analyses indicate that this is the ancestral area for all ophrynopine genera except *Guiglia*. *K. mexicana* is also found in the northern Neotropics. *Argentophrynopus*, *Ophrella*, and *Ophrynopus* are entirely restricted to the latter area; the distribution of these genera could be explained by dispersal of their common ancestor from the Nearctic to the northern Neotropics. This would imply that the diversification of the ophrynopine clade in the Neotropics happened in the late Cenozoic, i.e. subsequent to the rise of the Panama Isthmus (3.5 Mya) or at least not prior to the formation of the Panama Island Arc (15 Mya; Krzywinski, Wilkerson & Besansky, 2001). Alternatively, the presence of *Ophrynon* and *Kulcania* only in the southern part of the Nearctic might indicate that they dispersed there recently from South America, their absence from the latter region being caused by extinction or incomplete sampling (only three specimens of *Ophrynon* have been collected). According to this scenario, the common ancestor of all genera except *Guiglia* was restricted to the northern Neotropics. This allows a considerably longer time for the radiation of most of the ophrynopine genera in this area prior to the northward dispersal of the Nearctic taxa. Given the predominance of southern hemisphere taxa within the ophrynopine clade, south to north dispersal is perhaps a more intuitively appealing hypothesis than the opposite, even if it is not supported by the DIVA analyses.

The distribution of *Stirocorsia* in the Australian (New Guinea), Oriental (South-east Asia), and eastern Palaearctic (Japan) regions certainly requires dispersal, as this genus is nested within northern Neotropical taxa (Fig. 5; see also Vilhelmsen, 2003a for alternate placements of *Stirocorsia*). This could be explained by the common ancestor of *Stirocorsia* having dispersed from South America through the Nearctic to its present range across one of the three Beringian bridges available at different times during the Cenozoic (Sanmartín *et al*., 2001); however, considerable extinction has to be postulated. Furthermore, it is contradicted by the phylogeny of *Stirocorsia* spp., which has the species from New Guinea (*S. maculipennis*) as the sistergroup of the species from the eastern Palaearctic (*S. tosensis*) and Oriental regions (*S. kohli*). Another possibility is that the ancestor of the genus dispersed via Antarctica and Australia. Given the absence of representatives in areas along either hypothetical dispersal route, it is difficult to choose between these alternatives.

CONCLUSION: THE AGE OF ORUSSIDAE

Two sources of evidence can be brought to bear on the question of the age of the last common ancestor of Orussidae *s. s.*: the phylogenetic position of the fossils and the correlation between the phylogeny and tectonic events. *Mesorussus* and *Minyorussus* both date from the early Late Cretaceous. Given that they are basal to extant Orussidae, this indicates a minimum age of the last common ancestor of Orussidae *s. s.* of 95 Myr. In contrast, the putative sister groups, the Apocrita (e.g. Megalyridae, Proctotrupoidea; Rasnitsyn 1988, 2002) or Paroryssidae (e.g. *Paroryssus*) are both represented in the Late Jurassic, giving a minimum age for the lineage leading to Orussidae *s. s.* of at least 150 Myr. The earliest known Megalyridae are more than 180 Myr old, pushing the age of the ancestral orussid lineage back to the time before the breakup of Pangaea. This in itself does not prove that the Orussidae *s. s.* radiated at this time. However, the biogeographical scenario (see Fig. 5) suggests that some of the earliest splitting events within Orussidae *s. s.* coincided with the separation of Gondwana and Laurasia, and the earliest break up events within Gondwana. The earliest of these events have an age comparable to the paroryssid and early apocritan fossils. The discrepancy between this age and the much later one indicated by the fossil Orussidae *s. s.* is substantial. However, since Orussidae are only rarely encountered today and some of their ancestors perhaps were very small, it is unlikely that the fossil history of the Orussidae *s. s.* is sufficiently sampled. Consequently, I consider it most likely that the latest common ancestor of Orussidae *s. s.* has an age of more than 180 Myr, as indicated by the age of the earliest fossil representatives from the sistergroup and the distributional patterns within the family.

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APPENDIX

CHARACTER SCORINGS FOR FOSSIL ORUSSIDAE

Mesorussus taimyrensis Rasnitsyn consists of an amber inclusion of the head and anteroventral part of the thorax (see Rasnitsyn, 1977: fig. 5). Unfortunately, due to inexpert handling the fossil was damaged during the present study, so that the right dorsolateral parts of the head and thorax and the tips of the antennae are now missing. Antennae and the right fore femur could be clearly seen, as well as the ventral part of the head capsule. The mouthparts are partly occluded by opaque material, probably gut contents vomited by the dying animal. *Minyorussus luzzi* Basibuyuk *et al*. consists of an amber inclusion of an entire, presumably male specimen, as indicated by the shape of the antennae and the fore leg having more than three tarsomeres (Basibuyuk *et al*., 2000). Part of the specimen is occluded by opaque material in the matrix. The following characters from Vilhelmsen (2003a) could be scored for the two fossils. Illustrations of the characters are provided in Vilhelmsen (2003a). A complete matrix of the extant taxa (outgroup and Orussidae) is presented in Vilhelmsen (2003a). Reproducing this with the characters scored for *Mesorussus* and *Minyorussus* added would be largely repetitive; the matrix analysed in the present paper is available from the author on request.

(1) *Ocellar corona*: absent = 0; present = 1.
Mesorussus: 1. Due to the ventral view of the head capsule, it was not possible to observe the median ocellus and score the characters (2–8) describing the configuration of the coronal teeth relative to the ocellus and the dorsal coronal teeth. However, a pair of coronal teeth could be clearly observed.
Minyorussus: 1. Basibuyuk *et al*. (2000) stated that the head has an 'indication of a crown of spines (though not clearly seen because of a thick layer of foggy material)'. I fully concur with this, but was unable observe any further details about its configuration.

(9) *Median longitudinal frontal carina*: absent = 0; present = 1.
Mesorussus: 0. Since this carina is missing, characters 10 & 11 are inapplicable.
Minyorussus: unknown. The presence/absence of dorsal transverse and longitudinal carinae could not be ascertained due to the opaque layer surrounding the fossil.

(12) *Lateral longitudinal frontal carina*: absent = 0; well developed dorsally, but ventralmost part absent = 1; present along entire distance between ventral coronal tooth and ventral transverse frontal carinae = 2 (ordered).
Mesorussus: 0. Since this carina is missing, character 13 is inapplicable.
Minyorussus: unknown.

(18) *Transverse frontal furrow*: absent = 0; distinct furrow present just dorsally of ventral frontal transverse carina = 1.
Mesorussus: 0.
Minyorussus: 0.

(19) *Ventral transverse frontal carina*: entirely absent, torulus not overlapped dorsally by carina = 0; torulus overlapped dorsally by carina, these are not continuous medially = 1; carinae dorsally of toruli continuous medially through narrow ridge = 2; broad carina present along entire frons = 3 (ordered).
Mesorussus: 0. Since this carina is missing, characters 20–22 are inapplicable. *Mesorussus* resembles the outgroup taxa in not having a distinct carina above the torulus, but differs from the ground plan condition in extant Orussidae (as observed in *Orussella* and *Orussobaius*), which is state 1.
Minyorussus: 0/1. Some details of the ventral part of the head can be observed. Apparently, there is no fully developed ventral transverse frontal carina (state 3) like the one present in most extant Orussidae, or the more weakly developed version (state 2) present in *Orussonia*. However, it is impossible to decide whether state 0 or 1 is present.

(26) *Occipital carina*: absent = 0; present = 1.
Mesorussus: 1. *Mesorussus* could be observed to have a distinct, laterally situated (see character 27) occipital carina.
Minyorussus: 1. It is stated in Basibuyuk *et al*. (2000) that the 'occipital carina [is] complete'. I concur with this.

(27) *Configuration, occipital carina*: situated laterally, ventrally often continuous with lateral border of subantennal groove = 0; situated medially, never continuous with lateral border of subantennal groove = 1.
Mesorussus: 0.
Minyorussus: 0.

(28) *Occipital concavity*: absent = 0; occipital carina dorsally with distinctly deflected margin, delimiting concavity dorsoposteriorly on head = 1.
Mesorussus: unknown.
Minyorussus: 0.

(30) *Malar groove*: absent = 0; distinct groove extends between ventral margin of eye and mandibular base = 1.
Mesorussus: 0.
Minyorussus: unknown.

(31) *Subantennal groove*: at most shallow depressions not delimited laterally present posteroventrally of toruli = 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 = 2 (ordered).
Mesorussus: 0.
Minyorussus: 0.

(34) *Shape, scapus*: short, subcylindrical = 0; elongate, cylindrical = 1; elongate, at least slightly flattened = 2 (ordered).

Mesorussus: 1. The *Mesorussus* specimen is probably a female, but has a different antennal configuration from extant Orussidae, lacking the enlarged ninth antennomere (see characters 40 & 164). Therefore, the characters (38–39) describing the variation within this structure were scored as inapplicable.
Minyorussus: 1.

(35) *Ventral margin, scapus*: at most with slight projection distally = 0; distinct projection present distally, extends beyond base of pedicellus = 1; distal projection present, continuous with ventral carina along the entire margin of scapus (especially well developed in the males) = 2 (ordered).
Mesorussus: 0.
Minyorussus: 0.

(36) *Shape, antennomeres*: might be flattened, but not strongly constricted basally = 0; most (male) or some (female) segments constricted basally and very flattened = 1
Mesorussus: 0.
Minyorussus: 0.

(37) *Configuration, antennomere 3–6 (♀♀)*: combined length of A4 + 5 longer than A3 and/or A6 = 0; A4 + 5 same length or shorter than A3 and/or A6 = 1.
Mesorussus: 0.
Minyorussus: unknown.

(40) *Configuration, apical antennomere (A10) (♀♀)*: not modified, subequal in size to preceding antennomere = 0; **additional state** not constricted basally, but distinctly tapered distally and with somewhat flattened apex = 1; greatly diminished and constricted both proximally and distally, distinctly subcylindrical, with flattened apex = 2 (ordered).
Mesorussus: 1. Rasnitsyn (1977) tentatively suggested the *Mesorussus* specimen to be female, presumably based on the peculiar configuration of the apical antennomeres. These do not exactly resemble the state (2) observed in extant Orussidae, but something that might be intermediate between that and the unmodified outgroup state (0). Therefore, the condition in *Mesorussus* was assigned a unique state (1) and the character treated as ordered.
Minyorussus: unknown.

(46) *Configuration, maxillary palp*: elongate, with five or six segments, visible = 0; shortened, but still visible = 1; very reduced, barely discernible = 2 (ordered).
Mesorussus: 0. The maxillary palps are clearly observed, resembling the condition (0) in most extant Orussidae.
Minyorussus: 0. Basibuyuk *et al*. (2000) stated that the maxillary palp has '4 (possibly 5) segments'; while the exact number of segments may be difficult to decide, the palps are clearly longer than in *Pedicrista*, the only orussid taxon having state 1.

(48) *Shape, pronotum (dorsal view)*: of about equal length throughout = 0; distinctly longer laterally than medially = 1.
Mesorussus: unknown.
Minyorussus: 0.

(52) *Hindmargin, pronotum*: deeply excavated = 0; shallow, pronotum only slightly curved in dorsal view = 1.
Mesorussus: unknown.
Minyorussus: 1.

(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.
Mesorussus: 0. Clearly seen in ventral view.
Minyorussus: 0.

(56) *Ventral longitudinal carina, forefemur*: absent or inconspicuous = 0; present, distinct = 1.
Mesorussus: unknown.
Minyorussus: 0.

(64) *Length/width ratio of mesoscutum*: length/width more than 0.6 = 0; length/width equals or less than 0.6 = 1.
Mesorussus: unknown.
Minyorussus: 1.

(75) *Shape, mesoscutellum*: rounded posteriorly, lying parallel to the anterior margin of metanotum for a considerable distance = 0; rounded posteriorly, at most touching anterior margin of metanotum medially = 1; acute, triangular = 2 (ordered).
Mesorussus: unknown.
Minyorussus: 1. Even though the specimen is occluded, the shape of the mesoscutellum is discernible.

(84) *Mesosubalar carina*: not distinctly demarcated = 0; forming distinct smooth area overhanging dorsal part of mesepisternum = 1.
Mesorussus: unknown.
Minyorussus: 1.

(92) *Metepimera–T1 connection*: separate = 0; fused = 1.
Mesorussus: unknown.
Minyorussus: 0.

(97) *Denticles, hindfemur*: ventral part of hindfemora smooth = 0; with small denticles = 1.
Mesorussus: unknown.
Minyorussus: 0.

(98) *Ventral ridge, hindfemur*: absent = 0; present = 1.
Mesorussus: unknown.
Minyorussus: 0.

(99) *Posteroventral corners, hindfemur*: rounded, not protruding = 0; triangular, protruding = 1.
Mesorussus: unknown.
Minyorussus: 0.

(103) *Pegs, hindtibia*: entirely absent = 0; weakly developed, inconspicuous, sockets for hairs = 1; distinct pegs accommodating stout spines present = 2 (ordered).
Mesorussus: unknown.
Minyorussus: 0.

(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).
Mesorussus: unknown.
Minyorussus: 0.

(105) *Ventral longitudinal carina, hindtibia*: absent = 0; carina developed at least proximally on hindtibia present = 1.
Mesorussus: unknown.
Minyorussus: 0.

(107) *Apical flanges, hindtibia*: distal width of tibia less than twice the width of the tibia subapically = 0; distal width of tibia at least twice the width of the tibia subapically = 1.
Mesorussus: unknown.
Minyorussus: 0.

(112) *Vein 1r*: absent = 0; present = 1.
Mesorussus: unknown. Wings are not preserved in the fossil.
Minyorussus: 0. Only the forewings could be observed, the hind wings being concealed by the forewings, which are folded over the body.

(115) *Position, vein 2r*: arising more than 0.6 the total length of the pterostigma from the proximal part of the latter = 0; arising equal to or less than 0.6 the total length of the pterostigma from the proximal part of the latter = 1.
Mesorussus: unknown.
Minyorussus: 0.

(116) *Angle between veins 2r and Rs*: both veins distinct, usually separated by angle where they join = 0; smooth transition between veins = 1.
Mesorussus: unknown.
Minyorussus: 1.

(118) *Position, vein 2r-m*: at least anterior end situated distally of apex of pterostigma = 0; entire vein situated proximally of apex of pterostigma = 1.
Mesorussus: unknown.
Minyorussus: 1.

(119) *Configuration, discal cell*: rectangular, basal part not broader than distal part = 0; rhomboid, basal part broader than distal part, not reaching R anteriorly = 1; rhomboid, basal part broader than distal part, reaching R anteriorly = 2 (ordered).
Mesorussus: unknown.
Minyorussus: 0.

(120) *Vein 1r-Rs*: spectral = 0; present, elongate = 1; present, but very shortened = 2 (unordered).
Mesorussus: unknown.
Minyorussus: 1.

(121) *Vein 3r-m*: absent = 0; present = 1.
Mesorussus: unknown.
Minyorussus: 0.

(122) *Vein 2 m-cu*: absent = 0; present = 1.
Mesorussus: unknown.
Minyorussus: 0.

(123) *Vein cu-a insertion*: cu-a inserts on Cu1 at most slightly distally of M = 0; inserts on Cu1 more distally, close to the middle of the discal cell = 1.
Mesorussus: unknown.
Minyorussus: 1.

(124) *Anal vein configuration*: posterior anal veins fully developed, extending to base of wing = 0; absent proximally = 1; entirely absent = 2 (ordered).
Mesorussus: unknown.
Minyorussus: 1.

(140) *Constriction between 1st and 2nd abdominal segments*: absent = 0; present = 1.
Mesorussus: unknown.
Minyorussus: 0. Characters requiring a dorsal view of the abdomen could not be scored due to the position of the wings.

(144) *Lateral swellings, abdominal terga*: absent = 0; several terga, starting from the 2nd, with distinct longitudinal raised area laterally = 1.
Mesorussus: unknown.
Minyorussus: 0. Most of the abdomen, especially the posterior part, is heavily occluded; only a general outline can be discerned.

(163) *Body shape*: subcylindrical, not flattened = 0; distinctly flattened = 1.
Mesorussus: unknown.
Minyorussus: 0.

(164) ***Additional character****: number of antennomeres* (♀♀): more than 12 = 0; 12 = 1; 10 = 2 (ordered).
All outgroup: 0.
Mesorussus: 1.
Minyorussus: unknown.
Extant Orussidae. 2 (taxa where no ♀♀ are known scored as unknown). All extant female Orussidae have 10 segments, the ninth being twice as long as the preceding segment. In contrast, *Mesorussus* has 12 segments, the distal ones being subequal in size (except for the modification of the apical antennomere, see charac-

ter 40). All outgroup taxa have more than 12 segments. This variation was coded here and treated as ordered, with the state (1) in *Mesorussus* being intermediate between that of the outgroup (state 0) and that of extant Orussidae (state 2). See above for further discussion of the evolution of antennal structure within Orussidae *s. s.*

(165) ***Additional character:*** *number of antennomeres (♂♂)*: more than 11 = 0; 11 = 1
All outgroup: 0.
Mesorussus: unknown.
Minyorussus and extant Orussidae: 1 (taxa where no ♂♂ are known scored as unknown).