



<http://dx.doi.org/10.11646/zootaxa.3860.5.4>

<http://zoobank.org/urn:lsid:zoobank.org:pub:2894C38A-2CEC-4091-92D2-39198776820F>

Extension of historical range of Betylobraconinae (Hymenoptera: Braconidae) into Palaearctic Region based on a Baltic amber fossil, and description of a new species of *Mesocentrus* Szépligeti from Papua New Guinea

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Abstract

Two new species of the parasitic wasp genus *Mesocentrus* Szépligeti (Betylobraconinae) are described. One based on a new species from Papua New Guinea, the other the first Palaearctic member of the subfamily based on a 30+ mya, species from Baltic amber. The second species is illustrated using synchrotron X-ray microtomography. Whereas the extant Betylobraconinae are restricted to Australia, New Guinea and New Caledonia, their ancestral distribution is now known to have extended considerably further. A key to the four species of *Mesocentrus* known from Papua New Guinea is provided. Both species possess some putatively plesiomorphic characters absent in other extant *Mesocentrus* spp. The new extant species differs in having a considerably larger number of antennal segments and a less laterally depressed frons, while the extinct one has the clypeus separated from the face dorsally and strongly developed hypoclypeal depression. Availability of sequence data for this species enabled further analysis of the relationships of the subfamily, which we present in a phylogenetic analysis additionally including the release of a number of new sequences of related taxa.

Key words: *Betylobracon*, *Rhinoprotoma*, distribution, fossil, palaeontology, historical biogeography, new taxa

Introduction

Since its description by Tobias (1979), the Betylobraconinae has undergone expansion and subsequent contraction. It was based on a highly derived Australian genus, *Betylobracon*, which despite not being physically cyclostome, displayed other characters such as possession of hind wing vein m-cu, suggesting that it probably belonged to that group. Van Achterberg (1984) recognised that it was related to the less derived and distinctly cyclostome genus *Mesocentrus* described from Australia by Szépligeti (1900), both genera possessing robust legs with the fore tarsal segments shortened and telotarsus enlarged. Subsequently, three further tribes were added to the subfamily; van Achterberg added the Facitorini for three new tropical genera, and the Planitorini for the Australian genus *Planitorus*, and Belokobylskij & Long (2005) added the Aulosaphobraconini for their new genus *Aulosaphobracon* from Vietnam. However, Belokobylskij *et al.* (2008) using DNA sequence data showed that the Facitorini were actually not close to *Betylobracon* and *Mesocentrus*, but instead belonged in the rogadoine tribe Yeliconini, and further, they showed that most probably *Aulosaphobracon* belonged elsewhere, although in the absence of strong support for any other placement they left it the Betylobraconinae. Sharanowski *et al.* (2011) then showed that *Planitorus*, which like *Betylobracon* is not physically cyclostome, was really not a member of the cyclostome braconid lineage at all, but rather a member of the non-cyclostome subfamily Euphorinae. Thus the Betylobraconinae now comprises just *Betylobracon* and *Mesocentrus*, with *Aulosaphobracon incertae sedis* but most likely belonging to the Lysiterminae.

The extant specimen described here was collected as part of the *Our Planet Reviewed—IBISCA Niugini 2012-2013* project, which operated Malaise traps along an altitudinal transect at Mt. Wilhelm in Madang Province, New Guinea. By coincidence, two of us (DLJQ and TVDK) were studying a cyclostome wasp specimen from Baltic amber in the collection of Copenhagen University museum also apparently belonging to *Mesocentrus*, and we are therefore describing the two species together, and so extending the known range of the subfamily into the palaeo Palaearctic.

Despite being collected quite commonly, nothing is known about the biology of Betylobraconinae. They appear closely related to the cyclostome subfamily Rogadinae, and may belong there, but they are kept separate here as they appear to be distinguishable on the basis of wing venation and metasomal tergal sculpture features. The new taxon was successfully sequenced both for the barcoding region of cytochrome oxidase 1 and for the D2-D3 region of the nuclear 28S ribosomal DNA gene, making it only the second betylobraconine to be known from both gene fragments. We therefore carried out a molecular phylogenetic analysis including a range of related taxa in order better to assess the affinities of the subfamily.

Material and methods

Descriptive taxonomy. The type specimen of the extant species is deposited in the Muséum national d'Histoire naturelle, Paris, and that of the extinct species in the Natural History Museum of Denmark, København.

Wing vein terminology follows Sharkey & Wharton (1997); other terminology follows van Achterberg (1988). The † is used to indicate fossil taxa. Illustrations were made using an Olympus SXZ16 microscope with automated multiple image capture at preset focal levels using an Olympus DP72 camera, and image combination using the Cell^D image processing system.

Molecular analysis. Molecular methods were as in Zaldivar-Riverón *et al.* (2008b, 2013). Sequence data for the two gene fragments were assembled from a range of putatively related taxa (see Appendix 1 for Genbank accessions numbers and additional voucher information). The taxa chosen focused on the cyclostome branch including these groups and was rooted by *Doryctes erythromelas*, a relatively basal doryctine (Zaldivar-Riverón *et al.* 2008). Secondary structure interpretation followed the model of Gillespie *et al.* (2005), though with this more taxonomically restricted subset of taxa it was possible to identify a few additional pairing bases than in other recent studies on larger groupings (e.g. Zaldivar-Riverón *et al.* 2008a,b; 2013).

Data were analysed using the maximum parsimony programme RAXML (Stamatakis, 2006) with five data partitions, the three codon positions for CO1 and pairing and non-pairing bases for 28S; length-variable unalignable regions were excluded. The final analyses were carried out over the RAXML were carried out via the webserver interface (Stamatakis *et al.* 2008) which included 100 full bootstrap pseudoreplicates (file execution time approximately 30 minutes).

Synchrotron X-ray microtomography. Tomographic scans were performed at the TOPO-TOMO beamline of the ANKA Synchrotron Radiation Facility of Karlsruhe Institute of Technology. 2,500 radiographic projections covering an angular range of 180° were acquired using a filtered white beam with the spectral peak at about 15 keV. An indirect detector system composed of a 50 µm LuAG Ce scintillating screen, diffraction limited optical microscope and 12 bit pco.dimax high speed camera (2016 x 2016 pixels resolution) was employed to capture the projections. A 5x optical magnification led to an effective pixel size of 2.44 µm. The frame rate was set to 150 images per second, resulting in an overall scan duration of 16.6 seconds.

Before reconstruction, the projections were processed with the phase retrieval ImageJ plugin ANKAphase (Weitkamp *et al.* 2011). Volume reconstruction was done by the PyHST software developed at the European Synchrotron Radiation Facility in Grenoble, France.

Visualisation. The tomographic volume was imported into Amira® (version 5.5.0; FEI Visualization Sciences Group). The specimen was selected from the tomographic volume by its greyscale using the *Threshold* tool. Artifacts, bubbles and inclusions of dirt were removed manually with *Brush* and *Lasso*. Subsequently, a polygon mesh was created with the *SurfaceGen* module. The polygon count of the original mesh was reduced to 10% of its original value. The mesh was saved in the Wavefront format (OBJ) and imported into CINEMA 4D (version 14; Maxon Computer GmbH) to create the renderings (Figs 4–7).

Key to the species of *Mesocentrus* from Papua New Guinea

The following key is largely based on original descriptions (Szépligeti 1900, 1902) together with Papp (2005). The female lectotype and one male paralectotype of *M. crassipes* and the type and only known specimen of *M. pusillus* have been lost, so it is therefore impossible to be completely sure about all the features of *M. pusillus* and at some point, a neotype is likely to be needed.

- 1. Antenna with more than 25 flagellomeres (26) (Fig. 1A); frons hardly depressed behind antennal sockets and laterally (Fig. 1C)..... *M. sasquatch* **sp. nov.**
- Antenna with fewer than 16 flagellomeres (13–15); frons more strongly depressed laterally 2
- 2 3rd metasomal tergite distinctly longitudinally striate basally; 2nd metasomal tergite approximately as long as posteriorly wide (“fast quadratisch”); pterostigma entirely light brown *M. pusillus* Szépligeti
- 3rd metasomal tergite entirely smooth basally; 2nd metasomal tergite 1.35 to 1.8 x wider posteriorly than long; pterostigma either yellow brown with a darker median spot (*M. crassipes*) or brown with distinct yellow base (*M. reptus*) 3
- 3 Flagellum not narrowing (attenuating) distally, 1st flagellomere approximately 2 x longer than wide; head rather strongly narrowing immediately behind eyes; pterostigma yellow brown with a darker median spot; 2nd *M. crassipes* Szépligeti
- Flagellum strongly narrowing (attenuating) distally, 1st flagellomere approximately 4 x longer than wide; head nearly parallel-sided immediately behind eyes; pterostigma brown with distinct yellow base *M. reptus* Papp

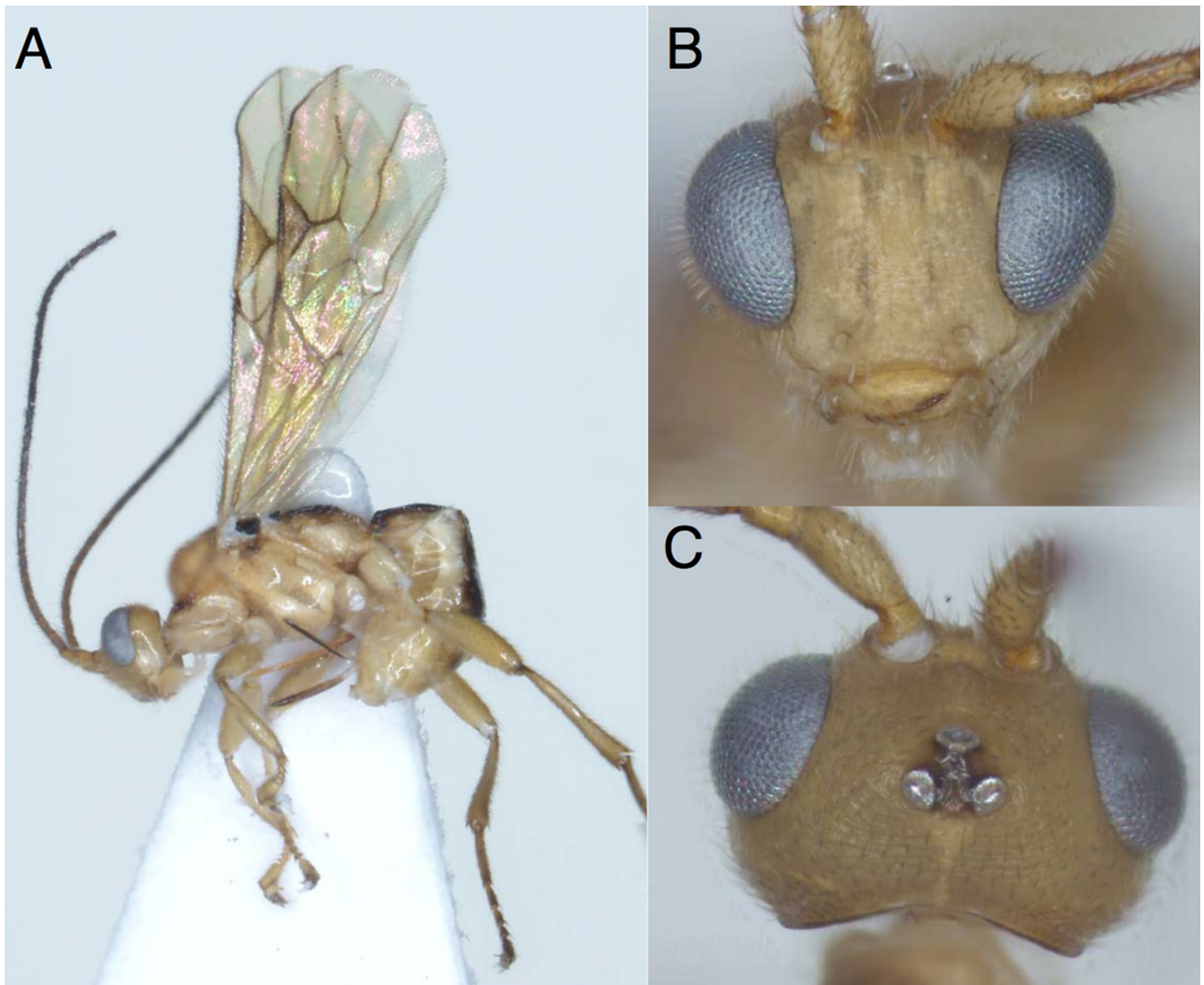


FIGURE 1. *Mesocentrus sasquatch* **sp. nov.** A, habitus; B, head, front view; C, head dorsal view.

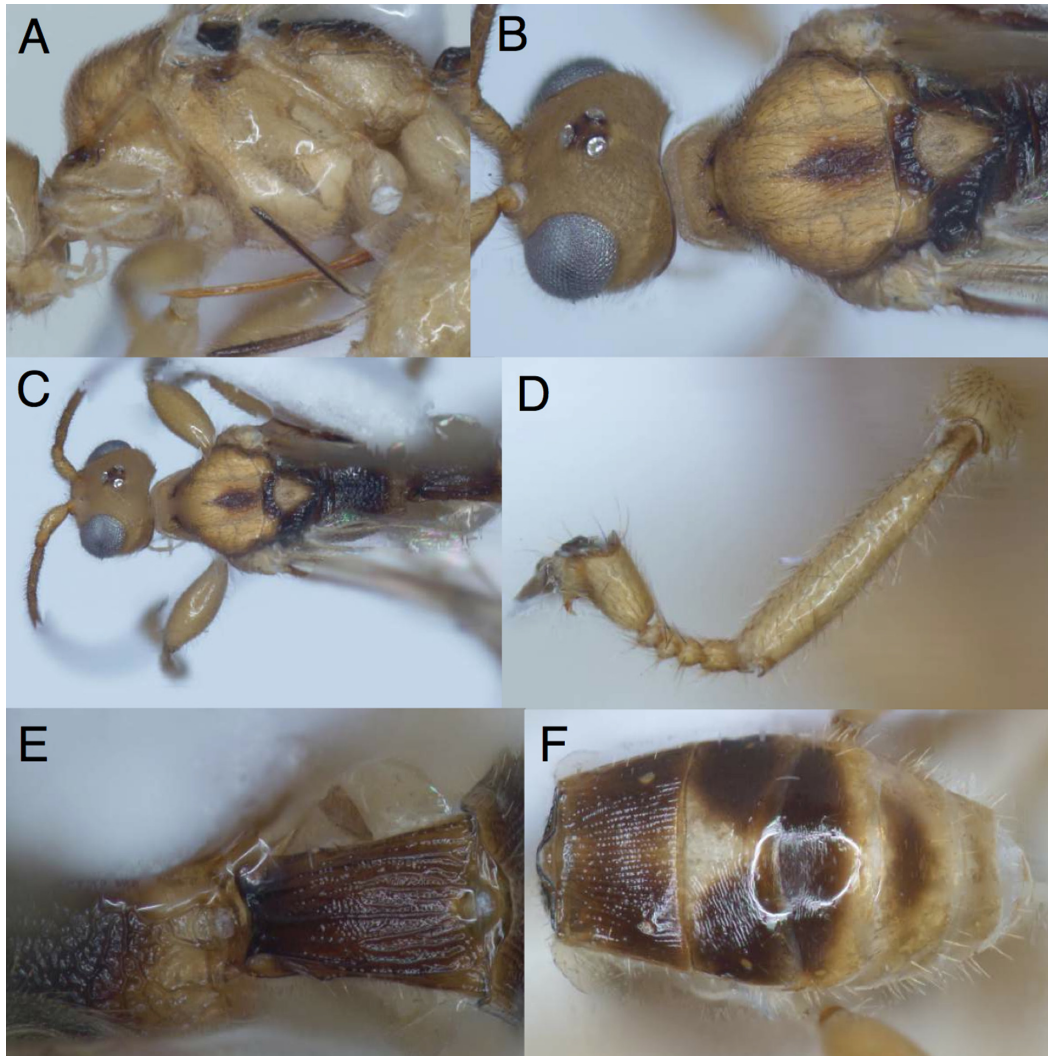


FIGURE 2. *Mesocentrus sasquatch* sp. nov. A, mesosoma and ovipositor, lateral view; B, thorax, dorsal view; C, head, mesosoma, fore femora, dorsal view; D, fore tibia and tarsus; E, propodeum and 1st metasomal tergite, dorsal view; F, metasomal tergites 2–6, dorsal view.

Descriptive taxonomy

Mesocentrus sasquatch sp. nov.

(Figs 1–3)

Holotype ♀. Papua-New-Guinea, Province Madang, Mount Wilhelm 1700m (-5.759269,145.2356) 1700m, 09-10/11/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise—MAL-MW1700A-16/16-d16.

Body length (corrected for bent metasoma) 3.5 mm, length of fore wing 3.0 mm.

Antenna with 26 flagellomeres. Terminal flagellomere pointed but not acuminate. Face transversely striate. Clypeus not separated from face medially. Eyes strongly setose, 1.1 x higher than width of face. Hypoclypeal depression moderately convex mediodorsally, rather shallow with labrum wide and largely exposed. Inter-tentorial distance 2.3 x shortest distance between tentorial pit and eye. Frons hardly depressed laterally. Mesosoma 1.6 x longer than maximally high. Pronotum without midlongitudinal carina. Mesopleuron smooth and shiny. Precoxal sulcus rugose to rugulose, approximately triangular in shape. Median area of metanotum with complete midlongitudinal carina. Fore wing vein 3RSa 3.6 x r-rs, 0.55 x 3RSb. Vein (RS+M)a weakly sinuous. Hind wing vein 1M 1.2 x M+CU. Vein m-cu weakly antefurcal. Hind basitarsus approximately 9 x longer than deep, approximately the same length as the next three segments combined. Propodeum largely irregularly rugose. First

metasomal tergite 1.4 x longer than posteriorly wide with prominent midlongitudinal carina (Fig. 2E); second metasomal suture narrow, shallow, sharply defined, nearly smooth. Metasomal tergites 3 to 5 progressively less conspicuously with fine, sub-transverse wrinkles, with sparse long setosity posteriorly. Ovipositor sheath 0.6 x hind tibia. Ovipositor distinctly laterally compressed.

Largely brown-yellow; dark brown are medioposterior mesoscutum, scutellar sulcus, sides of scutellum and axilla, anteromedial part of propodeum, 1st, and tergites, 3rd tergite except medio-anteriorly, 4th and 5th tergites broadly medially.

Etymology. Named after the cryptozoological North American creature, big-foot, otherwise known as the sasquatch; noun in apposition.

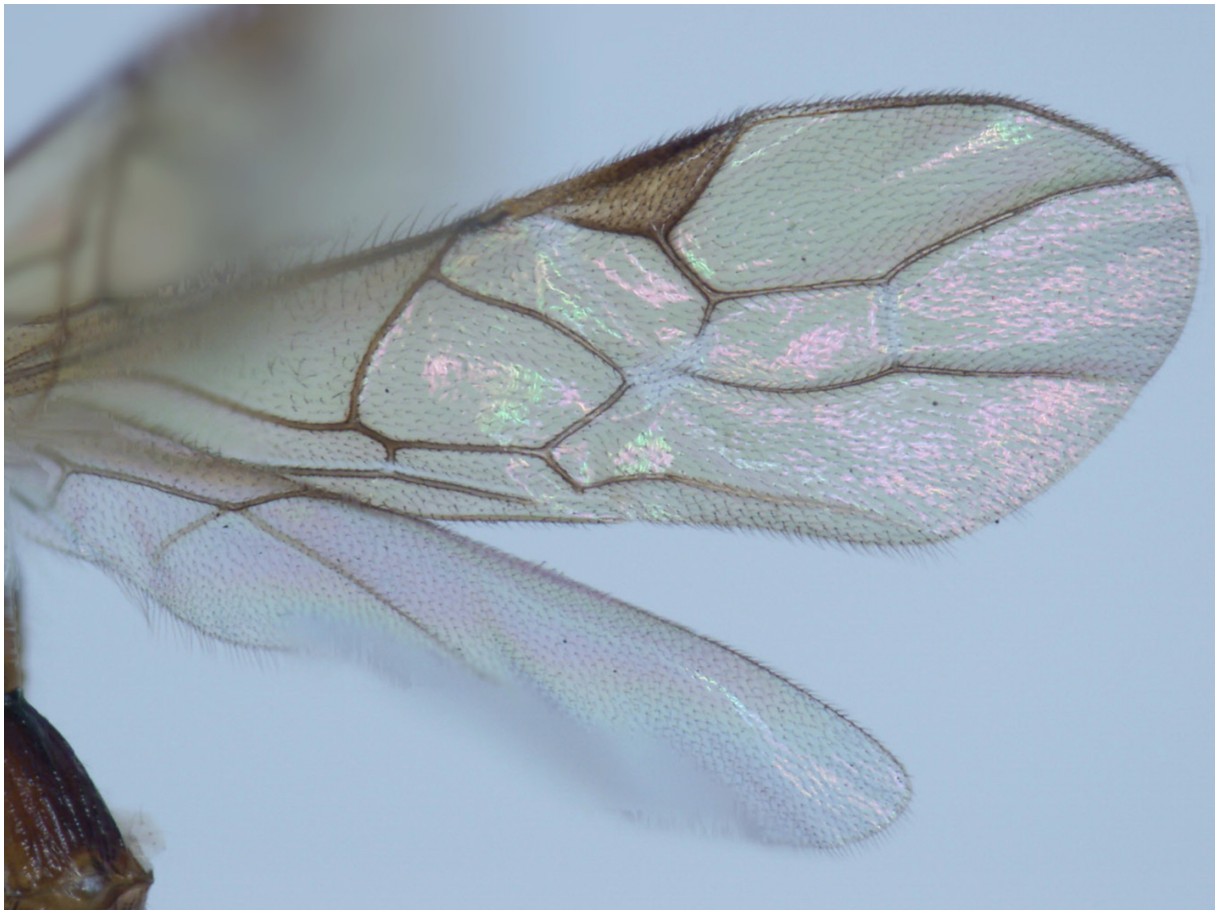


FIGURE 3. *Mesocentrus sasquatch* sp. nov. wings.

***Mesocentrus palaeoeuropaea* sp. nov. †**
(Figs 4–7)

Holotype ♂. Braconidae/C.V. Henningsen [the collector]/22-6-1953 [the collecting date]. No further information is available.

Length of body 3.25 mm and of fore wing c. 3.3 mm.

Antenna with 19 flagellomeres, median flagellomeres nearly quadrate, scapus weakly flared apically. Fore wing vein (RS+M)a strongly sinuate (Fig. 7). Width of head 1.6 x width of face. Face produced into a distinct point medio-dorsally between antennal sockets. Clypeus separated from face dorsally by a distinct groove. Hypoclypeal depression strongly convex medio-dorsally. Malar suture weak, curved. Occipital carina not weakened medio-dorsally. Frons strongly depressed laterally. Mesosoma 2 x longer than maximally high. Fore wing vein (RS+M)a strongly sinuate (Fig. 7). Fore wing vein 3RSa 1.5 x r-rs, 0.38 x 3RSb, vein (RS+M)a strongly sinuous. Hind wing

vein 1M 1.1 x M+CU, m-cu antefurcal. Fore tibia with weak longitudinal dorsal ridge (Fig. 5C). Fore telotarsus approximately 0.8 x length of fore basitarsus. First metasomal tergite approximately as long as posteriorly wide with submedial carinae apparently more prominent than medial carina. 2nd metasomal tergite longitudinally striate. 3rd tergite apparently entirely smooth.

Notes. Differs from extant species of *Mesocentrus* in having a distinct (though weak) midlongitudinal ridge on the fore tibia, a groove separating the clypeus from the face medio-dorsally, and flared basal flagellomeres. Whilst it could be argued that it might equally be placed in an extinct genus rather than *Mesocentrus*, the differences are rather slight and only the lack of dorsal separation of the clypeus in *Mesocentrus* would support its monophyly relative to the extinct species. Despite careful visual examination we were unable to determine whether the eyes of the fossil specimen are setose as in the extant species, and such detail is below the resolution of the synchrotron imaging system employed, though it seems likely that they are at least less setose if not completely glabrous.

Etymology. Name refers to its ancient European provenance.

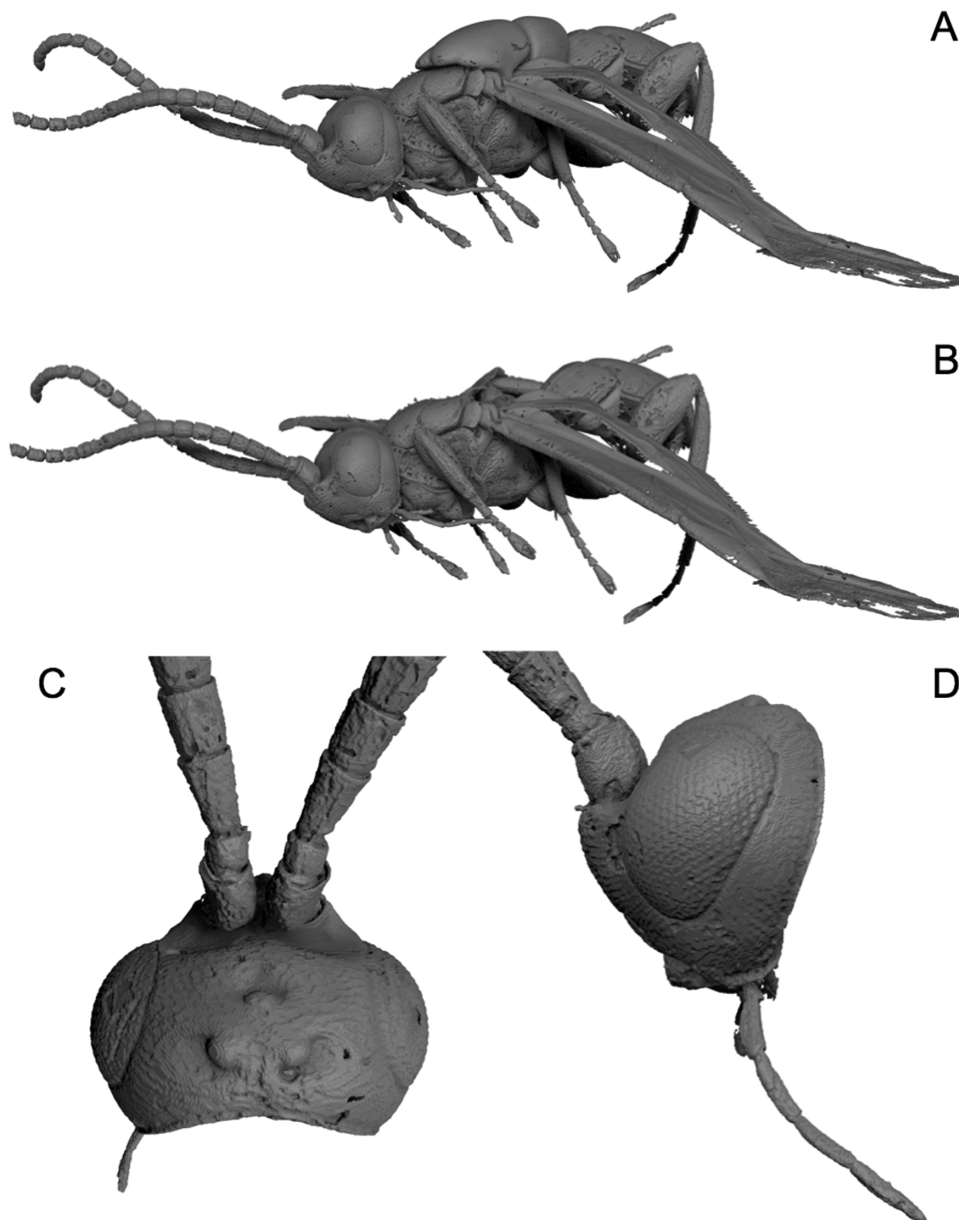


FIGURE 4. *Mesocentrus palaeoeuropaea* sp. nov. 3D surface rendering based on synchrotron X-ray microtomography data. A, B, approximately lateral views, showing raw surface with air bubbled over posterior of mesosoma, and with air bubbles removed, respectively; C, D, head, dorsal and lateral aspects respectively.

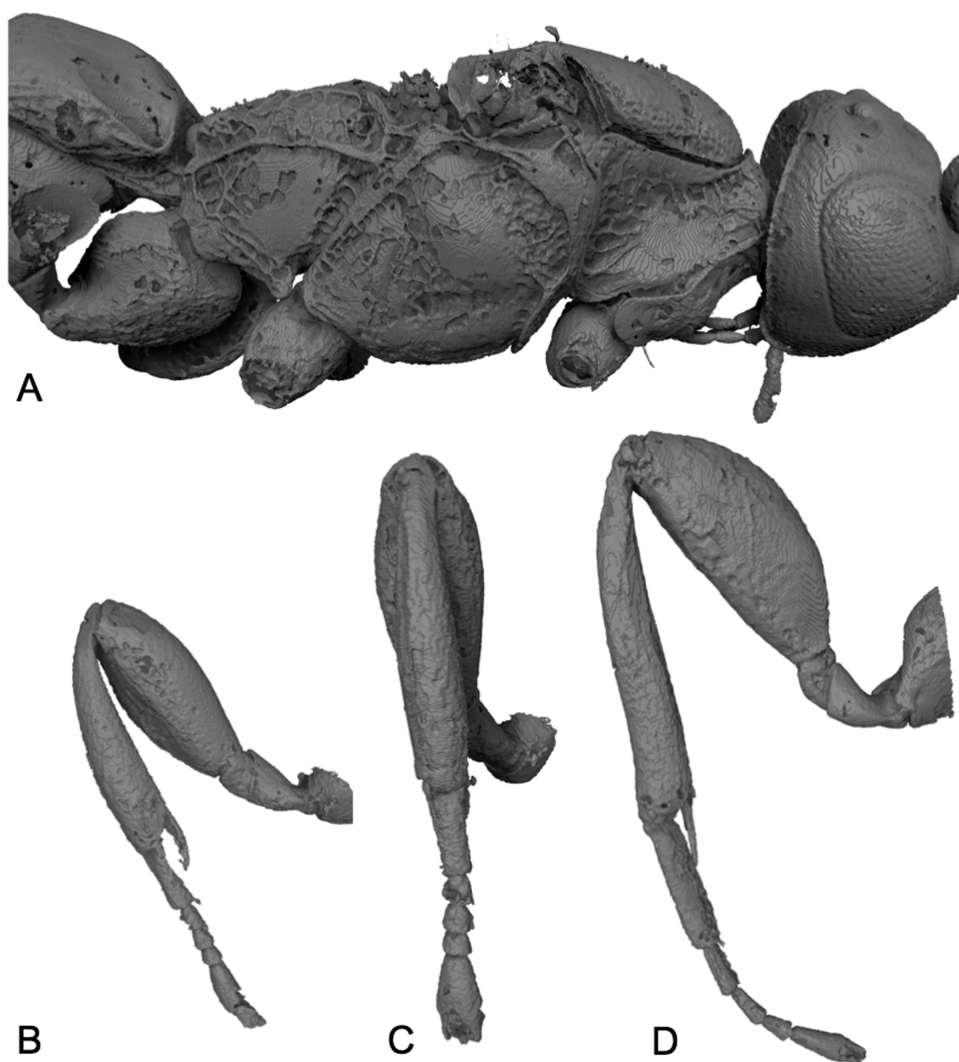


FIGURE 5. *Mesocentrus palaeoeuropaea* sp. nov. 3D surface rendering based on synchrotron X-ray microtomography data. A, mesosoma and most of 1st metasomal tergite, lateral view; B-D, fore, middle and hind legs respectively.

Molecular results

The maximum likelihood tree generated by RAxML analysis with a log likelihood score of -24157.275645 was very similar to the bootstrap tree shown in Fig. 8 which includes bootstrap values of nodes with more than 50% support. *M. sasquatch* sp. nov. is recovered as expected with the other betylobraconines but without significant bootstrap support for any internal relationships, most likely because only it and one other betylobraconine have both 28S and CO1 sequence data. This clade was recovered among a mixture of Clinocentrini (Rogadinae *sensu stricto*) and one Tetratermini (Lysiterminae), and is well-separated from the remainder of the Rogadinae (*viz.* Aleiodini, Rogadini and Yelicionini). However, in agreement with Belokobylskij *et al.* (2008), the Facitorina which had previously been included within the Betylobraconinae are recovered with 100% bootstrap support within the tribe Yelicionini, as sister group to *Pseudoyelicones* + *Bulborogas*, which here are represented by additional sequences, again with high support.

Also of interest is the placement of the New Zealand genus *Rhinoprotoma*, which also has rather shortened fore tarsi and a protruding face though not pronounced as in the Betylobraconinae and Yelicionini or indeed, some

Aleiodes. Van Achterberg (1995) provisionally included it within the Rogadini, though here it was recovered belonging to the Aleiodini with 82% bootstrap support (Fig. 8), though that is only based on CO1 data. It does not appear to be a derived *Aleiodes*, however, despite the fact that several species of that genus similarly have very robust femora and shortened medial tarsal articles, viz. *A. globifemurus* Butcher & Quicke, *A. nonicones* Butcher & Quicke and *A. pseudicones* Butcher & Quicke (Butcher *et al.* 2012), thus providing an independent example of leg and facial modification in the subfamily.

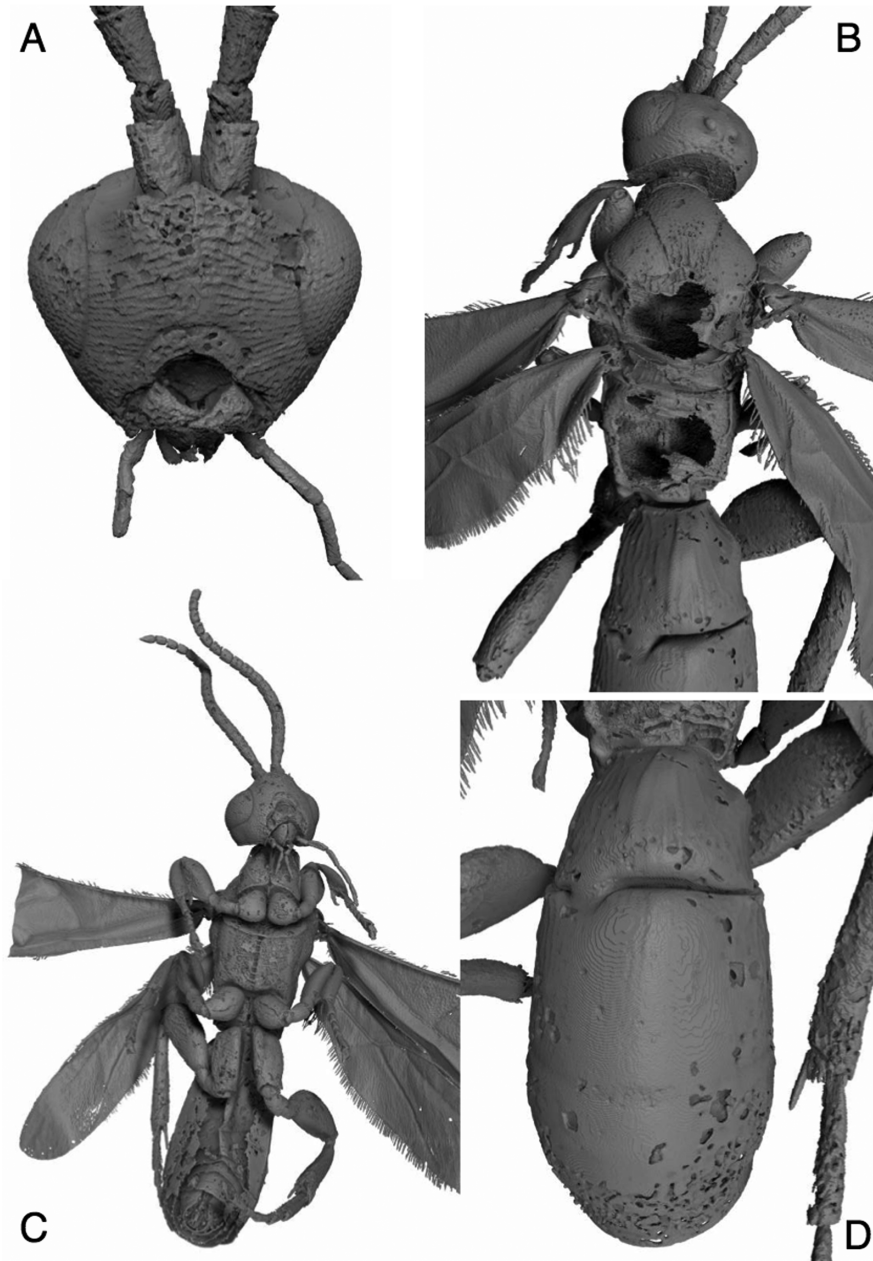


FIGURE 6. *Mesocentrus palaeoeuropaea* sp. nov. A, 3D surface rendering based on synchrotron X-ray microtomography data. A, head, front view; B, mesosoma and 1st metasomal tergite; C, ventral view of head and body; D, dorsal view of remains of propodeum and metasoma.

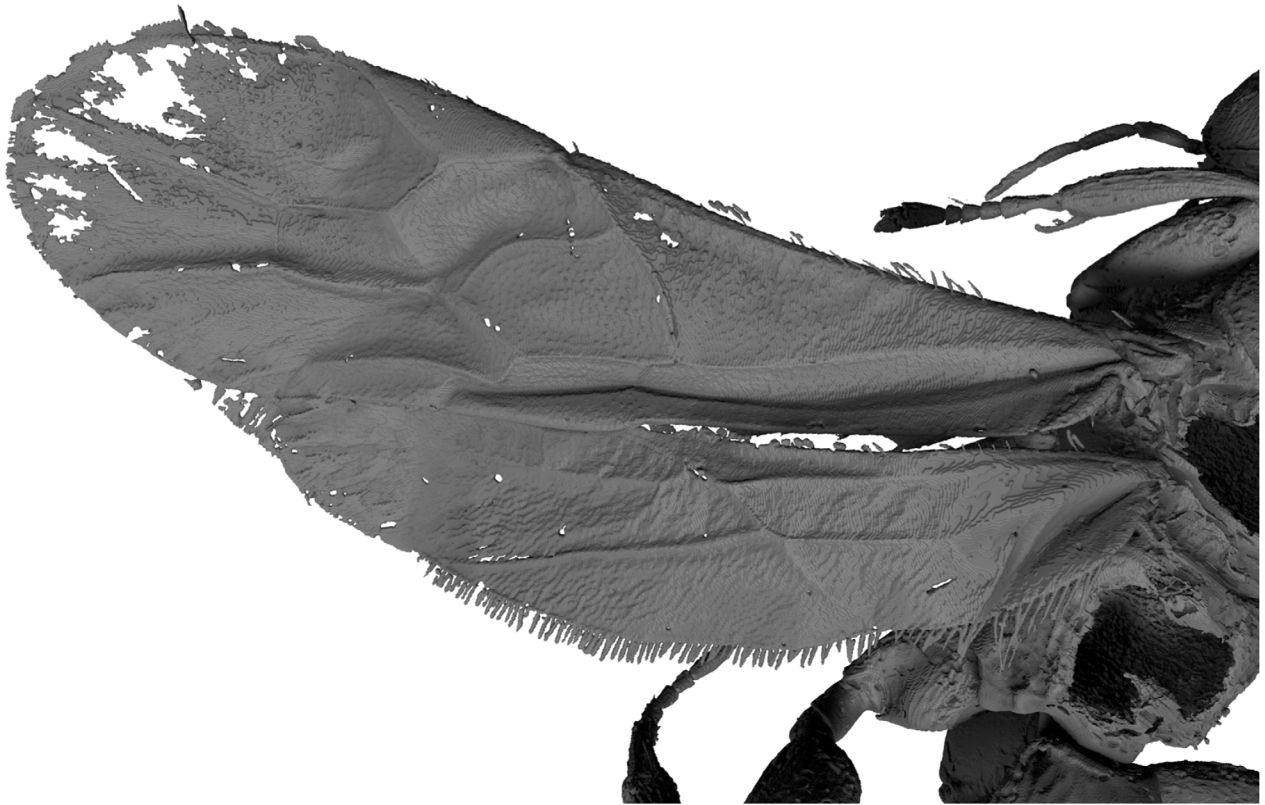


FIGURE 7. *Mesocentrus palaeoeuropaea* sp. nov. wings. 3D surface rendering based on synchrotron X-ray microtomography data showing wings.

Discussion

The new species extend the known range of variation in the Betylobraconinae as well as placing a minimum age on the group, Baltic amber most probably having an age of at least 44 million years (Ritzkowski 1997). Preservation of the fossil specimen is generally very good, though the darkness of the amber limited visual inspection, whereas synchrotron x-ray has allowed visualisation of the specimen from all angles as well as enabling obscured parts to be digitally revealed. The specimen has two large bubbles directly on top of the posterior of the mesosoma (Fig. 4A), but while it was possible to remove these digitally (Fig. 4B), quite a lot of the underlying cuticle no longer exists (Fig. 6B). Nevertheless, the ability to remove them has permitted some remaining otherwise hidden detail to be discerned, e.g. the median carina on the metanotum, and the presence of at least a short mid-longitudinal carina on the propodeum anteriorly.

Although there is quite a strong difference in the development of the hypoclypeal depression in the two species, this feature is also quite variable in the genus *Mesocentrus*, as well as in the Opiinae. Notably the fossil species resembles the extant species in many features such as the near triangular conformation of the precoxal sulcus (Fig. 5A cf. 2A), some irregular to slightly longitudinal rugosity between notauli posteriorly, the extent and general quality of the body sculpture. In general, the extant species appears somewhat more derived in some features, especially in the degree of enlargement of the fore telotarsus and the reduction in the fore basitarsus, which consequently look far more like those of *Yelicones*. The slight ridge on the fore tibia like that in *M. palaeoeuropaea* sp. nov. is also present in many *Yelicones* species but and is likely involved in strengthening the segment in association with the robust nature of the fore leg rather than indicating membership of that group. *M. palaeoeuropaea* sp. nov., unlike any extant *Mesocentrus* species, has a distinct groove separating the clypeus medially from the face. In contrast, *M. sasquatch* sp. nov., with its larger number of flagellar segments than any other extant member of the genus, and more or less unmodified (not laterally depressed) frons, appears in these likely to have retained the plesiomorphic state.

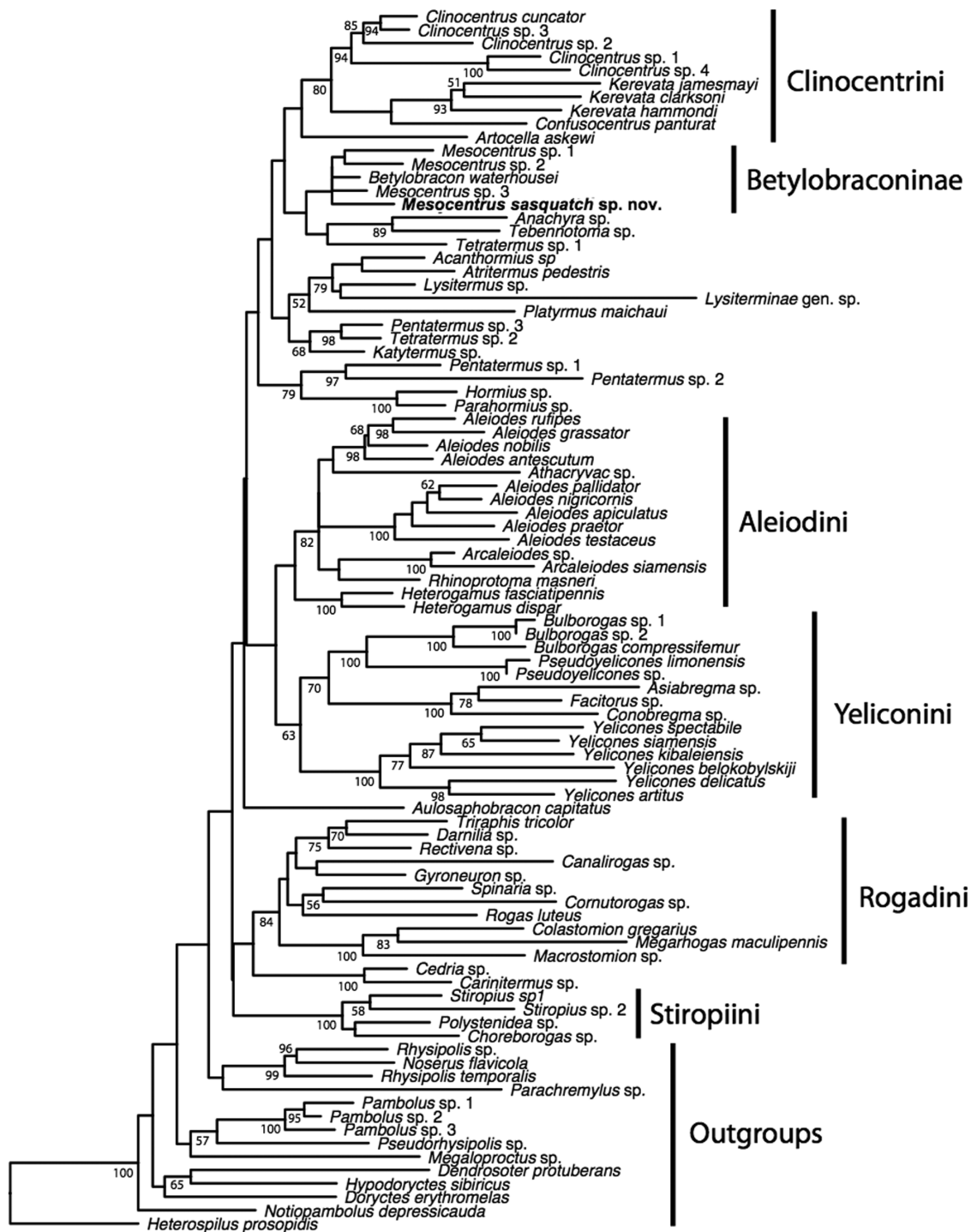


FIGURE 8. Bootstrapped maximum likelihood molecular tree showing major in-group clades, and the position of *Mesocentrus sasquatch* sp. nov.

Acknowledgements

We are greatly indebted to Claire Villemant (Paris) and Yves Braet (Brussels) for the loan of fascinating specimens from Papua New Guinea, Lars Vilhelmsen (Copenhagen) for arranging for DLJQ to study their collection of Baltic amber Ichneumonidea. Kees van Achterberg kindly sent us a copy of his unpublished illustrations of *Promesocentrus* for comparison. The ANKA Synchrotron Radiation Facility is acknowledged for providing beam

time. Mark Shaw (National Museums of Scotland) and Darren Ward (Landcare Research, New Zealand) allowed us to use sequence data from some of their specimens. We would like to thank Chulalongkorn University Centenary Academic Development Project for support to DQ.

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SUPPLEMENT

TABLE 1. Material included in molecular analysis and Genbank sequence accessions numbers.

Species	Voucher code	Provenance	Genbank accession numbers	
			28S D2-D3 rDNA	COI
Betylobraconinae				
<i>Betylobracon waterhousei</i>		Australia	AJ245686	-
<i>Mesocentrus sasquatch</i> sp. nov.	BKK0002	Papua New Guinea	KM067176	KM067253
<i>Mesocentrus</i> sp2.	BF000422	Australia	KM067175	JF963534
<i>Mesocentrus</i> sp1.	BCLDQ0636	Australia	-	JF963533
<i>Mesocentrus</i> sp3	JM645	Australia	AY935461	-
Doryctinae				
<i>Dendrosoter protuberans</i>	JM920	Turkey	EF645736	EF645775
<i>Doryctes erythromelas</i>		USA	GQ374709	GQ374627
<i>Heterospilus prosopidis</i>		lab. culture UK	AY935469	AY935396
<i>Hypodoryctes sibiricus</i> *	none & JM981	Finland & no data	AJ302895	DQ498965
<i>Megaloproctus</i> sp.		Colombia	AY935466	AY935393
Hormiinae				
<i>Hormius moniliatus</i>		Greenland	-	KF604624
<i>Hormius</i> sp.	JM582	Madagascar	AY935455	AY935385
<i>Parahormius</i> sp.	JM576	Cameroon	AY935456	AY935386
Lysiterminae				

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TABLE 1. (Continued)

Species	Voucher code	Provenance	Genbank accession numbers	
			28S D2-D3 rDNA	COI
<i>Acanthormius</i> sp.	JM692	Madagascar	AJ302883	AY935381
<i>Atritermus pedestris</i>	NHM675950	Madagascar	DQ414401	-
<i>Katytermus</i> sp.	Hym-08	Japan	EU854406	EU979624
<i>Lysitermus</i> sp.	BF000511	Nigeria	KM067177	JF963503
<i>Pentatermus</i> sp1	JM695	Benin	AY935453	AY935383
<i>Pentatermus</i> sp2	BCLDQ00264	Thailand	KM067179	KM067254
<i>Pentatermus</i> sp3	NHM671109 & NHM671669	Madagascar	KM067178	FN662435
<i>Platyrmus maichau</i>			EU854407	-
<i>Tetratermus</i> sp1	BF000596	Nigeria	KM067180	JF963422
<i>Tetratermus</i> sp2	AL0217	Uganda	AY935452	AY935452
<i>Lysiterminae</i> gen. sp.	DQBJ5001	Australia	KM067181	KM067255
Pambolinae-Chremylini				
<i>Cedria</i> sp.	JM579	Madagascar	AY935460	AY935390
<i>Carinitermus</i> sp..	NHM671037	Madagascar	DQ414402	JF963048
Pambolinae-Pambolini				
<i>Notiopambolus depressicauda</i>	JM651	Australia	AY935459	JF963049
<i>Pambolus</i> sp1	JM597	Venezuela	AY935458	AY935388
<i>Pambolus</i> sp 2	AW125	Costa Rica	JN212493	JN212220
<i>Pambolus</i> sp 3	BF000614	Nigeria	KM067185	JF963048
Parachremylus			EU854408	-
Rhysipolinae				
<i>Noserus ?flavicola</i>	JM696	Russia	AY935454	AY935384
<i>Pseudorhysipolis</i> sp.	JM758	Costa Rica	AY935450	AY935377
<i>Rhysipolis temporalis</i>	JM886	Russia	AY935449	AY935376
<i>Rhysipolis</i> sp.	JMH2010	-	GQ374708	GQ374626
Rogadinae-Aleiodini				
<i>Aleiodes antescutum</i>	BCLDQ00210	Thailand	KM067183	JF962536
<i>Aleiodes apiculatus</i>	MRS028	UK	EF115440	EF115455
<i>Aleiodes grassator</i>	MRS163	Hungary	EU854332	EU979584
<i>Aleiodes nigricornis</i>	MRS216	UK	AJ784934	EU979585
<i>Aleiodes nobilis</i>	BCLDQ00123	UK	KM067184	JF962562
<i>Aleiodes pallidator</i>	MRS001	Turkey	EU854333	EU979586
<i>Aleiodes praetor</i>	MRS067	UK	EU854334	KM067256
<i>Aleiodes rufipes</i>	MRS312	Sweden	KM067186	KM067257
<i>Aleiodes testaceus</i>	AL0058	UK	EF115493	EF115454
<i>Arcaleiodes siamensis</i>	BCLDQ00781	Thailand	KM067187	JQ388379
<i>Arcaleiodes</i> sp.	BCLDQ00286	Nepal	KM067188	JF962914
<i>Athacryvac</i> sp.	BCLDQ00697	French Guyana	KM067189	JF962609
<i>Heterogamus dispar</i>	AL201	UK	KM067190	JF963404
<i>Heterogamus fasciatipennis</i>	MRS394	Sweden	EU854358	EU979609

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TABLE 1. (Continued)

Species	Voucher code	Provenance	Genbank accession numbers	
			28S D2-D3 rDNA	COI
Rogadinae-Clinocentrini				
<i>Artocella askewi</i>		Spain	AY93335451	AY935379
<i>Clinocentrus cuncator</i>	JM702	UK	AJ784962	AY935378
<i>Clinocentrus</i> sp1	BCLDQ01211	Colombia	KM067192	HM435170
<i>Clinocentrus</i> sp 2	NHM671058	Madagascar	KM067194	-
<i>Clinocentrus</i> sp 3	BF000440	Hungary	KM067193	JF963115
<i>Clinocentrus</i> sp 4	BCLDQ00835	Colombia	KM067191	JF963113
<i>Confusocentrus panturati</i>	BCLDQ01571	Thailand	-	KM067258
<i>Kerevata clarksoni</i>	DQBKK0006	Papua New Guinea	KM067195	KM067259
<i>Kerevata hammondi</i>	DQBKK0008	Papua New Guinea	KM067196	KM067260
<i>Kerevata jamesmayi</i>	DQBKK0007	Papua New Guinea	KM067197	KM067261
Tebennotoma	AL170	Taiwan	AJ784933	AY935380
Rogadinae-Rogadini				
<i>Canalirogas</i> sp.	BCLDQ00235	Thailand	KM067198	JF963044
<i>Colastomion gregarius</i>	USNMENT00680021	Papua New Guinea	KM067200	JF963128
<i>Cornutorogas</i> sp.	BCLDQ00149	Thailand	KM067201	KM067262
<i>Darnilia</i> sp.	BCLDQ00165	Thailand	KM067199	KM067263
<i>Gyroneuron</i> sp.	BCLDQ00187	Thailand	KM067202	JF963364
<i>Macrostomion</i> sp.	BCLDQ00136	Thailand	KM067203	JF963522
<i>Megarhogas ?maculipennis</i>	AL0138	Thailand	EU854379	JF963804
<i>Rectivena</i> sp.	AL0204	Benin	EU854384	EU979618
<i>Rhinoprotoma masneri</i>	NZHYM174-10	New Zealand	-	KM201332
<i>Rogas luteus</i>	CNIN200	France	KM067204	KM067264
<i>Spinaria</i> sp.	BCLDQ0638	Thailand	KM067205	FN662444
<i>Triraphis tricolor</i>	MRS553	Netherlands	KM067206	KM067265
Rogadinae-Stiropiini				
<i>Choreborogas</i> sp.	AL508	Costa Rica	KM067207	JF963107
<i>Polystenidea</i> sp.	JM821	Colombia	AY935448	AY935374
<i>Stiropius</i> sp1	AW004	Costa Rica	JN212496	JN212223
<i>Stiropius</i> sp.	JM730	Costa Rica	AJ784961	AY935373
Rogadinae-Yeliconini-Facitorina				
<i>Asiabregma</i> sp.		Malaysia	AY935462	-
<i>Conobregma</i> sp.	Zoo27	Dominican Republic	JF979880	JF963138
<i>Facitorus</i> sp.	HYM011	Vietnam	EU450765	EU450766
Rogadinae-Yeliconini-Yeliconina				
<i>Bulborogas compressifemur</i>	BMNHE897754	Belize	KM067209	KM067266
<i>Bulborogas</i> sp.	AL0202	Colombia	AJ784930	-
<i>Bulborogas</i> sp.	AL0203	French Guyana	EU854359	AY935372
<i>Pseudoyelicones limonensis</i>	JM738	Costa Rica	AJ784929	-
<i>Pseudoyelicones</i> sp.	DHJPAP0035971	Costa Rica	KM067210	KM067267

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TABLE 1. (Continued)

Species	Voucher code	Provenance	Genbank accession numbers	
			28S D2-D3 rDNA	COI
<i>Yelicones artitus</i>	BCLDQ0457	Costa Rica	KM067211	JF963958
<i>Yelicones belokobylskiji</i>	BCLDQ01346	Taiwan	AJ784322	AJ784322
<i>Yelicones delicatus</i>	JM762	USA	AJ784327	KM067268
<i>Yelicones kibaleiensis</i>	AL0210	Uganda	AJ784321	AJ784321
<i>Yelicones siamensis</i> *	AL0115 & BCLDQ01451	Thailand	AJ784323	JN278234
<i>Yelicones spectabile</i>	JM734	Madagascar	AJ784319	AJ784319
unplaced				
<i>Anachyra</i> sp. **	-	Malaysia	AY935463	-
<i>Aulosaphobracon capitatus</i>	-	Vietnam	EU450764	-

* combined sequences from two individuals;

** In this and several other analyses, the genus appears to belong to the Clinocentrini rather than the Rhyssalinae.