A new lineage of Cretaceous jewel wasps (Chalcidoidea: Diversinitidae)

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Jewel wasps (Hymenoptera: Chalcidoidea) are extremely species-rich today, but have a sparse fossil record from the Cretaceous, the period of their early diversification. Three genera and three species, *Diversinitus attenboroughi* gen. & sp. n., *Burminata caputaeria* gen. & sp. n. and *Glabiala barbata* gen. & sp. n. are described in the family Diversinitidae fam. n., from Lower Cretaceous Burmese amber. Placement in Chalcidoidea is supported by the presence of multiporous plate sensilla on the antennal flagellum and a laterally exposed prepectus. The new taxa can be excluded from all extant family level chalcidoid lineages by the presence of multiporous plate sensilla on the first flagellomere in both sexes and lack of any synapomorphies. Accordingly, a new family is proposed for the fossils and its probable phylogenetic position within Chalcidoidea is discussed. Morphological cladistic analyses of the new fossils within the Heraty et al. (2013) dataset did not resolve the phylogenetic placement of Diversinitidae, but indicated its monophyly. Phylogenetically relevant morphological characters of the new fossils are discussed with reference to Cretaceous and extant chalcidoid taxa. Along with mymarid fossils and a few species of uncertain phylogenetic placement, the newly described members of Diversinitidae are among the earliest known chalcidoids and advance our knowledge of their Cretaceous diversity.

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2 **Diversinitidae)**

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Abstract

12 Jewel wasps (Hymenoptera: Chalcidoidea) are extremely species-rich today, but have a sparse
13 fossil record from the Cretaceous, the period of their early diversification. Three genera and
14 three species, *Diversinitus attenboroughi* gen. & sp. n.*, Burminata caputaeria* gen. & sp. n. and
15 *Glabiala barbata* gen. & sp. n. are described in the family Diversinitidae fam. n., from Lower
16 Cretaceous Burmese amber. Placement in Chalcidoidea is supported by the presence of
17 multiporous plate sensilla on the antennal flagellum and a laterally exposed prepectus. The new
18 taxa can be excluded from all extant family level chalcidoid lineages by the presence of
19 multiporous plate sensilla on the first flagellomere in both sexes and lack of any
20 synapomorphies. Accordingly, a new family is proposed for the fossils and its probable
21 phylogenetic position within Chalcidoidea is discussed. Morphological cladistic analyses of the
22 new fossils within the Heraty et al. (2013) dataset did not resolve the phylogenetic placement
23 of Diversinitidae, but indicated its monophyly. Phylogenetically relevant morphological
24 characters of the new fossils are discussed with reference to Cretaceous and extant chalcidoid
25 taxa. Along with mymarid fossils and a few species of uncertain phylogenetic placement, the
26 newly described members of Diversinitidae are among the earliest known chalcidoids and
27 advance our knowledge of their Cretaceous diversity.

Introduction

30 Jewel wasps (Hymenoptera: Chalcidoidea) are estimated to constitute one of the most species-
31 rich insect lineages. Estimated numbers range from 100,000 to 500,000 species, which may
32 comprise 10% of insect diversity, though only about 22,000 species have been described to
33 date (Noyes, 1978, 2000, 2017; Heraty & Gates, 2001). Their evolutionary success is mirrored by
34 and likely results from their varied biological life styles. Jewel wasps develop mainly as
35 parasitoids of 13 different insect orders, as well as some nematodes, pseudoscorpions and
36 arachnids, and thus are essential beneficial regulators, while some species are phytophages or
37 even obligate pollinators of figs (*Ficus*) (Gibson, Heraty & Woolley, 1999; Weiblen, 2002;
38 Heraty, 2009). Despite recent progress (Munro et al., 2011; Heraty et al., 2013; Peters et al.,
39 2018), the relationships among most chalcidoid taxa as well as their evolutionary history still
40 remain unresolved. The role of fossils in a phylogenetic framework is pivotal in understanding
41 some of the evolutionary processes that led to chalcidoid megadiversity and provide valuable
42 information on morphological character evolution (Donoghue et al., 1989; Peters et al., 2018).
43 Reliably placed fossils can shed light on the minimum age of taxa and allow calibrations of
44 molecular phylogenies to resolve timing and patterns of biological shifts (Ware & Barden, 2016;
45 Gunkel et al., 2017; Slater, Harmon & Alfaro, 2012).
46   Numerous chalcidoid fossils have been reported from different amber deposits
47 (Grimaldi & Engel, 2005; Penney, 2010), but few of them have been formally described. Most
48 described chalcidoids stem from young (Eocene and Miocene) deposits, which already host an
49 astonishing phylogenetic diversity of taxa (Darling, 1996; Gibson, 2008, 2009, 2013; Engel,
50 2009; Engel, McKellar & Huber, 2013; Heraty & Darling, 2009; Compton et al., 2010; McKellar &

51 Engel, 2012; Krogmann, 2013; Simutnik, Perkovsky & Gumovsky, 2014; Bläser, Krogmann &
52 Peters, 2015; Burks et al., 2015; Farache et al., 2016). It is believed that most chalcidoid families
53 diversified after the Upper Cretaceous (Heraty et al., 2013; Peters et al. 2018) during a period
54 that falls within a major gap in the chalcidoid fossil record, from which only few taxa have been
55 described or even discovered (Burks et al. 2015; Heraty & Darling, 2009; Penney, 2010). The
56 earliest reported and described chalcidoids date back to the Lower Cretaceous period, 106–115
57 million years ago (mya) (Kaddumi, 2005; Grimaldi & Engel, 2005; Penney, 2010; Barling, Heads
58 & Martill, 2013).
59   The fossil *Minutoma yathribi* Kaddumi, 2005 is currently the oldest described putative
60 chalcidoid wasp from Jordanian amber, dated about 115 million years old (myo) (Kaddumi,
61 2005). It was placed in Mymaridae, which is considered to be the sister group to all other
62 chalcidoid families (Heraty et al., 2013). Heraty et al. (2013) however commented, that the
63 photo of *M. yathribi* rather suggests affiliation with Bouceklytinae, an extinct subfamily of
64 uncertain placement. Kaddumi (2005) also mentioned a putative eupelmid fossil, which was not
65 formally described. The family assignment of the concerned fossil is questionable as the
66 metasomal and wing venational characters depicted in Kaddumi (2005, figs 95–97) are
67 characteristic for Scelioninae (Platygastridae) (own observation). *Myanmymar aresconoides*
68 Poinar & Huber, 2011 represents the oldest verified fossil record of Chalcidoidea, dating back to
69 the Early Upper Cretaceous, approximately 99 mya (Shi et al., 2012). Although there are some
70 reports of Eulophidae and Chalcididae from the transition between the Upper and Lower
71 Cretaceous, no information concerning their validity is available (Penney, 2010).
72   Schmidt et al. (2010) reported Eulophidae, Trichogrammatidae and Mymaridae from
73 Ethiopian amber, which they dated through chemical and spectroscopic methods to an Upper
74 Cretaceous origin (around 94 mya). Though the family identifications might be right, doubt was
75 raised concerning the age of Ethiopian amber. Coty, Lebon & Nel (2016) described a myrmecine
76 ant from the same deposit, which could readily be described in the tribe Crematogastrini,
77 suggesting through phylogenetic dating that the specimen cannot be of Cretaceous age.
78 Subsequent revised gas chromatography and infrared spectroscopy analyses showed, that
79 indeed, though not completely unequivocal, evidence strongly suggested that Ethiopian amber
80 is of Cenozoic origin, probably at least 50 million years younger than formerly suspected (Coty,
81 Lebon & Nel, 2016). Currently, the oldest verified record of the families Trichogrammatidae and
82 Aphelinidae are from Baltic amber, approximately 44 myo (Burks et al., 2015).
83   From the Upper Cretaceous Canadian amber (~75 myo), fossil Tetracampidae and
84 Trichogrammatidae were recorded by Yoshimoto (1975). Of the four genera described by
85 Yoshimoto (1975) within Mymaridae (*Carpenteriana, Macalpinia, Protooctonus* and
86 *Triadomerus*), *Protooctonus* was later transferred to Mymarommatidae and synonymized under
87 *Archaeromma* Yoshimoto, 1975 (Gibson, Read & Huber, 2007). *Enneagmus* Yoshimoto, 1975,
88 originally described within Trichogrammatidae, was transferred by Huber (2005) to Mymaridae.
89 The placement of *Distylopus, Bouceklytus* and *Baeomorpha* within Tetracampidae by Yoshimoto
90 (1975) was considered erroneous and even the position of *Distylopus* within Chalcidoidea was
91 presumed unlikely as stated by Gumovsky & Perkovsky (2005) and Heraty & Darling (2009).

92   After a recent revision, *Distylopus* and *Bouceklytus* are now regarded as Chalcidoidea *incertae*
93   *sedis* and *Baeomorpha* and its respective subfamily Baeomorphinae were transferred to
94   Rotoitidae (Gumovsky, Perkovsky & Rasnitsyn 2018). McKellar & Engel (2012) additionally
95   mention Torymidae and Eupelmidae as possibly present in Canadian amber, although the
96   specimens have not been thoroughly studied to date.
97   A putative member of Pteromalidae, *Parviformosus wohlrabeae* Barling, Heads &
98   Martill, 2013, was described from limestone originating from the Crato formation, dated to the
99   Aptian period, about 110 mya. Because of its age, it might be considered as one of the oldest
100 known fossils of Chalcidoidea, but evidence for its placement is ambiguous because none of the
101 diagnostic features of Chalcidoidea was preserved (Barling, Heads & Martill, 2013; Farache et
102 al., 2016). It was placed within Pteromalidae only because of a putative habitus resemblance to
103 Sycophaginae (now Agaonidae *sensu* Heraty et al., 2013). The limited morphological characters
104 of *P. wohlrabeae* need to be reassessed before phylogenetic conclusions can be drawn from
105 this fossil. The original placement of *P. wohlrabeae* in Pteromalidae is in this case highly
106 problematic, because the family, in its current concept, is indicated to be polyphyletic
107 (Campbell et al., 2000; Krogmann & Vilhelmsen, 2006; Heraty et al., 2013).
108   We here contribute to the scarce Cretaceous fossil record of Chalcidoidea by describing
109 three new fossil genera and species within a new family. These fossils lack synapomorphies
110 with any of the currently described chalcidoid families, but possess many putatively
111 plesiomorphic features, suggesting a basal position within Chalcidoidea.
112

Material & Methods

Specimens

115 Four specimens in four different pieces of Burmese amber were examined. Burmese amber is of
116 Upper Cretaceous origin, approximately 99 my old (Shi et al., 2012). Additional information
117 about the geographical origin of the individual pieces is not known. All pieces are deposited in
118 the amber collection of the State Museum of Natural History, Stuttgart, Germany (SMNS).

Imaging

120 Imaging was done, using a MZ 16 APO Leica® microscope, with an attached DXM 1200 Leica®
121 camera. The images were generated by stacking single images using the Automontage®
122 technique and the program Helicon Focus Pro® (Vers. 6.7.1). For additional and detail imaging
123 as well as measurements the digital microscopes Keyence VHX 600 and VHX 5000 were used.
124 Adobe Photoshop® CS4 Version: 11.0.2 was used to process all images. Drawings were made,
125 using a camera lucida on a Leica® M205 C microscope. Digitalization of the drawings and
126 arrangement of the image plates was done with Adobe Illustrator® CS4 Version: 14.0.0.

Terminology

128 Terminology follows the Hymenoptera Anatomy Ontology (HAO) (Yoder et al., 2010).
129 Abbreviations listed in Table 1 are used throughout the text and illustrations.

Cladistic analysis

131 Morphological cladistic analyses were performed using the 233 characters from Heraty et al.
132 (2013). Their comprehensive matrix, encompassing 19 families, 78 subfamilies, 268 genera and
133 283 species of Chalcidoidea was used as basis for the here conducted phylogenetic analysis.
134 Due to conservation state and inaccessibility, some characters could not be scored for the
135 fossils without reasonable doubt and were marked as unknown "?" (Appendix S1). Analyses
136 were conducted using the program TNT ver. 1.5 (Goloboff, Farris & Nixon, 2008) following
137 Heraty et al. (2013) in analysis setup. A sectorial search, with equally weighted characters,
138 under New Technology methods was performed, using a ratchet weighting probability of 5%
139 with 50 iterations, tree-drifting of 50 cycles, tree-fusing of five rounds and a best score hit of 10
140 times. New Technology searches in TNT provide refined algorithms more effective than simple
141 branch swapping techniques applied in traditional searches, leading to shorter analyze times,
142 especially in large datasets (Goloboff, Farris & Nixon, 2008). Nevertheless, traditional searches
143 with and without implied weighting were conducted as well to test consistency of the results.
144 Dependent on the used concavity constant (k), implied weighting aims to decrease the
145 phylogenetic impact of supposed homoplasious characters, in comparison to equal weighting,
146 (Congreve & Lamsdell, 2016). Morphological datasets of Chalcidoidea are reported to include a
147 multitude of potentially homoplasious characters (Krogmann & Vilhelmsen, 2006; Heraty et al.,
148 2013), therefore implied weights of k = 1, 3, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, and 60 were
149 used with 1000 replications and Tree Bisection and Re-connection (TBR) for the analyses.
150 **Nomenclature**
151 The electronic version of this article in Portable Document Format (PDF) will represent a
152 published work according to the International Commission on Zoological Nomenclature (ICZN),
153 and hence the new names contained in the electronic version are effectively published under
154 that Code from the electronic edition alone. This published work and the nomenclatural acts it
155 contains have been registered in ZooBank, the online registration system for the ICZN. The
156 ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed
157 through any standard web browser by appending the LSID to the prefix http://zoobank.org/.
158 The LSID for this publication is: LSID urn:lsid:zoobank.org:pub:B936D52D-7165-47CE-9C3E-
159 0B79A17AC5AC. The online version of this work is archived and available from the following
160 digital repositories: PeerJ, PubMed Central and CLOCKSS.
161

Results

162
Systematic Palaeontology

163
164

Diversinitidae fam. n.

165
166 LSID urn:lsid:zoobank.org:act:017E601E-FB88-4821-8EA7-16228EC61C37

167
Type genus. *Diversinitus* gen. n.

168
169

Diagnosis. Antenna 13-segmented in male (Figs. 1B–D, 2A, 3A and 3B) and female (Figs. 4C, 4E and 5A), with eight funiculars and 3-segmented clava, including a distinct terminal button; all funiculars (including F1) with multiporous plate sensilla (Figs. 1C, 4C and 4E). Eyes large, without pilosity, inner margins not divergent ventrally (Figs. 1B and 4B). Occipital carina absent. Labrum exposed below clypeus (Figs. 1B and 4B), semicircular, flap-like with setae at least at apical margin, broadly contiguous with clypeal margin. Mandibles two toothed (Figs. 2A and 3A). Pronotum lacking collar (Figs. 3A, 5A and 5B). Mesosoma with independent, large and triangular, laterally exposed prepectus (Figs. 3A, 5A and 5B). Mesothoracic spiracle situated at lateral margin of mesoscutum, at juncture of pronotum and prepectus. Mesonotum with notauli deep and complete (Figs. 1D, 3B, 5A and 5B). Mesoscutellum with frenum distinguishable (Figs. 1D, 3B and 4F). Mesopleuron concave with acropleuron not enlarged. Fore wing with short marginal fringe. Basal vein at least apically pigmented (Figs. 1E and 4A). Uncus elongate, bent in direction of postmarginal vein (Figs. 1E, 4A and 4D). Postmarginal vein distinctly longer than marginal vein (Figs. 1E, 4A and 4D). Hind wing normal, membrane extending to base of wing, three hamuli, first straight (Figs. 1E and 4A). Tibial spur formula 1:1:2; protibial spur slightly curved, slender, simple tip; mesotibial spur slender and straight. Tarsus on all legs five segmented. Metasoma with Mt_8 and Mt_9 fused into syntergum (Mt_{8+9}) in both sexes (Figs. 3A, 3B, 5A and 5B). Cercus peg-like (Figs. 3A, 5A and 5B).

Key to species of Diversinitidae

1. Head distinctly towering over mesosoma (Fig. 4A). Pronotum almost as long as mesoscutum (Figs. 4A and 5A). Basal cell bare, basal vein nearly completely pigmented (Figs. 2A, 4A). Ovipositor protruding about half the length of gaster (Fig. 4A). [only female known]
                                                                    Burminata caputaeria
-   Head only slightly towering over mesosoma (Figs. 2A, 2B and 4D). Pronotum short, about 1/4 length of mesoscutum (Figs. 1A and 4G) Basal cell pilose (Fig. 1E), basal vein only apically pigmented (Fig. 2B). Ovipositor only slightly protruding gaster (Fig. 4D).
                                                                    2.
2. Gaster sessile (Fig. 4D). Mouthmargin surrounded by long setae (Figs. 4D and 5B). Antenna inserted at about center of face, with toruli closer to each other than to margin of eye. Axilla advanced almost 1/4 length of mesoscutum (Fig. 4G). Speculum on forewing present (Fig. 4 D). Protibia with a row of stout setae on anterior margin. [only female known]
                                                                    Glabiala barbata
-   Gaster distinctly petiolate (Figs. 1A and 1D). Mouthmargin not surrounded by long setae (Fig. 1B). Antenna inserted in lower third of face, with toruli closer to eye margin than to each other (Fig. 1B). Axilla not advanced (Fig. 1D). Speculum on forewing absent (Fig. 1E). Protibia without row of stout setae on anterior margin. [only males known]
                                                                    Diversinitus attenboroughi

Diversinitus **gen. n.**

210   LSID urn:lsid:zoobank.org:act:F8B422B0-C83B-4718-8042-D7F07EA0DF7F

211

212   **Type species.** *Diversinitus attenboroughi* sp. n.

213

214   **Diagnosis.** Antenna inserted in lower third of face (Fig. 1B). Clypeus transverse. Scape ventrally
215   expanded (Figs. 2A and 3A). Pronotum less than 1/4 length of mesoscutum (Figs. 1D and 3B).
216   Axilla not advanced. Frenum anteriorly delimited by deep frenal groove (Figs. 1D and 3A). Fore
217   wing completely pilose, i.e. speculum absent (Fig. 1E), basal vein only anteriorly pigmented.
218   Gaster distinctly petiolate (Fig. 1D).

219   **Etymology.** The generic name *Diversinitus* is composed of two parts. The first being "Divers-*"*,
220   originating from the Latin adjective "*diversus*", meaning diverse or different. The second part, "-
221   initus*"*, is the Latin noun "*initus*" translating to "origin" or "start". Together the two parts can
222   be translated to "origin of diversity", referring to the age of the fossil and the diversity which
223   evolved since its appearance in the Upper Cretaceous. The generic name is masculine in
224   gender.

225

226   ***Diversinitus attenboroughi* sp. n.** (Figs. 1–3)
227   LSID urn:lsid:zoobank.org:act:3840E4D4-46A6-4192-8052-20E561DD913F

228

229   **Diagnosis.** As for the genus.

230   **Male.** Measurements: (h) = holotype, (p) = paratype. Total body length, excluding protruded
231   aedeagus 1.67 mm (h), metasoma of paratype destroyed.

232   *Head.* In frontal view oval, bare, broader than rest of body, breadth 0.41 (p)–0.52 mm
233   (h), height 0.34 mm (h), length in dorsal view 0.23 (p)–0.29 mm (h). Foramen magnum situated
234   higher than half height of head. Eye length 0.25 mm (h), height 0.28 mm (h), distance between
235   eyes 0.21 (p)–0.23 mm (h). Transfacial sulcus indiscernible. Antennal scrobes probably shallow.
236   Clypeus transverse, apically truncate, tentorial pits absent, dorsal margin straight. Mandible at
237   least two times as long as broad with slight curvature and few short setae on outer surface.
238   Maxillary palps with at least three segments. Labial palps with at least two segments. Malar
239   space shorter than 1/3 length of an eye.

240   *Antenna.* Inserted in lower third of face, hardly above ventral level of eyes, with toruli
241   closer to edge of eyes than to each other. Scape ventrally expanded and broadened over most
242   of its length, not reaching median ocellus. Pedicel length, measured laterally, 0.05 (h) – 0.06
243   mm (p) and breadth 0.04 mm (h, p). F1 subquadrate, fully developed (not anelliform); following
244   funiculars increasingly more transverse and broadening distally, F1 – F4 with sides diverging
245   (subconical), F5 – F8 more parallel sided (cylindrical) and asymmetrically formed, connections
246   between segments rather slanted; F1 dorsolateral length (mm): width (mm) = 0.03(p)–0.04 (h):
247   0.03 (p)–0.04 (h), F2 = 0.02 (h, p): 0.04 (h, p), F3 = 0.02 (p)–0.03 (h): 0.04 (h, p), F4 = 0.2 (p)–0.03
248   (h): 0.04 (h, p), F5 = 0.03 (h, p): 0.04 (h, p), F6 = 0.03 (h, p): 0.04 (h, p), F7 = 0.03 (p, h): 0.04 (p)–
249   0.05 (h), F8 = 0.03 (p)–0.04 (h): 0.04 (p)–0.05 (h). Clava differentiated, sutures rather straight;

250   F9 length (mm): width (mm) = 0.03 (h, p): 0.04 (p)–0.05 (h), F10 = 0.02 (h, p): 0.03 (p)–0.04 (h),
251   F11 + F12 = 0.02 (p)–0.04 (h): 0.02 (p)–0.03 (h).
252   *Mesosoma.* Length 0.60 (p)–0.74 mm (h), arched. Pronotum bare, posteriorly deeply
253   emarginated, u-shaped, medially much shorter (0.06 (p) – 0.07 mm (h)) than mesoscutum (0.25
254   (p)–0.27 mm (h)), regularly reticulate. Prepectus slightly convex, lightly sculptured, with thin
255   shiny rim along its dorsal and posterior margin. Tegula much smaller than prepectus.
256   Mesonotum finely regularly reticulate and with very sparse, short pilosity. Mesoscutum slightly
257   shorter than wide; notauli reaching transscutal articulation, widely separated posteriorly.
258   Mesoscutellum length 0.23 (p)–0.26 mm (h), with frenum delimited anteriorly by deep frenal
259   groove (length: 0.05 (p)–0.06 mm (h)); axillae not advanced, widely separated at transscutal
260   articulation. Metapleuron small, bare. Metanotum length 0.06 (p)–0.07 mm (h), with smooth
261   metascutellum not reaching anterior margin of metanotum, lateral panel foveolate.
262   Propodeum transverse, rectangular, slightly arched, length 0.09 (p)–0.11 mm (h), with coarse
263   irregular sculpture, lateral propodeal callus bare; spiracles round to slightly elliptical.
264   *Wings.* Fore wing hyaline, immaculate, entirely pilose; humeral plate with at least three
265   setae; basal vein apically pigmented and angled relative to submarginal vein at about 10–15°;
266   marginal vein slightly thickened relative to postmarginal vein; stigmal vein about 0.5 times
267   length of marginal vein; uncus bent at angle of about 95–100° in direction of postmarginal vein,
268   almost reaching it; postmarginal vein not reaching apex of wing, 1.5 times as long as marginal
269   vein. Hind wing apical 2/3 pilose, rest relatively bare; posterior marginal fringe moderately long.
270   *Legs.* Pro- and metacoxa larger than mesocoxa; metacoxa dorsally bare, except few hairs
271   posteriorly. Protibial setae inconspicuous and short. Basitarsal comb not visible. Metatibia
272   laterally flattened, bearing two spurs, one robust, the other short and more slender.
273   *Metasoma.* Petiole (Mt_1) cylindrical distinct and reticulate, length 0.09 mm (h), breadth
274   0.06 mm (h). Gaster of holotype 0.66 mm in length, lanceolate; terga smooth and bare except
275   of Mt_6–Mt_{8+9} with longitudinal rugosity and lateral setae, hindmargins straight, length of terga
276   of holotype: Mt_2: 0.24 mm, Mt_3: 0.07 mm, Mt_4: 0.07 mm, Mt_5: 0.07 mm, Mt_6: 0.11 mm, Mt_7:
277   0.06 mm, Mt_{8+9}: 0.04 mm. Cerci peg-like with few long setae.
278   **Female.** Unknown.
279   **Specimen examined.** Male holo- (SMNS Bu-4) and paratype (SMNS Bu-5) deposited in the
280   SMNS. The amber piece hosting the holotype also includes syninclusions: three complete
281   Diptera and three further Diptera, which are preserved only in part. Additionally, a Serphitidae
282   (Hymenoptera) is included in the same piece. The amber piece including the paratype also
283   hosts a Platygastridae: Scelioninae (Hymenoptera).
284   **Etymology.** Named after the well renowned British broadcaster and naturalist Sir David
285   Frederick Attenborough for his inspiring enthusiasm and devotion to natural sciences. This
286   species was dedicated to Sir Attenborough during his visit to the SMNS on the occasion of his
287   91st birthday.
288
289   ***Burminata* gen. nov.**
290   LSID urn:lsid:zoobank.org:act:71D5E586-8406-486A-85AC-FA5CA1F293D8

291

292 **Type species.** *Burminata caputaeria* sp. n.

293

294 **Diagnosis.** Foramen magnum situated at lower third of head (Fig. 4A). Tentorial pits deep (Fig.
295 4B). Clypeus transverse (Fig. 4B). Pronotum only slightly shorter than mesoscutum (Fig. 5A).
296 Axilla slightly advanced (Fig. 5A). Fore wing with speculum; basal cell bare; basal vein almost
297 completely pigmented (Fig. 4A). Posterior fringe on hind wing long (Fig. 4A). Ovipositor
298 protruding about half length of gaster (Fig. 4A).
299 **Etymology.** The generic name is composed of two parts. The first part "Burmi-", references the
300 origin of the amber piece whereas the second part, "–nata", originates from the Latin adjective
301 "*natus*" translating to "born". The generic name is feminine in gender.

302

303 *Burminata caputaeria* **sp. n.** (Fig. 4A–C and Fig. 5A)
304 LSID urn:lsid:zoobank.org:act:AA5C051D-90AB-4D21-80F1-90AE82A8125A

305

306 **Diagnosis**. As for the genus.
307 **Female.** Total body length, excluding protruding ovipositor 1.23 mm.
308   *Head.* In frontal view oval, bare, much broader than rest of body, breadth 0.40 mm,
309 height 0.23 mm, dorsal length not measurable. Foramen magnum situated at lower third of
310 head. Eye length 0.17 mm, height 0.16 mm, distance between eyes 0.22 mm. Putative
311 transfacial sulcus anterior to antennal scrobes length 0.10 mm. Antennal scrobes absent.
312 Clypeus transverse, apically truncate, laterally delimited by large tentorial pits, dorsal margin
313 straight. Mandible about 1.6 times as long as broad, rather straight, setae not distinguishable.
314 Maxillary palps with at least three segments. Labial palp segments not countable. Malar space
315 more than 1/3 length of an eye.
316   *Antenna.* Inserted at about center of face, at half height of eyes, with toruli slightly
317 closer to edge of eyes than to each other. Scape slender, not flattened, not reaching median
318 ocellus. Pedicel length, measured laterally, 0.04 mm and breadth 0.04 mm. F1 subquadrate,
319 subconical, fully developed (not anelliform); following funiculars transverse to quadrate,
320 conical, connections between segments rather slanted; F1 lateral length (mm): width (mm) =
321 0.03: 0.04, F2 = 0.03: 0.04, F3 = 0.03: 0.04, F4 = 0.04: 0.04, F5 = 0.04: 0.04, F6 = 0.04: 0.04, F7 =
322 0.04: 0.04, F8 = 0.04: 0.04. Clava differentiated, sutures oblique, F9 length (mm): width (mm) =
323 0.04: 0.04, F10 = 0.03: 0.04, F11 + F12 = 0.03: 0.03.
324   *Mesosoma.* Length 0.49 mm, weakly arched. Pronotum bare except of few long setae on
325 hind margin, posteriorly slightly emarginated, medially only slightly shorter (0.12 mm) than
326 mesoscutum (0.15 mm), regularly finely reticulate. Prepectus convex, lightly sculptured, with
327 thin shiny rim along its dorsal and posterior margin. Tegula much smaller than prepectus.
328 Mesonotum, finely regularly reticulate, largely bare, only few single setae on lateral lobe of
329 mesoscutum, msoscutellum and axilla. Mesoscutum breadth not measurable; notauli reaching
330 transscutal articulation, widely separated posteriorly. Mesoscutellum length 0.14 mm, with
331 frenum short (0.02 mm), delimited anteriorly by shallow frenal groove; axillae slightly

332   advanced, widely separated at transscutal articulation. Metapleuron small and triangular, bare.
333   Metanotum and propodeum hardly discernable because of cracked amber and air inclusions,
334   propodeum apparently arched.
335   *Wings.* Fore wing hyaline, immaculate, speculum present, basal cell bare, costal cell
336   pilose throughout; humeral plate with at least two setae; basal vein almost completely
337   pigmented, angled relative to submarginal vein at about 27°; marginal vein as thick as
338   postmarginal vein; stigmal vein about 0.4 times length of marginal vein; uncus bent at angle of
339   about 110° in direction of postmarginal vein, almost reaching it; postmarginal vein not reaching
340   apex of wing, 1.6 times as long as marginal vein. Hind wing apical 2/3 pilose, rest relatively
341   bare; posterior marginal fringe long.
342   *Legs.* Pro- and mesocoxa about same size, metacoxa slightly larger, dorsally completely
343   bare. Protibial setae inconspicuous and short. Basitarsal comb not visible. Metatibia hardly
344   flattened, bearing two equally short and robust spurs.
345   *Metasoma.* Petiole (Mt_1) indistinct. Gaster lanceolate, length excluding ovipositor 0.52
346   mm; terga smooth and bare except dorsal surface of Mt_7 and Mt_{8+9} with longitudinal rugosity,
347   hindmargins straight, length of terga: Mt_2: 0.12 mm, Mt_3: 0.04 mm, Mt_4: 0.04 mm, Mt_5: 0.05
348   mm, Mt_6: 0.06 mm, Mt_7: 0.11 mm, Mt_{8+9}: 0.09 mm. Cercus peg-like, appearing to be slightly
349   spatulate, arising from under syntergum, bearing at least three setae. Hypopygium folded
350   downwards, slightly longer than half of gaster. Ovipositor protruding about half length of
351   gaster, third valvulae broad.
352   **Male.** Unknown.
353   **Specimen examined.** The holotype (SMNS Bu-304) is deposited in the SMNS. Besides the
354   holotype the amber piece also includes two Diptera and one Platygastridae: Scelioninae
355   (Hymenoptera), amongst parts of other insects.
356   **Etymology.** The specific epithet "*caputaeria*" consists of two parts originating from the Latin
357   noun for "head" (*caput*) and adjective "towering up" (*aerius*), referring to the lowly situated
358   foramen magnum, leaving the head protruding especially high over the pronotum. The species
359   name is treated as an adjective.
360
361   ***Glabiala* gen. nov.**
362   LSID urn:lsid:zoobank.org:act:10644623-4534-4848-B961-1E608CBB773B
363
364   **Type species.** *Glabiala barbata* sp. n.
365
366   **Diagnosis.** Head densely pilose, with mouth margin surrounded by especially long setae (Figs.
367   4D and 5B). Clypeus quadrate. Toruli situated at about center of face, closer to each other than
368   to margin of eyes. All funiculars rather thistle shaped (Fig. 4E). Pronotum and mesonotum with
369   dense, short pilosity (Fig. 4F). Pronotum about 1/3 the length of the mesoscutum (Figs. 4G and
370   5B). Axillae advanced about 1/4 the length of the mesoscutum (Fig. 4G). Frenum large,
371   delimited by deep frenal groove (Fig. 4F). Lateral propodeal callus with dense pilosity. Fore wing

372 with speculum (Fig. 4D); basal cell pilose, basal vein only anteriorly pigmented. Metacoxa
373 dorsally with short pilosity. Ovipositor hardly protruding apex of gaster (Fig. 4D).
374 **Etymology.** The name consists of two parts originating from the Latin words for "hairless"
375 (*glabellus*) and "wing" (ala), referring to the distinct speculum on the wing of the specimen. The
376 generic name is feminine in gender.
377
378 ***Glabiala barbata* sp. n.** (Fig. 4D–G and Fig. 5B)
379 LSID urn:lsid:zoobank.org:act:01C89C3D-E207-4544-A5AD-3BA80EFE61CB
380
381 **Diagnosis.** As for the genus.
382 **Female.** Total body length, excluding protruding ovipositor: 2.21 mm.
383   *Head.* Frontal view largely blocked, appearing trapezoid, finely pilose, except quite long
384 pilosity on gena and mouth margin, about as broad as body, actual breadth and height not
385 measurable. Foramen magnum situated higher than half height of head. Eye length 0.23 mm,
386 height 0.27 mm, distance between eyes not measurable. Transfacial sulcus not discernable.
387 Antennal scrobes absent. Clypeus quadrate with subparallel sides, apically truncate, tentorial
388 pits absent, dorsal margin straight. Mandible not measurable, appearing broad and straight,
389 with numerous longer setae on its outer surface. Maxillary palps probably with four segments.
390 Labial palps with at least two segments. Malar space about 1/3 length of an eye.
391   *Antenna.* Inserted at about center of face (direct frontal view blocked), slightly below
392 half height of eyes, with toruli closer to each other than to eyes. Scape slightly broadened, not
393 reaching median ocellus. Pedicel lateral length not assessable. F1 subconical fully developed
394 (not anelliform), distal funiculars more transverse, F2 – F8 appearing thistle-shaped, with F2 –
395 F7 asymmetrically shaped, connections between segments rather slanted; F1 lateral length
396 (mm): width (mm) = 0.05: 0.05, F2 = 0.06: 0.05, F3 = 0.05: 0.05, F4 = 0.06: 0.05, F5 = 0.05: 0.05,
397 F6 = 0.05: 0.06, F7 = 0.05: 0.06, F8 = 0.05: 0.06. Clava not clearly differentiated, segments
398 separated by deep, rather straight sutures, F9 length (mm): width (mm) = 0.04: 0.05, F10 =
399 0.05: 0.05, F11 + F12 = 0.05: 0.04.
400   *Mesosoma.* Length 0.96 mm, weakly arched. Pronotum densely shortly pilose,
401 posteriorly deeply emarginated, u-shaped, medially much shorter (0.12 mm) than mesoscutum
402 (0.4 mm), regularly reticulate. Prepectus almost flat, lightly sculptured, view on rim not clear.
403 Tegula smaller than prepectus. Mesonotum regularly reticulate and densely, shortly pilose.
404 Mesoscutum about 2/3 as long as wide; notauli reaching transscutal articulation, widely
405 separated posteriorly. Mesoscutellum length 0.31 mm, with frenum delimited anteriorly by
406 deep frenal groove (length: 0.07 mm); axillae strongly advanced, about 1/4 length of
407 mesoscutum, widely separated at transscutal articulation. Metapleuron small and triangular,
408 with few scattered setae. Metanotum length 0.06 mm, with smooth metascutellum not
409 reaching anterior margin of metanotum, lateral panels prominent, foveolate. Propodeum
410 transverse, rectangular, relatively flat, length 0.11 mm, reticulation regular, lateral propodeal
411 callus with dense and long pilosity; spiracles round to slightly elliptical.

412   *Wings.* Fore wing hyaline, immaculate, speculum present, basal cell pilose, costal cell
413   pilose throughout; humeral plate with at least two setae; basal vein apically pigmented and
414   angled relative to submarginal vein at about 9°; marginal vein slightly thickened relative to
415   postmarginal vein; stigmal vein about 0.4 times length of marginal vein; uncus bent at angle of
416   about 95° in direction of postmarginal vein, almost reaching it; postmarginal vein not reaching
417   apex of wing, 1.6 times as long as marginal vein. Hind wing apical 1/2 densely pilose, the rest
418   relatively bare; posterior marginal fringe short.
419   *Legs.* Pro-, meso- and metacoxa about same size, metacoxa dorsally with short pilosity.
420   Protibia with stout setae on anterior margin, other setae more inconspicuous. Basitarsal comb
421   longitudinal. Metatibia laterally flattened bearing two slender spurs, subequal in length.
422   *Metasoma.* Petiole (Mt_1) indistinct. Gaster lanceolate, length excluding ovipositor 0.98
423   mm; terga smooth and bare, hindmargins straight, length of terga: Mt_2: 0.21 mm, Mt_3: 0.09
424   mm, Mt_4: 0.15 mm, Mt_5: 0.18 mm, Mt_6: 0.14 mm, Mt_7: 0.11 mm, Mt_{8+9}: 0.1 mm. Cercus peg-
425   like, club-shaped, arising from under syntergum, bearing at least three setae. Hypopygium
426   folded downwards, slightly longer than 2/3 of the gaster. Ovipositor protruding about length of
427      $Mt_{8+9,}$ third valvulae broad.
428   **Male.** Unknown
429   **Specimen examined.** Female holotype (SMNS Bu-303) deposited in the SMNS. The piece of
430   amber was cut to reveal a better view of the specimen. Both pieces are free of other inclusions.
431   **Etymology.** The specific epithet "*barbata*" is the feminine form of the adjective "barbatus"
432   which means "bearded" and refers to the setose lower face of the specimen. The species name
433   treated as an adjective.
434
435   **Taxonomic remarks:**
436   It may seem counterintuitive to place the only two known males of Diversinitidae in a separate
437   genus than the two females, especially since sexual dimorphism is widely spread in
438   Chalcidoidea, most notably in Agaonidae and Eupelmidae resulting in a separation of sexes in
439   morphological analysis of females and males, when coded separately (Krogmann & Vilhelmsen,
440   2006; Heraty et al. 2013). In most other chalcidoids however, those modifications do not
441   include severe changes to the body plan and are often confined to body size (Hurlbutt, 1987)
442   and antennal characters (Barlin & Vinson, 1981). Males of *D. attenboroughi* differ from both
443   known females of Diversinitidae by the absence of a speculum on the forewing (versus
444   presence of speculum), an elongate petiole (versus a transverse petiole) and an antennal
445   insertion in the lower 1/3 of the face (versus an insertion near center of face). In addition, they
446   also lack each of the diagnostic characters of the other two females (see below) so that a
447   separate generic placement seems to be justified.
448   Furthermore, we consider the two females as not congeneric based on significant
449   morphological differences: *Glabiala barbata* differs from *B. caputaeria* in having the foramen
450   magnum situated higher than half the height of the head (versus lower third of head), a
451   pronotum only 1/3 length of mesoscutum (versus slightly shorter than mesoscutum), distinctly
452   advanced axillae (versus slightly advanced), a large and clearly anteriorly delimited frenum

453   (versus short and shallowly delimited) and a pilose basal cell on the forewing (versus a bare
454   basal cell).
455
456   **Results of cladistics analyses**
457   The new technology analysis in TNT found 39 most parsimonious trees (5,395 steps) with the
458   strict consensus tree being 5,861 steps long. The general topology of Heraty et al. (2013) could
459   largely be retrieved (Fig. 6). As in Heraty et al. (2013) the following families appeared as
460   monophyletic: Agaonidae, Chalcididae, Encyrtidae, Eurytomidae, Leucospidae, Mymaridae,
461   Rotoitidae, Signiphoridae, Torymidae (including Megastigminae) and Trichogrammatidae.
462   Contrary to Heraty et al. (2013), Aphelinidae and Eucharitidae could be retrieved as
463   monophyletic as well. In the unweighted new technology analysis Mymarommatoidea was
464   nested within Chalcidoidea as part of a larger clade containing the chalcidoid families
465   Aphelinidae, Mymaridae, Rotoitidae and Signiphoridae, as well as few members of
466   Tetracampidae and Eulophidae. Leucospidae were recovered as sistergroup to all other
467   Chalcidoidea, including Mymarommatoidea. The fossils were recovered as a monophyletic
468   group with *Micradelus rotundus* Walker, 1834 as sister taxon, nested within a large polytomy.
469   Monophyly of the fossils could be retrieved in all analyses, however general tree topology
470   changed considerably between different analyses. Using a traditional search without implied
471   weighting (Appendix S2), Diversinitidae were recovered as sistergroup of all other Chalcidoidea
472   with the inclusion of Mymarommatoidea. Mymaridae as well as Rotoitidae clustered in deeper
473   clades far from the base of the tree. Using a traditional search with implied weights (Appendix
474   S2), Mymarommatoidea were almost always recovered as sistergroup of Chalcidoidea (except k
475   = 45), but topology changed drastically with increasing k value, as did the position of the fossils
476   within the tree. In most analyses with k values below 30, the fossils were closely affiliated with
477   the pteromalid genera *Habritys brevicornis* (Ratzeburg, 1844), *Cheiropachus quadrum*
478   (Fabricius, 1787) and other interchanging groups. Above a k of 30, *M. rotundus* was recovered
479   as a sistertaxon (k = 35 and 55) or only *Cheiropachus quadrum* (k= 40), Diversinitidae were
480   sister to all Chalcidoidea including Mymarommatoidea (k = 45) or they were recovered close to
481   *Platynocheilus cuprifrons* (Nees, 1834) and some Ormocerinae (k = 50 and 60).

482   # Discussion
483   The placement of Diversinitidae within Chalcidoidea is well supported by several morphological
484   synapomorphies. One of the key autapomorphies of Chalcidoidea are the structurally unique
485   multiporous plate sensilla (mps) on the antennal funicle, with their apices free of their
486   surrounding antennal cuticle, the lack of an encircling groove around the sensillum and
487   elevation of the multiporous plate above the antennal cuticular level (Barlin & Vinson, 1981;
488   Gibson, 1986; Basibuyuk & Quicke, 1999). Evidently, Diversinitidae have modified sensilla (Figs.
489   1C, 4C and 4E), which are raised above the antennal surface and have their apices not
490   completely surrounded by the antennal cuticle. Some mps, although not all, even protrude
491   slightly over the funicular apices, as seen with backlighting under high magnification. The lack of
492   an encircling groove cannot be unequivocally confirmed, but overall resemblance to mps of

493   other Chalcidoidea is apparent. Within those groups of Proctotrupomorpha that are most
494   closely related to Chalcidoidea (Peters et al., 2017), few possess mps on their antennae. Only
495   Cynipoidea and the family Pelecinidae within Proctotrupoidea share this feature, but show a
496   quite different sensillar morphology with their sensillae usually only slightly raised above the
497   antennal surface and possessing a groove surrounding the multiporous plate (Basibuyuk &
498   Quicke, 1999). Other Proctotrupoidea, Ceraphronoidea, Platygastroidea and Diaprioidea
499   possess setiform multiporous sensilla sharing little resemblance with the morphology of
500   chalcidoid mps (Gibson, 1986; Basibuyuk & Quicke, 1999). Even Mymarommatidae, the putative
501   sister group of Chalcidoidea, lack mps (Gibson, 1986; Munro et al., 2011; Heraty et al., 2013).
502   Another diagnostic feature of Chalcidoidea is the presence of a free, externally visible
503   prepectus between the pronotum and mesopleuron, which separates the pronotum from the
504   tegula (Gibson, 1985, 1999; Gibson, Heraty & Woolley, 1999). Diversinitidae have a large
505   triangular prepectus, neither fused to the pronotum or mesopleuron nor hidden beneath its
506   lateral margin (Figs. 3A, 4A, 5A and 5B). Additionally, like in other chalcidoids, the mesothoracic
507   spiracle is situated between the lateral margin of the mesoscutum and the pronotum directly
508   adjacent to the anterodorsal edge of the prepectus, another autapomorphy of Chalcidoidea
509   that is correlated with its external prepectus. Gibson (1999) hypothesized the more dorsal
510   position of the spiracle compared to other hymenopterans as a derived state. Other
511   hymenopterans having a concealed prepectus or a prepectus that is fused either to the
512   pronotum or mesopleuron have the spiracle originating somewhat more ventrally below the
513   level of the mesoscutum between the pronotum and mesepisternum. In Rotoitidae and
514   Mymaridae, the spiracle is situated between the lateral margin of the mesoscutum and the
515   pronotum, but in Rotoitidae and some Mymaridae the prepectus is slender and more or less
516   concealed under the pronotum. Mymaridae and Rotoitidae are hypothesized as basalmost
517   clades within Chalcidoidea (Gibson, 1986; Munro, 2011; Heraty et al. 2013; Peters et al. 2018)
518   and their prepectal structure may represent a transitional state (Gibson, 1999).
519   Assignment of the fossils to extant chalcidoid families is not possible due to the lack of
520   synapomorphies. The most prominent characteristic of Diversinitidae separating them from all
521   other chalcidoid families, except for some Mymaridae, is the possession of mps on the first
522   flagellomere (F1) in both sexes. Mps on F1 is found in Chalcidoidea only in very few cases. In
523   Mymaridae, most males possess mps on their first flagellomere and also females of very few
524   species (e.g., within the genera *Eustochomorpha* Girault 1915 and *Yoshimotoana* Huber, 2015)
525   have them (Heraty et al., 2013; Huber, 2015, 2017). Some Aphelininae (Aphelinidae) and
526   Eucharitidae also seemingly possess mps on their apparent F1, but this is only because the first
527   two flagellomeres are fused (Heraty et al., 2013). In Diversinitidae, the first visible flagellomere
528   is undoubtedly F1 in both sexes. A well-developed F1 that has mps is hypothesized as
529   plesiomorphic for Chalcidoidea (Heraty et al., 2013), suggesting a basal position of
530   Diversinitidae within Chalcidoidea. During the evolution of Chalcidoidea, the first funicular likely
531   secondarily lost mps in association with the segment being reduced in length to a ring-like
532   segment (anellus) as is suggested by some chalcidoids that have additional funiculars reduced
533   to anelli-like segments that lack mps. In those, comparatively few chalcidoids with F1 lacking

534   mps but being reduced in size, F1 is hypothesized to have been secondarily lengthened (see
535   character 11 in Gibson, 2003).
536   *Burminata caputaeria* is the only species in Diversinitidae possessing a discernible line
537   above the scrobal area, corresponding in position and size to a transfacial sulcus (Fig. 4B). A
538   transfacial sulcus or transfacial line, situated below the anterior ocellus right above the
539   antennal scrobes, is found in many, mostly soft-bodied families including Aphelinidae,
540   Encyrtidae, Eulophidae, Eupelmidae (only *Phenaceupelmus* Gibson, 1995), Pteromalidae,
541   Tetracampidae and Trichogrammatidae (Gibson, 1986, 1995; Burks et al., 2011; Kim & Heraty,
542   2012; Heraty et al., 2013). This transfacial sulcus is structurally different from the trabeculae of
543   Mymaridae, which are formed by several interconnected lines of cuticular invaginations,
544   separating the vertex as a distinct sclerite from the face and are therefore regarded as
545   autapomorphic for this family (Königsmann, 1978; Schauff, 1984; Gibson, 1986). Rotoitidae as
546   well as Mymarommatidae lack any indication of a transfacial sulcus (Bouček & Noyes, 1987;
547   Gibson & Huber, 2000; Huber et al., 2008), leaving the ground plan of this character for
548   Chalcidoidea uncertain.
549   The labrum of Diversinitidae can be described as free, semicircular or rectangular, flap-
550   like and broadly continuous with the clypeal margin. Darling (1988) postulated, that the ground
551   plan structure of the labrum for Chalcidoidea is flap-like, with many evenly distributed setae.
552   Darling (1988) referred to the labrum of Chalcididae as "remarkably uniform and [...] similar to
553   that hypothesized as the ground plan for Apocrita", being heavily sclerotized and contiguous
554   with the margin of the clypeus, bearing long, tapered setae on the entire surface, arising from
555   distinct sockets. In Pteromalidae, the plesiomorphic state of the labrum is found in
556   Cleonyminae, and the labrum is also exposed in Spalangiinae, Asaphinae, Eunotinae and others,
557   which bear in comparison to Cleonyminae setae only along their apical margin (Darling, 1988).
558   Some Mymaridae also possess an exposed labrum (Heraty et al., 2013; Huber, 2013).In
559   Diversinitidae, the setal pattern is difficult to assess due to refractions within the amber in
560   conjunction with the small size of the specimens. Setae are at least situated along the apical
561   margin in Diversinitidae, but whether they are also found on the surface remains uncertain. If
562   so, the labrum might also be putatively plesiomorphic for Diversinitidae.
563   Diversinitidae possess a bidentate mandible, which is widely distributed in Chalcidoidea,
564   although a three or more dentate mandible appears to be more common (Bouček & Noyes,
565   1987; Woolley, 1988; Dzhanokmen, 1996; Gibson, Heraty & Woolley, 1999; Gibson & Huber,
566   2000; Heraty et al., 2013). The plesiomorphic state for this character is not known and has so
567   far not been discussed for Chalcidoidea comprehensively so that the evolutionary patterns are
568   difficult to assess. Putatively basal chalcidoid families already exhibit varied states of mandible
569   dentation, with Rotoitidae having bidentate mandibles, of which *Chiloe micropteron* Gibson and
570   Huber, 2000 has the upper tooth finely serrated (Bouček & Noyes, 1987; Gibson & Huber,
571   2000). Denticulation in Mymaridae varies greatly, with taxa lacking mandibular teeth
572   (*Erythmelus rosascostai* Ogloblin, 1934) to taxa with many fine denticles (*Eubroncus* spp.)
573   (Heraty et al., 2013; Jin & Li, 2014). The mymarid genera *Triadomerus* Yoshimoto, 1975
574   (extinct)*, Macalpinia* Yoshimoto, 1975 (extinct) and *Neotriadomerus* Huber, 2017 (extant) are

575 considered to be the most basal taxa in this family (Huber, 2017). In those early groups
576 mandibular dentation is already differing, with bidentate mandibles in *Triadomerus* and
577 *Macalpinia* and four uneven teeth in *Neotriadomerus*, hampering phylogenetic implications.
578 Outgroup comparisons with Mymarommatoidea and other Proctotrupomorpha (*sensu* Peters et
579 al., 2017) reveal that also in those groups, mandibular dentation is highly variable (Naumann &
580 Masner, 1985), not permitting a stable hypothesis about the groundplan state for Chalcidoidea.
581 However, Diversinitidae as putative basal group within Chalcidoidea might indicate that
582 bidentate mandibles could be plesiomorphic for at least a smaller subset of chalcidoid taxa.
583   A frenum is found in Diversinitidae, which is likely a plesiomorphic character state for
584 Chalcidoidea (Krogmann & Vilhelmsen, 2006). Presence is observed in many chalcidoid families
585 and in closely related groups, such as Mymarommatidae, Diapriidae and Platygastridae:
586 Scelioninae (Heraty et al., 2013), suggesting that it is probably part of the ground plan structure
587 for a subgroup of Proctotrupomorpha. Frenal morphology is used in species and subfamily
588 distinction of Torymidae and Pteromalidae (Graham, 1969; Graham & Gijswijt, 1998; Gibson,
589 2003). The morphological variation of the frenum led to frequent discussions about its
590 homology between different taxonomic groups (Grissell, 1995; Gibson, Heraty & Woolley, 1999;
591 Vilhelmsen & Krogmann, 2006).
592   Diversinitidae possess peg-like cerci, which are more or less spatulate. This character
593 state has been considered as plesiomorphic in contrast to a button-like cercus (Gibson, 2003)
594 or, alternatively, as an apomorphic character state, which has independently evolved in
595 different chalcidoid groups (Grissell, 1995). Grissell (1995) postulated that though peg-like cerci
596 are found in Agaonidae *sensu lato*, Eulophidae (*Entia* Hedqvist, 1974), Pteromalidae (*Cea*
597 Walker, 1837 and *Chromeurytoma* Cameron, 1912), Torymidae and Megastigmidae, evolution
598 of this character must have been convergent because positioning of the cerci is different in
599 those groups. On the other hand, Gibson (2003) stated that many other groups have peg-like
600 cerci as well, though most often not as prominent as those listed above, and therefore he
601 considered exerted, basally articulated cerci as plesiomorphic relative to more reduced, plate-
602 like cerci. In Heraty et al. (2013) many taxa were also coded as possessing exerted cerci to
603 various degrees, such as Perilampidae (*Brachyelatus* sp.), Tetracampidae (*Platynocheilus* sp.),
604 Signiphoridae (*Signiphora* sp.), Mymaridae (*Borneomymar* sp.) and Tanaostigmatidae
605 (*Protanaostigma* sp.). Outgroup comparison for this character in Heraty et al. (2013) is however
606 not conclusive due to sparse taxon sampling. Mymarommatidae (*Mymaromella* sp.) was coded
607 as not possessing exerted cerci, compared to Scelioninae (*Archaeoteleia mellea* Masner, 1968),
608 which show slightly exerted cerci and Diapriidae (*Belyta* sp.) without coding for this character.
609 The wide distribution of peg-like cerci within Chalcidoidea and its appearance in Mymaridae
610 and Diversinitidae supports the hypothesis that they represent the plesiomorphic state over
611 button-like cerci.
612   Presenting a solid phylogenetic placement of Diversinitidae within Chalcidoidea is not
613 unequivocally possible. All cladistic analyses provided evidence for monophyly of Diversinitidae,
614 but did not resolve further relationships within Chalcidoidea, because placement of the fossils
615 and general tree topology remained highly variable between different analysis. Although

616   *Micradelus rotundus* was recovered as sister taxon of Diversinitidae in the new technology
617   analysis and few traditional searches with implied weighting, a true relationship is highly
618   doubtful. *Micradelus rotundus* belongs to the pteromalid subfamily Pireninae. This subfamily is
619   characterized, though not only, by a reduced number of antennal segments and at least one
620   annellus (Bouček, 1988), which is also the most prominent difference to Diversinitidae, sharing
621   little resemblance to *M. rotundus* aside from morphologically variable characters like a
622   bidentate mandible, lack of pronotal collar, deep notauli or exposed labrum. Additionally
623   placement of *M. rotundus* was inconsistent over the different analyses and it behaved like a
624   rogue taxon, jumping between several clades. However, high inconsistencies in the analyses
625   were expected, because the morphology-only analysis in Heraty et al. (2013) was also poorly
626   resolved. Due to the expected high rate of homoplasious characters in morphological datasets
627   of Chalcidoidea (Krogmann & Vilhelmsen, 2006; Heraty et al., 2013), especially the results from
628   analyses with and without implied weighting differed considerably. With increasing k values,
629   the base of the phylogenetic tree was mostly relatively well resolved. Mymmarommatoidea
630   were the sistergroup to Chalcidoidea and Rotoitidae and Mymaridae were retrieved as basal
631   lineages within the superfamily. However, changes in topology of higher relationships were
632   substantial. Through weighing down putative homoplasious characters, implied weighting is
633   capable of better resolving polytomies (Goloboff et al. 2008). This can lead to trees with more
634   correctly resolved clades, but also higher risks of erroneous placements and more inconsistent
635   topologies as demonstrated by Congreve & Lamsdell (2016). Implied weighting can therefore be
636   considered as less conservative over equal weighing of characters. There are conflicting views
637   on whether parsimony analyses (Goloboff, Torres & Arias, 2017), as conducted in this study, or
638   likelihood analyses (O'Reilly et al. 2017) perform better with morphological datasets. A
639   comparison between likelihood and parsimony methods performed by Heraty et al. (2013) on
640   the original dataset, however, resulted in a generally congruent tree with equally poor
641   resolution of taxa. Additionally, probabilistic methods infer an evolutionary model on the data,
642   based on subjective decisions and previous knowledge (Goloboff, Torres & Arias, 2017). We
643   therefore favored the conservative equal weight parsimony analysis over implied weighting and
644   likelihood analyses.
645   Unfortunately, there is no evident autapomorphic character of Diversinitidae, which
646   would support its monophyly and all characters that exclude this group from existing families
647   are seemingly plesiomorphic (see above). However, based on the unique combination of
648   morphological characters (see diagnosis) and the preliminary results from the cladistic analyses
649   (Fig. 6), we decided to place the new fossils into their own family rather than leaving them
650   unplaced within Chalcidoidea.
651   Morphologically, Diversinitidae appear to be an early lineage of Chalcidoidea, possessing
652   many putatively plesiomorphic characters (see discussion above). Mymaridae are thought to
653   form the sister group to all remaining Chalcidoidea and can be traced back at least to the mid-
654   Cretaceous (Gibson, 1986; Munro et al., 2011; Heraty et al., 2013). Resemblance between
655   Diversinitidae and Mymaridae is not obvious and they only possess few putatively
656   symplesiomorphic characters, such as an exposed labrum and mps on the true F1 in males and

657   some females. In general, the mymarid body plan is characterized by a number of derived

658   autapomorphies that have not changed much since the Mid Cretaceous (Poinar & Huber, 2011).

659   The phylogenetic position of Diversinitidae can therefore not be established with certainty and

660   several hypotheses are possible. Firstly, Diversinitidae could represent the sister group to all

661   remaining chalcidoids, since they show a multitude of plesiomorphic characters, foremost mps

662   on F1. During chalcidoid evolution mps on F1 might have been lost at first in females (as in most

663   Mymaridae) and subsequently also in males (as in all remaining Chalcidoidea). This would

664   imply, that the prepectus in Diversinitidae was either secondarily enlarged or that Mymaridae

665   and Rotoitidae reduced the prepectal size during their evolution. Diversinitidae might also

666   represent a sistergroup to a smaller subset of Chalcidoidea, suggesting that mps on F1 were

667   independently lost at least twice, once in most females in Mymaridae and once in all other

668   Chalcidoidea. Prepectal size might therefore have been increased in other Chalcidoidea relative

669   to the prepectus in Mymaridae and Rotoitidae.

670   Biological implications of the new fossils are difficult to draw, because their phylogenetic

671   position is not fully resolved. Egg parasitoidism is hypothesized to be the putative ground plan

672   biology of Chalcidoidea (Heraty et al., 2013, Peters et al., 2018). Diversinitidae share a relatively

673   small body size, which unites nearly all egg parasitizing taxa, but does not necessarily exclude

674   ectoparasitoid groups. Body shape is not indicative, because both ecto- and endoparasitoids

675   can be very diverse in this regard. The length of the ovipositor and its saw-like tip might be

676   indicative for concealed hosts inside plant material.

677

Conclusion

679   With the newly described fossils we reduce a significant fossil gap of Chalcidoidea from the

680   Cretaceous. The wasp species described herein provide important new information of

681   chalcidoid evolution because they are early representatives of a parasitoid lineage that was just

682   beginning to evolve. One hundred million years later we merely start to fully appreciate the

683   great morphological diversity and ecological significance of these "green myriads in the peopled

684   grass" (Walker, 1839), which still rank among the least known of all insects. Further Cretaceous

685   fossils will hopefully reduce the fossil gap even further to help us to understand how chalcidoid

686   wasps have evolved and shaped the evolution of their arthropod host groups and associated

687   plant species, as one of the most diverse and influential insect groups that life has ever seen.

688

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693

References

695   Barlin MR., Vinson SB. 1981. Multiporous plate sensilla in antennae of the chalcidoidea

696   (Hymenoptera). *International Journal of Insect Morphology and Embryology* 10:29–42.

697   DOI: 10.1016/0020-7322(81)90011-8.

698   Barling N., Heads SW., Martill DM. 2013. A new parasitoid wasp (Hymenoptera: Chalcidoidea)
699   from the Lower Cretaceous Crato Formation of Brazil: The first Mesozoic Pteromalidae.
700   *Cretaceous Research* 45:258–264. DOI: 10.1016/j.cretres.2013.05.001.

701   Basibuyuk HH., Quicke DLJ. 1999. Gross morphology of multiporous plate sensilla in the
702   Hymenoptera (Insecta). *Zoologica Scripta* 28:51–67. DOI: 10.1046/j.1463-
703   6409.1999.00007.x.

704   Bläser M., Krogmann L., Peters RS. 2015. Two new fossil genera and species of Cerocephalinae
705   (Hymenoptera, Chalcidoidea, Pteromalidae), including the first record from the Eocene.
706   *ZooKeys* 545:89–100. DOI: 10.3897/zookeys.545.6470.

707   Bouček Z., Noyes JS. 1987. Rotoitidae, a curious new family of Chalcidoidea (Hymenoptera)
708   from New Zealand. *Systematic Entomology* 12:407–412. DOI: 10.1111/j.1365-
709   3113.1987.tb00212.x.

710   Bouček Z. 1988. Australasian Chalcidoidea (Hymenoptera). A biosystematic revision of genera
711   of fourteen families, with a reclassification of species. *CAB International, Wallingford,*
712   *Oxon, U.K., Cambrian News Ltd; Aberystwyth, Wales.*

713   Burks RA., Heraty JM., Gebiola M., Hansson C. 2011. Combined molecular and morphological
714   phylogeny of Eulophidae (Hymenoptera: Chalcidoidea), with focus on the subfamily
715   Entedoninae. *Cladistics* 27:581–605. DOI: 10.1111/j.1096-0031.2011.00358.x.

716   Burks RA., Heraty JM., Pinto JD., Grimaldi D. 2015. Small but not ephemeral: Newly discovered
717   species of Aphelinidae and Trichogrammatidae (Insecta: Hymenoptera: Chalcidoidea) from
718   Eocene amber. *Systematic Entomology* 40:592–605. DOI: 10.1111/syen.12124.

719   Campbell B., Heraty JM., Rasplus J-Y., Chan K., Steffen-Campbell J., Babcock C. 2000. Molecular
720   systematics of the Chalcidoidea using 28S-D rDNA. In: Austin AD., Dowton M eds.
721   *Hymenoptera: evolution, biodiversity and biological control. Fourth International*
722   *Hymenoptera Conference, held in Canberra, Australia, in January 1999.* Collingwood,
723   Australia: CSIRO, 59–73.

724   Compton SG., Ball AD., Collinson ME., Hayes P., Rasnitsyn AP., Ross AJ. 2010. Ancient fig wasps
725   indicate at least 34 Myr of stasis in their mutualism with fig trees. *Biology letters* 6:838–
726   842. DOI: 10.1098/rsbl.2010.0389.

727   Congreve CR., Lamsdell JC. 2016. Implied weighting and its utility in palaeontological datasets: A
728   study using modelled phylogenetic matrices. *Palaeontology* 59:447–462. DOI:
729   10.1111/pala.12236.

730   Coty D., Lebon M., Nel A. 2016. When phylogeny meets geology and chemistry: doubts on the
731   dating of Ethiopian amber. *Annales de la Société entomologique de France (N.S.)* 52:161–
732   166. DOI: 10.1080/00379271.2016.1230477.

733   Darling DC. 1988. Comparative morphology of the labrum in Hymenoptera: the digitate labrum

734   of Perilampidae and Eucharitidae (Chalcidoidea). *Canadian Journal of Zoology* 66:2811–
735   2835. DOI: 10.1139/z88-409.

736   Darling DC. 1996. A new species of Spalangiopelta (Hymenoptera; Pteromalidae; Ceinae) from
737   Dominican Amber: Phylogenetic and Biogeographic Implications. *Journal of Kansas*
738   *Entomological Society* 69:248–259.

739   Donoghue MJ., Doyle JA., Gauthier J., Kluge AG., Rowe T. 1989. The Importance of Fossils in
740   Phylogeny Reconstruction. *Annual Review of Ecology and Systematics* 20:431–460. DOI:
741   10.1146/annurev.es.20.110189.002243.

742   Dzhanokmen KA. 1996. Morphology of Mouthparts in Chalcids (Hymenoptera, Pteromalidae).
743   *Entomological Review* 76:547–552.

744   Engel M. 2009. The first fossil leptofoenine wasp (Hymenoptera, Pteromalidae): A new species
745   of Leptofoenus in Miocene amber from the Dominican Republic. *ZooKeys* 13:57–66. DOI:
746   10.3897/zookeys.13.159.

747   Engel MS., McKellar RC., Huber JT. 2013. A fossil species of the primitive mymarid genus
748   Borneomymar (Hymenoptera: Mymaridae) in Eocene Baltic amber. *Novitates*
749   *Paleoentomologicae* 5:1–8. DOI: 10.17161/np.v0i5.4651.

750   Farache FHA., Rasplus J-Y., Azar D., Pereira RAS., Compton SG. 2016. First record of a non-
751   pollinating fig wasp (Hymenoptera: Sycophaginae) from Dominican amber, with estimation
752   of the size of its host figs. *Journal of Natural History* 50:2237–2247. DOI:
753   10.1080/00222933.2016.1193646.

754   Gibson GAP. 1985. Some Pro- and Mesothoracic Structures Important for Phylogenetic Analysis
755   of Hymenoptera, With a Review of Terms Used for the Structures. *The Canadian*
756   *Entomologist* 117:1395–1443. DOI: 10.4039/Ent1171395-11.

757   Gibson GAP. 1986. Evidence for monophyly and relationships of Chalcidoidea, Mymaridae and
758   Mymarommatidae (Hymenoptera: Terebrantes). *The Canadian Entomologist* 118:205–240.
759   DOI: 10.4039/Ent118205-3.

760   Gibson GAP. 1995. Parasitic wasps of the subfamily Eupelminae: classification and revision of
761   world genera (Hymenoptera: Chalcidoidea: Eupelmidae). *Memoirs on entomology*
762   *international* 5:1–421.

763   Gibson GAP. 1999. Sister-group relationships of the Platygastroidea and Chalcidoidea
764   (Hymenoptera) - an alternate hypothesis to Rasnitsyn (1988). *Zoologica Scripta* 28:125–
765   138. DOI: 10.1046/j.1463-6409.1999.00015.x.

766   Gibson GAP. 2003. Phylogenetics and classification of Cleonyminae (Hymenoptera:
767   Chalcidoidea: Pteromalidae). *Memoirs on Entomology, International* 16:100–101.

768   Gibson GAP. 2008. Description of Leptoomus janzeni, n. gen. and n. sp. (Hymenoptera:
769   Chalcidoidea) from Baltic amber, and discussion of its relationships and classification
770   relative to Eupelmidae, Tanaostigmatidae and Encyrtidae. *Zootaxa* 1730:1–26.

771   Gibson GAP. 2009. Description of three new genera and four new species of Neanastatinae
772   (Hymenoptera, Eupelmidae) from Baltic amber, with discussion of their relationships to
773   extant taxa. *ZooKeys* 20:175–214. DOI: 10.3897/ zookeys.20.161.

774   Gibson GAP. 2013. The extinct Baltic amber genus Propelma Trjapitzin, a valid genus of
775   Neanastatinae (Hymenoptera, Eupelmidae). *ZooKeys* 283:59–69. DOI:
776   10.3897/zookeys.283.4665.

777   Gibson GAP., Heraty JM., Woolley JB. 1999. Phylogenetics and classification of Chalcidoidea and
778   Mymarommatoidea - a review of current concepts (Hymenoptera, Apocrita). *Zoologica
779   Scripta* 28:87–124. DOI: 10.1046/j.1463-6409.1999.00016.x.

780   Gibson GAP., Huber JT. 2000. Review of the family Rotoitidae (Hymenoptera: Chalcidoidea),
781   with description of a new genus and species from Chile. *Journal of Natural History*
782   34:2293–2314. DOI: 10.1080/002229300750037901.Gibson GAP., Read J., Huber JT. 2007.
783   Diversity, classification and higher relationships of Mymarommatoidea (Hymenoptera).
784   *Journal of Hymenoptera Research* 16:51–146.

785   Goloboff PA., Farris JS., Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*
786   24:774–786. DOI: 10.1111/j.1096-0031.2008.00217.x.

787   Goloboff PA., Carpenter JM., Arias JS., Rafael D., Esquivel, Rafael M. 2008. Weighting against
788   homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* 24:1–16.
789   DOI: 10.1111/j.1096-0031.2008.00209.x.

790   Goloboff PA., Torres A., Arias JS. 2017. Weighted parsimony outperforms other methods of
791   phylogenetic inference under models appropriate for morphology. *Cladistics*. DOI:
792   10.1111/cla.12205.

793   Graham MW. 1969. The Pteromalidae of North- Western Europe the British Museum (Natural
794   History). *Bulletin of the British Museum (Natural History) Entomology* Suppl. 16:1–909.

795   Graham MDV., Gijswijt M. 1998. Revision of the European species of Torymus Dalman (s. lat.)
796   (Hymenoptera: Torymidae). *Zoologische Verhandelingen* 317:1–202.

797   Grimaldi D., Engel MS. 2005. *Evolution of the Insects*. Cambridge: Cambridge University Press.

798   Grissell EE. 1995. Toryminae (Hymenoptera: Chalcidoidea: Torymidae): a redefinition, generic
799   classification and annotated world catalogue of species. *Memoirs on entomology
800   international* 2:1–474.

801   Gumovsky A., Perkovsky E. 2005. Taxonomic notes on Tetracampidae (Hymenoptera:
802   Chalcidoidea) with description of a new fossil species of Dipricocampe from Rovno amber.
803   *Entomological Problems* 35:123–130.

804   Gumovsky A., Perkovsky E., Rasnitsyn A. 2018. Laurasian ancestors and "Gondwanan"
805   descendants of Rotoitidae (Hymenoptera: Chalcidoidea): What a review of Late Cretaceous
806   Baeomorpha revealed. *Cretaceous Research* 84:286–322. DOI:
807   10.1016/j.cretres.2017.10.027.

808 Gunkel S., Rust J., Wappler T., Mayer C., Niehuis O., Misof B. 2017. A posteriori evaluation of
809   molecular divergence dates using empirical estimates of time-heterogenous fossilization
810   rates. *bioRxiv*. DOI: 10.1101/128314.

811 Heraty JM. 2009. Parasitoid biodiversity and insect pest management. In: *Foottit, B., Adler, P.*
812   *(Eds.), Insect Biodiversity: Science and Society.* Hague, Netherlands: Springer-Verlag Press,
813   445–462.

814 Heraty JM., Burks RA., Cruaud A., Gibson GAP., Liljeblad J., Munro J., Rasplus J-Y., Delvare G.,
815   Janšta P., Gumovsky A., Huber J., Woolley JB., Krogmann L., Heydon S., Polaszek A.,
816   Schmidt S., Darling DC., Gates MW., Mottern J., Murray E., Dal Molin A., Triapitsyn S., Baur
817   H., Pinto JD., van Noort S., George J., Yoder M. 2013. A phylogenetic analysis of the
818   megadiverse Chalcidoidea (Hymenoptera). *Cladistics* 29:466–542. DOI: 10.1111/cla.12006.

819 Heraty JM., Darling DC. 2009. Fossil Eucharitidae and Perilampidae (Hymenoptera:
820   Chalcidoidea) from Baltic Amber. *Zootaxa* 16:1–16.

821 Heraty JM., Gates ME. 2001. Diversity of Chalcidoidea (Hymenoptera) at El Edén Reserve,
822   Mexico. In: *In: Gómez-Pompa, A., Allen, M.F., Fedick, S.L., R.C. McKellar, M.S. Engel /*
823   *Cretaceous Research 35 (2012) 258e279 277 Jiménez-Osornio, J.J. (Eds.), Proceedings of the*
824   *21st Symposium in Plant Biology, "Lowland Maya Area: Three Millenia at the Human-*
825   *Wildland Interface".* Haworth Press, New York, NY. 277–292.

826 Huber JT. 2005. The gender and derivation of genus-group names in Mymaridae and
827   Mymarommatidae (Hymenoptera). *Acta Societatis Zoologicae Bohemicae* 69:167–183.

828 Huber JT. 2013. Revision of Ooctonus in the Neotropical region and comparison with
829   Boudiennyia (Hymenoptera: Mymaridae). *Zootaxa* 3701:1–23. DOI:
830   10.11646/zootaxa.3701.1.1

831 Huber JT. 2015. World reclassification of the Gonatocerus group of genera (Hymenoptera:
832   Mymaridae). *Zootaxa* 3967:1. DOI: 10.11646/zootaxa.3967.1.1.

833 Huber JT. 2017. Eustochomorpha Girault, Neotriadomerus gen. n., and Proarescon gen. n.
834   (Hymenoptera, Mymaridae), early extant lineages in evolution of the family. *Journal of*
835   *Hymenoptera Research* 57:1–87. DOI: 10.3897/jhr.57.12892.

836 Huber JT., Gibson GAP., Bauer LS., Liu H., Gates MW. 2008. The Genus Mymaromella
837   (Hymenoptera: Mymarommatidae) in North America, with a Key to Described Extant
838   Species. *Journal of Hymenoptera Research* 17:175–194.

839 Hurlbutt B. 1987. Sexual size dimorphism in parasitoid wasps. *Biological Journal of the Linnean*
840   *Society* 30:63–89. DOI: 10.1111/j.1095-8312.1987.tb00290.x.

841 Jin X-X., Li C-D. 2014. First record of Eubroncus (Hymenoptera, Mymaridae) from China, with
842   description of three new species. *ZooKeys* 399:29–41. DOI: 10.3897/zookeys.399.6996.

843 Kaddumi HF. 2005. *Amber of Jordan The Oldest Prehistoric Insects in Fossilized Resin.*
844   Publications of the Eternal River Museum of Natural History, Amman.

845 Kim JW., Heraty JM. 2012. *A phylogenetic analysis of the genera of Aphelininae (Hymenoptera:*
846   *Aphelinidae), with a generic key and descriptions of new taxa*. DOI: 10.1111/j.1365-
847   3113.2012.00625.x.

848 Königsmann E. 1978. Das phylogenetische System der Hymenoptera Teil 3: "Terebrantes"
849   (Unterordnung Apocrita). *Deutsche Entomologische Zeitschrift* 25:1–55. DOI:
850   10.1002/mmnd.19780250102.

851 Krogmann L. 2013. First fossil record of cerocephaline wasps with a description of a new genus
852   and species from Dominican amber (Hymenoptera: Chalcidoidea: Pteromalidae:
853   Cerocephalinae). *Historical Biology* 25:43–49. DOI: 10.1080/08912963.2012.685729.

854 Krogmann L., Vilhelmsen L. 2006. Phylogenetic implications of the mesosomal skeleton in
855   Chalcidoidea (Hymenoptera, Apocrita) - Tree searches in a jungle of homoplasy.
856   *Invertebrate Systematics* 20:615–674. DOI: 10.1071/IS06012.

857 McKellar RC., Engel MS. 2012. Hymenoptera in Canadian Cretaceous amber (Insecta).
858   *Cretaceous Research* 35:258–279. DOI: 10.1016/j.cretres.2011.12.009.

859 Munro JB., Heraty JM., Burks RA., Hawks D., Mottern J., Cruaud A., Rasplus J-Y., Jansta P. 2011.
860   A Molecular Phylogeny of the Chalcidoidea (Hymenoptera). *PLoS ONE* 6:e27023. DOI:
861   10.1371/journal.pone.0027023.

862 Noyes JS. 1978. On the numbers of genera and species of Chalcidoidea (Hymenoptera) in the
863   World. *Entomologist's Gazette* 29:163–164.

864 Noyes JS. 2000. Encyrtidae of Costa Rica (Hymenoptera: Chalcidoidea), Part 1: The Subfamily
865   Tetracneminae, Parasitoids of Mealybugs (Homoptera: Pseudococcidae). *Memoirs of the*
866   *Entomological Institute* 62.

867 Noyes JS. 2017.Universal Chalcidoidea Database. *Available at*
868   *http://www.nhm.ac.uk/chalcidoids* (accessed 24 November 2017).

869 O'Reilly JE., Puttick MN., Pisani D., Donoghue PCJ. 2018. Probabilistic methods surpass
870   parsimony when assessing clade support in phylogenetic analyses of discrete
871   morphological data. *Palaeontology* 61:105–118. DOI: 10.1111/pala.12330.

872 Penney D. 2010. *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific
873   Press.

874 Peters RS., Krogmann L., Mayer C., Donath A., Gunkel S., Meusemann K., Kozlov A.,
875   Podsiadlowski L., Petersen M., Lanfear R., Diez PA., Heraty J., Kjer KM., Klopfstein S., Meier
876   R., Polidori C., Schmitt T., Liu S., Zhou X., Wappler T., Rust J., Misof B., Niehuis O. 2017.
877   Evolutionary History of the Hymenoptera. *Current Biology* 27:1013–1018. DOI:
878   10.1016/j.cub.2017.01.027.

879 Peters RS., Niehuis O., Gunkel S., Bläser M., Mayer C., Podsiadlowski L., Kozlov A., Donath A.,
880   van Noort S., Liu S., Zhou X., Misof B., Heraty J., Krogmann L. 2018. Transcriptome
881   sequence-based phylogeny of chalcidoid wasps (Hymenoptera: Chalcidoidea) reveals a

882   history of rapid radiations, convergence, and evolutionary success. *Molecular*
883   *Phylogenetics and Evolution* 120:286–296. DOI: 10.1016/j.ympev.2017.12.005.

884   Poinar G., Huber JT. 2011. A new genus of fossil mymaridae (Hymenoptera) from cretaceous
885   amber and key to cretaceous mymarid genera. *ZooKeys* 130:461–472. DOI:
886   10.3897/zookeys.130.1241.

887   Schauff ME. 1984. The Holarctic genera of Mymaridae (Hymenoptera: Chalcidoidea). *Memoirs*
888   *of the Entomological Society of Washington* 12:1–67.

889   Schmidt AR., Perrichot V., Svojtka M., Anderson KB., Belete KH., Bussert R., Dörfelt H., Jancke S.,
890   Mohr B., Mohrmann E., Nascimbene PC., Nel A., Nel P., Ragazzi E., Roghi G., Saupe EE.,
891   Schmidt K., Schneider H., Selden PA., Vávra N. 2010. Cretaceous African life captured in
892   amber. *Proceedings of the National Academy of Sciences of the United States of America*
893   107:7329–7334. DOI: 10.1073/pnas.1000948107.

894   Shi G., Grimaldi DA., Harlow GE., Wang J., Wang J., Yang M., Lei W., Li Q., Li X. 2012. Age
895   constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research*
896   37:155–163. DOI: 10.1016/j.cretres.2012.03.014.

897   Simutnik SA., Perkovsky EE., Gumovsky AV. 2014. Review of the Late Eocene Encyrtidae
898   (Hymenoptera, Chalcidoidea) with a description of the first fossil genus with filum
899   spinosum. *Paleontological Journal* 48:65–73. DOI: 10.1134/S0031030114010122.

900   Slater GJ., Harmon LJ., Alfaro ME. 2012. Integrating fossils with molecular phylogenies improves
901   inferences of trait evolution. *Evolution* 66:3931–3944. DOI: 10.5061/dryad.q96d7.

902   Vilhelmsen L., Krogmann L. 2006. Skeletal anatomy of the mesosoma of Palaeomymar
903   anomalum (Blood & Kryger, 1922)(Hymenoptera: Mymarommatidae). *Journal of*
904   *Hymenoptera Research* 15:290–306.

905   Walker F. 1839. *Monographia Chalcidium I*. London: Hyppolitus Baillière.

906   Ware JL., Barden P. 2016. Incorporating fossils into hypotheses of insect phylogeny. *Current*
907   *Opinion in Insect Science* 18:69–76. DOI: 10.1016/j.cois.2016.10.003.

908   Weiblen GD. 2002. How to be a fig wasp. *Annual Review of Entomology* 47:299–330.

909   Woolley JB. 1988. Phylogeny and classification of the Signiphoridae (Hymenoptera:
910   Chalcidoidea). *Systematic Entomology* 13:465–501. DOI: 10.1111/j.1365-
911   3113.1988.tb00256.x.

912   Yoder MJ., Mikó I., Seltmann KC., Bertone MA., Deans AR. 2010. A Gross Anatomy Ontology for
913   Hymenoptera. *PLoS ONE* 5:e15991. DOI: 10.1371/journal.pone.0015991.

914   Yoshimoto CM. 1975. Cretaceous chalcidoid fossils from canadian amber. *The Canadian*
915   *Entomologist* 107:499–528.

Abbreviations for morphological structures.

HAO-Numbers inserted in the following link (*) provide direct access to referenced structures in the HAO database (http://purl.obolibrary.org/obo/*).

Abbreviation	Morphological structure	HAO-Number
ax	Axilla	HAO_0000155
bv	Basal vein	HAO_0000170
cer	Cercus	HAO_0000191
cx_1	Procoxa	HAO_0001122
cx_2	Mesocoxa	HAO_0000635
cx_3	Metacoxa	HAO_0000587
F1-12	Flagellomeres 1-12	HAO_0000342
frn	Frenum	HAO_0000355
lbr	Labrum	HAO_0000456
mps	Multiporous plate sensillum	HAO_0000640
msc	Mesoscutum	HAO_0000575
Mt	Metasomal tergite	HAO_0002005
Mt_{8+9}	Syntergum	HAO_0000987
no_1	Pronotum	HAO_0000853
no_3	Metanotum	HAO_0000603
not	Notaulus	HAO_0000647
ov	Ovipositor	HAO_0000679
pl_1	Propleuron	HAO_0000862
pl_2	Mesopleuron	HAO_0000566
pre	Prepectus	HAO_0000811
prp	Propodeum	HAO_0000051
ptl	Petiole	HAO_0000020
set	Seta	HAO_0002299
sctl	Mesoscutellum	HAO_0000574
tfs	Transfacial sulcus	HAO_0002016
tgl	Tegula	HAO_0000993
tps	Tentorial pit	HAO_0000999

Figure 1

Digital microscopic images of *Diversinitus attenboroughi* holotype, male.

(A) Dorsal habitus. (B) Head frontal. (C) Antenna detail dorsal. (D) Head and mesosoma dorsal. (E) Wings left side. Scale bars: (A, C) 0.5 mm, (B, E) 2.5 mm, (D) 0.2 mm. Abbreviations: ax = axilla, F1/11 = funicular 1/11, frn = frenum, lbr = labrum, mps = multiporous plate sensilla, msc = mesoscutum, no_1 = pronotum, not = notaulus, sctl = scutellum, ptl = petiole. Photos by M Haas.
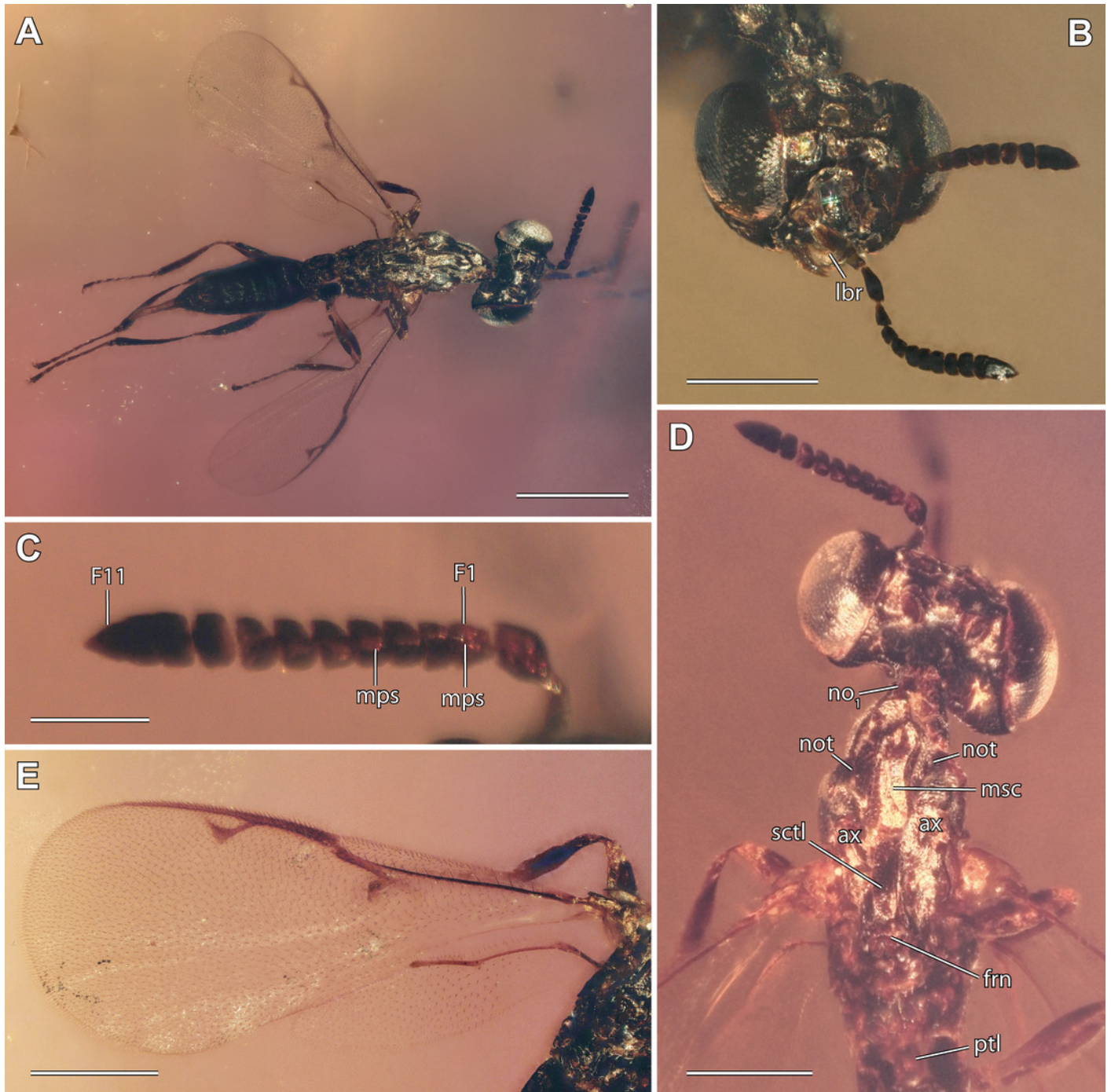
Figure 2

Digital microscopic images of *Diversinitus attenboroughi* lateral habitus, males.

(A) Holotype. (B) Paratype. Scale bars: 0.5 mm. Photos by M Haas.
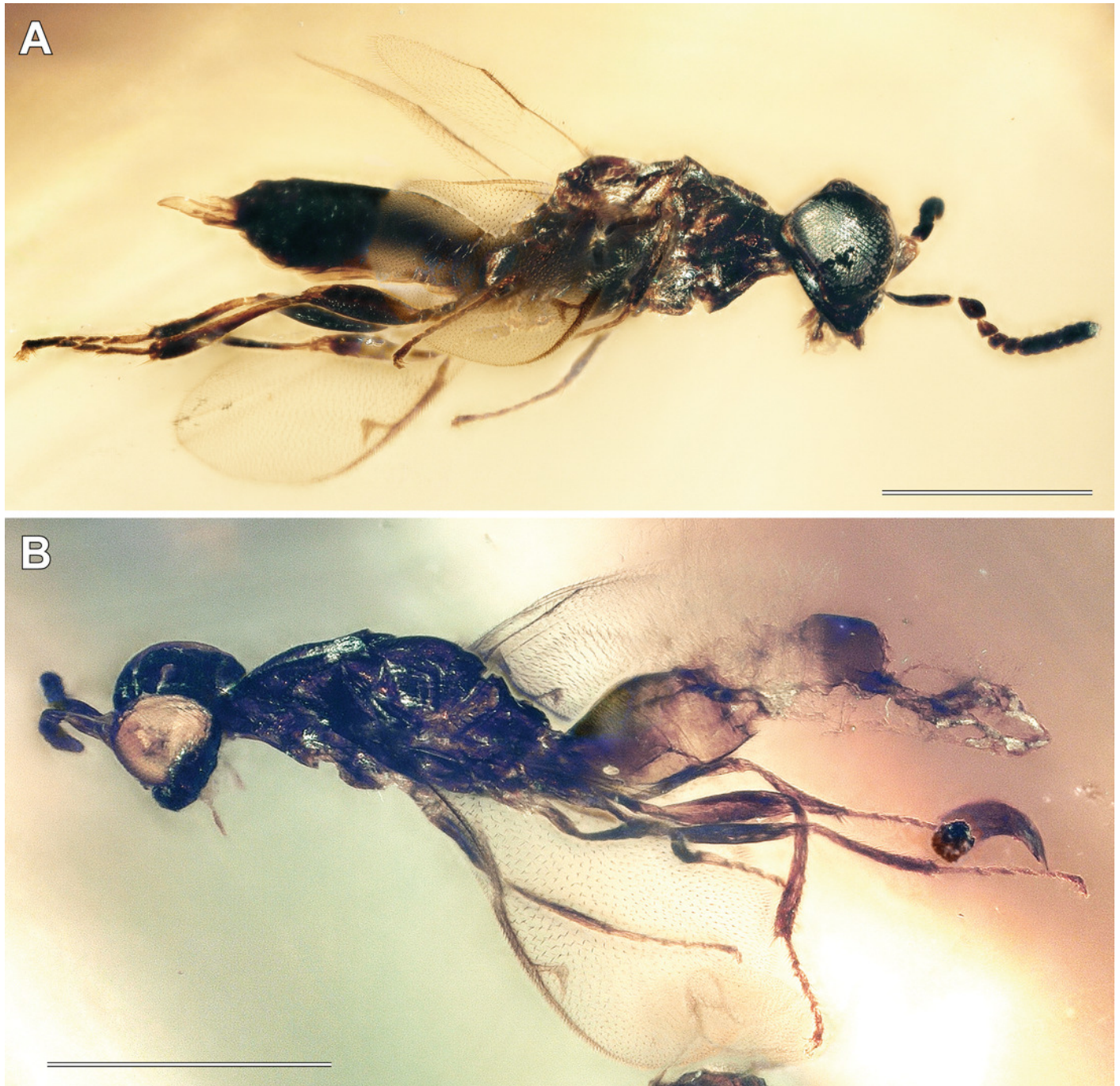
Figure 3

Habitus drawings of *Diversinitus attenboroughi* holotype, male.

(A) Habitus lateral. (B) Habitus dorsal. Scale bars: 0.5 mm. Abbreviations: ax = axilla, bv = basal vein, cer = cercus, $cx_{1/2/3}$ = pro-/ meso-/ metacoxa, F1/11 = funicular 1/11, frn = frenum, msc = mesoscutum, Mt_2 = metasomal tergum 2, Mt_{8+9} = syntergum, no_1 = pronotum, not = notaulus, pl_1 = propleuron, pre = prepectus, prp = propodeum, ptl = petiole, sctl = scutellum, tgl = tegula. Drawings by M Haas.
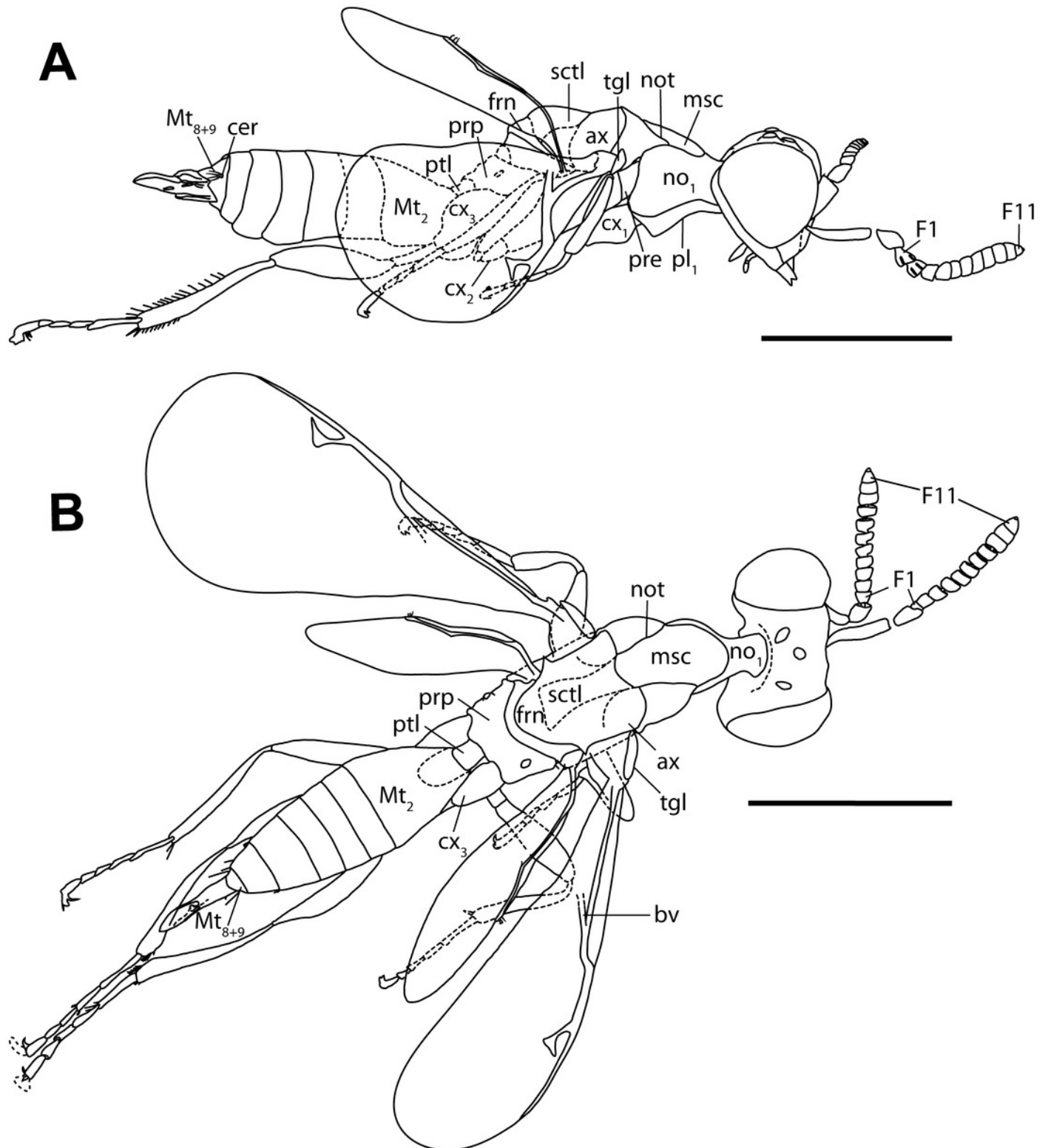
Figure 4

Digital microscopic images of *Burminata caputaeria* and *Glabiala barbata*, female.

(A, B, C) *Burminata caputaeria* (A) lateral habitus. (B) Head frontal. (C) Right antenna lateral. (D, E, F, G) *Glabiala barbata* (D) lateral habitus. (E) Left antenna dorsal. (F) Mesosoma lateral. (G) Mesosoma dorsal. Scale bars: (A, D) 0.5 mm, (B, C, E, F, G) 0.1 mm. Abbreviations: ax = axilla, F1/11 = funicular 1/11, frn = frenum, lbr = labrum, mps = multiporous plate sensilla, msc = mesoscutum, no_1 = pronotum, no_3 = metanotum, sctl = scutellum, tfs = transfacial sulcus, tps = tentorial pits. Photos by M Haas.

Figure 5

Habitus drawings of female holotypes of *Burminata caputaeria* (A) and *Glabiala barbata* (B).

Scale bars: 0.5 mm. Abbreviations: ax = axilla, bv = basal vein, cer = cercus, $cx_{1/2/3}$ = pro-/ meso-/ metacoxa, F1/11 = funicular 1/11, msc = mesoscutum, Mt_2 = metasomal tergum 2, Mt_{8+9} = syntergum, no_1 = pronotum, not = notaulus, ov = ovipositor, $pl_{1/2}$ = pro-/ mesopleuron, pre = prepectus, prp = propodeum, sctl = scutellum, tgl = tegula. Drawings by M Haas.

A

ov

cer
Mt$_{8+9}$

frn

Mt$_2$

sctl

ax

not msc

no$_1$

cx$_1$

pl$_1$

pl$_2$

cx$_3$

pre

tgl

cx$_2$

bv

F1

F11

B

cer
Mt$_{8+9}$

ov

bv frn

Mt$_2$

not

sctl

msc

ax

no$_1$

prp$_0$

cx$_3$

pl$_2$

cx$_1$

cx$_2$

pre

tgl

set
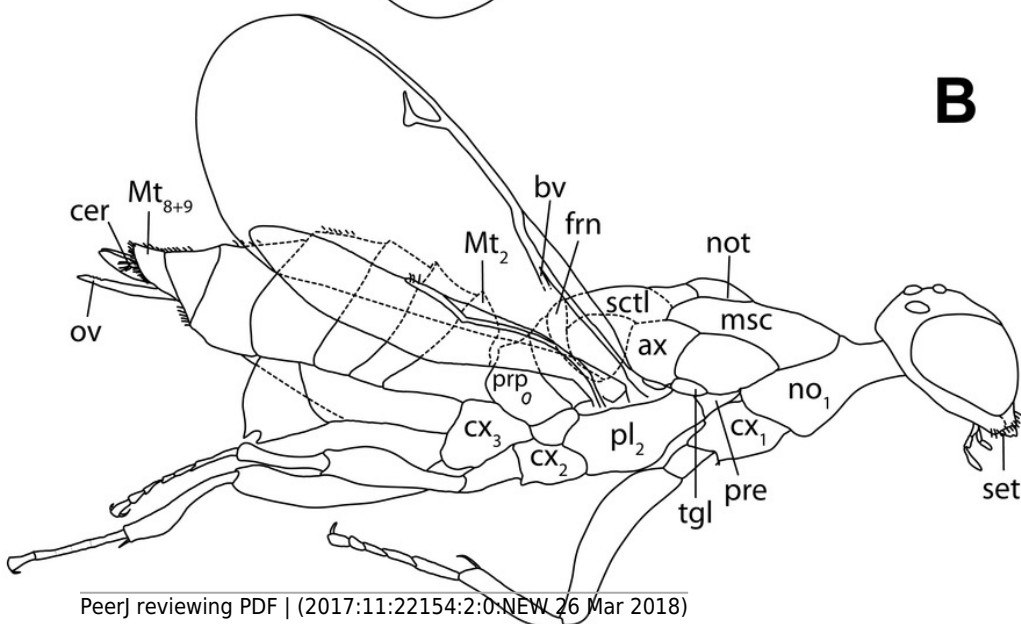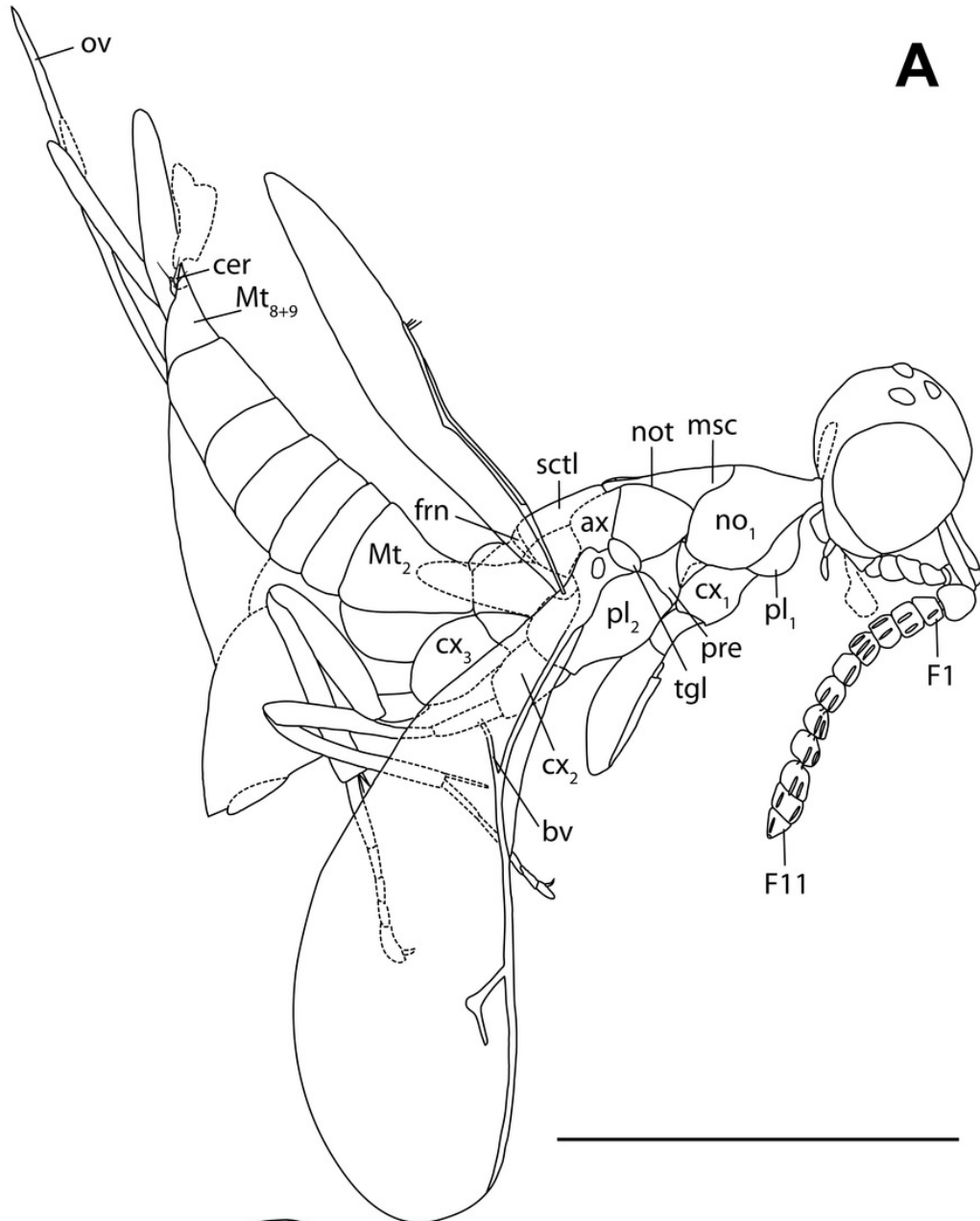
Figure 6

Phylogenetic placement of Diversinitidae within Chalcidoidea based on morphological characters.

Strict consensus tree calculated from 39 trees (tree length = 5861, CI = 0.077, RI = 0.567, 232 characters and 304 taxa, equal weights, new technology search). Yellow box highlights described fossils. Mymarommatoidea, potential sistergroup to all Chalcidoidea, collapsed and highlighted in blue. Green names indicate monophyletic and therefore collapsed families. Red names indicate monophyletic and therefore collapsed pteromalid subfamilies. Grey names indicate single taxa. For more information on the dataset of extant taxa refer to Heraty et al. (2013).