A new lineage of Cretaceous jewel wasps (Chalcidoidea: Diversinitidae) (#22154)

First submission

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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. Therefore, the evolutionary history of Chalcidoidea is still poorly understood, hampering recent efforts to uncover the phylogenetic relationships within this group. The three species *Diversinitus attenboroughi* gen. & sp. n., *Glabiala barbata* gen. & sp. n. and *Burminata caputaeria* gen. & sp. n. are described from Lower Cretaceous Burmese amber. Placement in Chalcidoidea is supported by the presence of multiporous plate sensilla and an exposed prepectus. The new fossils can be excluded from all extant chalcidoid lineages by the presence of multiporous plate sensilla on the first flagellomere in both sexes and a combination of other putatively plesiomorphic characters. Accordingly, the new family Diversinitidae is proposed 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 confirmed 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 few species of unclear 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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Abstract

Jewel wasps (Hymenoptera: Chalcidoidea) are extremely species-rich today, but have a sparse fossil record from the Cretaceous, the period of their early diversification. Therefore, the evolutionary history of Chalcidoidea is still poorly understood, hampering recent efforts to uncover the phylogenetic relationships within this group. The three species *Diversinitus attenboroughi* gen. & sp. n.*,* *Glabiala barbata* gen. & sp. n. and *Burminata caputaeria* gen. & sp. n. are described from Lower Cretaceous Burmese amber. Placement in Chalcidoidea is supported by the presence of multiporous plate sensilla and an exposed prepectus. The new fossils can be excluded from all extant chalcidoid lineages by the presence of multiporous plate sensilla on the first flagellomere in both sexes and a combination of other putatively plesiomorphic characters. Accordingly, the new family Diversinitidae is proposed 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 confirmed 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 few species of unclear phylogenetic placement, the newly described members of Diversinitidae are among the earliest known chalcidoids and advance our knowledge of their Cretaceous diversity.

Introduction

Jewel wasps (Hymenoptera: Chalcidoidea) are estimated to constitute one of the most species-rich insect lineages. Estimated numbers range from 100,000 to 500,000 species and they may comprise 10% of insect diversity, but only about 22,000 species have been described to date (Noyes, 1978, 2000, 2017; Heraty & Gates, 2003). Their evolutionary success is mirrored by and resulting from their varied biological life styles, mainly as parasitoids of 13 different insect orders, but also as phytophages, rendering them essential as regulators for other insects and as important pollinators (Gibson, Heraty & Woolley, 1999; Weiblen, 2002; Heraty, 2009). Despite recent progress (Munro et al., 2011; Heraty et al., 2013; Peters et al., subm.), the relationships among certain chalcidoid taxa as well as their evolutionary history still remain unresolved. The role of fossils in a phylogenetic framework is pivotal to understand some of the evolutionary processes, which led to chalcidoid megadiversity and provide valuable information on morphological character evolution. Reliably placed fossils can shed light on the minimum age of taxa and allow calibrations of molecular phylogenies to resolve timing and patterns of biological shifts (Ware & Barden, 2016).

Numerous chalcidoid fossils have been reported from different amber deposits (Grimaldi & Engel, 2005; Penney, 2010), but few of them have been formally described. Most described chalcidoids stem from young (Eocene and Miocene) deposits, which already host an astonishing phylogenetic diversity of taxa (Darling, 1996; Gibson, 2008, 2013; Engel, 2009; Heraty & Darling, 2009; Compton et al., 2010; McKellar & Engel, 2012; Krogmann, 2013; Simutnik, Perkovsky & Gumovsky, 2014; Bläser, Krogmann & Peters, 2015; Burks et al., 2015;

Farache et al., 2016). It is believed that most chalcidoid families diversified after the Upper Cretaceous (Heraty et al., 2013) during a period that falls within a major gap in the fossil record. The earliest reported and described chalcidoids date back to the Lower Cretaceous period, 106–115 million years ago (Kaddumi, 2005; Grimaldi & Engel, 2005; Penney, 2010; Barling, Heads & Martill, 2013).

The fossil *Minutoma yathribi* Kaddumi, 2005 is currently the oldest described putative chalcidoid wasp from Jordanian amber, dated about 115 million years old (Kaddumi, 2005). It was placed in Mymaridae, which is considered to be the sister group to all other chalcidoid families (Heraty et al., 2013). Heraty et al. (2013) however commented, that the photo of *M. yathribi* rather suggests affiliation with Bouceklytinae, an extinct subfamily of uncertain placement. Kaddumi (2005) also mentioned a putative eupelmid fossil, which was not formally described. The oldest fossil record of Eupelmidae is from the Eocene (Gibson, 2009), and we consider the concerned fossil as a member of Scelionidae based on the metasomal and wing venational characters depicted in Kaddumi (2005, figs 95–97). *Myanmymar aresconoides* Poinar & Huber, 2011 represents the oldest verified fossil record of Chalcidoidea, dating back to the Early Upper Cretaceous, approximately 99 mya (Shi et al., 2012). Although there are some reports of Eulophidae and Chalcididae from the transition between the Upper and Lower Cretaceous, no information concerning their validity is available (Penney, 2010).

Schmidt et al. (2010) reported Eulophidae, Trichogrammatidae and Mymaridae from Ethiopian amber, which they dated as Upper Cretaceous (around 94 mya). Though the family identifications might be right, doubt was raised concerning the age of Ethiopian amber. Coty, Lebon & Nel (2016) described a myrmecine ant from the same deposit, which could readily be described in the tribe Crematogastrini, suggesting through phylogenetic dating that the specimen cannot be of Cretaceous age. Subsequent analyses showed, that indeed, though not completely unequivocal, evidence strongly suggested that Ethiopian amber is of Cenozoic origin, probably at least 50 my younger than formerly suspected (Coty, Lebon & Nel, 2016). The first verified reports of the families Trichogrammatidae and Aphelinidae were however reported from Baltic amber, about 44 million years old (Burks et al., 2015).

From the Upper Cretaceous Canadian amber (~75 mya), fossil Tetracampidae and Trichogrammatidae were recorded (Yoshimoto, 1975). Of the four genera, *Carpenteriana, Macalpinia, Protooctonus* and *Triadomerus* described by Yoshimoto (1975) in the Mymaridae, *Protooctonus* was later transferred to Mymarommatidae and synonymized under *Archaeromma* Yoshimoto, 1975 (Gibson, Read & Huber, 2007). The genus of *Enneagmus* Yoshimoto, 1975, originally described as Trichogrammatidae was transferred by Huber (2005) to the Mymaridae. Though not revised in detail, the placement of the genera *Distylopus, Bouceklytus* and *Baeomorpha* described by Yoshimoto (1975) within the Teracampidae is erroneous, and even the position of *Distylopus* within the Chalcidoidea is unlikely (Gumovsky & Perkovsky, 2005; Heraty & Darling, 2009). McKellar & Engel (2012) additionally mention Torymidae and Eupelmidae as possibly present in Canadian amber, although the specimens have not been thoroughly studied to date.

A putative member of Pteromalidae, *Parviformosus wohlrabeae* Barling, Heads & Martill, 2013, was described from limestone originating from the Crato formation, dated to the Aptian period, about 110 mya. Because of its age, it might be considered as one of the oldest known fossils of Chalcidoidea, but evidence for its placement is lacking, because none of the diagnostic features of Chalcidoidea was preserved (Barling, Heads & Martill, 2013; Farache et al., 2016). It was placed within Pteromalidae only because of a putative habitual resemblance to Sycophaginae (now Agaonidae sensu Heraty et al., 2013). The limited morphological characters of *P. wohlrabeae* need to be reassessed before phylogenetic conclusions can be drawn from this fossil. The original placement of *P. wohlrabeae* in Pteromalidae is in this case highly problematic as the family in its current concept is polyphyletic (Campbell et al., 2000; Krogmann & Vilhelmsen, 2006; Heraty et al., 2013).

We here contribute to the scarce Cretaceous fossil record of Chalcidoidea by describing three new fossil genera and species. These fossils lack all apomorphies of Mymaridae, but possess plesiomorphic features that are not shared by any other extant chalcidoid lineage and are placed in a separate family.

Material & Methods

Specimens

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

Imaging

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

Terminology

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

Cladistic analysis

Morphological cladistic analyses were performed using the 233 characters from Heraty et al. (2013). Their comprehensive matrix, encompassing 19 families, 78 subfamilies, 268 genera and 283 species of Chalcidoidea, was used as basis for the here conducted phylogenetic analysis. Due to conservation state and inaccessibility, some characters could not be scored without reasonable doubt and were marked as unknown "?" (Table S1). Analyses were conducted using the program TNT ver. 1.5 (Goloboff, Farris & Nixon, 2008) following Heraty et al. (2013) in analysis setup. A sectorial search under new technology was done, using a ratchet weighting probability of 5% with 50 iterations, tree-drifting of 50 cycles, tree-fusing of five rounds and a best score hit of 10 times. Additionally, traditional searches with and without implied weighting were conducted to test consistency of the results. Implied weights of k= 1, 3, 5, 10, 15, 20, 25 and 30 were used with 1000 replications for the analyses.

Nomenclature

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: LSID urn:lsid:zoobank.org:pub:B936D52D-7165-47CE-9C3E-0B79A17AC5AC. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Results

Systematic Palaeontology

Diversinitidae fam. n.

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

Diagnosis. Male and female antenna 13-segmented, with eight funicular segments and three-segmented clava (plus distinct terminal button). All funicular segments (including first one) with row of multiporous plate sensilla. Eyes large and without pilosity, not divergent ventrally. Labrum flap-like, exposed. Head with transverse sulcus dorsal to antennal scrobe, occipital carina absent. Independent prepectus exposed, large and triangular. Wings with short marginal fringe. Notauli deep and complete. Male axillae only slightly advanced, female axillae distinctly advanced. Frenal groove developed. Propodeal spiracles situated almost in middle of propodeum, slightly closer to anterior propodeal margin. Trochanters distinctly elongate at least one quarter length of femora. Male forewing fully pilose, female forewing with speculum. Postmarginal vein distinctly longer than marginal vein. Basal vein developed. Hindwing normal, not stalked. Male petiole distinct, at least as long as broad, female petiole hardly visible in dorsal view. Cerci peg-like. Syntergum (Mt_{8+9}) present.

Key to species of Diversinitidae

1. Antenna symmetric with segments transverse (Fig. 1B and Fig. 2). Axillae not advanced (Fig. 1D and Fig. 2B). Mesotibial spur half as long as basitarsus.
Diversinitus attenboroughi

- Antenna asymmetric (Fig. 3C and E). Axillae advanced into mesoscutum (Fig. 4). Mesotibial spur almost as long as basitarsus. **2.**

2. Oral fossa surrounded by long hairs (Fig. 4B). Pronotum only 0.4 times as long as mesoscutum (Fig. 3G). Head densely pilose. Basal funicular segments longer than broad with following segments getting increasingly more quadrate/transverse (Fig, 3C). Foramen magnum situated halfway down the head (Fig. 4B). Funicular segments somewhat thistle-shaped (Fig. 3C). Axillae advanced almost 1/4 length of mesoscutum (Fig. 3G). Short but dense pilosity on mesoscutum and mesoscutellum. Ovipositor protruding only slightly (Fig. 3D and Fig. 4B). ***Glabiala barbata***

- Oral fossa bare (Fig. 3B). Pronotum 0.8 times as long as mesoscutum (Fig. 4A). Head mainly bare (Fig. 3B). All funicular segments rather transverse to quadrate (Fig. 3C). Foramen magnum at lower third of head (Fig. 4A). Axilla advanced only 1/7 length of mesoscutum (Fig. 4A). Pilosity on mesoscutum and mesoscutellum less dense. Ovipositor protruding almost half the length of the metasoma (Fig. 3A and Fig. 4A).
Burminata caputaeria

***Diversinitus* gen. n.**
LSID urn:lsid:zoobank.org:act:F8B422B0-C83B-4718-8042-D7F07EA0DF7F

Type species. *Diversinitus attenboroughi* sp. n.

Diagnosis. Antenna symmetrical. Axillae not advanced. Forewing completely pilose. Mesotibial spur half as long as basitarsus.

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

***Diversinitus attenboroughi* sp. n.** (Fig. 1 and Fig. 2)
LSID urn:lsid:zoobank.org:act:3840E4D4-46A6-4192-8052-20E561DD913F

Diagnosis. As for the genus.

Description of male. Total body length, excluding the protruded aedeagus: 1.67 mm.

Head. In frontal view oval, median length of head in dorsal view: 0.19–0.22 mm median breadth: 0.43–0.51 mm, broader than rest of body, height: 0.34 mm; eyes very large without visible sensilla, eye length: 0.15–0.25 mm, eye height: 0.17–0.28 mm, distance between eyes: 0.21–0.23 mm, not diverging ventrally; median ocellus round, lateral ocelli lens-shaped; antennal scrobes probably shallow; occipital carina absent; clypeus truncate; labrum broadly contiguous with clypeal margin and visible as a semicircular plate bearing setae at least at apical margin; two toothed mandibles long and narrow with a slight curvature.

Antenna. Inserted slightly above ventral level of eyes, toruli closer to edge of eyes than to each other; scape length: 0.13–0.16 mm, flattened and broadened over most of its length, not reaching median ocellus; pedicel length (measured in dorsal view): 0.05–0.06 mm and breadth: 0.04 mm; funicle eight-segmented, each segment, including F1, bearing one row of mps, F1 not anelliform; funicle from proximal to distal increasingly more transverse and broadening, F1 – F4 with sides diverging (subconical), F5 – F8 parallel sided (cylindrical), (F1: length: 0.03 mm x width: 0.03–0.04 mm; F2: 0.02–0.03 mm x 0.04 mm; F3: 0.02–0.03 x 0.04 mm; F4: 0.03 mm x 0.04 mm; F5: 0.03 mm x 0.04 mm; F6: 0.02–0.03 mm x 0.04 mm; F7: 0.03–0.04 mm x 0.04–0.05 mm; F8: 0.03 mm x 0.04–0.05 mm); joints between funicle segments visible; clava differentiated and with three segments distinguishable by constrictions plus a distinct but small terminal button (F9: 0.02–0.03 mm x 0.04–0.05 mm; F10: 0.03 mm x 0.04–0.05 mm; F11: 0.02–0.03 mm x 0.02–0.03 mm).

Mesosoma. Length: 0.65–0.74 mm; length of medially rather short dorsally u–shaped pronotum: 0.06 mm, pronotum lacking collar, lateral panels prominent, regularly reticulate; prepectus convex, lightly sculptured, without pilosity, large and triangular, possessing thin shiny rim; mesothoracic spiracle situated at lateral margin of mesoscutum, directly at the meeting point of pronotum and prepectus; length of mesoscutum: 0.24–0.28 mm, with midlobe longer than wide; deep notauli completely reaching transscutal articulation, widely separated posteriorly; length of mesoscutellum: 0.24–0.27 mm, including frenum (length: 0.07–0.09 mm) which is delimited anteriorly by a deep frenal groove; axillae not advanced and widely separated at transscutal articulation; mesoscutum and mesoscutellum with short fine pilosity; mesopleuron concave with acropleuron not enlarged, bearing no pilosity; length of metanotum: 0.03–0.04 mm, smooth metascutellum not reaching anterior margin of metanotum; lateral panel of metanotum foveolate; metapleuron bare; length of rectangular propodeum: 0.07–0.08 mm, breadth: 0.18–0.24 mm; propodeum with coarse irregular sculpture; elliptical spiracles situated slightly closer to anterior margin of propodeum.

Metasoma. Cylindrical petiole (Mt_1) distinct and weakly reticulate, length of petiole 0.05–0.09, breadth: 0.05 -0.08 mm; length of metasoma: 0.66 mm, smooth except of last three tergites bearing longitudinal rugosity, lanceolate with lengths of tergites (Mt_2: 0.18–0.24 mm, Mt_3: 0.08 mm, Mt_4: 0.06 mm, Mt_5: 0.07 mm, Mt_6: 0.12 mm, Mt_7: 0.06 mm, Mt_{8+9}: 0.03 mm), last three tergites with lateral setae; cerci peg-like with long setae.

Wings. Forewing hyaline, immaculate, entirely pilose except of base and subcubital cell; humeral plate large, nearly as long as tegula, bearing at least three setae; parastigma elongated into basal cell angulated with the submarginal vein at about 10–15°; stigmal vein about 1/3 of postmarginal vein; uncus about 95–100° bent in the direction of the postmarginal vein, almost reaching it; postmarginal vein not nearly reaching apex; length of postmarginal to marginal vein

= 1.4–1.5. Hindwing with three hamuli of which the first one is straight; apical 2/3 of hindwing densely pilose, rest relatively bare; costal cell bare.

Legs. Pro- and mesocoxae about same size; protibia with long, slender and slightly curved spur; mesotibial spur straight, 0.5 times as long as basitarsus; metatibia bearing two spurs, one robust, the other short and more slender; trochanters quite long in comparison to corresponding femora (ratios trochanter/femur: 0.33 (pro-), 0.35–0.4 (meso-), 0.3–0.31 (metafemur)); all legs with five tarsomeres.

Female. Unknown.

Specimen examined. Male holo- (SMNS Bu-4) and paratype (SMNS Bu-5) deposited in the amber collection of the State Museum of Natural History in Stuttgart (SMNS). The amber piece hosting the holotype also includes syninclusions: three Empididae (Diptera), probably three further Empididae, which are preserved only in part. Additionally, a small wasp, presumably a Serphitidae is included in the same piece. The amber piece including the paratype hosts a microhymenopteran syninclusion, possibly a Scelionidae.

Etymology. Named after the well renowned British broadcaster and naturalist Sir David Frederick Attenborough for his inspiring enthusiasm and devotion to natural sciences. This species was presented to Sir Attenborough during a visit to the SMNS on the occasion of his 91st birthday.

***Burminata* gen. nov.**

LSID urn:lsid:zoobank.org:act:71D5E586-8406-486A-85AC-FA5CA1F293D8

Type species. *Burminata caputaeria* sp. n.

Diagnosis. Funicular segments rather transverse to quadrate. Pronotum 0.8 times as long as mesoscutum. Axilla advanced 1/7 length of mesoscutum. Foramen magnum about half way between mouth margin and vertex. Mesoscutum and mesoscutellum with sparse pilosity. Ovipositor protruding almost half the length of the metasoma.

Etymology. The generic name is composed of two parts. The first being "*Burmi-"*, referencing the origin of the amber piece and *"–nata"* originating from the Latin adjective "natus" translated to "born". The generic name is feminine in gender.

***Burminata caputaeria* sp. n.** (Fig. 3A−C and Fig. 4A)

LSID urn:lsid:zoobank.org:act:AA5C051D-90AB-4D21-80F1-90AE82A8125A

Diagnosis. As for the genus.

Description of female. Total body length, excluding protruding ovipositor: 1.19 mm.

Head. Ovate in frontal view, median breadth: 0.41 mm and median height 0.25 mm; eyes large and bare, eye length: 0.17 mm, eye height: 0.16 mm high; distance between eyes: 0.22 mm; eyes not diverging ventrally; median ocellus round, lateral ocelli lens-shaped; transfacial sulcus developed; occipital carina absent; clypeal margin truncate; clypeus laterally delimited by large tentorial pits and with upper margin rather straight; labrum semicircular and broadly sitting on clypeal margin; small mandibles with two teeth; maxillary palps with at least three segments; malar space more than 1/3 length of an eye.

Antenna. Inserted at about center of face, toruli situated closer to margin of eyes than to each other; scape slender and relatively short, probably not reaching vertex; pedicel quadrate (length: 0.04 x width: 0.04) F1 shaped like F2; F1 bearing mps; funicle segments slightly transverse with one row of mps; funicle with eight transverse to quadrate segments (F1: length: 0.03 mm x width 0.04 mm; F2: 0.03 mm x 0.04 mm; F3: 0.03 mm x 0.04 mm; F4: 0.04 mm x 0.04 mm; F5: 0.04 mm x 0.04 mm; F6: 0.04 mm x 0.04 mm; F7: 0.04 mm x 0.04 mm; F8: 0.04 mm x 0.04 mm); clava differentiated and with three segments distinguishable by oblique constrictions plus a distinct but small terminal button (F9: 0.04 mm x 0.04 mm; F10: 0.03 mm x 0.04 mm; F11: 0.03 mm x 0.03 mm).

Mesosoma. Length: 0.49 mm, weakly arched; pronotum lacking collar, dorsally only slightly shorter (length: 0.13 mm) than mesoscutum (length: 0.15 mm) with prominent lateral panels, with propleura protruding slightly from underneath; pronotal hind margin with few longer setae; prosternum without process; prepectus triangular and large, with slight sculpturing and without hairs; tegula much smaller than prepectus; pronotum, mesoscutum and mesoscutellum with rather thin and short pilosity and regular reticulation; notauli deep and meeting on transscutal articulation; mesopleuron large, bearing smooth area beneath wing articulation; acropleuron not enlarged; mesopleuron concave; upper mesepimeron without hairs; axillae advanced about 1/7 of the mesoscutal length; mesoscutellum bearing short frenum; metapleuron small and triangular; metanotum and propodeum hardly discernable because of cracked amber and air inclusions; propodeum apparently arched.

Metasoma. Petiole not elongate; metasoma lanceolate, sessile and smooth surface, length excluding ovipositor: 0.5 mm; syntergum present; length of single tergites: Mt_2: 0.11 mm, Mt_3: 0.04 mm, Mt_4: 0.05 mm, Mt_5: 0.05 mm, Mt_6: 0.06 mm, Mt_7: 0.11 mm, Mt_{8+9}: 0.07 mm; cercus peg-like, appearing to be slightly spatulate and bearing at least four hairs; hypopygium folded downwards, probably reaching slightly more than halfway along the metasoma; ovipositor protruding nearly half the length of metasoma, with broad third valvulae.

Wings. Forewing hyaline and immaculate; humeral plate large, with at least two hairs; speculum large; basal cell bare; costal cell pilose throughout; basal vein distinct, angled 27° from the submarginal vein, with pigmentation reaching more than halfway down, continued by setal line; stigmal vein 1/3 the length of the marginal vein, uncus almost reaching postmarginal vein (angle from stigmal vein greater than 110°); postmarginal vein almost reaching apex of wing, 1.4 times as long as marginal vein. Hindwing with three hamuli of which the first one is straight; margin with fringe of long setae; apical 2/3 of hindwing densely pilose, base relatively bare.

Legs. Slender; metacoxae slightly larger than fore and mid coxae and bearing basally some hairs; protibial spur curved; mesotibial spur slender and almost as long as basitarsus; the two metatibial spurs short and robust; trochanters quite long in comparison to corresponding femur (ratios trochanter/femur: 0.32 (pro-), 0.43 (meso-), 0.26 (metafemur)); all legs with five tarsomeres.

Male. Unknown.

Specimen examined. The holotype (SMNS Bu-304) is deposited in the amber collection of the State Museum of Natural History in Stuttgart. The original amber piece, in which the female holotype is encased, broke along a fissure within the amber. The piece hosting the specimen also includes two Diptera and one Scelionidae (Hymenoptera), amongst parts of other insects. The other piece is free of inclusions.

Etymology. The specific epithet "*caputaeria*" consists of two parts originating from the Latin noun for "head" (caput) and adjective "towering up" (aerius), referring to the lowly situated foramen magnum, leaving the head protruding especially high over the pronotum. The species name is feminine in gender.

***Glabiala* gen. nov.**

LSID urn:lsid:zoobank.org:act:10644623-4534-4848-B961-1E608CBB773B

Type species. *Glabiala barbata* sp. n.

Diagnosis. Basal funicular segments longer than broad with following segments getting increasingly more quadrate/transverse. Head and especially margin of oral fossa with dense pilosity. Pronotum dorsally only about 0.4 times the length of the mesoscutum. Axillae advanced about 1/4 the length of the mesoscutum. Mesoscutum and mesoscutellum densely pilose. Foramen magnum situated one third down the head. Ovipositor exerted only slightly. Basal vein distinct as a small spur, forming acute angle with submarginal vein. Uncus of stigma almost reaching postmarginal vein.

Etymology. The name consists of two parts originating from the Latin words for "hairless" (glabellus) and "wing" (ala), referring to the basally bare wing of the specimen. The generic name is feminine in gender.

***Glabiala barbata* sp. n.** (Fig. 3D−G and Fig. 4B)

LSID urn:lsid:zoobank.org:act:01C89C3D-E207-4544-A5AD-3BA80EFE61CB

Diagnosis. As for the genus.

Description of female. Total body length, excluding protruding ovipositor: 2.23 mm.

Head. Foramen magnum situated on upper third of head; eyes relatively large and bare, length: 232 mm, height: 267 mm; antennal scrobes absent; head seemingly finely pilose, except quite long pilosity on gena and mouthmargin; clypeus small, truncate with semicircular labrum; mandibles not clearly visible, but appearing to have two teeth.

Antenna. Inserted at center of head; toruli closer to each other than to eyes; 13-segmented plus a terminal button; scape small; funicle eight-segmented, each segment, including F1, bearing one row of mps, F1 not anelliform; funicular segments quadrate to transverse; segments slightly asymmetrically arranged, appearing thistle-shaped (F1: length: 0.05 mm x width 0.04 mm; F2: 0.05 mm x 0.04 mm; F3: 0.05 mm x 0.05 mm; F4: 0.05 mm x 0.05 mm; F5: 0.06 mm x 0.04 mm; F6: 0.06 mm x 0.06 mm; F7: 0.06 mm x 0.05 mm; F8: 0.05 mm x 0.06 mm); clava not clearly differentiated, with three segments distinguishable plus a distinct but small terminal button (F9: 0.04 mm x 0.06 mm; F10: 0.04 mm x 0.05 mm; F11: 0.05 mm x 0.04 mm).

Mesosoma. Length: 1.0 mm; Pronotum dorsally short, length: 0.15 mm, u-shaped without collar, lateral panels large; prepectus triangular, with light sculpturing; mesoscutum length: 0.36 mm with notauli deep and reaching transscutal articulation; axillae advanced almost 1/4 length of the mesoscutum; mesoscutellum median length: 0.33 mm including frenum length: 0.06 mm separated from mesoscutellum by deep frenal groove; pronotum, mesoscutum and mesoscutellum densely pilose, with frenum bearing slightly longer hairs; frenal groove and frenum present; mesopleuron concave, without enlarged acropleuron; length of metanotum: 0.06 mm; length of propodeum: 0.1 mm; propodeal spiracles situated close to middle of convex propodeum; propodeum without indication of median carina or plicae; lateral propodeal callus with dense and long pilosity; metapleuron with few scattered hairs.

Metasoma. Length: 9.79 mm; Petiole not clearly visible, metasoma therefore appearing sessile; metasoma lanceolate, surface smooth, with length of tergites (Mt_2: 0.22 mm, Mt_3: 0.09 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); tergites with straight dorsal margin; cerci peg-like and club-shaped, arising from under syntergum with setae on the apical margin; ovipositor protruding about the length of Mt_{8+9}.

Wings. Forewing hyaline, immaculate; large speculum and bare basal cell; basal vein shortly distinct, continued by a setal line, forming acute angle of 9° with submarginal vein; length of stigmal vein close to ½ of marginal vein; length of postmarginal vein 1.54 times the marginal vein; uncus almost reaching postmarginal vein, angled from stigmal vein about 95°; postmarginal vein almost reaching apex of wing. Hindwing with three hamuli of which the first one is straight.

Legs. Slender; protibial spur slender, curved and with single tip; protibia with stout setae on dorsal margin; basitarsal comb longitudinal; mesotibial spur almost as long as basitarsus; metatibia bearing two spurs, one much larger than the other; trochanters quite long in comparison to corresponding femur (ratios trochanter/femur: 0.25 (pro-), 0.43 (meso-), 0.3 (meta-)); all legs with five tarsomeres.

Male. Unknown

Specimen examined. Female holotype (SMNS Bu-303) deposited in the amber collection of the State Museum of Natural History in Stuttgart. The piece of amber was cut to reveal a better view on the specimen. Both pieces are free of other inclusions.

Etymology. The specific epithet “*barbata*” is the feminine form of the adjective “barbatus” which means “bearded” and refers to the setose lower face of the specimen. The species name is feminine in gender.

Results of cladistics analyses

The new technology analysis in TNT found 38 most parsimonious trees with the strict consensus tree being 6,306 steps long. The general topology of Heraty et al. (2013) could largely be retrieved (Fig. 5). As in Heraty et al. (2013) the following families appeared as monophyletic: Agaonidae, Chalcididae, Encyrtidae, Eurytomidae, Leucospidae, Mymaridae, Signiphoridae, Torymidae, and Trichogrammatidae. Contrary to Heraty et al. (2013) Aphelinidae and Eucharitidae could be retrieved as monophyletic, while Rotoitidae remained unresolved. In the unweighted analysis Mymarommatoidea was nested within Chalcidoidea as part of a large polytomy including most of the other groups. Leucospidae, Leptofoeninae, Spalangiinae and *Chalcedectus* sp. clustered in one smaller polytomy at the base of the tree. The fossils were recovered as a monophyletic group nested within the large polytomy. Monophyly of the fossils could be retrieved in the traditional search analysis as well, general topology changed however considerably. Using a traditional search without implied weighting, Leucospidae were recovered as sistergroup of all other Chalcidoidea with the inclusion of Mymarommatoidea and the fossils clustered close to the pteromalid subfamily Ormocerinae and the tetracampid *Platynocheilus cuprifrons*. Using a traditional search with implied weights, Mymarommatidae were always recovered as sistergroup of Chalcidoidea and topology changed drastically with increasing k value, as did the position of fossils within the tree. In most analysis with k values below 20, the fossils were closely affiliated with the pteromalid genera *Habritys*, *Cheiropachus* and other interchanging groups. With a k value of 25, they were nested as sistergroup of Agaonidae and with a k value of 30, again, affiliation to some Ormocerinae and the tetracampid genus *Platynocheilus* were retrieved as in the unweighted traditional search.

Discussion

The placement of Diversinitidae within Chalcidoidea is well supported by several putative morphological synapomorphies. All Diversinitidae bear the same type of multiporous plate sensilla (mps), which are structurally unique to Chalcidoidea, with their apices free of their surrounding antennal cuticle, the lack of an encircling groove around the sensillum and elevation of the multiporous plate above the antennal cuticular level (Barlin & Bradleigh, 1981; Gibson, 1986; Basibuyuk & Quicke, 1999). Within those groups of Proctotrupomorpha that are most closely related to Chalcidoidea (Peters et al., 2017), few possess mps on their antennae. Only Cynipoidea and the family Pelecinidae within Proctotrupoidea share this feature, but show a quite different antennal morphology with their sensilla usually only slightly raised above the antennal surface and possessing a groove surrounding the multiporous plate (Basibuyuk & Quicke, 1999). Other Proctotrupidae, Ceraphronoidea, Platygastroidea and Diaprioidea possess setiform multiporous sensilla sharing little resemblance with the morphology of chalcidoid mps (Gibson, 1986; Basibuyuk & Quicke, 1999). Even Mymarommatidae, the putative sister group of Chalcidoidea, lack mps (Gibson, 1986; Munro et al., 2011; Heraty et al., 2013).

Another diagnostic feature of Chalcidoidea is the presence of an externally visible prepectus, separating the pronotum from the tegula (Gibson, 1985, 1999; Gibson, Heraty & Woolley, 1999). A prepectus is present in many groups and is postulated to be a ground plan character of Hymenoptera, but an independent and exposed lateral prepectus is unique for Chalcidoidea and therefore believed to be apomorphic within Apocrita (Gibson, 1985, 1986). Diversinitidae possess a large triangular prepectus, neither fused to the pronotum nor hidden. Additionally, like in other chalcidoids, the mesothoracic spiracle is situated between the lateral margin of the mesoscutum and the pronotum directly adjacent to the anterodorsal edge of the prepectus. Gibson (1999) hypothesized this to be the derived state from a concealed prepectus with the spiracle originating from between the pronotum and mesepisternum. Rotoitidae may therefore exhibit a transitional state where the spiracle is already situated between the lateral margin of the mesoscutum and the pronotum, but the prepectus is slender and almost completely concealed under the pronotum (Gibson, 1999).

Assignment of the fossils to extant chalcidoid families is not possible due to the presence of many plesiomorphic features and the lack of synapomorphies. The most prominent characteristic of Diversinitidae that separates them from all other chalcidoid families is the possession of mps on the first flagellomere (F1) in both sexes. Mps on F1 can be found in Chalcidoidea only in very few cases. In Mymaridae, most males possess mps on their first flagellomere, but they are always absent in females (Heraty et al., 2013). Some Aphelininae (Aphelinidae) and Eucharitidae also seemingly possess mps on their apparent F1, but it has been shown that this is only because the first two flagellomeres are united (Heraty et al., 2013). In Diversinitidae, the first visible flagellomere is undoubtedly F1 in both sexes. The well-developed F1 bearing mps is hypothesized as plesiomorphic for Chalcidoidea (Heraty et al., 2013), suggesting a basal position of Diversinitidae within Chalcidoidea. During their evolution, Chalcidoidea probably subsequently lost mps on their F1 and reduced the F1 into a ring-like anellus that is present in almost all extant chalcidoids.

Another phylogenetically relevant character of Diversinitidae is the presence of a transfacial sulcus. A transfacial sulcus or line, situated below the anterior ocellus right above the antennal scrobes, can be found in many, mostly soft-bodied families including Aphelinidae, Encyrtidae, Eulophidae, Eupelmidae, Mymaridae, Pteromalidae and Trichogrammatidae (Gibson, 1986; Kim & Heraty, 2012; Heraty et al., 2013). Its form in combination with other sulci on the frons of the head was believed to be apomorphic for Mymaridae, but with other families including Diversinitidae possessing a transfacial sulcus as well, it might be a ground plan character for Chalcidoidea as already postulated by Gibson (1986).

Darling (1988) argued, that the ground plan structure of the labrum for Chalcidoidea is flap-like, with many evenly distributed setae. Darling (1988) referred to the labrum of Chalcididae as “remarkably uniform and […] similar to that hypothesized as the ground plan for Apocrita”, being heavily sclerotized and contiguous with the margin of the clypeus, bearing long, tapered setae on the whole surface, arising from distinct sockets. In Pteromalidae, the plesiomorphic state of the labrum can be found in Cleonyminae, and the labrum is also exposed in Spalangiinae, Asaphinae, Eunotinae and others, which bear in comparison to Cleonyminae setae only near their apical margin (Darling, 1988). The labrum of Diversinitidae can be described as free, semicircular, flap-like and broadly continuous with the clypeal margin. However, the setal pattern is difficult to assess due to refractions within the amber in conjunction with the small size of the specimens. Setae are at least situated along the apical margin in Diversinitidae, whether they are also found on the surface remains uncertain. If so, the labrum might also be putatively plesiomorphic for Diversinitidae.

A clearly delimited frenal area can be found in Diversinitidae, which is likely a plesiomorphic character state for Chalcidoidea (Krogmann & Vilhelmsen, 2006). A frenum can be observed in many chalcidoid families and in closely related groups, such as Mymmaromatidae, Diapriidae and Scelionidae (Heraty et al., 2013), suggesting that it is probably part of the ground plan structure for a subgroup of Proctotrupomorpha. Frenal morphology is used in species and subfamily distinction of Torymidae and Pteromalidae (Graham, 1969; Graham & Gijswijt, 1998; Gibson, 2003). The morphological variation of the frenum led to frequent discussions about its homology between different taxonomic groups (Grissell, 1995; Gibson, Heraty & Woolley, 1999; Vilhelmsen & Krogmann, 2006).

Metasomal cercal structures of Chalcidoidea have been discussed in the literature, with often opposing views on which character state should be regarded as plesiomorphic (Grissell, 1995; Gibson, 2003). Female Diversinitidae possess peg-like cerci, which are more or less spatulate. This character state has been considered as plesiomorphic in contrast to a button-like cercus (Gibson, 2003) or, alternatively, as apomorphic character, which has independently evolved in different chalcidoid groups (Grissell, 1995). Grissell (1995) argued that though peg-like cerci are found in Agaonidae *sensu lato*, Eulophidae (*Entia* Hedqvist, 1974), Pteromalidae (*Cea* Walker, 1837, *Chromeurytoma* Cameron, 1912) and Torymidae, evolution of this character must have been convergent since positioning of the cerci is different in those groups. On the other hand, Gibson (2003) stated that many other groups have peg-like cerci as well, though most often not as prominent as those listed above, and therefore he considered exerted cerci as plesiomorphic relative to plate-like cerci. In Heraty et al. (2013) many taxa were also coded as possessing exerted cerci to various degrees, such as Perilampidae (*Brachyelatus* sp.), Tetracampidae (*Platynocheilus* sp.), Signiphoridae (*Signiphora* sp.), Mymaridae (*Borneomymar* sp.) and Tanaostigmatidae (*Protanaostigma* sp.). Outgroup comparison for this character in Heraty et al. (2013) is however not conclusive due to sparse taxon sampling. Mymarommatidae (*Mymaromella* sp.) was coded as not possessing exerted cerci, compared to Scelionidae (*Archaeoteleia mellea* Masner, 1968), which show slightly exerted cerci and Diapriidae (*Belyta* sp.) without coding for this character. The wide distribution of peg-like cerci within Chalcidoidea and its early appearance in Mymaridae and Diversinitidae emphasizes the hypotheses that they represent the plesiomorphic state over button-like cerci.

Presenting a solid phylogenetic placement of Diversinitidae within Chalcidoidea is not unequivocally possible. All cladistic analyses provided evidence for monophyly of Diversinitidae, but do not resolve further relationships within Chalcidoidea, since placement of the fossils and general tree topology remained highly variable in different analyses. This was expected, since the morphology-only analysis in Heraty et al. (2013) was also poorly resolved. Morphologically, Diversinitidae appear to be an early lineage of Chalcidoidea, possessing many putatively plesiomorphic characters (see discussion above). Mymaridae are thought to form the sister group to all remaining Chalcidoidea and can be traced back at least to the mid-Cretaceous

(Gibson, 1986; Munro et al., 2011; Heraty et al., 2013). Resemblance between Diversinitidae and Mymaridae is not obvious and they only possess few putatively symplesiomorphic characters, such as a transfacial sulcus and mps on the true F1 in males. In general, the mymarid body plan appears very derived and is characterized by a number of apomorphies that have not changed much since the Mid Cretaceous (Poinar & Huber, 2011). The phylogenetic position of Diversinitidae cannot be established with certainty and several hypotheses are possible. Firstly, Diversinitidae could represent the sister group to all remaining chalcidoids, since they show a multitude of plesiomorphic characters, foremost mps on F1. During chalcidoid evolution mps on F1 might have been lost at first in females (as in Mymaridae) and subsequently also in males (as in all remaining Chalcidoidea). However, a sister group relationship of Diversinitidae to a smaller subset of Chalcidoidea is also possible though less parsimonious as it would suggest that mps on F1 were independently lost twice, once in Mymaridae and once in all other Chalcidoidea.

Biological implications of the new fossils are difficult to draw, since their phylogenetic position is not fully resolved. Egg parasitoidism is considered to be the putative ground plan biology of Chalcidoidea (Heraty et al., 2013, Peters et al., subm.). Diversinitidae share a relatively small body size, which unites nearly all egg parasitizing taxa, but does not necessarily exclude ectoparasitoid groups. Body shape is not indicative, since both ecto- and endoparasitoids can be very diverse in this regard. The length of the ovipositor and its saw-like tip might be indicative for concealed hosts.

With the described fossils we close a significant fossil gap of Chalcidoidea from the Cretaceous. The wasp species diagnosed herein provide an important snapshot of chalcidoid evolution as they are early representatives of a parasitoid lineage that was about to rise. Hundred million years later we are just beginning to fully appreciate the ecological significance of these “green myriads in the peopled grass” (Walker, 1839) that still rank among the least known of all insects. Further Cretaceous fossils will hopefully help us to understand how chalcidoid wasps have shaped the evolution of their arthropod host groups and associated plant species, while they evolved to become one of the most diverse and influential insect groups that life has ever seen.

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Table 1(on next page)

Abbreviations for morphological structures.

Numbers provide direct access to referenced structures in the HAO database (http://portal.hymao.org/projects/32/public/ontology_class/show/*).

Table 1. Abbreviations for morphological structures. Numbers provide direct access to referenced structures in the HAO database (http://portal.hymao.org/projects/32/public/ontology_class/show/*)

ax	Axilla	883
F1-11	Flagellomeres 1-11	526
frn	Frenum	869
lbr	Labrum	499
mps	Multiporous plate sensillum	1046
Mt	Metasomal tergite	9475
Mt_{8+9}	Syntergum	1721
no_3	Metanotum	532
pre	Prepectus	872
ptl	Petiole	4542
sctl	Mesoscutellum	622
tfs	Transfacial sulcus	9485
tps	Tentorial pit	1310

Figure 1

Digital microscopic images of *Diversinitus attenboroughi*, male.

(A, B, D, E) holotype. (A) Lateral habitus. (B) Detail of left antenna. (C) Lateral habitus of paratype. (D) Dorsal habitus. (E) Wings left side. Scale bars: (A, C) 0.5 mm, (B) 0.1 mm, (D) 0.2 mm, (E) 0.25 mm. Abbreviations: mps = multiporous plate sensilla, ptl = petiole.

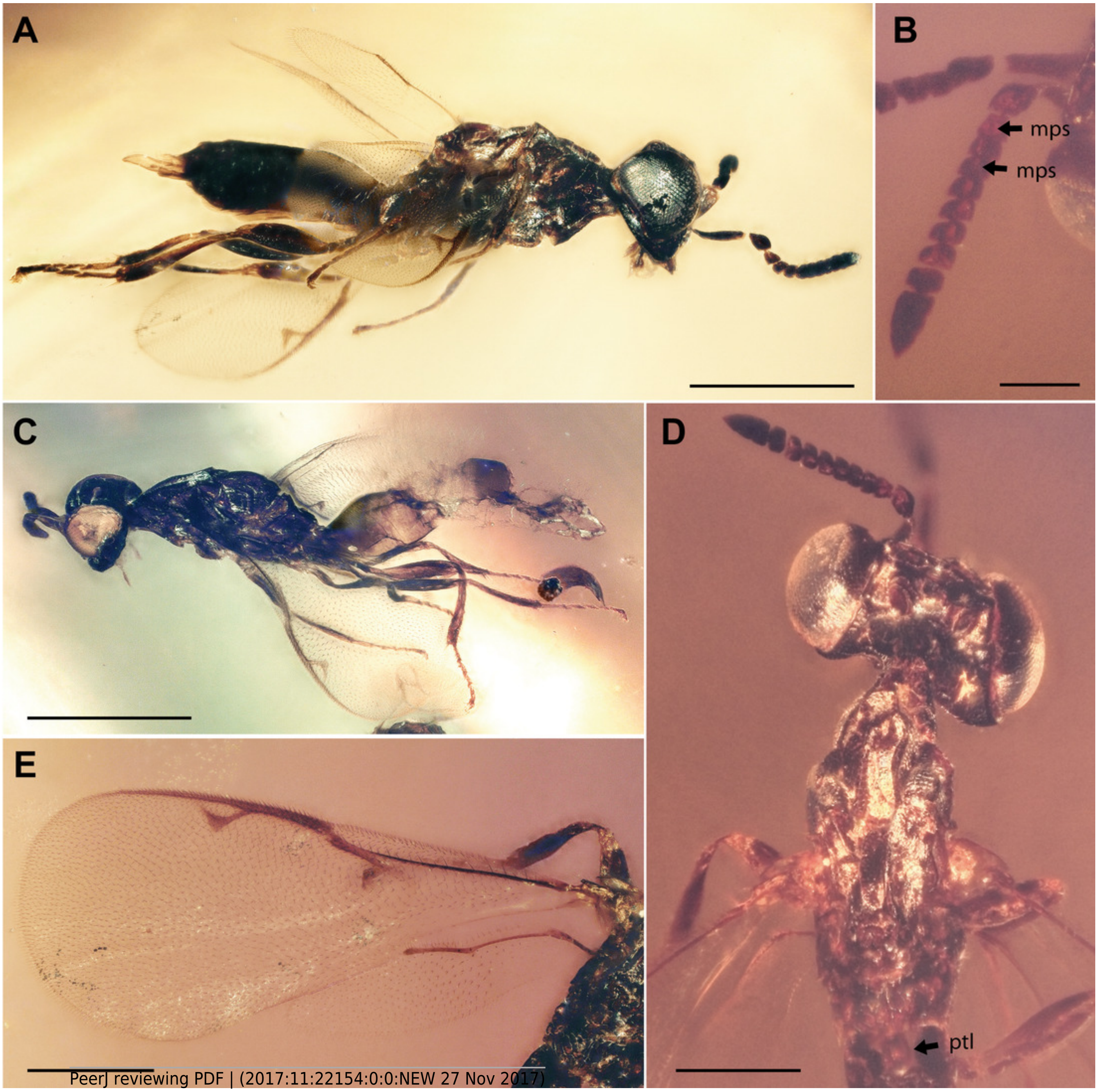


Figure 2

Habitus drawings of *Diversinitus attenboroughi*, male.

Holotype (A) habitus lateral. (B) Habitus dorsal. Scale bars: 0.5 mm.

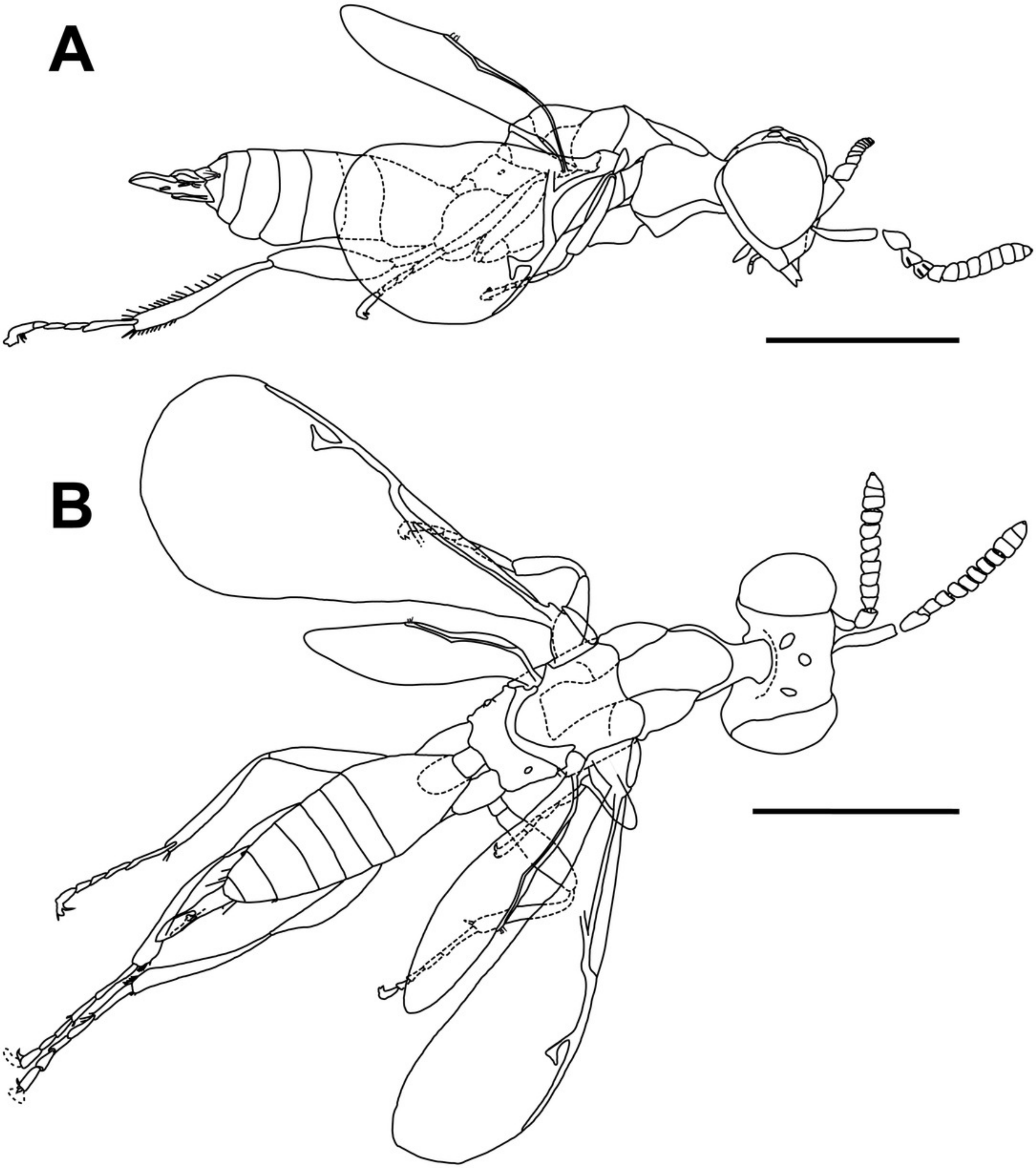

A
B

Figure 3

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) 0.25 mm, (B, C, E, F) 0.1 mm, (D, G) 0.5 mm. Abbreviations: ax = axilla, frn = frenum, lbr = labrum, mps = multiporous plate sensilla, no3 = metanotum, pre = prepectus, sctl = scutellum, tfs = transfacial sulcus, tps = tentorial pits.

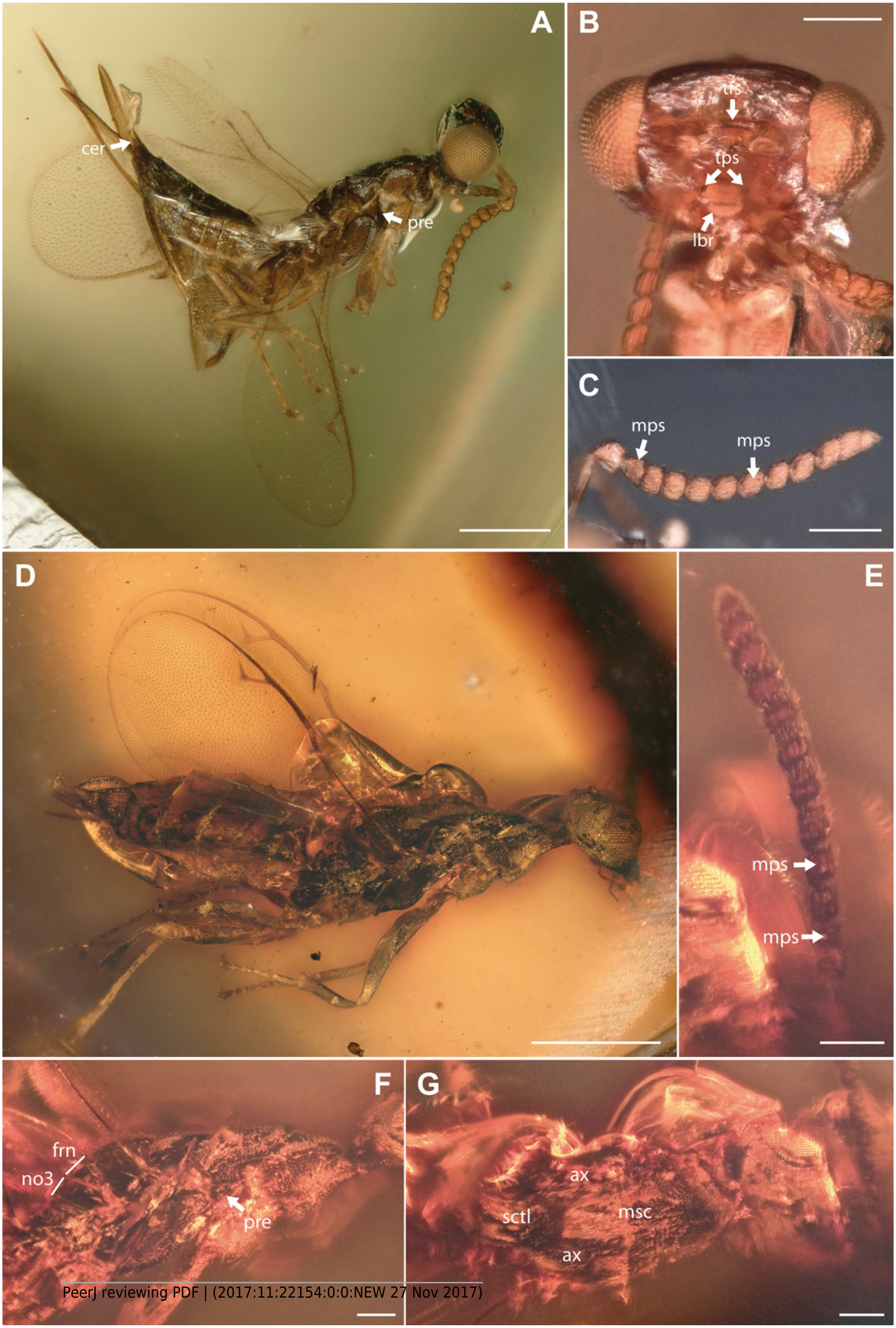

A
cer
pre
B
tfs
tps
lbr
C
mps
mps
D
E
mps
mps
F
frn
no3
pre
G
ax
sctl
msc
ax

Figure 4

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

Scale bars: 0.5 mm.

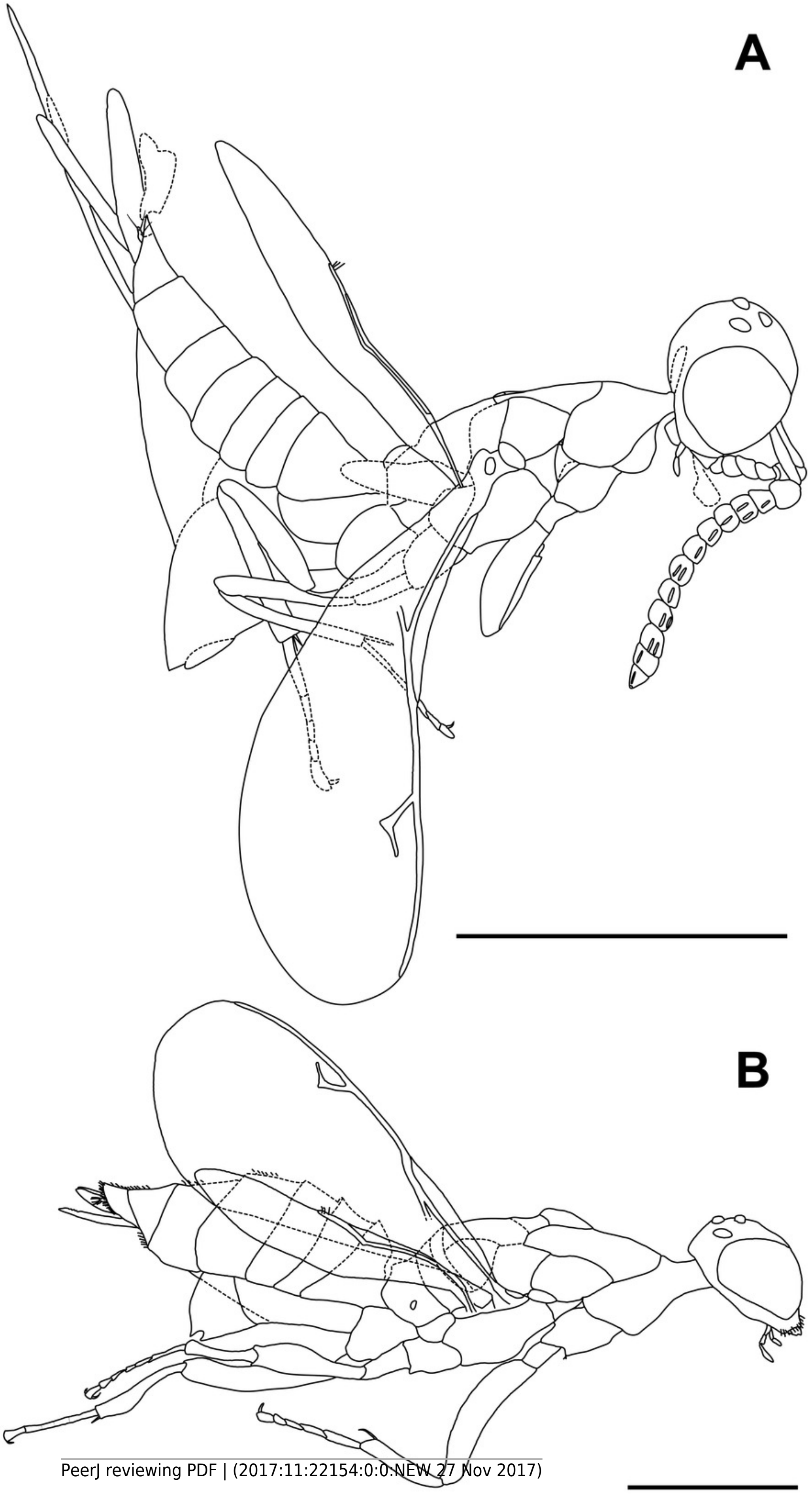
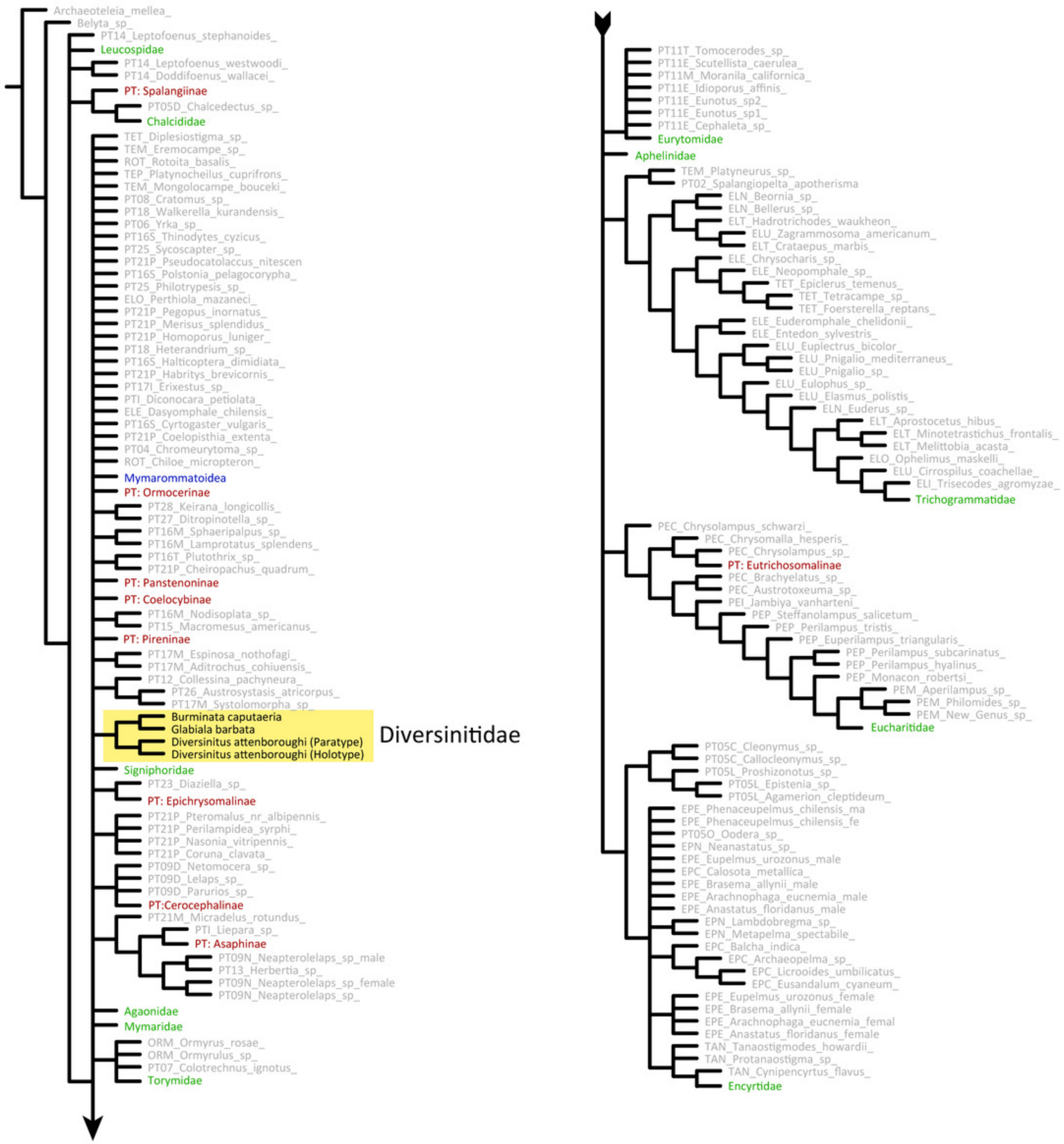

A
B

Figure 5

Phylogenetic placement of Diversinitidae within Chalcidoidea based on morphological characters.

Strict consensus tree calculated from 38 trees (tree length = 6306, CI = 0.072, RI = 0.532, 232 characters and 304 taxa, equal weights, new technology search). Yellow box highlights described fossils. Green names indicate monophyletic and therefore collapsed families. Mymarommatoidea, potential sistergroup to all Chalcidoidea, collapsed and highlighted in blue. 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).


Archaeoteleia_mellea_
Belyta_sp_
PT14_Leptofoenus_stephanoides_
Leucospidae
PT14_Leptofoenus_westwoodi_
PT14_Doddifoenus_wallacei_
PT: Spalangiinae
PT05D_Chalcedectus_sp_
Chalcididae
TET_Diplesiostigma_sp_
TEM_Eremocampe_sp_
ROT_Rotoita_basalis_
TEP_Platynocheilus_cuprifrons_
TEM_Mongolocampe_bouceki_
PT08_Cratomus_sp_
PT18_Walkerella_kurandensis_
PT06_Yrka_sp_
PT16S_Thinodytes_cyzicus_
PT25_Sycoscapter_sp_
PT21P_Pseudocatolaccus_nitescen
PT16S_Polstonia_pelagocorypha_
PT25_Philotrypesis_sp_
ELO_Perthiola_mazaneci_
PT21P_Pegopus_inornatus_
PT21P_Merisus_splendidus_
PT21P_Homoporus_luniger_
PT18_Heterandrium_sp_
PT16S_Halticoptera_dimidiata_
PT21P_Habritys_brevicornis_
PT17I_Erixestus_sp_
PTI_Diconocara_petiolata_
ELE_Dasyomphale_chilensis_
PT16S_Cyrtogaster_vulgaris_
PT21P_Coelopisthia_extenta_
PT04_Chromeurytoma_sp_
ROT_Chiloe_micropteron_
Mymarommatoidea
PT: Ormocerinae
PT28_Keirana_longicollis_
PT27_Ditropinotella_sp_
PT16M_Sphaeripalpus_sp_
PT16M_Lamprotatus_splendens_
PT16T_Plutothrix_sp_
PT21P_Cheiropachus_quadrum_
PT: Panstenoninae
PT: Coelocybinae
PT16M_Nodisoplata_sp_
PT15_Macromesus_americanus_
PT: Pireninae
PT17M_Espinosa_nothofagi_
PT17M_Aditrochus_cohiuensis_
PT12_Collessina_pachyneura_
PT26_Austrosystasis_atricorpus_
PT17M_Systolomorpha_sp_
Burminata caputaeria
Glabiala barbata
Diversinitus attenboroughi (Paratype)
Diversinitus attenboroughi (Holotype)
Diversinitidae
Signiphoridae
PT23_Diaziella_sp_
PT: Epichrysomalinae
PT21P_Pteromalus_nr_albipennis_
PT21P_Perilampidea_syrphi_
PT21P_Nasonia_vitripennis_
PT21P_Coruna_clavata_
PT09D_Netomocera_sp_
PT09D_Lelaps_sp_
PT09D_Parurios_sp_
PT:Cerocephalinae
PT21M_Micradelus_rotundus_
PTI_Liepara_sp_
PT: Asaphinae
PT09N_Neapterolelaps_sp_male
PT13_Herbertia_sp_
PT09N_Neapterolelaps_sp_female
PT09N_Neapterolelaps_sp_
Agaonidae
Mymaridae
ORM_Ormyrus_rosae_
ORM_Ormyrulus_sp_
PT07_Colotrechnus_ignotus_
Torymidae
PT11T_Tomocerodes_sp_
PT11E_Scutellista_caerulea_
PT11M_Moranila_californica_
PT11E_Idioporus_affinis_
PT11E_Eunotus_sp2_
PT11E_Eunotus_sp1_
PT11E_Cephaleta_sp_
Eurytomidae
Aphelinidae
TEM_Platyneurus_sp_
PT02_Spalangiopelta_apotherisma
ELN_Beornia_sp_
ELN_Bellerus_sp_
ELT_Hadrotrichodes_waukheon_
ELU_Zagrammosoma_americanum_
ELT_Crataepus_marbis_
ELE_Chrysocharis_sp_
ELE_Neopomphale_sp_
TET_Epiclerus_temenus_
TET_Tetracampe_sp_
TET_Foersterella_reptans_
ELE_Euderomphale_chelidonii_
ELE_Entedon_sylvestris_
ELU_Euplectrus_bicolor_
ELU_Pnigalio_mediterraneus_
ELU_Pnigalio_sp_
ELU_Eulophus_sp_
ELU_Elasmus_polistis_
ELN_Euderus_sp_
ELT_Aprostocetus_hibus_
ELT_Minotetrastichus_frontalis_
ELT_Melittobia_acasta_
ELO_Ophelimus_maskelli_
ELU_Cirrospilus_coachellae_
ELI_Trisecodes_agromyzae_
Trichogrammatidae
PEC_Chrysolampus_schwarzi_
PEC_Chrysomalla_hesperis_
PEC_Chrysolampus_sp_
PT: Eutrichosomalinae
PEC_Brachyelatus_sp_
PEC_Austrotoxeuma_sp_
PEI_Jambiya_vanharteni_
PEP_Steffanolampus_salicetum_
PEP_Perilampus_tristis_
PEP_Euperilampus_triangularis_
PEP_Perilampus_subcarinatus_
PEP_Perilampus_hyalinus_
PEP_Monacon_robertsi_
PEM_Aperilampus_sp_
PEM_Philomides_sp_
PEM_New_Genus_sp_
Eucharitidae
PT05C_Cleonymus_sp_
PT05C_Callocleonymus_sp_
PT05L_Proshizonotus_sp_
PT05L_Epistenia_sp_
PT05L_Agamerion_cleptideum_
EPE_Phenaceupelmus_chilensis_ma
EPE_Phenaceupelmus_chilensis_fe
PT05O_Oodera_sp_
EPN_Neanastatus_sp_
EPE_Eupelmus_urozonus_male
EPC_Calosota_metallica_
EPE_Brasema_allynii_male
EPE_Arachnophaga_eucnemia_male
EPE_Anastatus_floridanus_male
EPN_Lambdobregma_sp_
EPN_Metapelma_spectabile_
EPC_Balcha_indica_
EPC_Archaeopelma_sp_
EPC_Licrooides_umbilicatus_
EPC_Eusandalum_cyaneum_
EPE_Eupelmus_urozonus_female
EPE_Brasema_allynii_female
EPE_Arachnophaga_eucnemia_femal
EPE_Anastatus_floridanus_female
TAN_Tanaostigmodes_howardii_
TAN_Protanaostigma_sp_
TAN_Cynipencyrtus_flavus_
Encyrtidae