Diversinitidae, a new family of Cretaceous jewel wasps (Hymenoptera: Chalcidoidea)

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Comment [G1]: The title is not as informative as it should be. A new „taxon“ could be anything from a new species to a new Class. It is better to state the name, that it is a new family, and the Order to which it belongs.

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Abstract

Two new genera and three new species, *Diversinitus attenboroughi* gen. & sp. n., *Glabiala barbata* gen. & sp. n. and *Burminata caputaeria* gen. & sp. n., are described in the new 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 familial level chalcidoid lineages by the presence of multiporous plate sensilla on the first flagellomere in both sexes. 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 support 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 uncertain 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, which may comprise 10% of insect diversity, though only about 22,000 species have been described to date (Noyes, 1978, 2000, 2017; Heraty & Gates, 2003). Their evolutionary success is mirrored by and likely result from their varied biological life styles, being mainly parasitoids of 13 different insect orders, and thus essential beneficial regulators of other insects, but also as phytophages so as sometimes harmful pests but also important obligate pollinators of figs (*Ficus*) (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 most chalcidoid taxa as well as their evolutionary history still remain unresolved. The role of fossils in a phylogenetic framework is pivotal to understanding some of the evolutionary processes that 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.

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Deleted: 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.

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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 by Yoshimoto (1975). Of the four genera described by Yoshimoto (1975) in Mymaridae (*Carpenteriana, Macalpinia, Protooctonus* and *Triadomerus*), *Protooctonus* was later transferred to Mymarommatidae and synonymized under *Archaeromma* Yoshimoto, 1975 (Gibson, Read & Huber, 2007). The genus *Enneagmus* Yoshimoto, 1975, originally described within Trichogrammatidae was transferred by Huber (2005) to Mymaridae. Though not revised in detail, the placement of *Distylopus, Boucekytus* and *Baeomorpha* within Tetracampidae by Yoshimoto (1975) 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

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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 habitus 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 because the family, in its current concept, is indicated to be polyphyletic (Campbell et al., 2000; Krogmann & Vilhelmsen, 2006; Heraty et al., 2013).

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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, Stuttgart, Germany (SMNS).

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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 3-segmented clava, including a distinct terminal button; all funicular segments (including F1) with a row of multiporous plate sensilla. Eyes large, without pilosity, with inner margins not divergent ventrally. Labrum exposed below clypeus, flap-like. Head with transverse, transfacial sulcus dorsal to antennal scrobe; occipital carina absent. Mesosoma with independent, large and triangular, laterally exposed prepectus. Mesonotum with notauli deep and complete; male axillae only slightly advanced, female axillae distinctly advanced relative to posterior margin of mesoscutum; scutellum with frenal groove developed. Wings with short marginal fringe; male fore wing completely pilose, female fore wing with basal cell bare and with speculum; postmarginal vein distinctly longer than marginal vein; basal vein developed; hind wing normal, not stalked. Trochanters distinctly elongate, at least one quarter length of femora. Propodeal spiracles situated almost in middle of propodeum, but slightly closer to anterior margin. Male petiole distinct, at least as long as broad, female petiole hardly visible in dorsal view. Metasoma with Mt8 and Mt9 fused into a syntergum in both sexes; cerci peg-like.

Key to species of Diversinitidae

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1. Antenna symmetric, with funiculars 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), with funiculars ?????. Axillae advanced into mesoscutum (Fig. 4). Mesotibial spur almost as long as basitarsus. **2.**

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

- Head mostly bare, including around oral fossa (Fig. 3B). Pronotum 0.8 times as long as mesoscutum (Fig. 4A). Funicular segments ????? shaped and all rather quadrate to transverse (Fig. 3C). Foramen magnum situated at lower third of head (Fig. 4A). Axilla advanced only 1/7 length of mesoscutum (Fig. 4A). Mesoscutum and mesoscutellum with pilosity less dense than above. Ovipositor protruding almost half length of 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. Fore wing completely pilose. Mesotibial spur half as long as basitarsus.

Etymology. The generic name *Diversinitus* is composed of two parts. The first part, “Divers-“, originates from the Latin adjective “*diversus*”, meaning diverse or different. The second part, “-initus”, is the Latin noun *“initus”* 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.

Male. Total body length, excluding protruded aedeagus: 1.67 mm.

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

Antenna. Inserted slightly above ventral level of eyes, with 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 8-segmented, each segment, including F1, bearing one row of mps; F1 ??????? (not anelliform); funiculars with joints between segments visible and increasingly more transverse and broadening distally, F1 – F4 with sides diverging (subconical), F5 – F8 parallel sided (cylindrical); F1 length (mm):width (mm) = 0.03:0.03–0.04, F2 = 0.02–0.03:0.04, F3 = 0.02–0.03:0.04; F4 = 0.03:0.04; F5 = 0.03:0.04, F6 = 0.02–0.03:0.04, F7 = 0.03–0.04:0.04–0.05; F8 = 0.03:0.04–0.05. Clava differentiated from funicle, with three segments distinguishable by constrictions plus a distinct but small terminal button; F9 length (mm):width (mm) = 0.02–0.03:0.04–0.05, F10 = 0.03: 0.04–0.05, F11 = 0.02–0.03: 0.02–0.03.

Mesosoma. Length: 0.65–0.74 mm. Pronotum in dorsal view u–shaped, medially rather short (0.06 mm), lacking collar, lateral panels prominent, regularly reticulate. Prepectus convex, lightly sculptured, bare, large and triangular, with thin shiny rim along ?????. Mesothoracic spiracle situated at lateral margin of mesoscutum at juncture of pronotum and prepectus. Mesoscutum length 0.24–0.28 mm, with midlobe longer than wide; notauli deep, reaching transscutal articulation, widely separated posteriorly; mesoscutellum length 0.24–0.27 mm, with frenum delimited anteriorly by deep frenal groove, frenum length 0.07–0.09 mm; axillae not advanced and widely separated at transscutal articulation; mesoscutum and mesoscutellum with short fine pilosity; mesopleuron concave with acropleuron not enlarged, bare; length of metanotum 0.03–0.04 mm, with smooth metascutellum not reaching anterior margin of metanotum and lateral panel of metanotum foveolate; metapleuron bare; propodeum rectangular, length 0.07–0.08 mm, breadth 0.18–0.24 mm, with coarse irregular sculpture; spiracles elliptical, situated slightly closer to anterior than posterior margin.

Wings. Fore wing hyaline, immaculate, entirely pilose except basally and subcubital cell; humeral plate large, nearly as long as tegula, with at least three setae; parastigma elongated into basal cell and angled relative to submarginal vein at about 10–15°; stigmal vein about 1/3 length of postmarginal vein; uncus bent at angle of about 95–100° in direction of postmarginal vein and almost reaching it; postmarginal vein not nearly reaching apex of wing, 1.4–1.5 times as long as marginal vein. Hind wing with three hamuli, the first straight; apical 2/3 densely pilose, the rest relatively bare; costal cell bare.

Legs. Pro- and mesocoxae of similar size; protibia with long, slender, slightly curved spur; mesotibial spur straight, 0.5 times as long as basitarsus; metatibia with two spurs, one robust, the other short and more slender; trochanters quite long in comparison to

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corresponding femora, with ratio of trochanter:femur = 0.33 (pro-), 0.35–0.4 (meso-), and 0.3–0.31 (metafemur); all legs with five tarsomeres.

Metasoma. Petiole (Mt_1) distinct, cylindrical and weakly reticulate, length 0.05–0.09 mm, breadth 0.05–0.08 mm. Gaster 0.66 mm in length, lanceolate; tergites smooth and bare except last three with longitudinal rugosity and lateral setae; length 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; cerci peg-like, with long setae.

Female. Unknown.

Specimen examined. Male holo- (SMNS Bu-4) and paratype (SMNS Bu-5) deposited in SMNS. The amber piece with the holotype also includes syninclusions: three Empididae (Diptera), and probably three other 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 quadrate to rather transverse. 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 length of metasoma.

Etymology. The generic name is composed of two parts. The first part, "Burmi-", references the origin of the amber piece whereas the second part, "–*nata*", originates 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.

Female. Total body length, excluding protruding ovipositor: 1.19 mm.

Comment [G28]: I find this very hard to believe, are you sure that you are not confusing the trochanter + trochantellus with the trochanter? Because you have two specimens I assume that it is visible in both and not just a preservation artefact. Based on your figure 3D I suspect the length is a composite of both the trochanter and trochantellus and, if so, not all that unusual compared to many other chalcids.

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Head. Ovate in frontal view, median breadth 0.41 mm and median height 0.25 mm; eyes large, bare and with inner margins not diverging ventrally, length 0.17 mm, height 0.16 mm, distance between eyes 0.22 mm; median ocellus round, lateral ocelli lens-shaped; transfacial sulcus developed; occipital carina absent; clypeus laterally delimited by large tentorial pits, with upper margin rather straight and apically truncate; labrum semicircular and broadly contiguous with clypeal margin; mandibles small, 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:width = 0.04:0.04. Funicle ?-segmented; F1 shaped like F2 and with 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.

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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 SMNS. The original amber piece, in which the female holotype is encased, broke along a fissure within the amber. The piece containing 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*), and refers to the lowly situated foramen magnum, which leaves 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. Funicle with basal segments longer than broad and following segments increasingly more quadrate to transverse. Head and especially margin of oral fossa with dense pilosity. Pronotum dorsally only about 0.4 times length of mesoscutum. Axillae advanced about 1/4 length of mesoscutum. Mesoscutum and mesoscutellum densely pilose. Foramen magnum situated one third distance from ventral margin of 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.

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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 SMNS. The piece of amber was cut to reveal a better view of 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.

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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 plus Leptofoeninae, Spalangiinae and *Chalcedectus* sp. (Pteromalidae) clustered in one smaller polytomy at the base of the tree. The fossils were recovered as a monophyletic group nested within a much larger polytomy. Monophyly of the fossils could be retrieved in the traditional search analysis as well, however general topology changed 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 analyses 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 have the same type of structurally unique multiporous plate sensilla (mps) as other 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 sensillar morphology with the 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).

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Another diagnostic feature of Chalcidoidea is the presence of an externally visible prepectus between the pronotum and mesopleuron, which separates the pronotum from the tegula (Gibson, 1985, 1999; Gibson, Heraty & Woolley, 1999). A free prepectus is present in many groups of Hymenoptera and is postulated to be a ground plan character of the Order. Some Apocrita retain a free prepectus, but one that is laterally exposed is unique for Chalcidoidea. The presence of a laterally visible prectus is postulated as secondary and therefore as a second autapomorphy of Chalcidoidea within Apocrita (Gibson, 1985, 1986). Diversinitidae have a large triangular prepectus, neither fused to the pronotum or mesopleuron nor hidden beneath its lateral margin. 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, another autapomorphy of Chalcidoidea that is correlated with its external prepectus. Gibson (1999) hypothesized the more dorsal position of the spiracle compared to other hymenopterans is a derived state. Other hymenopterans having a concealed prepectus or a prepectus that is fused either to the pronotum or mesopleuron have the spiracle originating somewhat more ventrally below the level of the mesoscutum between the pronotum and mesepisternum. In Rotoitidae and Mymaridae the spiracle is situated between the lateral margin of the mesoscutum and the pronotum, but in Rotoitidae and some Mymaridae the prepectus is slender and almost completely concealed under the pronotum. Because Mymaridae and Rotoitidae are hypothesized as basal clades within Chalcidoidea (references) their prepectal structure may therefore represent a transitional state (Gibson, 1999).

Assignment of the fossils to extant chalcidoid families is not possible due to the lack of synapomorphies. The most prominent characteristic of Diversinitidae, which separates them from all other chalcidoid families, is the possession of mps on the first flagellomere (F1) in both sexes. Mps on F1 is found in Chalcidoidea only in very few cases. In Mymaridae, most males possess mps on their first flagellomere, but they are always absent from females (Heraty et al., 2013). Some Aphelininae (Aphelinidae) and Eucharitidae also seemingly possess mps on their apparent F1, but 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. A well-developed F1 that has mps is hypothesized as plesiomorphic for Chalcidoidea (Heraty et al., 2013), suggesting a basal position of Diversinitidae within Chalcidoidea. During the evolution of Chalcidoidea, the first funicular likely secondarily lost mps in association with the segment being reduced in length to a ring-like segment (anellus), as is suggested by some chalcidoids that have additional funiculars reduced to anelli-like segments that lack mps. In those, comparatively few, chalcidoids with F1 lacking mps but being similarly as long as the subsequent funiculars, F1 is hypothesized to have been secondarily lengthend.

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, is 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

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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) postulated 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 entire surface, arising from distinct sockets. In Pteromalidae, the plesiomorphic state of the labrum is 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, but 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 is found in Diversinitidae, which is likely a plesiomorphic character state for Chalcidoidea (Krogmann & Vilhelmsen, 2006). A frenum is 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 an apomorphic character state, which has independently evolved in different chalcidoid groups (Grissell, 1995). Grissell (1995) postulated that though peg-like cerci are found in Agaonidae *sensu lato*, Eulophidae (*Entia* Hedqvist, 1974), Pteromalidae (*Cea* Walker, 1837, *Chromeurytoma* Cameron, 1912) and Torymidae and Megastigmadae, evolution of this character must have been convergent because 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, basally articulated cerci as plesiomorphic relative to more reduced, 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.

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(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 appearance in Mymaridae and Diversinitidae supports the hypothesis 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, because placement of the fossils and general tree topology remained highly variable in different analyses. This was expected because 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 hypothesized 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 in several respects to be derived and is characterized by several 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, including Mymaridae, because they possess mps on F1 in both sexes. 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 this would suggest that mps on F1 were independently lost twice, once from female Mymaridae and once from both sexes of all other Chalcidoidea.

Biological implications of the new fossils are difficult to draw, because their phylogenetic position is not fully resolved. Egg parasitoidism is hypothsized 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, because 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.

Conclusion

With the newly described fossils we reduce a significant fossil gap of Chalcidoidea from the Cretaceous. The wasp species described herein provide important new information of chalcidoid evolution because they are early representatives of a parasitoid lineage that was just beginning to evolve. One hundred million years later we are just beginning to fully appreciate

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the great morphological diversity and ecological significance of these “green myriads in the peopled grass” (Walker, 1839), which still rank among the least known of all insects. Further Cretaceous fossils will hopefully reduce the fossil gap even further to help us to understand how chalcidoid wasps have evolved and shaped the evolution of their arthropod host groups and associated plant species, as one of the most diverse and influential insect groups that life has ever seen.

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Acknowledgements

We thank Patrick Müller (Käshofen) for the kind donation of the holotype of *Burminata caputaeria* and Karin Wolf-Schwenninger (SMNS) for providing access to the amber collection and for technical support.

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Figures:

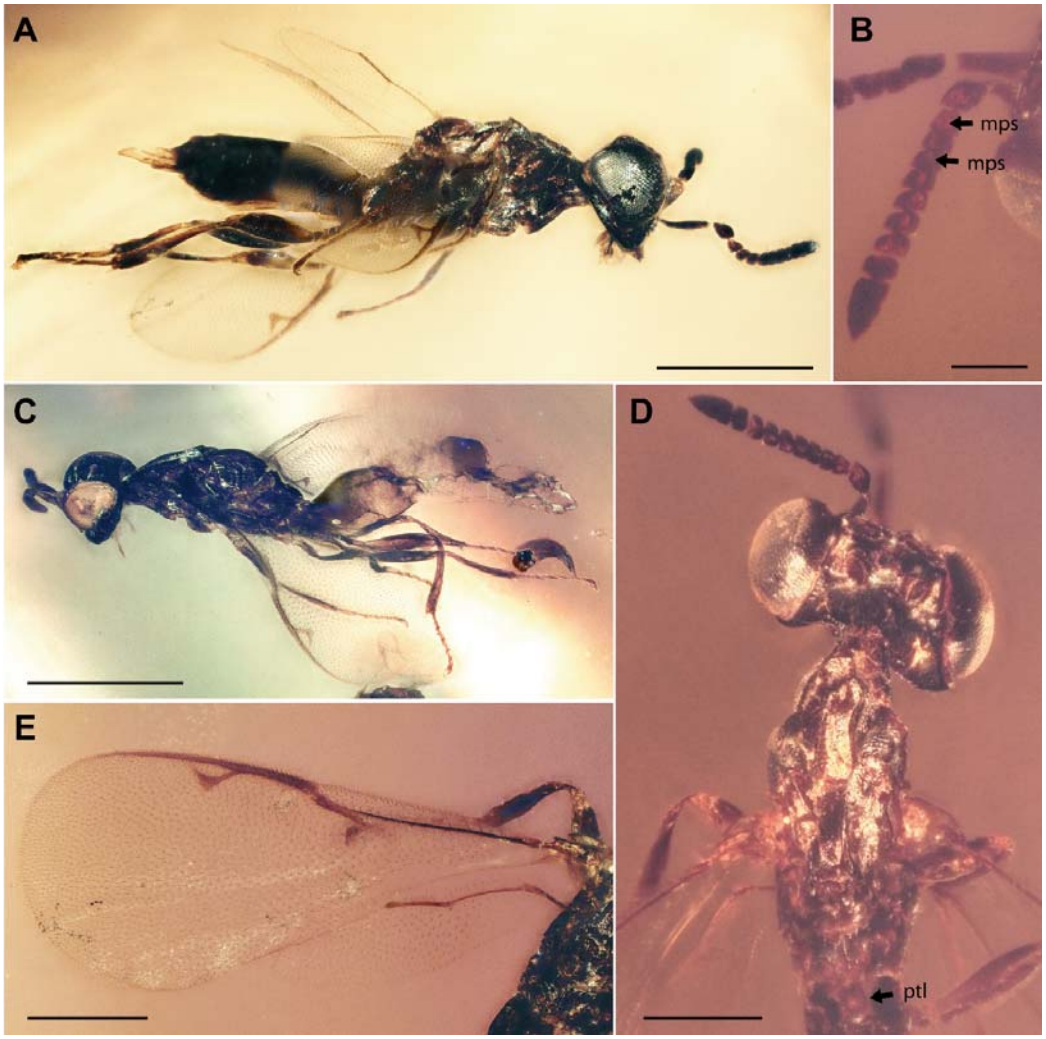

Figure 1: Digital microscopic images of *Diversinitus attenboroughi*, male. (A, B, D, E) holotype. (A) Lateral habitus. (B) Detail of left antenna. (C) Lateral habitus of paratype. (D) Dorsal habitus. (E) Wings left side. Scale bars: (A, C) 0.5 mm, (B) 0.1 mm, (D) 0.2 mm, (E) 0.25 mm. Abbreviations: mps = multiporous plate sensilla, ptl = petiole.

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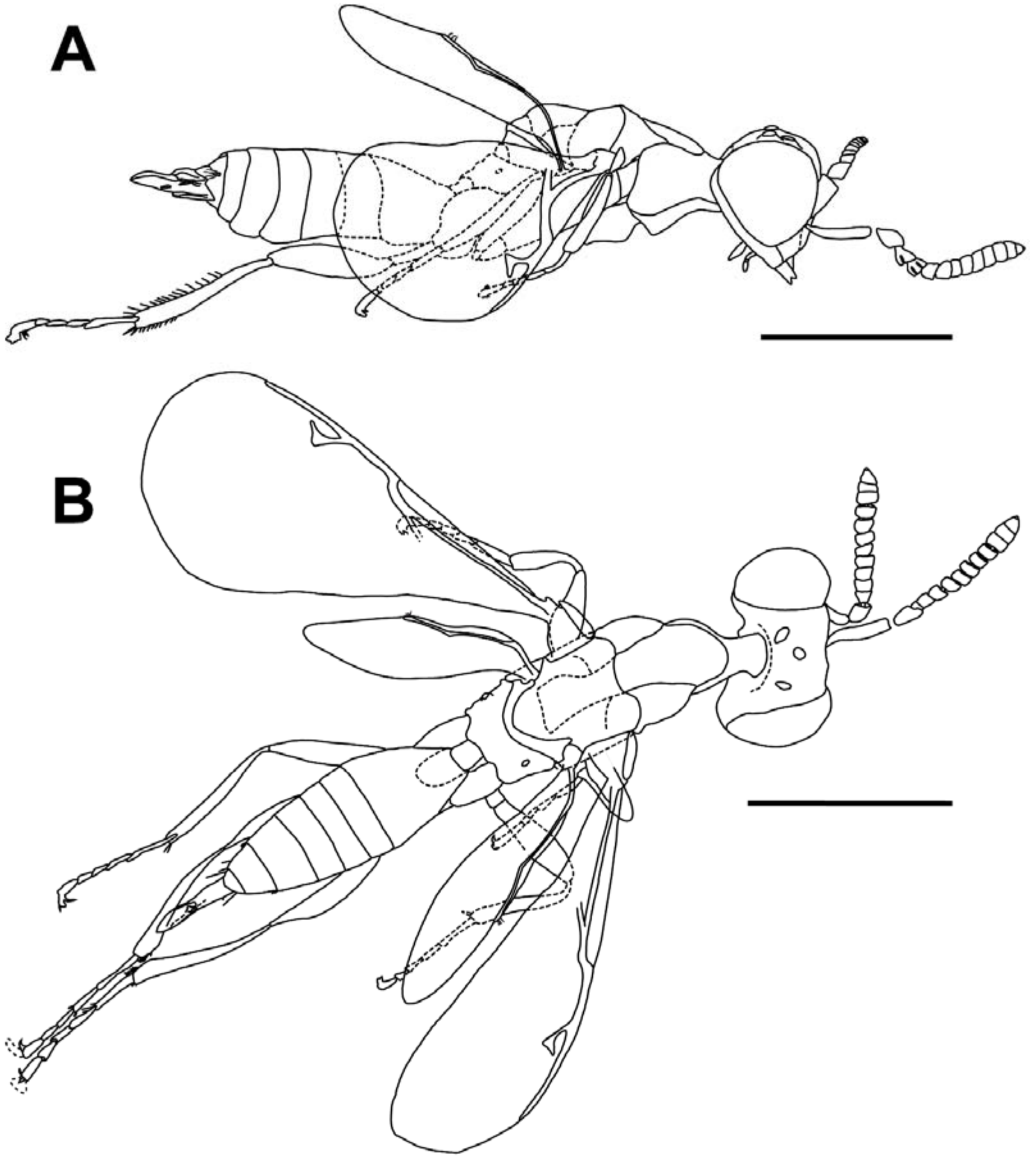

Figure 2: Habitus drawings of *Diversinitus attenboroughi*, male. Holotype (A) habitus lateral. (B) Habitus dorsal. Scale bars: 0.5 mm.

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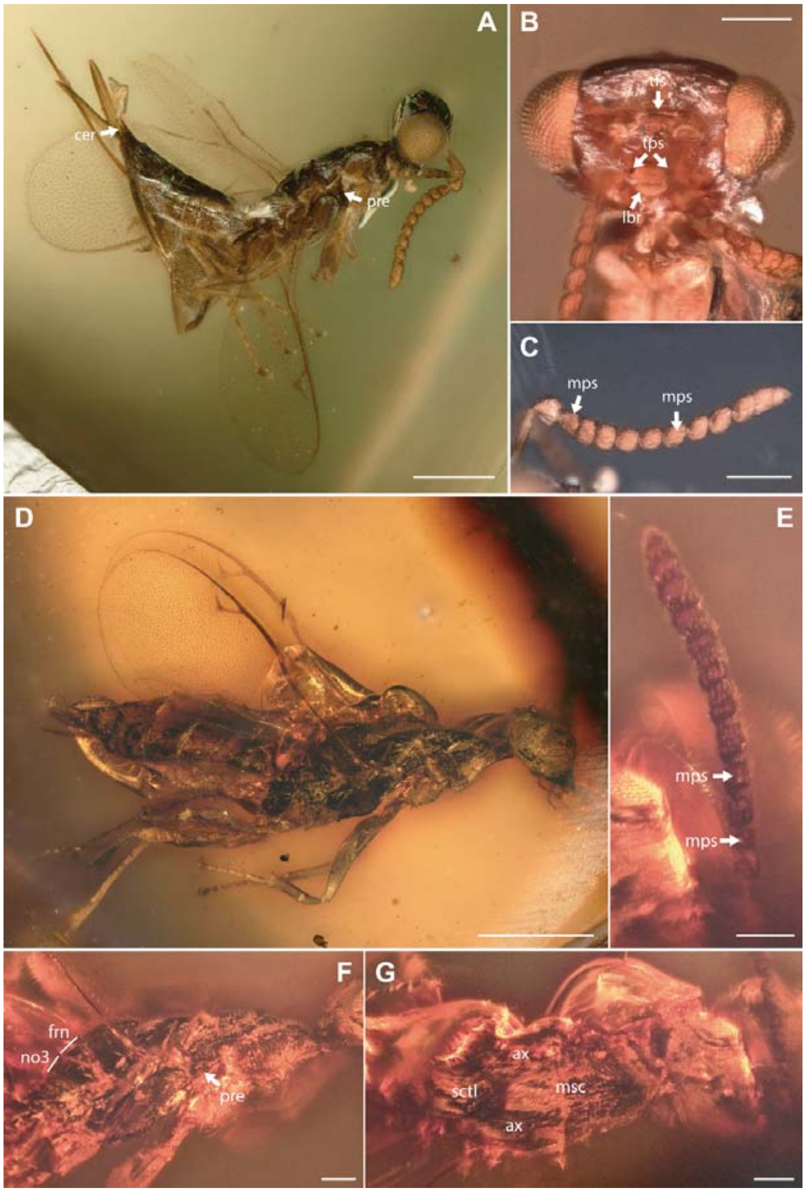

Figure 3: Digital microscopic images of *Burminata caputaeria* and *Glabiala barbata*, female. (A, B, C) *Burminata caputaeria* (A) lateral habitus. (B) Head frontal. (C) Right antenna lateral. (D, E, F, G) *Glabiala barbata* (D) lateral habitus. (E) Left antenna dorsal. (F) Mesosoma lateral. (G) Mesosoma 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.

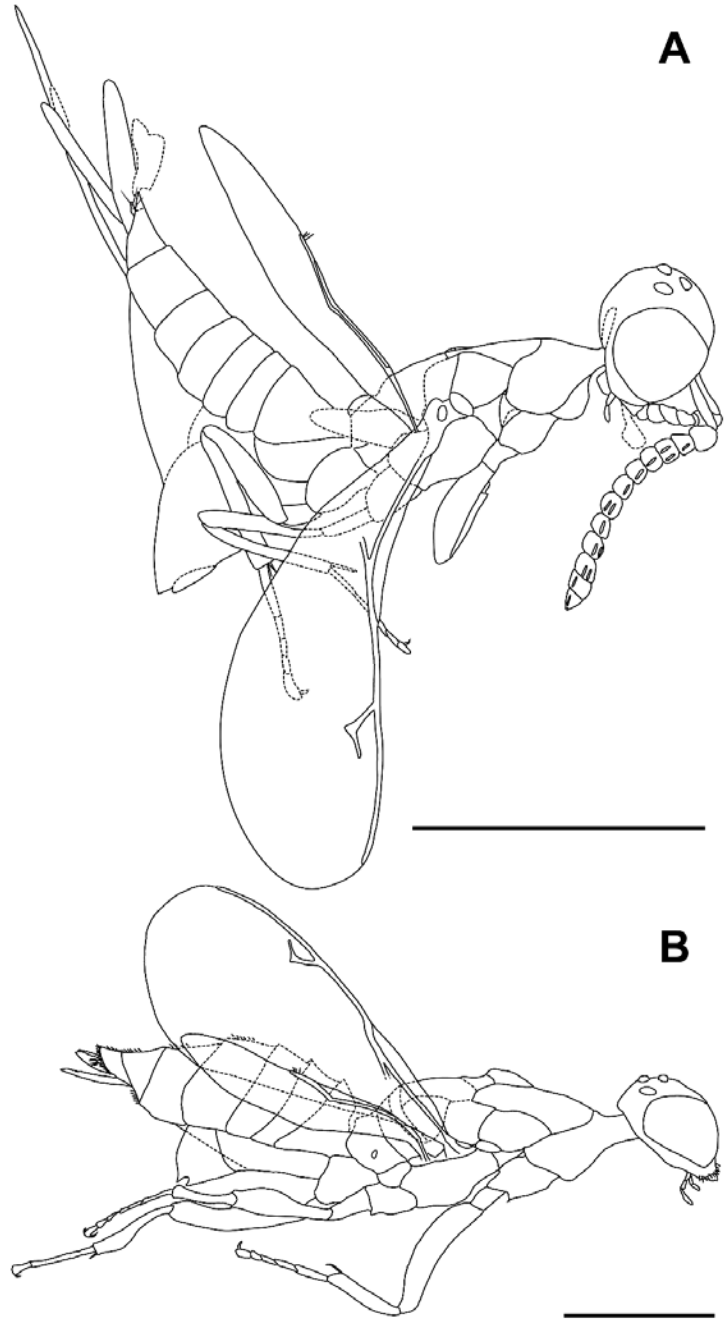

Figure 4: Habitus drawings of female holotypes of *Burminata caputaeria* (A) and *Glabiala barbata* (B). Scale bars: 0.5 mm.

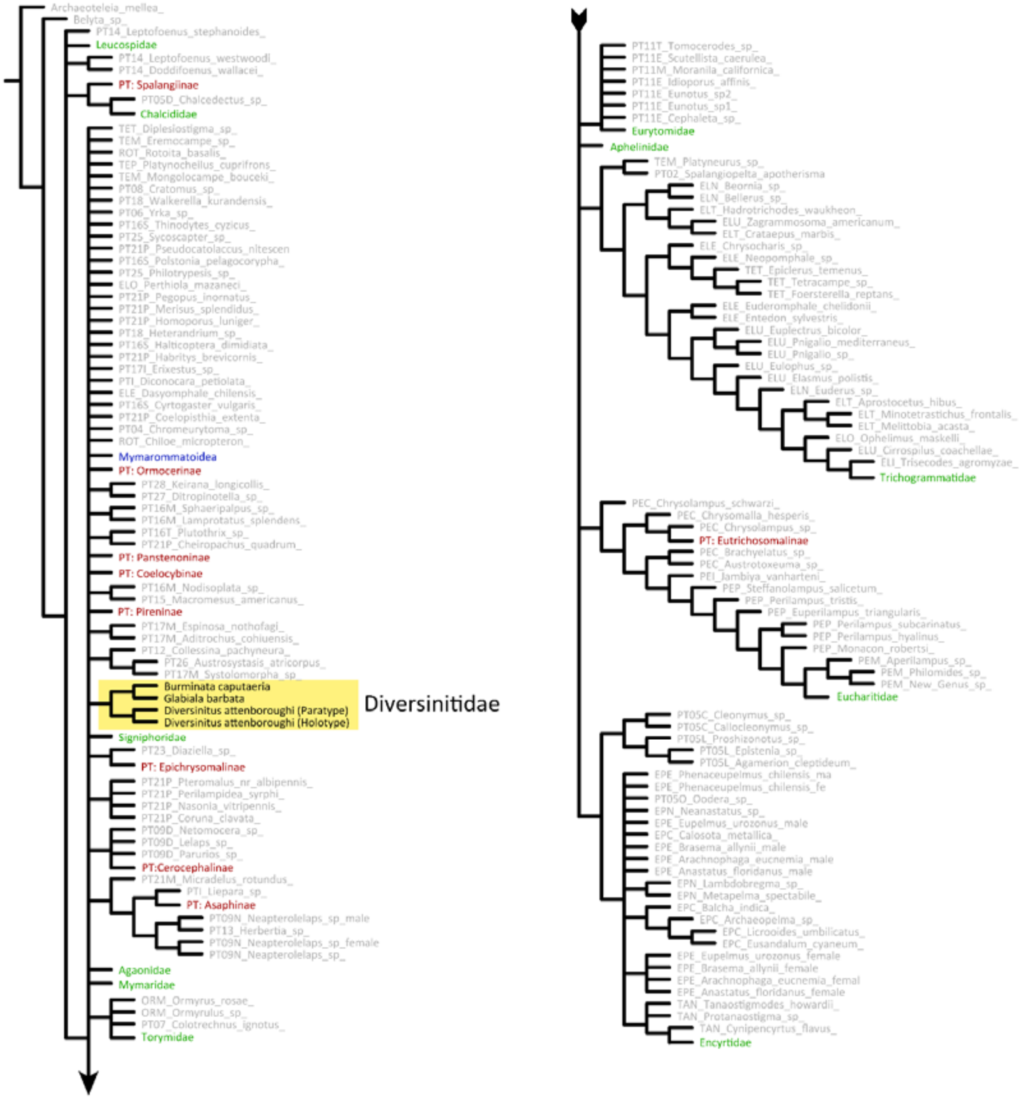

Figure 5: Phylogenetic placement of Diversinitidae within Chalcidoidea based on morphological characters. Strict consensus tree calculated from 38 trees (tree length = 6306, CI = 0.072, RI = 0.532, 232 characters and 304 taxa, equal weights, new technology search). Yellow box highlights described fossils. 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).

Tables:

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

Supplementary Table:

Supplementary Table 1: Data matrix constructed for all available members of the family Diversinitidae, using the character list of Heraty et al. (2013).

Page 2: [1] Comment [G4] Gibson 2017-12-18 2:22:00 PM

Any individual studies can only support or not support a hypothesis such as monophyly, they can not ‚confirm' hypotheses, they can only ‚confirm' the presence or absence of a structure, etc.

Page 2: [2] Comment [G5] Gibson 2017-12-18 9:22:00 AM

Also known from nematodes, pseudoscorpions and other arachnids. Your word „mainly" may cover these exceptions, but you should perhaps list these also in the beneficial category because „mainly" in the sentence also covers the phytophages, and thus the sentence is inaccurate.

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, rendering them essential as regulators for other insects and as

Page 2: [4] Comment [G6] Gibson 2017-12-18 9:29:00 AM

If you use the word „taxa", which again includes species, then relationships among almost all chalcid taxa remain unresolved. However, even if you use „families" I would say that most still remain unresolved, as does the familial status of a good number of currenctly „accepted" families.

Page 5: [5] Comment [G9] Gibson 2017-12-18 2:07:00 PM

Is this rewording accurate? A speculum is a bare region of the disc beyond the basal fold. I think from your images of the females the wing is bare basally, including the basal cell and apparently beyond this to behind the parastigma. A bare or pilose basal cell as well as the presence or absence of a speculum should be stated explicitly here and in the descriptions.

Page 5: [6] Comment [G10] Gibson 2017-12-18 2:10:00 PM

Based on your figure 4 I would definitely not agree with „distinctly longer".

Page 5: [7] Comment [G11] Gibson 2017-12-18 2:11:00 PM

Based on your images certainly not a complete basal vein, but apparently only a small section near the parastigma.

Page 5: [8] Comment [G12] Gibson 2017-12-18 11:05:00 AM

I find this very hard to believe, see comment below under description.

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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.

Page 5: [10] Comment [G13] Gibson 2017-12-18 2:13:00 PM

I do not suppose you can tell whether the cerci are articulated with the tergum basally or fused basally to the tergum? See discussion.

Page 5: [11] Comment [G14] Gibson 2017-12-18 9:51:00 AM

This paper and the description of the new family likely will be of interest to others than just chalcidologists knowledgeable of chalcid jargon. I therefore suggest adding a bit more information about the more general body part a specifica part, such as „frenum", „prepectus" is on. Certainly not absolutely necessary, but a bit more informative.

Page 6: [12] Comment [G16] Gibson 2017-12-18 2:27:00 PM

Are you sure that the asymmetry is not just an artefact of preservation? In your figure 3E the funiculars appear more symmetrical, as you draw in figure 4. In any event, you should also state in the key that Diversinitus is based on males and the other two genera on females. Because you do not have the alternative sex for any of the three genera you cannot know with certainty what features might be sexually dimorphic. Another feature that appears to be very distinctive, setal pattern of the fore wing, should be included in the key because this likely is more visible than the other key features given.

Page 6: [13] Comment [G17] Gibson 2017-12-18 10:01:00 AM

The key should be rigorously comparative for all included features.

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Head densely pilose.

1.

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Funicular segments somewhat thistle-shaped (Fig. 3C).

2.

Page 6: [16] Comment [G18] Gibson 2017-12-18 2:35:00 PM

Including axillae? See comment below.

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on mesoscutum and mesoscutellum

3.

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. Head mainly bare (Fig. 3B)

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on mesoscutum and mesoscutellum

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For the benefit of the reader it is always good practice to first state the structure being described, then (if necessary) the view from which it is viewed, and then the state(s).

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Page 7: [27] Comment [G23]	**Gibson**	**2017-12-18 10:33:00 AM**

Along which margins, all or just one or both of dorsal and posterior? Please state explicitly.

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Because the mesoscutellum does not include the axillae, does this mean the axillae are bare?

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bearing no pilosity

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bearing no pilosity

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bearing no pilosity

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bearing no pilosity

Page 7: [30] Deleted Gibson 2017-12-18 10:41:00 AM

bearing no pilosity

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bearing no pilosity

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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.

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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.

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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.

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bearing

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Page 7: [33] Comment [G26] **Gibson** **2017-12-18 10:57:00 AM**

I am not sure of the significance of this comparison, but you should also describe in particular the size and shape of the metacoxa, which is a familial feature for some families.

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Can you tell if it is bifurcate or simple, which is also very important.

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and

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and

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This is a family feature. Family features should not be included in generic descriptions (see for example first description). Also as much as possible, the descriptions should be as similar as possible, with any feature described for one taxon described for all, or a statment given that the feature is not visible. For example you describe the maxillary palps as being at least three segmented in this taxon, but do not mention it for the previous taxon, which leaves the reader to wonder whether the absence is because you just did not describe it for that taxon or because it is not visible to describe.

Page 9: [37] Comment [G32]	**Gibson**	**2017-12-18 12:25:00 PM**

Measured in dorsal length?

Page 9: [38] Comment [G33]	**Gibson**	**2017-12-18 12:27:00 PM**

If the same as for previous taxon then describe the same way as for the previous description. Because I realize the descriptions are not rigorously comparable I did not go any further editing them.

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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

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You should comment that the large prepectus of Diversinitidae is not congruent with it having an undifferentiated F1 with mps if the prepectal states of Rotoitidae and some Mymaridae are plesiomorphies. Consequently, the F1 structure of Diversinitidae may indicate the prepectal structures of Rotoitidae and some Mymaridae represent secondary reductions within Chalcidoidea.

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presence of many plesiomorphic features and the

Page 13: [42] Comment [G37]	**Gibson**	**2017-12-18 2:49:00 PM**

Assignment of taxa to families is, or should be, based on shared derived features (synapomorphies) and thus the presence of symplesiomorphies is non-informative.

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that is present in almost all extant chalcidoids

Page 13: [44] Comment [G38]	**Gibson**	**2017-12-18 1:08:00 PM**

Known from only one genus, albeit the hypothesized most basal group of the subfamily Eupelminae.

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Not in Mymaridae because the transverse line in Mymaridae consists internally of inrolled cuticle, part of the trabeculae, and not homologous to the transverse lines in the other groups. See Debauche ( ) for structure.

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Another important character that should be discussed relative to Diaprioidea and other Proctotrupomorpha, Tetracampidae, Mymaridae, etc. is the presence of bidentate rather than tridentate mandibles. Also, somewhere in the discussion you need to note the unusually long trochanters of Diversinitidae, assuming you are correct in this feature (see previous comment).

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An arcane difference between „since“ and „because“ in English is that „since“ implies a ‚time‘ whereas „because“ implies a ‚causal‘ effect. For example, „Chalcidoidea have been around since at least the Cretaceous“ compared to „Diversinitidae are Chalcidoidea because they have mps“. Not important, just shows I have been editing papers too long.

Page 15: [48] Comment [G44] Gibson 2017-12-18 2:56:00 PM

Again, structures not homologous.

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show a multitude of plesiomorphic characters, foremost

Page 15: [50] Comment [G45] Gibson 2017-12-18 1:24:00 PM

None of the other plesiomorphic character states possessed by Diversinitidae are more plesiomorphic than found in Mymaridae and other Chalcidoidea.

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Here is where you might discuss the non-congruence of the size of the prepectus relative to Rotoitidae and some Mymaridae. If the F1 sensillar pattern is plesiomorphic then either Rotoitidae and some Mymaridae independently similarly reduced the size of their prepectus or Diversinitidae independently increased the size of their prepectus similarly to other non-Rotoitid chalcids.