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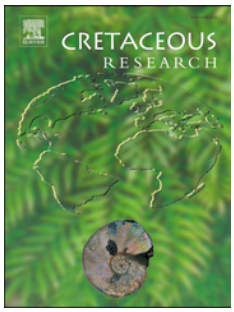

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Corentin Jouault: Data curation, Formal analysis, Investigation, Writing - Original draft, Writing - Review & Editing. **Alexandr P. Rasnitsyn:** Conceptualization, Formal analysis, Resources, Investigation, Validation, Writing - Original draft. **Vincent Perrichot:** Conceptualization, Resources, Data curation, Investigation, Formal analysis, Validation, Writing - Original draft, Writing – Review & Editing, Supervision.

Ohlhoffiidae, a new Cretaceous family of basal parasitic wasps (Hymenoptera: Stephanoidea)

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ABSTRACT 0000-0002-7973-0430

A new family of stephanoid wasps is established based on Cretaceous amber inclusions and rock imprints. Ohlhoffiidae fam. nov. comprises four species in three genera: Ohlhoffia robusta gen. et sp. nov., and Myanmephialtites bashkuevi gen. et sp. nov., which are newly described and figured from mid-Cretaceous amber of northern Myanmar; and Cretephialtites pedrerae Rasnitsyn & Ansorge, 2000, and C.(?) hispanicus (Rasnitsyn & Martínez-Delclòs, 2000) comb. nov., transferred here from Karataus hispanicus, both from the Barremian of Spain. A key to the genera of the family is proposed, and we also discuss the shifting proportion of non-aculeate wasps between the Early Cretaceous and Cenozoic.

Keywords. *Apocrita, Ohlhoffiidae, Kachin amber, Montsec, Cenomanian, Barremian*

1. Introduction

The Stephanoidea is considered an old lineage of parasitoid wasps that previously diverged from the parasitoid Euhymenoptera (Grimaldi and Engel, 2005). In recent analyses of the higher-level hymenopteran relationships, the sole living family Stephanidae has been retrieved as the sister-group to the remaining Apocrita (Sharkey et al., 2012; Mao et al., 2015) or closer to the Evanioidea or Trigonaloidea (Peters et al., 2017; Tang et al., 2019). But little is known on the evolutionary history of Stephanidae, particularly its past distribution and diversity, since the family has a scant fossil record. Indeed, while there are about 350 extant species (Aguiar et al., 2013) and the earliest occurrences extend back to the mid-Cretaceous (ca. 100 Ma), only twelve extinct species of Stephanidae are currently recognized, five of which from the Cretaceous (Engel and Grimaldi, 2004, Engel et al., 2013; Engel and Huang, 2017; Li et al., 2017; Engel, 2019). The geological record provides a better glimpse into the remaining Stephanoidea, hitherto comprising three extinct-only families: the Ephialtitidae, known from 89 species ranging from early Jurassic to mid-Cretaceous of China, India, Kazakhstan, Kyrgyzstan, Mongolia, Russia, Spain, Germany, and Brazil (Li et al., 2020; Zhang, 2020 and references therein); the Aptenoperissidae, with eight species in mid-Cretaceous Burmese amber (Rasnitsyn et al., 2017; Rasnitsyn and Öhm-Kühnle, 2018; Zhang et al., 2018a, 2018d); and the Myanmarinidae, with four species similarly in mid-Cretaceous Burmese amber only (Li et al., 2018; Zhang et al., 2018b). Stephanoidea are thus mostly extinct except for the relictual, nominotypical family Stephanidae, with their generic diversity peak from the Jurassic to mid-Cretaceous.

Here we propose a fifth family, Ohlhoffiidae fam. nov., based on two specimens that are newly described from Albian–Cenomanian Burmese amber, in which we also tentatively place the genus Cretephialtites Rasnitsyn & Ansorge, 2000, known from Lower Cretaceous rock imprints.

2. Material and methods

The two amber specimens described herein originate from mines of the Noije Bum Hill in Hukawng Valley, Kachin State, northern Myanmar (see Grimaldi and Ross, 2017: fig. 2 for a

detailed map). After more than a century of uncertainty regarding the age of this amber, there seems to be a recent consensus toward a latest Albian–earliest Cenomanian age, based on radiometric studies of volcanic clasts from within the amber-bearing stratum (dated to 98.79 ± 0.62 Ma; Shi et al., 2012), the palynomorphs and ammonoid content of this amber bed (Cruickshank and Ko, 2003), and ammonoid and bivalve inclusions in amber (Smith and Ross, 2018; Yu et al., 2019).

Specimen MB.I.12345 is complete and exquisitely preserved in a piece of clear yellow amber. It was spotted by one of us (VP) among the amber collection of Rainer Ohlhoff (Saarbrücken, Germany) who kindly provided it for study; it is now housed in the amber collection of the Museum für Naturkunde, Berlin. It was examined and photographed using a Zeiss Axio Zoom.V16 stereomicroscope and Axiocam 512 digital camera with Zen software allowing for measurements and digital photography. All images are digitally stacked photomicrographic composites of several individual focal planes, which were processed using HeliconFocus software in B mode. The figures were composed with Adobe CC 2019 softwares (Illustrator and Photoshop).

Specimen PIN no. 5608/55 is nearly complete, missing only the apex of fore wings, but is somewhat distorted and altered by preservation, and surrounded by organic debris; it is preserved in a piece of clear yellow amber that was donated to the Paleontological Institute, Russian Academy of Sciences, Moscow (PIN), by Alexei Bashkuev. The piece was trimmed and polished by Dr. Dmitry D. Vorontsov (Moscow) who also photographed the specimen. It was studied using a Leica M165C stereomicroscope, and imaged using a compound microscope Nikon E-800 with dry (4×) equipped with an Olympus OM-D E-M10II camera. A combination of brightfield and incident light was used, and stacks of images were processed with Helicon Focus software in B mode. *The figures were composed with Adobe Photoshop CS2 and CorelDRAW 2019.*

The morphological terminology used in description generally follows that of Huber and Sharkey (1993), except van Achterberg (1993) or Quicke (2015) for the wing cell nomenclature, and Engel et al. (2013) for the nomenclature of coronal teeth. This published work and the nomenclatural acts it contains have been registered in ZooBank (http://www.zoobank.org/, last access: 18 June 2020),

with the following LSID (reference): "urn:lsid:zoobank.org:pub:518E7020-1E4D-4DFD-B6D0-97F960379A32.

3. Systematic paleontology

Order Hymenoptera Linnaeus, 1958

Superfamily Stephanoidea Leach, 1815

Diagnosis. Fore wing with vein 1-RS short and proclivous, vertical, or reclivous (never long and proclivous), and vein 2A, when present, never with complete sub-basal loop. In lateral view, propodeum lacking a posterior surface or declivity, instead with a single, weakly sloping surface not bent downward toward hind coxa, nor enclosed widely below metasomal articulatory orifice.

Included families. Stephanidae (mid-Cretaceous to Recent), Ephialtitidae (late Early Jurassic to mid-Cretaceous), Ohlhoffiidae fam. nov. (Early to mid-Cretaceous), Aptenoperissidae and Myanmarinidae (mid-Cretaceous only).

Comment. The superfamily Stephanoidea differs from the more basal Orussoidea (including Karatavitidae, Orussidae and Paroryssidae) in the fore wing lacking the sub-basal loop of vein 2A, which is indicative of the lost apparatus of wing fixation at resting position, as is retained in most Orussoidea and more basal Hymenoptera. The Stephanoidea differs from higher Apocrita in the propodeum that is not bent downward toward hind coxae (as in non-evanioid higher Apocrita) nor widely sclerotized ventrally of the metasomal attachment (unlike Evanioidea).

Family **Ohlhoffiidae** *fam. nov.*

urn:lsid:zoobank.org:act:658F42E2-2BA7-4EAC-B7F1-6DC3A981C89A

Type genus: Ohlhoffia gen. nov.

Diagnosis. Males and females fully winged. Head with series of teeth or tubercles arranged in transverse rows on frons and vertex. Antenna polymerous, with more than 20 segments, not geniculate. Mesosoma not much elongate nor strictly cylindrical, with standard sclerotization (no fused carapace); mesonotum with median, longitudinal sulcus and notauli. Fore wing with vein 1-Rs reclivous, 2m-cu entering second submarginal cell, and cu-a not distinctly postfurcal. Hind wing with marginal cell widely open, vein 2-M+Cu long. Legs, including metacoxae and all femora, long and slender; tibiae not inflated (without hypertrophied vibration detector inside), protibia with one apical spur. Basal metasomal segments I and II transformed into petiole and postpetiole, respectively; ovipositor short.

Included genera. Type genus Ohlhoffia gen. nov., Myanmephialtites gen. nov., and Cretephialtites Rasnitsyn & Ansorge, 2000.

Comment. The new family is placed in Stephanoidea based on the following combination of characters unique of the latter: (i) propodeum not bent downward to hind coxae (apparently without free posterior surface) and not widely sclerotized below metasomal base, unlike in remaining Apocrita with metasomal articulatory orifice small due to propodeum either bent downward to hind coxae (in majority of taxa), or posterior propodeal surface widely sclerotized below metasomal base (in Evanioidea); (ii) fore wing vein 2A, if present, lacking complete sub-basal loop indicative of wing coupling apparatus (metanotal cenchri and rough area on lower wing surface within 2A loop that fits to fix on cenchrus): the coupling mechanism is characteristic of lower Hymenoptera including Orussoidea (Orussidae, Paroryssidae and Karatavitidae; see Rasnitsyn and Zhang, 2010).

Ohlhoffiidae is mostly similar to Stephanidae in the presence of teeth or tubercles on the head, a nearly complete wing venation, and the tibiae not inflated. But it differs notably from Stephanidae and all other Stephanoidea by its two-segmented metasomal petiole. Additionally, Ohlhoffiidae differs from Stephanidae and Ephialtitidae: Ephialtitinae by its short ovipositor, and from Ephialtitidae: Symphytopterinae by its fore wing crossvein cu-a not far postfurcal. It differs from

Aptenoperissidae by its antennae not geniculate, the fore tibia bearing a single spur, the female winged and with a standard mesosomal sclerotization (aptenoperissid females are wingless and with a mesosomal carapace), and the male with fore wing vein cu-a interstitial or antefurcal (cu-a well postfurcal in aptenoperissid males). And it differs from Myanmarinidae by a more complete wing venation (deeply reduced and modified in Myanmarinidae), polymerous antennae (11-14 segments in Myanmarinidae), a standard mesosomal sclerotization (elongate, cylindrical mesosoma with smooth and desclerotized dorsum in Myanmarinidae, particularly in female), and a short ovipositor.

Genus ***Ohlhoffia*** *gen. nov.*

urn:lsid:zoobank.org:act:7A7ADDB7-11F6-4786-A4D1-5E9FBDE0B366

Type species: Ohlhoffia robusta sp. nov.

Etymology. The generic name is a patronym honoring Rainer Ohlhoff who provided the type specimen described here. The name is feminine.

Diagnosis. Stature stout, with body and appendages long and robust. Frons and vertex with 10-12 transverse ridges, 6 of which surmounted by series of distinct teeth or tubercles. Mandibles small, tridentate. Fore wing with costal space much narrow, pterostigma narrow and elongate, marginal cell long and narrow, third submarginal cell 3× as short as second submarginal cell, vein 2m-cu well basad 2r-m. Hind wing vein 2A absent. Petiolar segments hardly longer than high. Tibial spurs relatively short.

Ohlhoffia robusta *sp. nov.*

urn:lsid:zoobank.org:act:8E78F44A-D299-4E61-8B0C-8BAE91B17F59

(Figs. 1–3)

Holotype. MB.I.12345, a complete female exquisitely preserved in a small piece of polished, translucent, yellow amber; housed in the Museum für Naturkunde Berlin, Germany.

Horizon and locality. Mid-Cretaceous, upper Albian–lower Cenomanian (ca. 99 Ma), in amber from the Hukawng Valley, Kachin State, Myanmar.

Etymology. The specific epithet is taken from the Latin robustus, meaning strong, in reference to the robust appearance of this morphotype.

Diagnosis. As for the genus.

Description. Total body length 6.30 mm. Integument apparently thick. Head globose, 0.98 mm high; compound eye large, 0.74 mm high, 0.51 mm wide, occupying much of lateral surface of the head; gena apparently coriaceous, rounded (Figs. 2B, 2E, 3B). In lateral view, vertex strongly rounded above compound eye, with distinct ocelli, ocellar diameter about as large as pedicel width. Frons with median-anterior tubercle (tbA) followed by slightly larger, second median-anterior tubercle (tbB); and row of two large tubercles (tbC-tbC') located right in front and at either side of median ocellus. Vertex with one row of two large tubercles (tbD-D') located just behind median ocellus and in front of lateral ocelli, at about the same position and size as tbC-C'; one single, large, median tubercle (tbE) located between lateral ocelli; and one single, median tubercle (tbF) smaller than tbE and located posterior to lateral ocelli (Figs. 2B, 2D, 3B). Each row or tubercle extending laterally into transverse ridges reaching margin of compound eyes; additionally, 1–2 similar ridges between each row of tubercles. Occiput slightly concave and roughened; malar space slightly longer than first flagellomere, 0.24 mm long, with malar sulcus. Antenna relatively short (3.83 mm long), filiform, with 21 flagellomeres gradually slightly decreasing in width toward apex; scape robust, pedicel short (0.12mm), longer than wide, and slightly narrower than scape; individual flagellomeres longer than wide, each about 0.06 mm wide; length of first flagellomere 0.16 mm, second 0.22 mm; flagellomeres decreasing in length after antennal midlength; mandibles short, stout, projecting forward, the outer surface strongly convex and with apical half densely covered by long, fine, decumbent setae; masticatory margin of mandible with 3 blunt teeth, the apical tooth large, the others progressively decreasing in size toward base. Maxillary palps with four long palpomeres, labial palps much shorter, with apical palpomere the only visible segment, which barely surpasses the first maxillary palpomere (Figs. 2E, 3B).

Mesosoma (Figs. 2A, 3A) with only few pronounced sculpturing, densely covered by fimbriate setae; mesosomal length 2 mm, maximal height 1.10 mm. Pronotum slightly elongate into a neck, reaching tegula, pronotal fold reduced; anterior declivity of pronotum smooth; neck without distinctive sculpture; dorsal mesonotal area convex, with weak median longitudinal sulcus not reaching to posterior mesonotal margin, and distinct notauli converging but not touching posteriorly; mesoscutellum short; mesopleuron with a depression for reception of leg delimited above with furrow running from mesopleural pit (entrance of mesopleural apodeme) to small triangular external part of prepectus; metanotum and mesoscutellum subequal in length, slightly costulate; metanotal trough (metapostnotum) foveate; metapleuron fused immovably with propodeum, posteriorly with transverse, foveate groove; propodeum flat to slightly convex, anteriorly with a transverse row of shallow foveae, with long, slit-like spiracle.

Fore wing (Fig. 3C) 4.30 mm long, with ten cells (incl. costal one) entirely enclosed by tubular veins; C and R adjacent for 2/3 of their length, then slightly diverging to form a narrow costal cell which is mostly distinct above prestigma; pterostigma elongate, more than 8× as long as wide, only feebly swollen medially; 1-Rs reclivous, 1.5× as long as 1-M, nearly straight, aligned with slightly arched 1-M; 2r-rs proclivous, about as long as RS+M; fork of 2-RS and 2-M only slightly anterior to 1m-cu (2-M very short); 2-Rs distinctly arched basally, with no trace of 1r-rs; 2r-m oblique, slightly sinuate, meeting RS slightly behind 2r-rs, and well behind 2m-cu, enclosing long and almost triangular submarginal cell 2; 3r-m sinuate, subparallel to 2r-m, delimitating short and skewed submarginal cell 3; 5-RS almost half length of marginal cell, meeting R1 at acute angle near wing apex; 1m-cu subequal in length and subparallel to 1-M (discal cell subparallel-sided, more than twice as long as high); 2r-m, 3r-m, and 2m-cu each with two bullae; cu-a only slightly anterior to fork of 1-M and 1-Cu, oblique, longer than 1-M; 2-Cu longer than 1m-cu; A straight, prolonged apically by claval furrow which forms a spurious vein margined with incrassate membrane. Hind wing (Fig 3C) 2.70 mm long, with basal and sub-basal cells entirely enclosed by tubular veins; basal cell long, 1.5× as long as sub-basal one; neither longitudinal vein reaching wing margin as a tubular vein; 1-RS and 1-M long, subequal in length, more than twice as long as

subvertical r-m, 1-M distinctly arched basally, 2-M+Cu only slightly shorter than 1-M, longer than cu-a; fork of 1-M and 1-Cu basal to fork of RS and R1; 2A present, jugal lobe only incipiently delimited; anterior margin of wing with 8 distal hamuli.

Legs elongate, without distinct sculpturing (Figs. 1, 3A); tibial spur formula 1-2-2; protibial spur bifid at apex, shorter than meso and meta-tibial spurs that are subequal in length, straight and simple; metacoxa distinctly larger than pro- and meso-coxae, its outer margin expanded apically by a lateral flange covering articulation of metatrochanter; metafemur moderately swollen medially (0.30 mm at maximum width) and nearly as long as metatibia (1.95 vs 2.00 mm); tarsi pentamerous; metabasitarsus (0.91 mm) as long as remaining ones combined, second metatarsus 0.43 mm long; fourth metatarsomere shortest; pretarsal claws with small preapical tooth.

Metasoma bipetiolate (Figs. 1, 2A, 2C, 3A), both petiolar segments cushion-shaped, short and thick, hardly as long as high (0.50 and 0.53 mm long, respectively), without tergosternal fusion and with deep, foveate pretergite; remaining metasoma ('gaster') oval, short, only twice as long as petiolar segments combined; first and second gastral tergites largest of metasomal tergites, following gastral tergites gradually decreasing in size toward apex. Ovipositor short, third valvula 0.40 mm long, sheaths 0.30 mm long; sheaths narrow, tapering apically to broadly rounded apex, covered with short subdecumbent setae. Gastral integument without pronounced sculpturing, covered with scattered, short, subdecumbent setae.

Myanmephialtites *gen. nov.*

urn:lsid:zoobank.org:act:53BB71B4-1736-4FC4-8E73-CDD6120F259F

Type species: Myanmephialtites bashkuevi sp. nov.

Etymology. The genus name is a combination of a corrupted name of the country of origin (Myanmar), and Ephialtites, type genus of the related family Ephialtitidae.

Diagnosis. Stature relatively slender, with body and appendages long and narrow; antennae 28 or 29-segmented, with first flagellomere elongate. Hind wing vein 2A present. Posterior propodeal

foramen much wider than metasomal base. Metatibial spurs long. Petiolar segments more than twice as long as high.

Myanmephialtites bashkuevi *sp. nov.*

urn:lsid:zoobank.org:act:A1211E5A-7FBA-4EB4-83D9-35F6B16B4DD9

(Figs. 4–5)

Holotype. PIN no. 5608/55, sex unknown; specimen approximating the amber surface, with right half of head and apical portion of fore wings missing, destroyed during trimming of the amber piece; housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN).

Horizon and locality. Upper Cretaceous, upper Albian–lower Cenomanian (ca. 99 Ma); in amber from Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar.

Etymology. The specific epithet is a patronym honoring Mr. Alexei Bashkuev who donated the fossil to the PIN collection.

Diagnosis. As for the genus, by monotypy.

Description. Body length 5.2 mm, wing length as preserved 3.2 mm, estimated total wing length 4.7 mm. Preserved fragment of head with 5 visible teeth on frons / vertex; mandibles small, elongate, symmetrically pointed apical as preserved (dentition obliterate due to integument degradation). Antenna elongate, with 28-29 segments (apparently different in two antennae), pedicel slightly thinner than scape and thicker than flagellum; flagellar segments subequal in width, all more than twice as long as broad, gradually slightly decreasing in length toward apex, except disproportionally long first flagellomere, subapical and apical segments shortest.

Mesosomal structures poorly visible by preservation except propodeum which is, in lateral view, only slightly convex dorsally and without posterior face; instead, posterior propodeum entirely open to form a wide articulatory foramen which is much wider than metasomal base, as is

described for some Ephialtitidae (see Rasnitsyn and Zhang, 2010; Li et al., 2015), dorsal posterior propodeal margin extending backward above metasomal base.

Fore wing (Fig. 5B), as preserved, much similar to that of Ohlhoffia robusta; costal cell much narrow, both veins C and R incrassate distally; pterostigma not much elongate, with 2r-rs originating near its midlength; 1-RS distant from pterostigma for less than its length, subequal to 1-M in length, angular at junction with 1-M; RS+M parallel to 1-Cu, almost as long as pterostigma; 2-RS long, distinctly arched basally, with no trace of 1r-rs; 2r-m meeting RS slightly distal of 2r-rs, oblique, delimiting long, low, nearly triangular submarginal cell 2; 1m-cu not parallel to 1-M, distinctly shorter that 2-Cu; 2m-cu joining M well before 2r-m; cu-a interstitial; first sub-discal cell higher than discal one. Hind wing (Fig. 5B) with 1-RS and 1-M subequal in length, much longer than subvertical r-m, both distinctly arched basally; 2-M+Cu longer than cu-a and about 0.75× as long as 1-M; RS, M, Cu and A with distinct but short abscissae not reaching wing margin; 2A distinct, much approximated to hind margin of wing; jugal lobe apparently not delimited; anterior margin of wing with seven basal hamuli, distal hamuli not visible.

Legs long and thin, with particularly long trochanters (and probably with trochantelli, although these are not reliably identifiable), basitarsi, and hind tibial spurs; basitarsus subequal to remaining tarsomeres combined, fourth tarsomere elongate, fifth one subequal to second, third and fourth combined (precise proportions unknown because of deformation); pretarsal claws small, with a small preapical tooth.

Metasoma. Petiolar segments elongate, each more than twice as long as high, with first segment slightly longer than second, and second segment barrel-shaped in lateral view. Remaining mesosoma (gaster) apparently distorted, segmentation obscured by preservation; as preserved, gaster roughly as long as petiolar segments combined, less than 3× as high as petiolar segments, slightly higher in its apical half; genitalia not preserved.

Comment. Myanmephialtites gen. nov. primarily differs from Ohlhoffia gen. nov. in its slender stature, particularly the more elongate petiolar segments, and in the antennae more segmented, the

290 *hind wing vein 2A present, and the long hind tibial spurs. Both fore wings of Myanmephialtites gen.*
291 *nov. and Ohlhoffia gen. nov. are much similar.*
292
293 ***Cretephialtites*** *Rasnitsyn & Ansorge, 2000*
294 *Type species: Cretephialtites pedrerae Rasnitsyn & Ansorge, 2000: 62, figs. 3, 4 (isolated fore wing*
295 *only).*
296
297 *Diagnosis. Fore wing as in Ohlhoffia gen. nov. and Myanmephialtites gen. nov., except for the*
298 *costal cell which is distinctly wider. Additionally, the veins 2r-m, 3r-m, and 2m-cu lack the bullae*
299 *that are present in Ohlhoffia. Metacoxa and metafemur (known in C. hispanicus only) shorter and*
300 *thicker than in Ohlhoffia and Myanmephialtites.*
301
302 *Included species. Type species, and possibly C.(?) hispanicus (Rasnitsyn & Martínez-Delclòs,*
303 *2000) (= Karataus hispanicus Rasnitsyn & Martínez-Delclòs, 2000) (see below).*
304
305 *Comment. Cretephialtites was described based solely on an isolated fore wing from the Barremian*
306 *of Spain (Rasnitsyn and Ansorge, 2000) which is nearly identical to those of Ohlhoffia and*
307 *Myanmephialtites, except for the wider costal cell. Based on the current knowledge on stephanoid*
308 *wasps, this difference is considered sufficient to distinguish the fossils as separate genera.*
309 *Rasnitsyn and Ansorge (2000) also guessed that Karataus hispanicus, and possibly Karataus*
310 *kourios (misspelled therein as kourius) Sharkey, in Darling and Sharkey (1990), may belong in*
311 *Cretephialtites as well. This could be correct for K. hispanicus, except that it was restored with the*
312 *costal cell wide although the preservation of the fore wing is poor and this inference would need*
313 *confirmation. Otherwise, the general appearance of the fossil agrees well with that of Ohlhoffia*
314 *gen. nov. (stature robust, petiolar segments short and thick, hind trochanters long), though with a*
315 *hind wing vein 1-M more strongly arched. This would make possible to assign K. hispanicus to a*

316 *genus of its own, but the incomplete preservation state of the fossil rather suggests its tentative*
317 *attribution to Cretephialtites, as C.(?) hispanicus comb. nov., until new information appears.*
318 *Karataus kourios differs more profoundly from Ohlhoffia, and by extension the Ohlhoffiidae, by*
319 *its ovipositor much longer and, based on additional material found since its original description*
320 (Grimaldi and Engel, 2005: fig. 11.11; Osten, 2007: fig. 11.75d, pl. 15j, 15k)*, by the absence of*
321 *metasomal petiolar segments. Karataus kourios was attributed to a particular genus Cratephialtites*
322 *Rasnitsyn, 1999 (again misspelled as C. koiurus) and in our opinion would be left there in the*
323 *family Ephialtitidae.*
324
325 *Key to genera of Ohlhoffiidae:*
326
327 1. Fore wing with costal cell wide ……..…. *Cretephialtites* Rasnitsyn & Ansorge, 2000
328 – Fore wing with costal cell long and narrow …….……. 2
329 2. Stature stout; tibial spurs short; first and second metasomal (petiolar) segments compact, barely
330 longer than high, cushion-shaped; hind wing vein 2A absent ……..… *Ohlhoffia* gen.
331 nov.
332 – Stature slim; tibial spurs long; petiolar segments elongate, more than twice as long as high, barrel-
333 shaped; hind wing vein 2A present ……..…..…..…… *Myanmephialtites* gen. nov.
334
335 **4. Discussion**
336 *Most Stephanoidea and Orussidae share the coronal teeth or tubercles on the vertex, a*
337 *symplesiomorphy which may be considered as a convergent response to a same constraint of*
338 *leaving the galleries dug by their hosts. However, it seems that stephanoid wasps possess one*
339 *single, median, anterior tooth while this character is lacking in Orussidae. The latter also possess a*
340 *plesiomorphic wing venation (Rasnitsyn, 1978) and a "Symphyta-like" habitus which allows an*
341 *clear distinction from the Apocrita. The specimens described above display a unique combination*
342 *of characters that are otherwise found independently in Stephanidae or Ephialtitidae, but cannot be*

assigned to any of these families without altering their diagnosis. In our opinion, these taxa belong to a sister family of Stephanidae. The perfect preservation of Ohlhoffia robusta gen. et sp. nov and the wing venation of Myanmephialtites bashkuevi gen. et sp. nov. allow the diagnosis of typical morphological characters only known from these specimens and distinctive enough to warrant the description of the fossils as a family of their own. The Ohlhoffiidae differ from other stephanoid families (Aptenoperissidae, Ephialtitidae, Myanmarinidae, and Stephanidae) primarily by a plesiomorphic wing venation, unmodified legs (plesiomorphic character), a bipetiolate metasoma (synapomorphy), and a different organization of the coronal teeth (difficult to categorize for the moment).

We propose to place C. pedrerae among the new family Ohlhoffiidae based on its strikingly similar wing venation, which is distinguishable from Myanmephialtites and Ohlhoffia only by its broader costal cell, broader cell 3rm, and the shorter distance separating the veins 2r-m and 2m-cu. However, C. pedrerae is known from an isolated fore wing (Rasnitsyn and Ansorge, 2000) so the comparison remains limited, as the wing venation of Cratephialtites kourios (Ephialtitidae) is also rather close. The discovery of a complete C. pedrerae specimen would strengthen the membership of this taxa in Ohlhoffiidae and would enhance the discussion about the character states as well as the paleobiogeographical implications.

An island endemism has been recently suggested for the Burmese amber biota (Zhang et al., 2018c; Westerweel et al., 2019), providing elements for a better understanding of this highly peculiar fauna. Insularity generally favors speciation and therefore the establishment of a unique fauna. These assumptions are consistent with the unique stephanoid diversity observed in Burmese amber and its possible affinities with the Gondwanan fauna. The Cretaceous Stephanoidea were hitherto represented by 26 species, including few amber taxa (Fossilworks, available at http://fossilworks.org, accessed 16 April 2020). Unlike the well represented ichneumonoids which show a distinct increase of diversity since the Early Cretaceous, the stephanoid wasps were apparently more diverse during the Cretaceous than today (Fig. 6). The group comprised only 4% of the non-aculeate wasps recorded in the Early Cretaceous, reached its maximal diversity (ca.

11%) during the Late Cretaceous, then dropped to less than 1% today. A similar trend is observed in Evanioidea and Proctotrupoidea. In contrast, ichneumonoids comprised 24% of non-aculeate wasps in the Early Cretaceous, 70% during the Oligocene, and 55% today. This fossil record may be biased, for example a bias over rock-imprint preservation in the Oligocene, as this period is largely devoid of fossiliferous amber deposits.

But this may reflects more or less accurate trends in the diversity of these parasitoid wasps, due to their subservient life condition in peculiar habitats, correlated with the extinction or diversification of their host. The diversity of both ichneumonoids and stephanoids in Burmese amber is yet underestimated, but systematic descriptions of ichneumonoids have probably been more neglected owing to the often difficult-to-place fossil taxa between extant or even extinct subfamilies (Quicke, 2015).

5. Concluding remarks

The bi-segmented petiole, mobile gaster, long antennae and comparatively large, movable head of Ohlhoffiidae are suggestive of insects parasitizing cryptic preys. This supposed behavior agrees with the proposed taxonomic position of Ohlhoffiidae in Stephanoidea. Extant stephanid wasps are known to develop at the expense of xylophagous beetles (van Achterberg, 2002), however using a long ovipositor to reach the hosts deep in wood galleries. In contrast, the short ovipositor displayed by Ohlhoffia may suggest they were parasitic on non-xylophagous insects.

The description of Ohlhoffiidae fam. nov. adds to the uniqueness of the hymenopteran Burmese amber fauna. In Ross' (2020) latest inventory, 1173 hexapod species are listed in no less than 412 families. Among these, the order Hymenoptera comprises a significant diversity of 189 species in 53 families, encompassing 16 percent of the total hexapod diversity in Burmese amber. It is certain that undescribed, potentially endemic taxa are yet to be discovered from this extraordinary fossil deposit.

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Figures captions

Fig. 1. *Photomicrograph of Ohlhoffia robusta gen. et sp. nov., female holotype MB.I.12345, from mid-Cretaceous Burmese amber. Habitus in left lateral view. Scale bar: 2 mm.*

Fig. 2. *Photomicrographs of Ohlhoffia robusta gen. et sp. nov., female holotype MB.I.12345, from mid-Cretaceous Burmese amber. A, Mesosoma and petiolar segments in left lateral view. B, Head in left lateral view. C, Metasoma in left lateral view. D, Detail of head dorsum in right lateral view. E, Head in frontal view. Scale bars: 0.5 mm (C), 0.2 mm (A, B, E), 0.1 mm (D).*

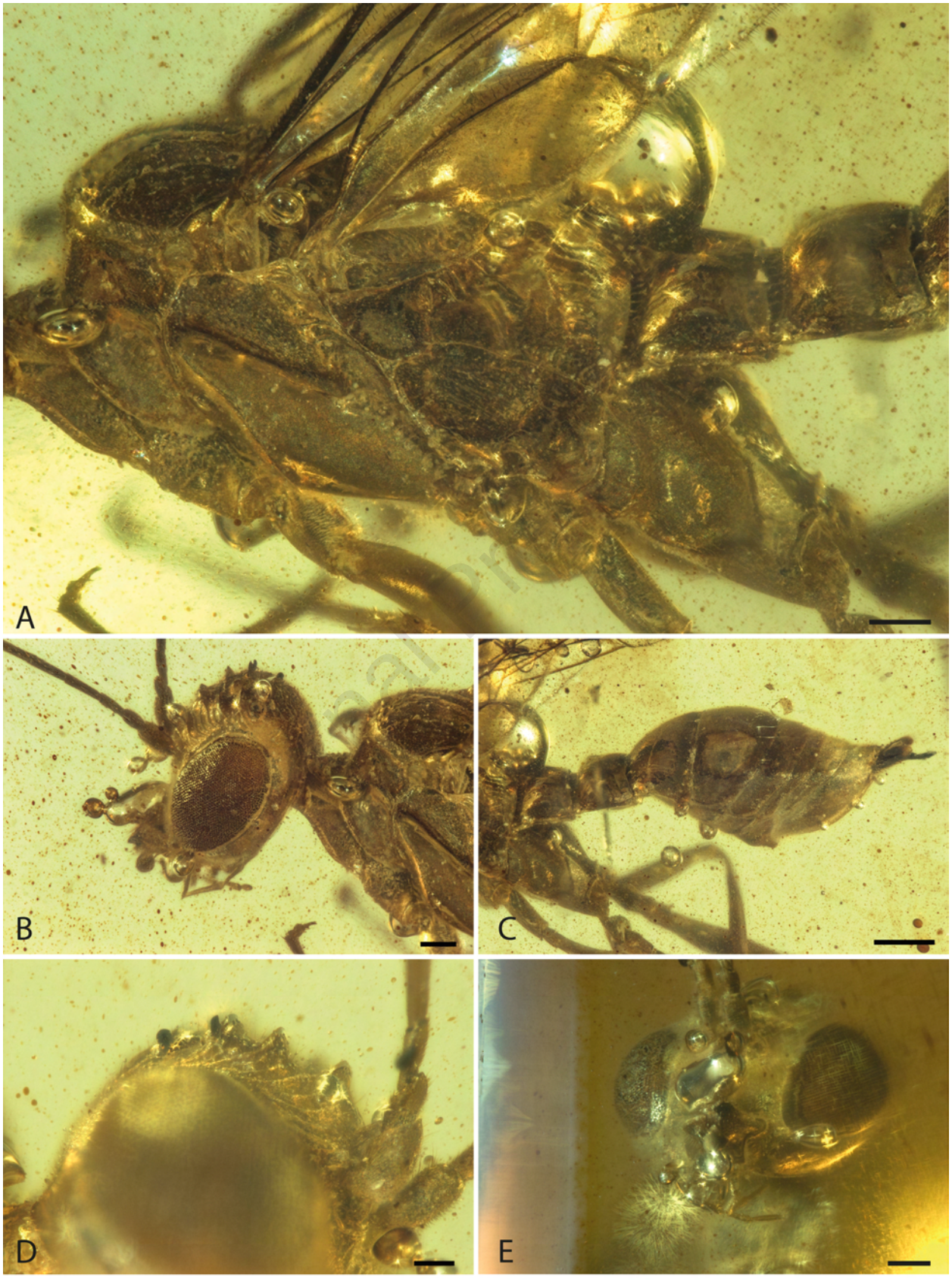
Fig. 3. *Line drawings of Ohlhoffia robusta gen. et sp. nov., female holotype MB.I.12345, from mid-Cretaceous Burmese amber. A, Habitus in left lateral view. B, Head in lateral right view. C, Wings with indication of the vein nomenclature used herein. Scale bars: 2 mm (A), 0.5 mm (C), 0.2 mm (B).*

Fig. 4. *Photomicrograph of Myanmephialtites bashkuevi gen. et sp. nov., holotype PIN no. 5608/55, from mid-Cretaceous Burmese amber. Habitus in right lateral view. Scale bar: 1 mm.*

Fig. 5. *Myanmephialtites bashkuevi gen. et sp. nov., holotype PIN no. 5608/55, from mid-Cretaceous Burmese amber. Interpretation of general appearance and wing venation. Abbreviations: ct, circumocellar teeth; cx_1, cx_2, cx_3, pro-, meso- and metacoxa; f_1, f_2, f_3, pro-, meso- and metafemur; ha – hamuli; md, mandible; N_1, N_2, pro- and mesonotum; ppd, propodeum; scl_1, scl_2, meso- and metascutellum; sp, tibial spurs; t_1, t_2, metasomal petiolar tergites; ta_1, ta_2, ta_3, pro-, meso- and metatarsus; ti_1, ti_2, ti_3, pro-, meso- and metatibia. Scale bar: 1 mm.*

Fig. 6. *Relative proportions of non-aculeate superfamilies as recorded by geological epochs from the Early Cretaceous to Recent, highlighting the current dominance of Ichneumonoidea. Data*

compiled from the fossil taxon count request at http://fossilworks.org/ and the species list of extant taxa at https://hol.osu.edu (both accessed 16 April 2020).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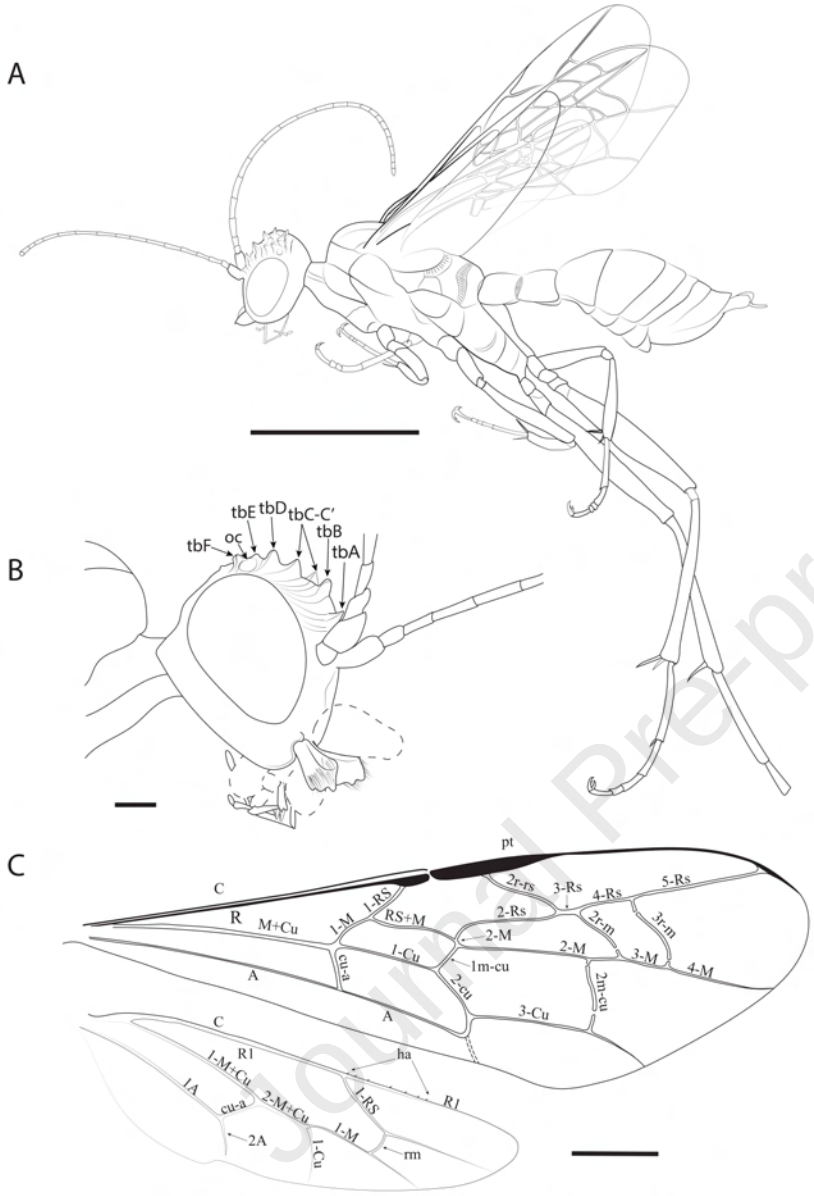

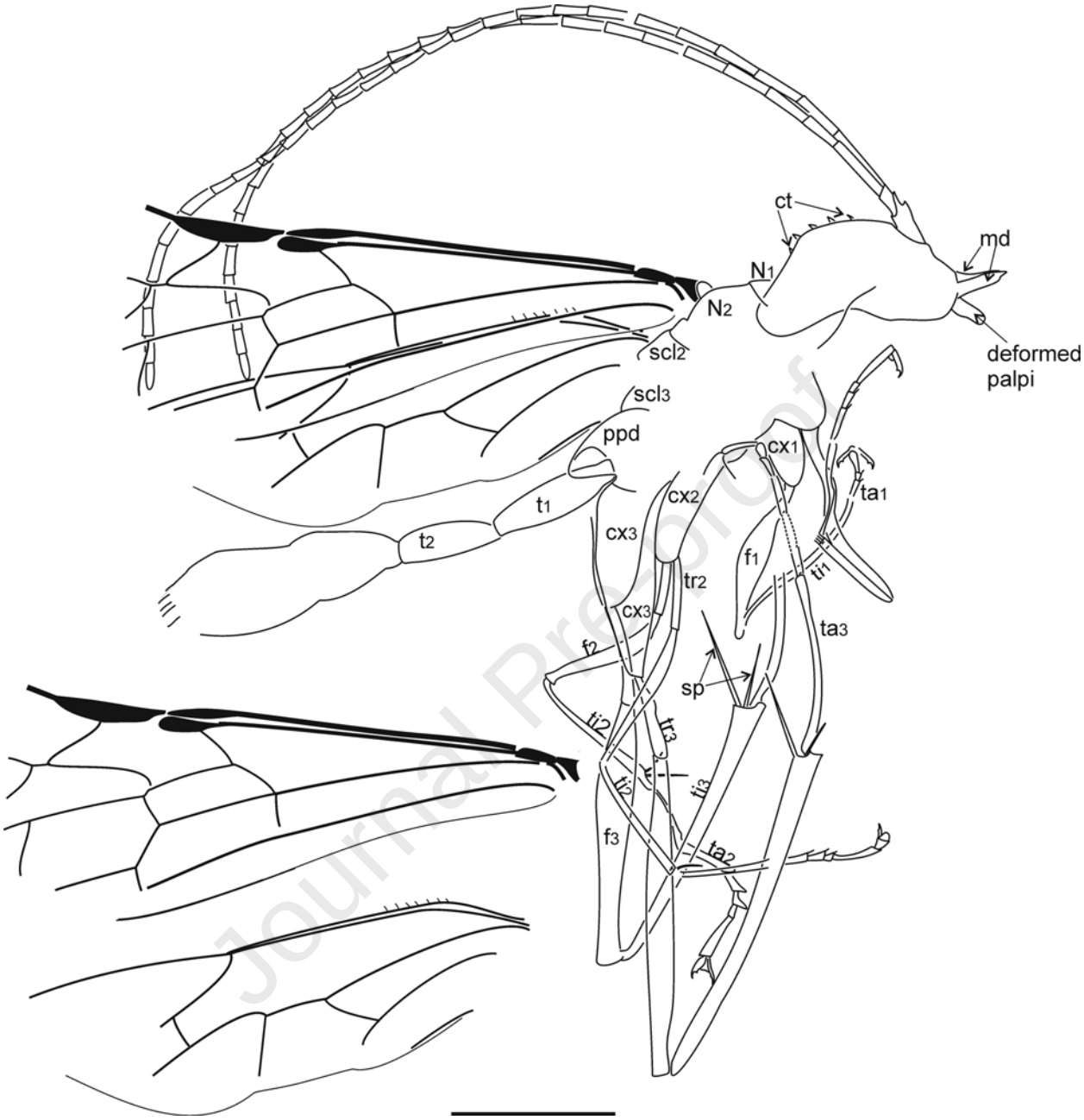

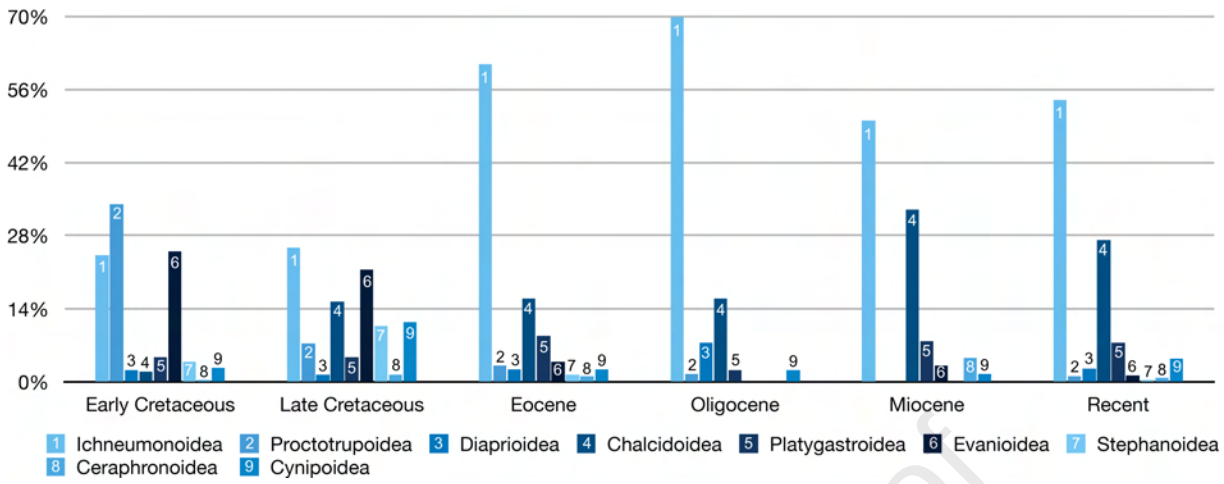

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: