Cretaceous Research

A remarkable evanioid wasp in mid-Cretaceous amber from northern Myanmar (Hymenoptera: Evanioidea)

Michael S. Engel^{a,b}, Diying Huang^c, Abdulaziz S. Alqarni^d, Chenyang Cai^c

^a Division of Entomology, Natural History Museum, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045, USA (msengel@ku.edu).

^b Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, USA.

^c State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China (dyhuang@nigpas.ac.cn).

^d Department of Plant Protection, College of Food and Agriculture Sciences, King Saud University, P.O. Box 2460, Riyadh 11451, Kingdom of Saudi Arabia (alqarni@ksu.edu.sa).

Abstract

A remarkable new wasp of the superfamily Evanioidea (Apocrita: Evaniomorpha) is described and figured from a female preserved in mid-Cretaceous amber from the Hukawng Valley of northern Myanmar. *Othniodellitha mantichora* Engel and Huang, gen. et sp. nov., is characterized by its unique combination of primitive and derived features in mesosomal and metasomal construction and wing venation, along with its peculiarly blocky head with a prominent facial horn, clypeal projection, and massive, squared mandibles, among other traits. The genus is placed in the new family, Othniodellithidae Engel and Huang, fam. nov., and is among the lower Evanioidea and distinguished from the Praeaulacidae and other Mesozoic evanioid families.

Keywords:

Apocrita

Burmese amber

Cenomanian

Evaniomorpha

Mesozoic

taxonomy

1. Introduction

The apocritan superfamily Evanioidea includes three extant families of distinctive wasps (Mason, 1993; Grimaldi and Engel, 2005), with a collective modern diversity of about 2200 species (Huber, 2009; Engel and Krombein, 2012; Aguiar et al., 2013). The smallest of the three families, the Aulacidae, retains the greatest number of generalized traits and also have a more characteristically primitive biology — parasitoids of wood-boring beetles and wood wasps (Jennings and Austin, 2004; Grimaldi and Engel, 2005). The aulacids are most closely related to, and sometimes united with, the Gasteruptiidae, a group of what are best termed predators in the nests of wasps and solitary bees, preying on the host larva outright rather than living on them ectoparasitically, and before then becoming acting as a kind of cleptoparasite and consuming the host's brood cell provisions (e.g., Grimaldi and Engel, 2005). The most distinctive of these families, the ensign wasps (Evaniidae), are predators on the eggs of roaches. The adult females oviposit into the oothecae and the larva consumes the developing roach immatures before pupating (Grimaldi and Engel, 2005). The superfamily is supported by the articulation of the metasoma in a strongly dorsal position, well above and separated from the metacoxal articulations, among other traits largely from the endoskeletal and musculature (e.g., Vilhelmsen et al., 2010) as well as molecular data (e.g., Dowton and Austin, 1994; Dowton et al., 1997; Sharkey et al., 2012).

Evanioidea are known from as far back as the Middle Jurassic, and were then diverse by the latest Jurassic and Early Cretaceous (e.g., Rasnitsyn, 1972, 1990; Oberprieler et al., 2012; Li et al., 2014), although largely represented by the plesiomorphic Praeaulacidae. Praeaulacidae were a perhaps a stem group to all other Evanioidea, and the family is presently defined largely by the lack of more derived evanioid features (e.g., Rasnitsyn, 1972, 1990; Zhang and Rasnitsyn, 2008; Li et al., 2013). Additional extinct families among the lower Evanioidea are also known from the same time periods (e.g., Rasnitsyn, 1975, 1980, 1991; Zhang and Rasnitsyn, 2004, 2007; Li et al., 2013), and reflect a broad morphological disparity than is present today, particularly as by the Cretaceous stem groups to the Evaniidae and Aulacidae become apparent. By the start of the Cenozoic only the three extant families remained among evanioid diversity. While the more familiar Evaniidae and Aulacidae are documented from Cretaceous amber (e.g., Basibuyuk et al., 2000, 2002; Deans et al., 2004; Jennings et al., 2004, 2013; Engel, 2006; Peñalver et al., 2010), the various extinct families are poorly documented from these same deposits, save for isolated Baissidae and Praeaulacidae (e.g., Engel, 2013; Li et al., 2015).

Here we report a rather monstrous appearing evanioid wasp discovered in the mid-Cretaceous amber of northern Myanmar. The new wasp intermingles features of the lower Evanioidea, while still having a more tubular petiolate and compressed metasoma, analogous to the Evaniidae. The new fossil is described here in order to bring its unique features to the attention of hymenopterists and in the hopes that the as-of-yet unknown males might be discovered.

2. Material and methods

The unique female was found in a moderately sizeable piece of clear yellow Burmese amber, the piece is roughly scalene triangular in cross section, with its largest face of length 24 mm by 18 mm wide, and a maximum depth of 8.5 mm. It was possible to polish flat surfaces

alongside the right of the wasp (Fig. 1) and for a slightly oblique frontal view, but surrounding inclusions and internal fractures prevented optimal perspectives from other angles. Nonetheless, virtually all details of the wasp are observable. The legs are positioned beneath the body and the wings, although folded back and slightly alongside the body, have no imperfections hampering an interpretation of the venation. The hind wing can be discerned through the forewing and its venation and margins throughout are clear. There are a number of internal fractures around the petiole and gaster, and across the hind legs and antennae, but these do not obscure or distort important characters. There is some organic debris about in the piece but again, these are in positions whereby they do not present any difficulty to studying the wasp. Descriptive terminology generally follows that presented by Huber and Sharkey (1993), and the description is presented in the context of furthering data for the eventual exploration of evolutionary patterns (sensu Grimaldi and Engel, 2007). Microphotography was done using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens, and measurements of the specimen were taken with an ocular micrometer on an Olympus SZX12 stereomicroscope. The classification of Evanioidea followed herein is outlined in Table 1.

The geological setting of Burmese amber has been outlined in detail by Cruickshank and Ko (2003), and maps of the locality provided by those authors as well as Grimaldi et al. (2002). The fossiliferous resins of these sediments have been dated to the earliest Cenomanian, near the Albian boundary based on U-Pb radiometric dating (Shi et al., 2012). To date a broad spectrum of biological inclusions have been recovered, and the vast majority of these represent virtually all terrestrial arthropod lineages (e.g., Grimaldi et al., 2002; Ross et al., 2010).

3. Systematic Palaeontology

Superfamily Evanioidea Latreille, 1802

Family: Othniodellithidae Engel & Huang, fam. nov.

Type genus. Othniodellitha Engel & Huang, gen. nov.

Diagnosis. ♀: Small wasps (approximately 5 mm in total length, excluding antennae and ovipositor), integument of head and mesosoma not transversely striate or rugose (variously transversely striate in Praeaulacidae, Andreneliidae, and Nevaniidae); head comparatively large (Figs. 1, 2A), with pronounced cephalic horn projecting from frons and well in front of face in profile, with toruli situated on lateral sloping surfaces of horn (Figs. 1, 2A, 2B, 3A); antenna filiform, with 21 flagellomeres; scape relatively long; flagellomeres longer than wide, tapering in length toward apex of flagellum. Clypeus with base indistinct owing to absence of epistomal sulcus, thus clypeus and frons apparently fused; clypeus with strong, elevated, longitudinal medial ridge projecting apically beyond lower margin of face as narrowly rounded, triangular process between mandibles (Figs. 2B, 3A). Mandibles massive, blocky, almost square-shaped, with series of blunt teeth along margin except large, pointed apical tooth overlapping other mandible (Figs. 2B, 3A). Maxillary palpus elongate, with four palpomeres, basal palpomere slightly longer than wide, remaining palpomeres thin and greatly elongate such that palpus is distinctly longer than compound eye length (Fig. 2B). Ocelli present, positioned close together on top of vertex and above upper tangent of compound eyes (Fig. 2A); compound eyes large, semi-circular, with inner margins slightly convergent below; occipital carina complete, less prominent mediodorsally, but present. Mesosoma somewhat laterally compressed, narrower than head, height more than two-thirds length; pronotum comparatively long medially, creating a

short neck (Fig. 2A); propleurae not projected forward beyond pronotum; mesoscutum with faint median sulcus, notauli weak but complete; mesoscutal transverse sulcus present; mesopleuron with weak oblique depression (apparently for reception of midleg when appressed to body); propodeum with prominent dorsal surface, twice as long as metanotum; articulation of metasoma high on propodeum, well above metacoxae and at angle between dorsal and posterior surfaces of propodeum (Figs. 1, 2A). Legs long and slender (Fig. 1); pro- and meso-trochantelli largely fused into base of associated femora, metatrochantellus reduced, largely present only ventrobasally against metafemur; tarsi pentamerous; tibial spur formula 1-2-2; pretarsal claws long, thin, comparatively straight except at apex, with minute subapical tooth, arolium small. Forewing venation nearly complete (Fig. 3B), albeit rs-m crossveins weakened and 2m-cu lacking (Fig. 3C); basal vein forking slightly distad midlength of Sc+R; cu-a postfurcal, slightly distad basal vein; marginal cell large, wide at tangent with apex of pterostigma and elongate, nearly reaching to wing apex. Hind wing venation complete except lacking C (Fig. 3B), lacking jugal lobe. Metasoma petiolate (Figs. 1, 2C), with gaster laterally compressed (similar to Evaniidae), articulation with mesosoma high, well above metacoxae, articulation well separated from metanotum, anterior petiolar width less than length of dorsal-facing surface of propodeum; first metasomal segment tubular, apparently with tergum and sternum fused, remaining metasomal segments (those comprising the gaster, i.e., all metasomal segments beyond the petiolar segments) large and laterally compressed, ovoid in profile (Fig. 2C); exerted ovipositor and sheaths moderately long, extending beyond metasomal apex (Fig. 2C), approximately two-thirds gaster length (i.e., length of only those metasomal segments posterior to the petiolar segment).

♂: *Latet*.

Genus: *Othniodellitha* Engel and Huang, gen. nov.

Type species. *Othniodellitha mantichora* Engel and Huang, sp. nov.

Diagnosis. As for the family (*vide supra*).

Etymology. The new generic name is a combination of the Greek words, *othneios* (meaning, “strange”) and *dellithos* (meaning, a kind of “wasp” or “wasp-like”). The gender of the name is feminine.

Othniodellitha mantichora Engel and Huang, sp. nov.

(Figs. 1–3)

Etymology. The specific epithet is taken from the Greek, *mantichoras*, which referred to a mythical beast that intermingled the traits of several animals, and is a general allusion to the enigmatic combination of features in the species.

Holotype. ♀, NIGP 163254, lowermost Cenomanian (near Albian boundary), Hukawng Valley, northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Diagnosis. As for the genus (*vide supra*).

Description. ♀: Total length as preserved (excluding antennae and ovipositor) 5.1 mm; forewing length 2.8 mm; integument largely brown to dark brown (where not distorted taphonomically), sparsely setose (largely glabrous), and without pronounced sculpturing or

punctuation except as noted below (integument at most faintly and finely imbricate in places); wings hyaline and clear, veins brown to light brown.

Head as long as wide in frontal view, width and length 0.92 mm; rounded in frontal view; genae large, broader than compound eyes, genal width 0.43 mm; distinct malar space separating mandibular base from lower border of compound eye, space slightly shorter than basal mandibular width; compound eyes semi-circular with lower borders blunt, without prominent circumocular carina, inner margins slightly converging below, compound eye length 0.51 mm, width 0.31 mm; ocelli present and situated in a small triangle on top of vertex above compound eyes and immediately before beginning of facial prominence, ocelli separated by approximately 1.5 times their diameter and from posterior border of head by slightly more than twice their diameter. Prominent facial horn projecting to length of 0.41 mm in profile, horn length greater than compound eye width, extending well in front of compound eyes, apex broad with blunt, squarish anterior surface the frontal view and with acute apicolateral corners above and below, surface between upper and lower ridges of anterior-facing surface slightly concave, lower ridged lip projecting further forward than upper ridge (Figs. 2A, 2B, 3A). Antennal toruli broadly separated by facial prominence, situated on lateral sloping surfaces of horn such that they open largely laterally and sit in front of compound eyes (Figs. 2A, 2B); scape comparatively long, length about 5.6 times width, length 0.33 mm, maximum width 0.06 mm; pedicel about 1.8 times as long as wide; flagellomeres each longer than wide, flagellum tapering gradually in length and slightly in width toward apex; first flagellomere longest, slightly longer than scape. Clypeal base indistinct from frons (epistomal sulcus lacking), with strong medial longitudinal ridge, ridge extends basally upward along to ventral origin of facial horn and apically projects as small triangular prominence between mandibles (Fig. 3A). Mandible massive, square in frontal view, with straight outer and apical margins, margins meeting at acutely rounded orthogonal outer angle; inner margin with ridges demarcating blunt 'teeth', and with elongate and acutely pointed apical tooth, apical tooth projects well over opposing mandible (Fig. 3A).

Mesosoma laterally compressed, slightly longer than high, length 1.94 mm, maximum height 1.34 mm; pronotum prominent, with poorly defined raised posterior surface, medially longer than wide and projecting forward as distinct neck, with gently and broadly concave posterodorsal margin, lateral surfaces large and slightly depressed; propleura long but not projecting anterior to pronotum; mesoscutum with faint medial line and weak notauli, notauli reaching to transverse sulcus but not meeting, mesoscutal length 0.59 mm; mesoscutellum arched in profile, medial length 0.38 mm; mesopleuron with oblique depression and small, single row of faint areolae demarcating border with pronotal lateral surface and more distinct, single row of areolae along border with metepisternum, ventrally surface somewhat broadly wrinkled; metanotum subvertical, short, length 0.14 mm; propodeum weakly areolate, with prominent dorsal surface, dorsal length (between metanotum and articulation with metasomal petiole) 0.29 mm. Legs long, with slender podites (metatibia not clavate), particularly hind legs; metafemur length 1.78 mm, metatibia length 1.69 mm; metabasitarsus elongate but shorter than combined lengths of remaining tarsomeres, metabasitarsus length 0.82 mm, lengths of remaining tarsomeres (from base to apex), 0.39 mm, 0.27 mm, 0.14 mm, and 0.25 mm. Forewing (Fig. 3B) with costal space apically slightly broader than pterostigma; pterostigma longer than width, tapering gradually in width to acute apex, margin inside marginal cell faintly concave; basal vein M+Cu forking slightly distad midlength of Sc+R, first abscissa M straight forming slightly angle at juncture with first abscissa Rs, slightly longer than Rs; Rs originating prior to pterostigma a distance less than its length; Rs+M straight, forking at about tangent with pterostigmal base;

second abscissa Rs greatly longer than adjoining abscissa of M which angles strongly posteriorly to meet 1m-cu, then extending out toward wing apex; second abscissa Rs straight, without kink or rudiment of crossvein; r-rs as basal quarter of pterostigmal length, elongate, longer than second abscissa Rs; marginal cell broad, greatest width at tangent of pterostigmal apex, elongate, extending to distance from wing apex about that of length of pterostigma, with Rs comparatively straight for majority of marginal cell length; two rs-m crossveins present, but distinctly weaker than surrounding veins; second submarginal cell with exceedingly narrow anterior border along Rs, posterior border longer than posterior border of third submarginal cell; third submarginal cell slightly wider posteriorly than anteriorly; discoidal cell almost a slanted rectangle (not distinctly pentagonal owing to exceptional short second abscissa of M), 1m-cu straight and almost parallel to basal vein; cu-a originating postfurcal, slightly distal of M+Cu bifurcation; 2m-cu absent; second abscissa A1 present and meeting Cu apically (demarcating subdiscoidal cell). Hind wing with venation largely complete (Fig. 3B) except lacking C; R with six distal hamuli, terminating immediately beyond hamuli, not meeting Rs; rs-m oblique, slightly longer than first abscissa Rs, shorter than first free abscissa M; Cu+cu-a present, nearly orthogonal to M+Cu; apical abscissa Cu absent; jugal lobe lacking.

Metasoma with first segment forming tubular petiole, petiole length 0.59 mm, narrower basally, basal width at articulation with mesosoma 0.08 mm, of consistent width in basal half of length, then becoming slightly thicker to an apical width at juncture with remainder of metasoma (i.e., juncture with gaster = all metasomal segments posterior to petiolar segment) 0.14 mm, tergum and sternum fused without apparent indication of individual sclerites; metasomal segments posterior to petiole (= gaster) compressed laterally, ovoid in profile, slightly longer than high, length 1.88 mm, maximum height 1.06 mm; ovipositor exerted, moderately long, length 1.18 mm, length of sheaths 1.21 mm (similar to stem-group Evaniidae).

♂: *Latet.*

4. Discussion

The new family can be placed easily within the Evanioidea owing to the high placement of the metasoma on the propodeum, articulating in this case near the angle between the dorsal and posterior surfaces of the propodeum. Therein, the plesiomorphic retention of a rather complete venation in both the forewing and hind wing, a larger number of flagellomeres (more than 12 flagellomeres in females), the medially long pronotum, as well as the medial and transverse mesoscutal sulci, are all indicative of placement among the basal grade of evanioid wasps, often classified as the family Praeaulacidae, but more accurately representing a series of families as they are otherwise united only by symplesiomorphies relative to the Neoevanioides. While *Othniodellitha mantichora* has several rather unique features, such as the massive blocky mandibles, elongate maxillary palpi, and prominent facial horn that render it readily identifiable among praeaulacid-like taxa, there are any number of characters that further reflect a combination of traits unique to the group and serving to distinguish it from other Mesozoic Evanioidea. Perhaps the next most distinctive of the lower Evanioidea are the Nevaniidae, formerly a subfamily within Praeaulacidae and the only group to have a distinctive bipetiolate metasoma (Zhang and Rasnitsyn, 2007), a character more famously known from the unrelated Mymarommatoidea and Serphitoidea in the Proctotrupomorpha (e.g., McKellar and Engel, 2011; Ortega-Blanco et al., 2011a, 2011b; Engel et al., 2011; Engel, unpubl. data). The new family differs from Nevaniidae by the unsegmented petiole, the absence of veins A2 and 2m-cu in the

forewing and C in the hind wing, the forking of M+Cu at or distad the midlength of Sc+R in the forewing, the absence of transverse striae or rugae on the mesosoma, and the more prominent ovipositor (Zhang and Rasnitsyn, 2007, 2008).

The Praeaulacidae s.str. are the most generalized of the lower evanioids, and therefore are difficult to characterize on the basis of putative synapomorphies. Othniodellithidae are easy to distinguish owing to the more elongate scape; absence of transverse striae or rugae on the mesosoma; in the forewing the weakening of the rs-m crossveins, absence of a kink or the second abscissa of Rs bearing a rudiment of 1r-rs, the absence of 2m-cu, and the more strongly apically angled basal vein; the hind wing R and Rs not meeting apically; the laterally compressed and distinctly petiolate metasoma, and the shorter ovipositor (e.g., Zhang and Rasnitsyn, 2008). The family Anomopterellidae, another family embodying many primitive traits among Evanioidea, is more derived in the presence of a reduced antennal flagellum (12 flagellomeres in females), the presence of 2m-cu, and the absence of 1rs-m such that there is a single, long second submarginal cell (e.g., Li et al., 2013). Anomopterellids also primitively retain the median and transverse mesoscutal sulci.

The poorly understood Andreneliidae are difficult to characterize owing to a lack of information, but differ from *O. mantichora* in the presence of transverse striae on the dorsum of the head, the medially shortened pronotum, and the more incomplete forewing venation owing to the absence of C and many veins posteroapically (e.g., 2m-cu and all rs-m crossveins, and apical abscissae of M, Cu, and A) (Rasnitsyn and Martínez-Delclòs, 2000). Given the incomplete nature of the material, it is possible that *Andrenelia pinnata* Rasnitsyn and Martínez-Delclòs is a derived anomopterellid, but this requires more complete specimens to ascertain.

The possible function of the cephalic horn is not clear, and given that the male is unknown, whether or not the presence of such a structure is sexually dimorphic is similarly impossible to determine. Exaggerated morphological traits are not entirely unknown among Hymenoptera in Cretaceous amber. For example, among the ants (Formicidae), various unique cephalic arrangements are well documented, ranging from trap jaws constructed and oriented differently to their modern analogs (e.g., Barden and Grimaldi, 2012; McKellar et al., 2013) to coronal rugosities and peculiar clypeal, labral, and mandibular combs (e.g., Barden and Grimaldi, 2013). Among the evanioids, stem-group Evaniidae often have swollen metatibiae and metabasitarsi (e.g., Basibuyuk et al., 2000; Peñalver et al., 2010). These ‘lost’ morphologies within their respective clades reveal functions and associated biologies that are distinct, and likely apomorphic in their own right, from that which we know from most of their modern relatives. It is therefore all the more interesting to wonder as to what the hosts of *O. mantichora* might have included, and for which it possible employed its many unique head morphologies. For now, it is impossible to speculate and this shall have to await the discovery of further material, ideally including males, and the even rarer find of putative victims as syninclusions.

5. Concluding remarks

The newly discovered Othniodellithidae further emphasize the grand variety of evanioid wasps present in the Mesozoic, particularly in their uniquely peculiar cephalic horn and massive mandibles. The exaggerated cephalic morphology of *Othniodellitha mantichora* certainly reflects distinctive biologies in which these traits would have functioned, but the sparsity of information on the possible paleobiology of lower Evanioidea and the lack of modern analogs among Aulacidae hinders any meaningful speculation regarding the life history of this species.

The family possesses a unique combination of traits among lower Evanioidea but seems to at least more basal to the Anomopterellidae + higher Evanioidea, yet more derived than the Praeaulacidae s.str. The finding of *O. mantichora* in the mid-Cretaceous emphasizes the need for more direct exploration of Mesozoic deposits for additional Hymenoptera and their associated implications for the diversification of this major insect lineage.

Acknowledgements

We are thankful to John T. Jennings and an anonymous reviewer for positive feedback on an earlier version of the manuscript. D.-Y.H. and C.-Y.C. were supported by the National Basic Research Program of China (2012CB821903), while the participation of M.S.E. was partially supported by U.S. National Science Foundation grant DEB-1144162. This work was supported by the Visiting Professor Program at King Saud University, Deanship of Scientific Research.

References

- Aguiar, A.P., Deans, A.R., Engel, M.S., Forshage, M., Huber, J.T., Jennings, J.T., Johnson, N.F., Lelej, A.S., Longino, J.T., Lohrmann, V., Mikó, I., Ohl, M., Rasmussen, C., Taeger, A., Yu, D.S.K., 2013. Order Hymenoptera. *Zootaxa* 3703(1), 51–62.
- Barden, P., Grimaldi, D., 2012. Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. *American Museum Novitates* 3755, 1–16.
- Barden, P., Grimaldi, D., 2013. A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa* 3681(4), 405–412.
- Basibuyuk, H.H., Rasnitsyn, A.P., Fitton, M.G., Quicke, D.L.J., 2000. An archaic new genus of Evaniidae (Insecta: Hymenoptera) and implications for the biology of ancestral evanioids. *Bulletin of the Natural History Museum, London, Geology* 56(1), 53–58.
- Basibuyuk, H.H., Rasnitsyn, A.P., Fitton, M.G., Quicke, D.L.J., 2002. The limits of the family Evaniidae (Insecta: Hymenoptera) and a new genus from Lebanese amber. *Insect Systematics and Evolution* 33(1), 23–34.
- Cruickshank, D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences* 21(5), 441–455.
- Deans, A.R., Basibuyuk, H.H., Azar, D., Nel, A., 2004. Descriptions of two new Early Cretaceous (Hauterivian) ensign wasp genera (Hymenoptera: Evaniidae) from Lebanese amber. *Cretaceous Research* 25(4), 509–516.
- Dowton, M., Austin, A., 1994. Molecular phylogeny of the insect order Hymenoptera: apocritan relationships. *Proceedings of the National Academy of Sciences, U.S.A.* 91(21), 9911–9915.
- Dowton, M., Austin, A., Dillon, N., Bartowsky, E., 1997. Molecular phylogeny of the apocritan wasps: the Proctotrupomorpha and Evaniomorpha. *Systematic Entomology* 22(3), 245–255.
- Engel, M.S., 2006. Two ensign wasps in Cretaceous amber from New Jersey and Myanmar (Hymenoptera: Evaniidae). *Polskie Pismo Entomologiczne* 75(3), 443–454.
- Engel, M.S., 2013. A new genus and species of Baissidae in Late Cretaceous amber from New Jersey (Hymenoptera: Evanioidea). *Novitates Paleontologicae* 3, 1–8.

- Engel, M.S., Krombein, K.V., 2012. Hymenoptera. In: McGraw-Hill Encyclopedia of Science and Technology [11th Edition, Volume 8]. MacGraw-Hill, New York, pp. 787–798.
- Engel, M.S., Grimaldi, D.A., Ortega-Blanco, J., 2011. Serphitid wasps in Cretaceous amber from New Jersey (Hymenoptera: Serphitidae). *Insect Systematics and Evolution* 42(2), 197–204.
- Grimaldi, D., Engel, M.S., 2005. *Evolution of the Insects*. Cambridge University Press, Cambridge, xv+755 pp.
- Grimaldi, D., Engel, M.S., 2007. Why descriptive science still matters. *BioScience* 57(8), 646–647.
- Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361, 1–72.
- Huber, J.T., 2009. Biodiversity of Hymenoptera. In: Footitt, R.G., Adler, P.H. (Eds.), *Insect Biodiversity: Science and Society*. Wiley-Blackwell, Oxford, pp. 303–323.
- Huber, J.T., Sharkey, M.J., 1993. Structure. In: Goulet, H., Huber, J.T. (Eds.), *Hymenoptera of the World: An Identification Guide to Families*. Agriculture Canada, Ottawa, pp. 13–59.
- Jennings, J.T., Austin, A.D., 2004. Biology and host relationships of aulacid and gasteruptionid wasps (Hymenoptera: Evanoidea): a review. In: Rajmohana, K., Sudheer, K., Girish Kumar, P., Santhosh, S. (Eds.), *Perspectives on Biosystematics and Biodiversity* [Prof. T.C. Narendran Commemoration Volume]. University of Calicut, Kerala, pp. 187–215.
- Jennings, J.T., Austin, A.D., Stevens, N.B., 2004. *Hyptiogastrites electrinus* Cockerell, 1917, from Myanmar (Burmese) amber: redescription and its placement within the Evanoidea (Insecta: Hymenoptera). *Journal of Systematic Palaeontology* 2(2), 127–132.
- Jennings, J.T., Krogmann, L., Mew, S.L., 2013. *Cretevania bechlyi* sp. nov., from Cretaceous Burmese amber (Hymenoptera: Evaniidae). *Zootaxa* 3609(1), 91–95.
- Latreille, P.A., 1802. *Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes*. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C. S. Sonnini, membre de plusieurs sociétés savantes [Tome troisième]. Dufart, Paris, xii+467 pp.
- Li, L.-F., Rasnitsyn, A.P., Shih, C.-K., Ren, D., 2013. Anomopterellidae restored, with two new genera and its phylogeny in Evanoidea (Hymenoptera). *PLoS ONE* 8(12), e82587.
- Li, L.-F., Shih, C.-K., Ren, D., 2014. New fossil Praeaulacinae wasps (Insect: Hymenoptera: Evanoidea: Praeaulacidae) from the Middle Jurassic of China. *Zootaxa* 3814(3), 432–442.
- Li, L.-F., Rasnitsyn, A.P., Shih, C.-K., Ren, D., 2015. A new genus and species of Praeaulacidae (Hymenoptera: Evanoidea) from Upper Cretaceous Myanmar amber. *Cretaceous Research* 55, 19–24.
- Mason, W.R.M., 1993. Superfamilies Evanoidea, Stephanoidea, Megalyroidea, and Trigonalioidea. In: Goulet, H., Huber, J.T. (Eds.), *Hymenoptera of the World: An Identification Guide to Families*. Agriculture Canada, Ottawa, pp. 510–520.
- McKellar, R.C., Engel, M.S., 2011. The serphitid wasps (Hymenoptera: Proctotrupomorpha: Serphitoidea) of Canadian Cretaceous amber. *Systematic Entomology* 36(1), 192–208.
- McKellar, R.C., Glasier, J.R.N., Engel, M.S., 2013. A new trap-jawed ant (Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous amber. *Canadian Entomologist* 145(4), 454–465.

- Oberprieler, S.K., Rasnitsyn, A.P., Brothers, D.J., 2012. The first wasps from the Upper Jurassic of Australia (Hymenoptera: Evanioidea, Praeaulacidae). *Zootaxa* 3503, 47–54.
- Ortega-Blanco, J., Peñalver, E., Delclòs, X., Engel, M.S., 2011a. False fairy wasps in Early Cretaceous amber from Spain (Hymenoptera: Mymarommatoidea). *Palaeontology* 54(3), 511–523.
- Ortega-Blanco, J., Delclòs, X., Peñalver, E., Engel, M.S., 2011b. Serphitid wasps in Early Cretaceous amber from Spain (Hymenoptera: Serphitidae). *Cretaceous Research* 32(2), 143–154.
- Peñalver, E., Ortega-Blanco, J., Nel, A., Delclòs, X., 2010. Mesozoic EvanIIDae (Insecta: Hymenoptera) in Spanish amber: reanalysis of the phylogeny of the Evanioidea. *Acta Geologica Sinica* 84(4), 809–827.
- Rasnitsyn, A.P., 1972. Praeaulacidae (Hymenoptera) from the Late Jurassic of Karatau. *Paleontologicheskii Zhurnal* 1972(1), 70–87 [In Russian].
- Rasnitsyn, A.P., 1975. Hymenoptera Apocrita of the Mesozoic. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 147, 1–134 [In Russian].
- Rasnitsyn, A.P., 1980. On the system of the family Aulacidae (Hymenoptera) in connection with a new finding in the Lower Cretaceous of Manlay. *Trudy Sovmestnoy Sovetsko-Mongol'skoy Paleontologicheskoy Ekspeditsii* 13, 65–67. [In Russian]
- Rasnitsyn, A.P., 1990. New representatives of the hymenopterous family Praeaulacidae from Early Cretaceous Buryatia and Mongolia. *Vestnik Zoologii* 1990(6), 27–31 [In Russian].
- Rasnitsyn, A.P., 1991. New hymenopterans of the genus *Baissa* (Gasteruptiidae s.l.) from the Early Cretaceous in Buryatia and Mongolia. *Vestnik Zoologii* 1991(1), 78–79. [In Russian, with English summary].
- Rasnitsyn, A.P., Martínez-Delclòs, X., 2000. Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain. *Acta Geológica Hispánica* 35(1–2), 65–95.
- Ross, A.J., Mellish, C., Crichton, B., 2010. Burmese amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 208–235.
- Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P.G., Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L., Wheeler, W.C., 2012. Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* 28(1), 80–112.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37, 155–163.
- Vilhelmsen, L., Mikó, I., Krogmann, L., 2010. Beyond the wasp waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). *Zoological Journal of the Linnean Society* 159(1), 22–194.
- Zhang, H.-C., Rasnitsyn, A.P., 2007. Nevaniinae subfam. n., a new fossil taxon (Insecta: Hymenoptera: Evanioidea: Praeaulacidae) from the Middle Jurassic of Daohugou in Inner Mongolia, China. *Insect Systematics and Evolution* 38(2), 149–166.
- Zhang, H.-C., Rasnitsyn, A.P., 2008. Middle Jurassic Praeaulacidae (Insecta: Hymenoptera: Evanioidea) of Inner Mongolia and Kazakhstan. *Journal of Systematic Palaeontology* 6(4), 463–487.

Zhang, J.-F., Rasnitsyn, A.P., 2004. Minute members of Baissinae (Insecta: Hymenoptera: Gasteruptiidae) from the Upper Mesozoic of China and limits of the genus *Manlaya*
Rasnitsyn, 1980. Cretaceous Research 25(6), 797–805.

Table 1

Hierarchical classification of evanioid wasps (Evanioidea s.l.).

Superfamily Evanioidea Latreille	
	Family †Praeaulacidae Rasnitsyn
	Family †Nevaniidae Zhang and Rasnitsyn
	Family †Andreneliidae Rasnitsyn and Martínez-Delclòs
	Family †Othniodellithidae, fam. nov.
Neoevanioides Engel	
	Family †Anomopterellidae Rasnitsyn
Aulaciformes Grimaldi and Engel	
	Family †Baissidae Rasnitsyn
Euaulacides Engel	
	Family Gasteruptiidae Ashmead
	Subfamily †Kotujellitinae Rasnitsyn
	Subfamily Hyptiogastrinae Crosskey
	Subfamily Gasteruptiinae Ashmead
	Family Aulacidae Hedicke
	Subfamily †Hyptiogastritinae Engel
	Subfamily Aulacinae Hedicke
Evaniiformes Grimaldi and Engel	
	Family Evaniidae Latreille*

*Inclusive of Cretevaniidae Rasnitsyn as this comprises a grade to modern Evaniidae (Peñalver et al., 2010).

FIGURE CAPTIONS

Fig. 1. Microphotograph of holotype (NIGP 163254) female of *Othniodellitha mantichora* Engel and Huang, gen. et sp. nov., in mid-Cretaceous amber from Myanmar (Scale bar = 1 mm).

Fig. 2. Microphotographs of holotype (NIGP 163254) female of *Othniodellitha mantichora* Engel and Huang, gen. et sp. nov. A, Lateral detail of mesosoma and head (scale bar = 0.5 mm). B, Frontal-oblique view of head as preserved (scale bar = 0.25 mm). C, Lateral detail of metasoma (scale bar = 0.5 mm).

Fig. 3. Line drawings of the holotype (NIGP 163254) female of *Othniodellitha mantichora* Engel and Huang, gen. et sp. nov. A, Detail of head in frontal-oblique view (scale bar = 0.25 mm). B, Forewing and hind wing venation (scale bar = 1 mm).

Figure 1

Figure 2

Figure 3