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An unusual new lineage of sawflies (Hymenoptera) in Upper Cretaceous amber from northern Myanmar

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Abstract

A peculiar new lineage of sawflies ('Symphyta') is described and figured from a female beautifully preserved in Upper Cretaceous (Cenomanian) amber from northern Myanmar.

Syspastoxyela rhapsidia Engel and Huang, gen. et sp. nov., shares many plesiomorphic features with the primitive Xyelidae, †Xyelotomidae, and †Xyelydidae such as enlarged and thickened first flagellomere succeeded by a series of thinner and shorter flagellomeres, absence of a transverse mesoscutal sulcus, multiple preapical spurs, and two protibial spurs among other traits. However, the new lineage has an apomorphically contracted forewing venation, lacks a subcostal vein, has a single marginal cell, and lacks crossvein 1r-rs, and thus it is segregated into a new family, Syspastoxyelidae Engel and Huang, fam. nov. The phylogenetic affinities of the new family are discussed and a position near Pamphilioidea or Pamphilioidea + Unicalcarida is advocated.

Keywords:

Burmese amber

Cenomanian

Mesozoic

Xyeloidea

Symphyta

taxonomy

1. Introduction

The Hymenoptera are one of the four remarkably diverse lineages of the ubiquitous Holometabola (Grimaldi & Engel, 2005; Engel, 2015), with over 155,000 described species, more than double the number of all known vertebrates, but believed to consist of anywhere from 3 to 7 times this value (Huber, 2009; Engel & Krombein, 2012; Aguiar et al., 2013). The bulk of hymenopteran diversity is principally comprised of parasitoids, although significant secondary shifts to predatory and phytophagous modes of life are scattered throughout. However, at the base of this diversity resides a grade of superfamilies of primitively phytophagous wasps, commonly referred to as ‘sawflies’ and ‘wood wasps’. These families collectively number slightly more than 8000 extant species and, along with the parasitoid Orussoidea, formerly comprised the ‘Symphyta’ (Taeger et al., 2010). At the root of this stem to the parasitoid radiation (Euhymenoptera) and representing the earliest crown-group Hymenoptera are the Xyeloidea (Archihymenoptera) (e.g., Rasnitsyn, 1988; Vilhelmsen, 2001; Grimaldi and Engel, 2005; Sharkey, 2007; Sharkey et al., 2012). The 63 living species of distinctive xyeloid sawflies stand in opposition to the Neohymenoptera (all other clades of the order), and can be recognized by their unique combination of numerous primitive features such as the presence of an apical bifurcation to vein Rs in the forewing, resulting in two marginal cells, and an overall enriched wing venation; presence of two protibial apical spurs and multiple preapical spurs on all legs; a characteristically large maxillary palpus in which the palpomeres have the form of a small leg; and the lack of a mesoscutal transverse sulcus, among other features.

Not surprisingly given their auspicious phylogenetic position, fossil xyeloids include the earliest of crown-group Hymenoptera, dating back to the Late Triassic (e.g., Riek, 1955; Rasnitsyn, 1964; Schlüter, 2000; Engel, 2005, unpubl. data; Kopylov, 2014; Lara et al., 2014), and exhibit a more enriched diversity in both form, distribution, and number of species (e.g., Rasnitsyn, 1966, 1969, 1971; Taeger et al., 2010). Prior to the Triassic xyeloids, only stem groups to the Hymenopterida are known, extending the superordinal lineage back to the Late Carboniferous (Nel et al., 2013). Various extinct xyelid-like groups have also been described but each show some degree of more derived traits suggesting that they are among the Neohymenoptera and more closely allied to other superfamilies, such as Xyelotomidae basal to Tenthredinoidea and Xyelydidae near Pamphilioidea (Rasnitsyn, 1988; Grimaldi and Engel, 2005). Even among the diversity of fossil xyelids there is considerable variation, and the superfamily as circumscribed to include these taxa may be paraphyletic. Here we describe a remarkable addition to this diversity of xyelid-like lineages and from a well-preserved female in Upper Cretaceous (approximately 98.8 Ma: Shi et al., 2012) amber from northern Myanmar (Fig. 1).

2. Material and methods

A single female wasp was discovered in a comparatively clear piece of light Burmese amber, there being few distortions or imperfections impacting views. There are some internal flow lines within the amber that result in a distorted view when the individual is examined head on or in profile from either side. However, the direct dorsal and ventral views are unhindered. There is isolated particular matter but it does not obscure the wasp. Some small bubbles are positioned along the thorax and left wing (just prior to the pterostigma), and a density of pollen grains blocks portions of the abdominal apex. The antennae are projected in front of the head and the legs are situated beneath the animal, with the wings reclined back over the body. The venation is quite lightly colored, and while a few veins from the hind wings can be seen, their overall courses and connections are not possible to detect. This is hampered by some clearing of the integument which impacted the wings to the degree that the membranes are exceedingly

faint, and even the extent of the forewing is challenging to discern (best followed in the left forewing, although the venation is easiest to trace in the right forewing). The body appears a bit dorsoventrally compressed, but given the form of the terga and sterna, this seems to be due to postmortem compression. The amber piece was trimmed and polished to a small rectangle of length 9 x 6 x 3 mm.

The descriptions here are meant to expand available character information in the exploration of relationships among basal Hymenoptera, and as the foundation for wider evolutionary patterns (Grimaldi and Engel, 2007). Morphological terminology generally follows that of Huber and Sharkey (1993), and measurements were made with the aid of an ocular micrometer on an Olympus SZX12 stereomicroscope. Photography was done with a Canon 7D digital camera attached to an Infinity K-2 long-distance lens. The amber-bearing deposits of the Hukawng Valley have been studied extensively, with detailed maps of the locality provided by Grimaldi et al. (2002) and Cruickshank and Ko (2003). The geological setting is most extensively covered by Cruickshank and Ko (2003), while the age of the deposit has been covered by Shi et al. (2012).

3. Systematic palaeontology

Family: Syspastoxyelidae Engel and Huang, fam. nov.

Type genus. *Syspastoxyela* Engel and Huang, gen. nov.

Diagnosis. ♀: Body size small (*ca.* 2.8 mm, excluding ovipositor); antenna with nine flagellomeres; first flagellomere greatly elongate and thickened (Figs. 1, 2B), apparently composite resulting from fusion of seven basal flagellomeres as evidenced by lines of weakness in cuticle: Fig. 2B), longer than remaining portion of flagellum; remaining flagellomeres thin, short, and forming apical flagellar ‘thread’ (Figs. 1, 2B); antennal toruli low on face, at lower tangent of compound eyes, near clypeal basal margin; clypeus narrow, not as wide as face, extending laterally to just outside tangent with outer rim of antennal toruli, short medially; mandibles positioned close together, elongate, longer than scape, scythe-like, flattened, and crossing scissor-like, apical tooth acutely pointed, with a single medial tooth; maxillary palpus with six palpomeres, leg-like in form (as in Xyelidae); ocelli positioned on top of vertex in small equilateral triangle; occipital carina lacking. Pronotum with pronounced collar, dorsal surface not greatly reduced medially, posterodorsal margin faintly concave; propleura contiguous medially throughout their length; mesoscutum with well delineated medial line and notauli, the latter converging to form a ‘V’ prior to mesoscutellum (Figs. 1A, 2A); mesoscutum without transverse sulcus anterior to mesoscutal-mesoscutellar sulcus; mesoscutellum tapering to acutely rounded apex; mesoscutellar appendage not evident; metascutum with cenchri present and large (Fig. 2A); metapostnotum indistinguishable (there is no clearly demarcated metapostnotum, however, the posterior border of the metascutum is clearly thickened and more heavily sclerotized across the entire margin and this may represent an exceedingly short, undivided metapostnotum or be a fusion of the metapostnotum into the metascutum). All tibiae with at least two preapical spurs (two on protibia, meso- and metatibiae with three and additional spurs on outer surfaces); apical spur formula of tibiae 2-2-2, with protibial spurs of equal length and both simple; tarsi pentamerous; pretarsal claws long, with exceedingly minute subapical tooth, small arolium present between claws. Forewing with venation (Fig. 2C) generally contracted proximad, all veins lightly pigmented but tubular, no traces (spectral or otherwise) of distal abscissae of longitudinal veins beyond closed cells; all cells closed; costal cell wide; Sc completely fused with R (thus Sc+R); Sc+R straight except slightly angling at origin of Rs; first abscissa Rs with anterior end slightly proximal relative to its posterior end, much shorter than first abscissa of M, Rs-M juncture slightly angled; first abscissa Rs+M slightly arched; only one r-rs present (owing to position it is equivalent to 2r-rs among symphytans, thus 1r-rs absent), positioned near midlength of pterostigma; pterostigma large, anterior border swollen, with

bordering veins poorly defined at base and along anterior margin, more easily discerned posteriorly and apically, without fenestral bullae between pterostigma and juncture with C and Sc+R; R extending along anterior margin as merely a stub beyond marginal cell apex; marginal cell exceedingly short, with Rs mirroring course of pterostigmal border to form narrow arched cell; Rs apically not bifurcate; 1cu-a and 2cu-a present, thus demarcating second cubital cell; A2+3 with shallow arch midway before a-a crossvein. Abdomen broadly joined to thorax; first tergum broadly divided medially (Fig. 2A); terga not sharply folded laterally (abdomen compressed as preserved and so a weak, artificial crease is present but appears to be taphonomic); apical tergum without medial horn; cercus exceedingly short, with three cercomeres; ovipositor elongate (Fig. 1), thin, needle-like, nearly one-half abdominal length.

♂: *Latet*.

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

Type species. *Syspastoxyela raphidia* Engel and Huang, sp. nov.

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

Etymology. The new genus-group name is a combination of *sypastos* (Greek, meaning, “drawn together” or “contracted”) and the generic name *Xyela* Dalman, a common root upon which many primitive sawfly generic names are based (itself based from the Greek *xyele*, a device for scraping wood). The gender of the name is feminine.

Syspastoxyela raphidia Engel and Huang, sp. nov.
(Figs. 1–2)

Etymology. The specific epithet is from the Greek *raphidos*, meaning “needle”, and is a reference to the long, thin, needle-like ovipositor.

Holotype. ♀ (Fig. 1), NIGP 163252, 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 ovipositor and antennae) 2.81 mm, length with ovipositor 3.48 mm; forewing length 1.67 mm, maximum width 0.69 mm. Integument generally brown to dark brown, partially cleared in places, impunctate and finely to distinctly imbricate, without scattered setae. Head broad, width across compound eyes 0.56 mm, length 0.38 mm, distance between compound eyes (0.39 mm) greater than compound eye length (0.19 mm), compound eyes parallel. Malar space broad, base of mandibles situated more medially on head. Labrum apparently situated between and posterior to mandibles (labrum exceedingly difficult to discern and so this character requires further verification). Maxillary palp large, leg-like (as in many Xyelidae; e.g., *Xyela*: Beutel and Vilhelmsen, 2007), combined lengths of palpomeres 0.64 mm (longer than head width), basal palpomere as wide as long (length 0.01 mm), second palpomere elongate and thicker (resembling a small femur) (length 0.16 mm), third palpomere elongate, similar to second palpomere but slightly thicker (0.19 mm); fourth palpomere longer than wide, about one-half length of third palpomere (length 0.10 mm); fifth palpomere longer than wide, about as long as fourth palpomere (it is difficult to discern but the fifth palpomere may be medially weakened and twisted; if so, then it would resemble somewhat the condition present in *Xyela* and *Pleroneura* Konow) (length 0.09 mm); fourth and fifth palpomeres distinctly thinner and less strongly sclerotized than second and third palpomeres; a

minute, apparently apically divided sixth palpomere present, distinctly thinner than preceding palpomere and exceedingly short (difficult to see but apparently shorter than basalmost palpomere). Antennal toruli separated by about twice torular diameter, separated from compound eyes by over twice torular diameter; scape length 0.17 mm, maximum width 0.052 mm; pedicel length 0.069 mm, maximum width 0.52 mm; thickened first flagellomere width 0.056 mm, length 0.35 mm; remainder of flagellum length 0.24 mm, maximum width 0.031 mm; first flagellomere with numerous placoid sensilla. Ocelli small, separated from each other by about diameter, separated from posterior of head by more than diameter, distant from compound eyes.

Thorax wide, width across tegulae 0.71 mm; pronotum long, with prominent collar; mesoscutum with medial line and notauli strongly impressed; cenchri large, encompassing large area of metascutum. Legs slender; propleurae massive, contiguous throughout length; protibia with two apical spurs, spurs of equal length, both simple; protibia with two preapical spurs, one near midlength, second midway between first preapical spur and protibial apex; meso- and metatibiae with spurs like those of protibia except also with spurs or spur-like setae on outer anterior surface at position of inner preapical spurs (*i.e.*, first at midlength, next near three-quarters length, with a pair at three-quarters length position); numerous prominent, stiff setae apically on metatibia, superficially resembling additional spurs; metafemur length 0.45 mm; metatibia length 0.57 mm; basitarsi long but shorter than remaining tarsomeres combined; fifth tarsomere elongate but shorter than basitarsi; medial tarsomeres about twice as long as wide except on protarsus where they are about as long as wide; pretarsal claws long, with curved apices and minute subapical tooth, individual claw more than one-half length of fifth tarsomere. Wing membranes hyaline clear, venation tubular but with faint brown pigmentation.

Abdominal terga wider than long, first broadly divided medially by membranous region, integument more distinctly, albeit still weakly, imbricate, sides generally parallel except expanding slightly by third segment with weakly convex margins, widest at junction of fourth and fifth segments, then tapering posteriorly; apical width of fourth tergum (widest point) 0.87 mm, medial length of fourth tergum 0.25 mm; eighth tergum narrowed apically, medial width 0.31 mm, medial length 0.13 mm; ninth tergum more strongly narrowed, medial width 0.21 mm, medial length 0.17 mm. Cercus minute, length 0.105 mm, with three cercomeres, each of length 0.035 mm, but of decreasing widths – first cercomere width 0.017 mm, second cercomere width 0.0104 mm, third cercomere width 0.0069 mm; basal cercomere with several prominent, suberect, apically directed setae; apical cercomere with a single, prominent, elongate seta at apex. Ovipositor needle-like; sheaths narrow, elongate, and flattened.

4. Discussion

Given that we surely know merely the tiniest fraction of the diversity of basal Hymenoptera during the Mesozoic, it is exciting to find another group exhibiting a unique combination of traits and that may, in time, aid our attempts to estimate phylogenetic relationships among living and fossil sawflies. This is particularly true for the various early xyelid and xyeloid-like groups. Syspastoxyelidae are clearly more derived than Xyeloidea as evidenced in the forewing by the complete fusion of Sc, the apically unbranched Rs, the absence of 1r-rs, and the reduced number of flagellomeres in the antennal thread. Among some xyelid-like fossil groups Sc can be wanting, such as in the Madygellinae, an assemblage in which Rs is also unbranched apically and where a fenestral bulla is lacking at the point of contact between R and the pterostigma. However, in madygellines the costal cell is narrow and 1r-rs is present (*e.g.*, Kopylov, 2014), aside from the lack of a contraction to the wing venation as observed in Syspastoxyelidae (Fig. 2C). Nonetheless, *Syspastoxyela rhapsidia* primitively retains two protibial spurs of equal length, multiple preapical spurs on all tibiae, a transversely narrow clypeus, a thickened and elongate first flagellomere (composite of at least seven flagellomeres as evidenced by the lines of weakening present in the holotype: Figs. 1, 2B), a nearly straight pronotal posterior border (Fig. 2A), absence of fenestral bullae at the point of contact between the pterostigma and C and Sc+R;

the absence of a transverse mesoscutal sulcus (Fig. 2A), and the long, almost leg-like maxillary palpi. This combination of characters is indicative of a basal position somewhere around the superfamilies Tenthredinoidea and Pamphilioidea (e.g., Vilhelmsen, 1997, 2001). The divided first metasomal tergum is similar to that observed in Pamphiliidae (Pamphilioidea) as well as some Tenthredinoidea (Benson, 1945; Goulet, 1992; Vilhelmsen, 2001: the first tergum is also deeply cleft in Xiphydriidae, e.g., Smith and Shinohara, 2011). However, unlike tenthredinoids, *S. rhapsidia* lacks the extreme medial narrowing of the pronotum and its antennal form and venation is unlike anything within the superfamily, including the Xyelotomidae (e.g., lack of 1r-rs, first abscissa Rs present and posteriorly not more proximal than its anterior, 2r-rs positioned medially on pterostigma in *S. rhapsidia*) (e.g., Rasnitsyn, 1969; Vilhelmsen, 2001). Similarly, the venation, antennal form, and structure of the ovipositor is unlike that of Pamphilioidea (Benson, 1945; Smith, 1988), and most notably unlike the Xyelydidae, a group of xyeloid-like stem pamphilioids in which the first metasomal tergum is not divided although the first flagellomere is thickened and elongate with a terminal flagellar thread (e.g., Rasnitsyn, 1969, 1988; Gao et al., 2013). If the compression of the abdomen is not an artifact of preservation, then one might interpret there to be a weakly formed crease laterally on the terga superficially similar to those in extant Pamphiliidae (Achterberg and Aartsen, 1986; Goulet, 1993). However, it seems possible that *S. rhapsidia* is either near to Pamphilioidea, on the stem of the branch comprising Pamphilioidea and Unicalcarida, or, perhaps much less likely, along the branch leading to Unicalcarida alone. It is difficult to discern the head in facial view but it seems as though the labrum may be positioned posterior to the mandibular apices and covered by them, a trait which would indicate some placement close to the pamphilioid+Unicalcarida clade (Vilhelmsen, 1996, 1997, 2001; Schulmeister et al., 2002). Accordingly, we for now tend to consider Syspastoxyelidae as representing a stem branch near to this latter grouping.

It is unclear what the biology of *S. rhapsidia* might have been but there are abundant pollen grains around the apex of the abdomen and around the ovipositor, trailing in the amber to the right of the individual. None of these are elsewhere on the body, most notably not present around the mouthparts. It is possible that females of *S. rhapsidia* oviposited into the male cones (microstrobili) of conifers, thereby bringing the apex of the abdomen into contact with pollen, with this accounting for the occurrence of grains on the specimen. Unfortunately, this is largely speculative and we cannot for now state with certainty that *S. rhapsidia* was associated with conifers over some form of angiosperm, which would certainly have been present in the Burmese amber forest, albeit not yet dominant. Indeed, it is not impossible that *S. rhapsidia* was ovipositing into the male catkins of early relatives of the fagaleans, a group that includes plant hosts of many pamphiliids. This would seem unlikely as crown-group Fagales are too young to have been present in the Burmese amber forest (e.g., Herendeen et al., 1995; Sims et al., 1998; Bell et al., 2010), and it is more probable that specialization on this group among symphytans occurred during the Late Cretaceous. The identity of the grains could not be ascertained at present but future work focusing on the pollen specifically, particularly using confocal imaging, should reveal much further information. The paleobiology of the many and diverse lineages of Mesozoic symphytans remains an open field of inquiry and one deserving of much attention given its implications for the groundplan life history of the entire order.

5. Concluding remarks

The discovery of *Syspastoxyela rhapsidia* reveals a fascinating new lineage of basal Hymenoptera, persisting into the mid-Cretaceous and perhaps allied to the Pamphilioidea or Pamphilioidea + Unicalcarida. Indeed, there are many features suggestive of a pamphilioid in the placement of the labrum, divided abdominal tergum, and possible compression of the abdomen, although the elongate, needle-like ovipositor, antennal morphology, and wing venation, among other traits exclude *S. rhapsidia* from the superfamily as circumscribed. Its true phylogenetic placement must await the discovery of additional material. Regardless, *S.*

rhaphidia and the numerous Mesozoic xyeloid-like groups demonstrate that the lower Hymenoptera were remarkably diverse during these periods, and that their modern diversity belies the richness that once was. As the ‘first’ hymenopterans, these varied lineages are crucial for any meaningful understanding of the order’s origins and their initial diversification during the Late Triassic and Jurassic. It may be that groups such as Sypastoxyelidae were already relict by the mid-Cretaceous, persisting as long as possible in a world that was rapidly becoming dominated by flower plants and while their distant cousins among the Apocrita were flourishing through their parasitoid mode of life. In this context, the exploration of Lower Mesozoic deposits for symphytan sawflies and wood wasps is all the more critical.

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FIGURE CAPTIONS

Fig. 1. Microphotograph of holotype female (NIGP 163252) of *Syspastoxyela rhaphidia* Engel and Huang, gen. et sp. nov., in Lower Cretaceous amber from Myanmar (Scale bar = 1 mm). A, Dorsal view. B, Ventral view.

Fig. 2. Camera lucida drawings of holotype female (NIGP 163252) of *Syspastoxyela rhaphidia* Engel and Huang, gen. et sp. nov., as preserved. A, Dorsal view of head, thorax, and first two abdominal segments (Scale bar = 0.25 mm). B, Detail of antenna (Scale bar = 0.1 mm). C, Right forewing venation (Scale bar = 0.5 mm).