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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 rhaphidia* 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.

1. Introduction

The Hymenoptera are one of the four remarkably diverse lineages of the ubiquitous Holometabola (Grimaldi and 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 and 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.,

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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 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 × 6 × 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

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.