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A new genus of alderflies (Megaloptera: Sialidae) in Upper Cretaceous Burmese amber

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ABSTRACT

A new genus and species of Mesozoic alderfly is described as *Haplosialodes liui* gen. et sp. nov., and from an adult male preserved in Cretaceous Burmese amber. The new genus is closely related to the genera *Haplosialis* Navás (Recent fauna of Madagascar), *Indosialis* Lestage (Recent fauna of Southeast Asia), and *Eosialis* Nel et al. (Eocene of France), suggesting a possible Early Cretaceous age for the clade that comprises these groups.

Keywords: Megaloptera, Phylogeny, Myanmar, Cretaceous, Cenomanian, taxonomy

1. Introduction

The family Sialidae, commonly called alderflies, is a group of insects belonging to the neuropterid order Megaloptera, with approximately 75 extant species and a sparse fossil record (Liu et al., 2015). Despite the allusion to great size in the ordinal name, alderflies are generally small, particularly by comparison to their relatives in the Corydalidae (Grimaldi and Engel, 2005). Adult alderflies are often short-lived, usually living only long enough to locate a mate and oviposit, and occasionally feed on pollen and nectar. The longer portion of the life cycle is spent as a predaceous larva, living in streams, rivers, and lakes, or sometimes in more ephemeral water sources such as phytotelmata (Grimaldi and Engel, 2005). The earliest definitive alderfly is *Dobbertinia reticulata* Handlirsch, 1920 (Lower Jurassic of Germany) (Ansorge, 2001). Aside from *D. reticulata*, only two further records are known from the Mesozoic, those being *Sharasialis fusiformis* Ponomarenko, 2012 based on a larva from the Upper Jurassic of Mongolia (Ponomarenko, 2012) and a fragmentary adult in Lower Cretaceous amber from Myanmar (Engel and Grimaldi, 2008). All other alderfly fossils occur in Cenozoic deposits and include 10 species placed in six genera (Lambkin, 1992; Fehler, 1999; Nel et al., 2002; Wichard and Engel, 2006; Engel and Grimaldi, 2007; Liu et al., 2015a).

Here we describe a complete and beautifully preserved alderfly from Burmese amber, representing the first named sialid from the Cretaceous. As noted, the first record of an alderfly from these deposits was provided by Engel and Grimaldi (2008), but it was not formally described given the incomplete nature of that specimen. There are insufficient details preserved in the earlier specimen to determine whether or not it is conspecific with the species established herein, but the two are certainly exceptionally similar. The present species is quite

modern in appearance, and is the earliest record of an alderfly that can be included in a modern sialid subclade.

2. Material and methods

The amber piece was ground and polished in order to make all of the anatomical features of the inclusion accessible for observation. Fortunately, there are no inclusions or imperfections in the amber piece that obscure the alderfly in dorsal or lateral views (Figs. 1-2). The wings are folded back over the body and make an unobscured dorsal view of the abdomen impossible and discernment of the hind wing venation challenging, but otherwise the fossil is exceedingly well preserved. The fossil was examined and measured using an incident light stereomicroscope (Olympus SZX9) and a stereomicroscope (Nikon SMZ 1500), along with a Leitz-Wetzlar binocular microscope. Observations and photographs were taken using a Zeiss Discovery V20 stereomicroscope and a Zeiss Axio Imager Z2 light microscope with a digital camera (AxioCam HRc) attached, respectively. Images were then digitally compiled using Helicon Focus software, and arranged in Adobe Photoshop.

The fossil described herein originates from the Hukawng Valley, Kachin State, northern Myanmar (Burma). The specific mine locality from which the specimen was collected is uncertain as it was acquired from fossil traders, but all of the amber derives from the same horizon in a general area and within the Hukawng Valley. Until recently, the precise age of the amber of Myanmar ('burmite') has been elusive. Recently an absolute age of 98.79 ± 0.62 Ma (earliest Cenomanian) was given for Burmese amber and based on U-Pb dating of zircons (Shi et al., 2012). Nevertheless, the amber from these sediments could be somewhat older, as frequently amber pebbles from this origin underwent surface perforation, suggesting that the amber was already hardened when deposited. But the amber material has to be

considered approximately coeval with the amber-bearing deposits. The history of Burmese amber and the geology of the locality has been reviewed by various authors (*vide* Cruickshank and Ko, 2003). This deposit arguably contains the greatest diversity of inclusions among those Cretaceous ambers presently known (Grimaldi et al., 2002), and continues to reveal orders and families as well as biological traits and behaviors not previously known from the Mesozoic (e.g., Davis and Engel, 2014; Parker and Grimaldi, 2014; Engel and Grimaldi, 2014; Cai et al., 2014; Peñalver et al., 2015; Myskowiak et al., 2016; Engel et al., 2016a, 2016b, 2016c). A map of the area where the amber has been found is available in Cruickshank and Ko (2003) and Dong et al. (2015).

We have followed the internal classification of Sialidae and the nomenclature of wing venation and male genitalia as proposed by Liu et al. (2015a; 2016). Abbreviations for wing venation terms are as follow: Sc, subcosta; R1, first branch of radius; Rs, radial sector; MA, media anterior; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; and A1, A2, A3, for the respective anal veins. All taxonomic actions established herein are registered under ZooBank LSID [zoobank.org:pub:FF6EC4D2-1532-44AF-982D-968DE98B77CD](http://zoobank.org/pub:FF6EC4D2-1532-44AF-982D-968DE98B77CD).

3. Systematic palaeontology

Order Megaloptera Latreille, 1802

Family Sialidae Leach, 1815

Haplosialodes gen. nov.

Type species. Haplosialodes liui, sp. nov.

Etymology. The new generic name is derived from the genus *Haplosialis* and the suffix *-odes*, and denotes the general similarity of the two groups. The gender of the name is masculine.

The generic name is registered under ZooBank LSID [zoobank.org:pub:FF6EC4D2-1532-44AF-982D-968DE98B77CD](https://zoobank.org/pub:FF6EC4D2-1532-44AF-982D-968DE98B77CD).

Diagnosis. ♂: Forewing MP with simple anterior branch and distally bifurcate posterior branch; a crossvein between Sc and R1; Rs distally two-branched in both fore- and hind wings; gonocoxites IX widely separated, broad, largely protruding beyond tergite IX in dorsal view; gonocoxite XI with median processes directed posterodorsad; ectoproct with a slender, elongate and feebly sclerotized projection (putative apomorphy with *Haplosialis* Navás).

♀: unknown.

***Haplosialodes liui* sp. nov.**

(Figs. 1–2)

Etymology. The specific epithet honors Dr. Xingyue Liu, prominent specialist on Recent Megaloptera and in recognition of his contributions to the systematics of these amazing insects. The specific epithet is registered under ZooBank LSID [zoobank.org:pub:FF6EC4D2-1532-44AF-982D-968DE98B77CD](https://zoobank.org/pub:FF6EC4D2-1532-44AF-982D-968DE98B77CD).

Holotype. ♂, NIGP163666, deposited in the collection of the Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGP), China.

Horizon and locality. Lowermost Cenomanian (Shi et al., 2012), Tanai Village, Hukawng Valley, Kachin, northern Myanmar.

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

Description. ♂: Total body length ca. 4.8 mm; integument of body dark brown. Head approximately 1.0 mm long, 1.2 mm wide; antenna pilose, with 28 flagellomeres, approximately 3/4 length of forewing; compound eyes strongly produced; ocelli absent; labrum apparently shorter than wide; mandibles not well visible. Prothorax approximately two

times wider than long. Fourth tarsomere bilobed. Wing surface with minute setae, such setae with nodulose bases giving membrane a microscopically ‘warty’ appearance. Forewing 4.8 mm long, 1.7 mm wide, 2.8 times longer than wide, minutely hirsute, margins pilose; costal area feebly broadened proximally, with four distinct costal veinlets, all basal to fusion of Sc with R1; sc-r1 present; Rs two-branched; MA two-branched; MP with weakened stem, two-branched, anterior branch simple, posterior branch bifurcate; CuA two-branched; CuP, A1, and A3 simple, A2 forked; three r1-rs crossveins present. Hind wing nearly as long as but slightly broader than forewing; four distinct costal crossveins proximal to fusion of Sc with R1; venation similar to that of forewing, with three crossveins between R1 and Rs, MA with two simple branches. Male gonocoxite IX gx9 largely protruding beyond tergite IX in dorsal view; gonocoxite XI gx11 with median processes directed posterodorsad, with hook-like tips; ectoproct e paired, with a slender, elongate, dorsally curved, and feebly sclerotized projection (only left lateral projection visible from below); tergum IX transversely arched, posterior margin medially produced in lateral view.

4. Discussion

It almost goes without saying that *Haplosialodes* can be attributed to the Sialidae, as it is fully modern in character and clearly a crown-group alderfly. Most specifically, the following synapomorphies attest to its placement within crown-group Sialidae (after Liu et al., 2015a): Rs bifurcate, forewing MP with weakened stem, prothorax wider than long, and fourth tarsomere bilobed. Following their key to genera, *Haplosialodes* would run out near to the genus *Haplosialis* owing to the simple anterior branch and distally bifurcate posterior branch of MP in the forewing, Rs distally two-branched in both the fore- and hind wings, male gonocoxites IX widely separated and broad, and the male ectoproct with a slender,

elongate, and feebly sclerotized projection (compare fig. 2B-C to Liu et al., 2015: fig. 12c, character 55.1). The gonocoxite IX largely protruding beyond tergite IX in dorsal view and the gonocoxite XI with median processes directed posterodorsad are synapomorphies of the clade consisting of *Haplosialis* + (*Indosialis* + *Eosialis*), and indicates a relationship between the fossil and this group of genera. The forewing with the posterior branch of MP bifurcate is a plesiomorphy absent in *Indosialis* and *Eosialis*, but present in both *Haplosialodes* and *Haplosialis*. Also, the presence of a crossvein between Sc and R1 is a trait of *Haplosialis*, and its absence in *Indosialis* is considered apomorphic (Liu et al., 2008, 2014, 2015a: their figures 8e-f). The ectoproct with a slender, elongate, and feebly sclerotized projection is present only in *Haplosialodes*, *Haplosialis*, and the Eocene *Eosialis*, and while suggesting that they may be most closely related, it could easily be homoplastic or even secondarily lost in *Indosialis*, and therefore is not easily interpreted at this time.

Liu et al. (2015a) proposed a chronogram for intergeneric relationships within the Sialidae and in which the clade *Haplosialis* + (*Indosialis* + *Eosialis*) diverged from their sister genus *Ilyobius* Enderlein at approximately 120 Ma and this split putatively representing vicariance from the breakup of Gondwanaland. *Haplosialis* are endemic to Madagascar, *Indosialis* are distributed in India and Indochina, while modern *Ilyobius* are known only from Central and South America, but include two species in Eocene amber from the Baltic region. Given the presence of Eocene *Ilyobius* in Europe (Wichard, 1997, 2002; Liu et al., 2015a, 2015b), it is likely that stem-group species of the 'Ilyobius lineage' (i.e., *Ilyobius*, *Haplosialis*, *Indosialis*, and *Eosialis*) and of *Ilyobius* itself were widespread in the Early Cretaceous, having experienced significant extinction during the Late Cretaceous and Cenozoic. The presence of *Eosialis* in the lower Eocene of France could be explained by a Late Cretaceous or Palaeocene spreading of the clade from India towards Europe owing to the warm palaeoclimates in the area during the early Palaeogene, but the aforementioned presence of

species of *Ilyobius* in the Eocene of Europe tends to suggest that the groups experienced Cenozoic contractions in distribution rather than biogeographic expansions. The discovery of *Haplosialodes* in Burmese amber and as clear relative of *Haplosialis*, *Indosialis*, and *Eosialis* in the '*Ilyobius* lineage' further challenges any notions of vicariance clearly explaining the majority of the modern distributions in this clade. *Haplosialodes liui* does not support the idea of an origin of the subclade within the Early Cretaceous of the combined continental mass of Africa, Madagascar, and India, as the latter was not in contact with Asia during the Mesozoic. Instead, the present fossil rather suggests a much older age for the entire clade as well as a broad distribution for their generic stem groups during the Early Cretaceous.

5. Concluding remarks

The discovery of *H. liui* serves to not only support the hypothesized antiquity of the *Haplosialis-Indosialis* subclade, but tends to suggest that the group may be even older than initially surmised. Moreover, given the great similarity between this 100 myr fossil and its modern relatives, one is struck by the morphological conservatism across the group, and all while spanning vast epochs of environmental and biotic change. This general tendency toward stasis in anatomy is analogous to various groups in Cretaceous amber that occupy comparatively stable ecological niches (e.g., Chatzimanolis et al., 2013; Engel et al., 2016a), in this case represented by a tendency for a long-lived, generalized, predatory larva and a short-lived adult. Such a pattern, along with the broad distribution of rather ancient sialid clades (Liu et al., 2015a), implies that there should be a rich palaeofauna extending back into at least the Jurassic and that has remained hidden. The discovery of *H. liui* will hopefully therefore represent only the first of many taxa to be forthcoming from Cretaceous

Lagerstätten, permitting us a more enriched perspective on the evolutionary diversity and history of alderflies.

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Figure 1. Holotype male (NIGP 163666) of *Haplosialodes liui* gen. et sp. nov., in amber from northern Myanmar. A, dorsal habitus; B, ventral habitus (to same scale as A); C, head in ventral view; D, pretarsi and apical tarsomeres of fore- and midleg.

Figure 2. Holotype male (NIGP 163666) of *Haplosialodes liui* gen. et sp. nov., in Cretaceous Burmese amber. A, drawing of forewing; B, male terminalia in ventral view; C, same view as in B except with different lighting (to same scale as B).



