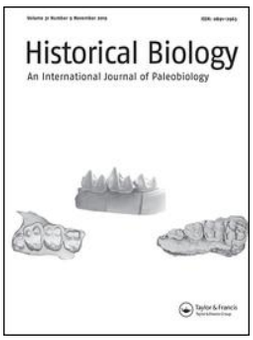

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ARTICLE

New sawflies from the mid-Cretaceous Myanmar amber (Insecta: Hymenoptera: Syspastoxyelidae)

Yimo Wang[a,b], Xiaodan Lin[a], Mei Wang[c], Chungkun Shih[a,d], Ren Dong[a,b] and Taiping Gao[a,b]

[a]College of Life Sciences, Capital Normal University, Beijing, China; [b]Academy for Multidisciplinary Studies, Capital Normal University, Beijing, China; [c]Key Laboratory of Forest Protection, State Forestry Administration, Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing, China; [d]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

ABSTRACT

Many insects have been described from the mid-Cretaceous Myanmar (Burmese) amber in recent years, including about 50 families of wasps. However, only two species of sawfly, *Syspastoxyela rhaphidia* and *Striaexyela longicornis* (Syspastoxyelidae), have been described in Myanmar amber, in contrast to more than 100 species of sawflies from the Mesozoic of Kazakhstan and China. Herein, we describe three new taxa of sawflies, *Deltoxyela engeli* gen. et sp. nov., *Syspastoxyela pinguis* sp. nov. and *Syspastoxyela simpla* sp. nov., based on six amber pieces with 21 specimens of sawflies from the mid-Cretaceous Myanmar amber. The new findings suggest that syspastoxyelids were speciose and prosperous in the ecosystem, even though only one family of sawflies, Syspastoxyelidae, has been reported hitherto.

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KEYWORDS
Mid-Cretaceous; Myanmar amber; Syspastoxyelidae; taxonomy

Introduction

The Myanmar (Burmese) amber probably harbours the most diverse biota in amber from the Cretaceous (Grimaldi et al. 2002; Zhang et al. 2018; Lin et al. 2019; Yang et al. 2019; Zhao et al. 2019). The latest version of the Myanmar amber online checklist (v.2019.2) reports the number of insect families as to 518 as of October 2019, which is the richest known assemblage from any Cretaceous amber deposit (Rasnitsyn et al. 2017; Zhang et al. 2017; Chen et al. 2018; Liu et al. 2018; Ross 2019). In the checklist, Hymenoptera is the most abundant order comprising 152 species in 100 genera and 50 families (Ross 2019). These species represent a significant part of the world biodiversity in mid-Cretaceous (Zhang et al. 2018). Most of these species represent groups of small parasitoid wasps (Grimaldi et al. 2002; Li et al. 2018).

Hymenoptera is traditionally divided into 'Symphyta' and Apocrita, but phylogenetic analyses based on morphological characters and/or molecular data suggest the 'Symphyta' is not a monophyletic group. Xyelidae is commonly considered to be the sister group to all other Hymenoptera (Ronquist et al. 2012; Sharkey et al. 2012). The early history of xyelid-like groups, in which the first flagellomere is long and swollen, is mainly documented by poorly preserved compression fossils (Rasnitsyn and Quicke 2002; Ronquist et al. 2012), although many well-preserved 'Symphyta' fossils, 64 species of 37 genera belonging to 6 families, from the Middle Jurassic and Early Cretaceous of Northeastern China have been described hitherto (Zhang and Zhang 2000; Wang et al. 2015b; Ren et al. 2019).

Symphytans are exceptionally rare in the Myanmar amber, with two described species, *Syspastoxyela rhaphidia* Engel & Huang, 2016 and *Striaexyela longicornis* Zheng, 2019 (Syspastoxyelidae) reported up to now. It possesses many unusual features, i.e., an apomorphically contracted forewing venation, a single marginal cell, but without a subcostal vein and cross-vein 1r-rs (Engel et al. 2016). Zheng *et al.* suggested that Syspastoxyelidae might be at a sister position in respect to all other Hymenoptera unless any of the oldest (Triassic) and currently insufficiently known Xyelidae are found to have segmented cercus (Zheng et al. 2019).

Herein, we report a new genus with a new species, *Deltoxyela engeli* gen. et sp. nov., and two new species, *Syspastoxyela pinguis* sp. nov. and *S. simpla* sp. nov., of Syspastoxyelidae, based on six pieces of well-preserved amber from the mid-Cretaceous of Myanmar. Three male and two female specimens are preserved in one piece, while one male and nine female specimens preserved in another. We suggest that syspastoxyelids were speciose and prosperous in the ecosystem. We also discuss the structures of antennae, venation, legs and ovipositor.

Material and methods

Examined taxa and terminology

The amber pieces examined for this paper were collected from the mid-Cretaceous (Cenomanian) of northern Myanmar. All type specimens are housed in the Key Laboratory of Insect Evolution and Environmental Changes at the Capital Normal University, Beijing, China (CNUB; Dong Ren, curator).

The amber specimens were examined and photographed, either dry or wetted with glycerine, by using a Nikon SMZ25 with an attached camera system. Line drawings were prepared using Adobe Illustrator CC and Adobe Photoshop CC graphics software. Morphological terminology follows that of Huber and Sharkey (1993).

Geological setting

The amber was collected from Kachin (Hukawng Valley) of Northern Myanmar. The amber mines are located at the north end of Noije Bum that is approximately at 26°15′N, 96°34′E, 18 km south-west of Tanai (Wang et al. 2015a; Li et al. 2018). The amber-bearing deposits of the Hukawng Valley have been studied widely, with detailed maps of the locality provided by Grimaldi et al. (2002) and Cruickshank and Ko (2003). The age of the deposit has been dated to 98.79 ± 0.62 Ma

CONTACT Taiping Gao tpgao@cnu.edu.cn College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China

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(earliest Cenomanian) by Shi et al. (2012). However, some evidence, including a high degree of roundness of the amber and bivalve borings on the surface, suggests that the amber was probably reworked before deposition in the volcanoclastic matrix, which implies that the age of the amber may be older than that of the matrix (Ross et al. 2010; Wang et al. 2015a).

Systematic palaeontology

Order **Hymenoptera** Linnaeus, 1758
Family **Syspastoxyelidae** Engel & Huang, 2016

Genus ***Deltoxyela*** Wang, Shih, Ren & Gao, gen. nov.
(Figure 1–3, 6)

Type species

Deltoxyela engeli sp. nov.

Diagnosis

Antenna with 13 flagellomeres, first flagellomere composite resulting from a fusion of eight primary segments as evidenced by lines of weakness in cuticle, shorter than remaining portion of flagellum; Pronotum elongate, triangle-shaped, apex angular; Pterostigma large, completely sclerotised; Rs-M juncture strongly angled; Rs much shorter than M.

Derivation of name

The generic name is a combination of the Greek word of 'delt-', meaning triangular, referring to the triangular and long pronotum and the generic name *Xyela* Dalman, 1819, a common root upon which many generic names of primitive sawfly are based (it is based on the Greek word of '*xyele*', a device for scraping wood). The gender is feminine.

Remarks

The new genus can be assigned to Syspastoxyelidae for the contracted forewing lacking a subcostal vein and cross-vein 1r-rs and having a single marginal cell (Engel et al. 2016). *Deltoxyela* gen. nov. is differentiated from *Syspastoxyela* by the following characters: pronotum long and triangular, protibia with many spur-like spines and additional appendages, forewing with pterostigma large and completely sclerotised, Rs much shorter than M, juncture of Rs-M strongly angled, cell 1M broad and nearly pentagon-shaped, cell 2M and 2Cu long and broad, 2cu-a smooth, A2 + 3 sharply bent. *Deltoxyela* gen. nov. is also differentiated from *Striaexyela* by the following characters: antenna with first flagellomere composite resulting from fusion of eight primary segments; pedicel funnel-shaped; pronotum long and triangular with medial line; forewing with marginal cell present.

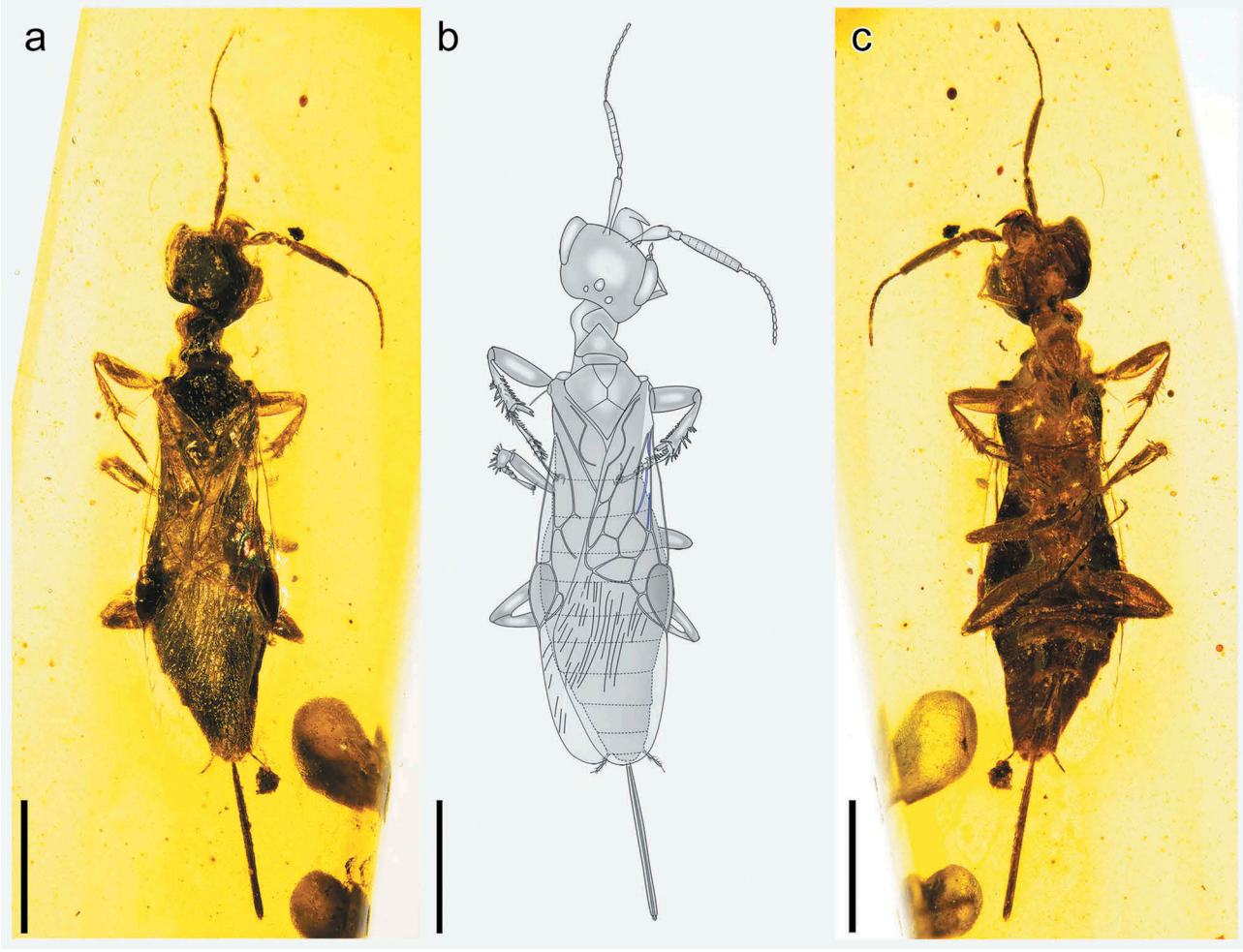

Figure 1. *Deltoxyela engeli* gen. et sp. nov. Holotype No. CNU-HYM-MA2018011. (a) Photograph of habitus in dorsal view. (b) Line drawing in dorsal view. (c) Photograph of habitus in ventral view. Scale bars: A–C = 1 mm.

Deltoxyela engeli Wang, Shih, Ren & Gao, sp. nov.
(Figure 1–3, 6)

Diagnosis
As for the genus.

Derivation of name
The specific name is dedicated to palaeoentomologist Dr Michael S. Engel, for his guidance and advice to Dr Gao.

Material
Holotype: No. CNU-HYM-MA2018011; Paratype: No. CNU-HYM -MA2018012.

Occurrence
Kachin (Hukawng Valley) of northern Myanmar. The lowermost Cenomanian (near Albian boundary); mid-Cretaceous.

Description. Holotype
♀, well-preserved specimen. Thorax and abdomen visible in ventral view but partly covered by folded forewings in dorsal view. Body about 4.32 mm in length excluding ovipositor and antennae in dorsal view, antenna 1.69 mm and ovipositor about 1.25 mm; forewing 2.92 mm in length, maximum width 0.92 mm.

Body (Figure 1) and appendages: black to dark brown as preserved, covered with scattered setae. Body thin and long. Head 0.82 mm wide and 0.54 mm long, inverted trapezoidal shape. Compound eyes large, ocelli small, displayed appreciably as a triangle. Malar space broad. Mandibles elongate, scythe-like, and apical tooth acute (Figure 2(b)). Maxillary palpus with five palpomeres, and the fifth segment bifurcated. Labial palps hairy with three palpomeres. The space between antennal (Figure 1) toruli about twice as wide as torular diameter, separated from compound eyes by over twice of torular diameter; scape 0.38 mm long, maximum 0.12 mm in width; pedicel 0.09 mm long, maximum 0.08 mm wide; first flagellomere thickest, 0.10 mm wide, 0.54 mm long; remainder flagellum 0.68 mm in length, maximum 0.03 mm in width.

Thorax (Figure 2(c)): narrow, width across tegulae 0.74 mm; pronotum long, triangular with long collar; mesoscutum with medial line and notauli strongly impressed; mesoscutellum tapering towards acute apex; metascutum with cenchri indistinguishable (they are covered by wings). Legs slender, metafemur length 0.74 mm, metatibiae length 0.82 mm. Foreleg with the protibia

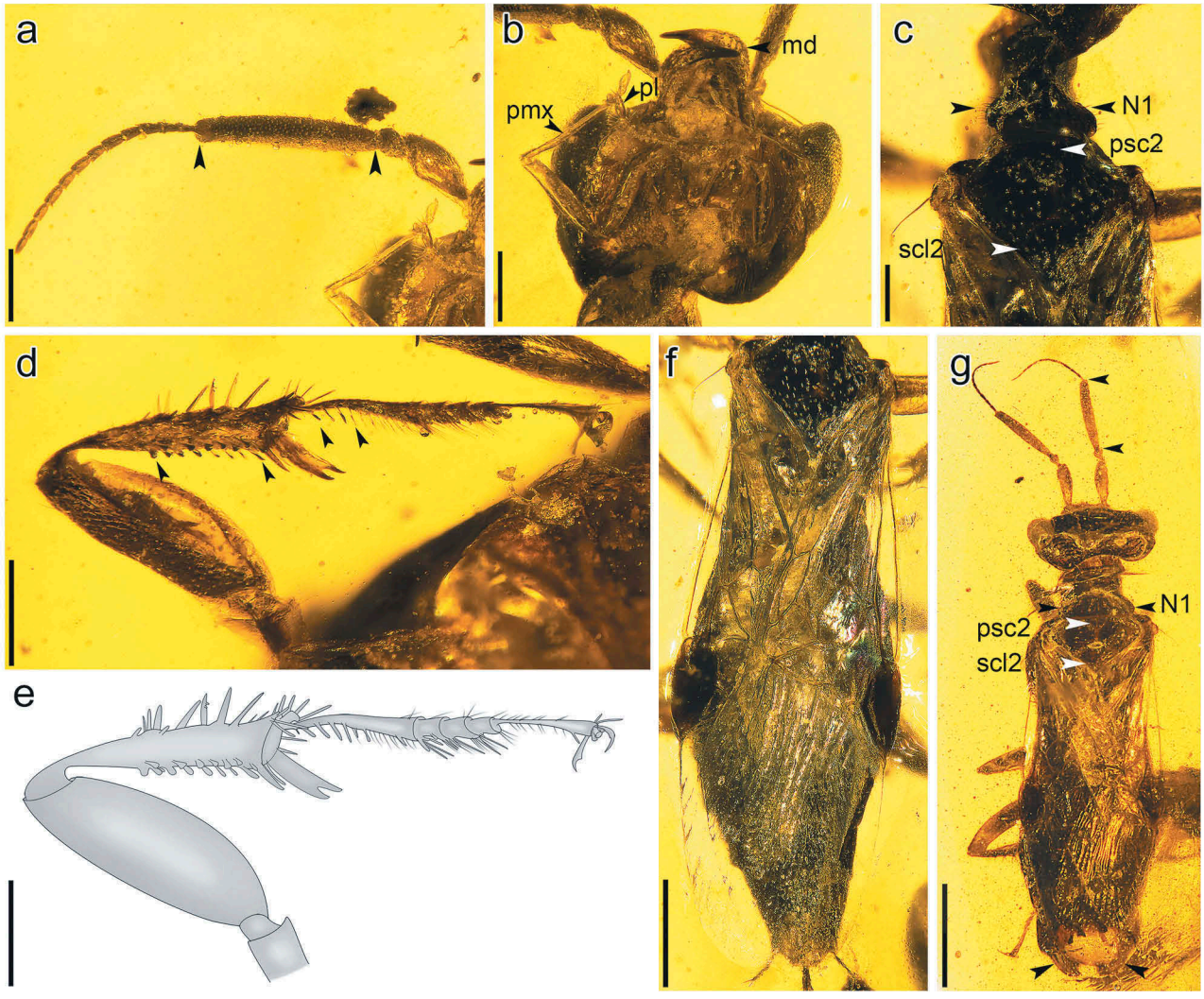

Figure 2. *Deltoxyela engeli* gen. et sp. nov. Holotype No. CNU-HYM-MA2018011. (a) Photograph of antenna in ventral view. (b) Photograph of mouthparts in ventral view. (c) Photograph of thorax in dorsal view. (d) Photograph of foreleg in ventral view. (e) Line drawing of foreleg in ventral view. (f) Photograph of forewing in dorsal view. *Deltoxyela engeli* gen. et sp. nov. Paratype No. CNU-HYM-MA2018012. (g) Photograph of habitus in dorsal view. Scale bars: A–E = 0.2 mm; F, G = 1 mm. Abbreviations: md = mandible, pl = palpus labial, pmx = palpus maxillary, N1 = pronotum, psc2 = mesoscutum, scl2 = mesoscutellum.

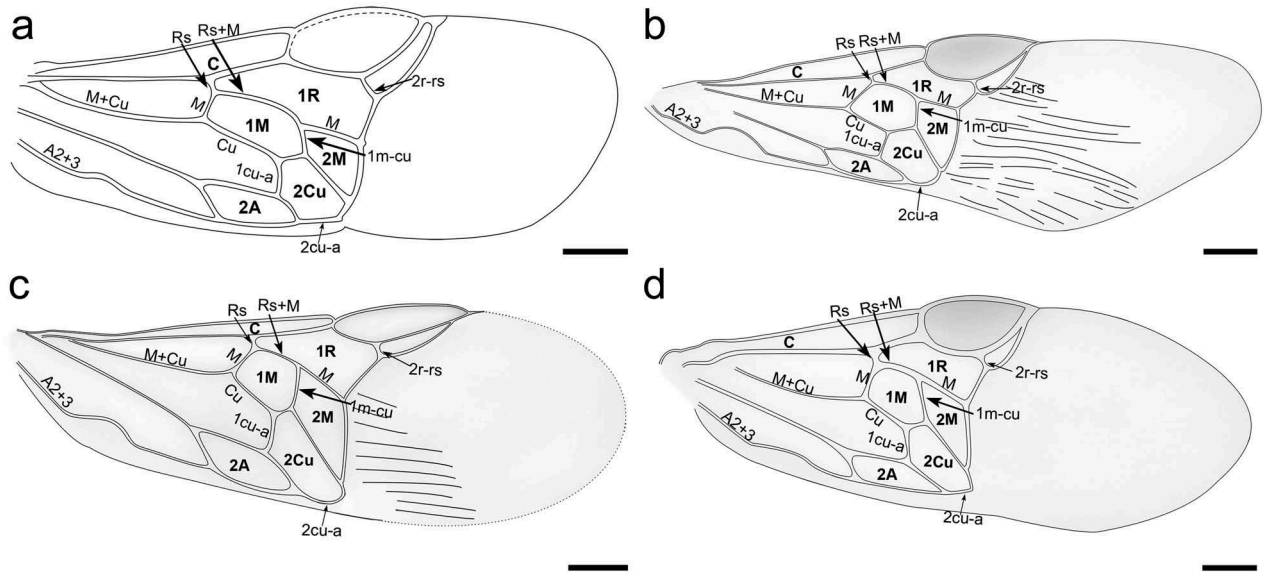

Figure 3. Line drawings of wings of Syspastoxyelidae. (a) *Syspastoxyela rhaphidia* Engel & Huang, 2016. (b) *Deltoxyela engeli* gen. et sp. nov. (c) *Syspastoxyela pinguis* sp. nov. (d) *Syspastoxyela simpla* sp. nov. Scale bars: A–D = 0.2 mm.

coniform with additional appendages, and only one apical spur present (Figure 2(d,e)). Meso- and metatibiae with at least two preapical spurs and all tibiae with many additional spines. Basitarsi of foreleg and hind leg with slender appendages, a sparse row of setae instead of usual preening brush, long but shorter than remaining tarsomeres combined. All tarsi with spur-like setae on outer anterior surface at position of inner preapical spurs. Claws symmetrical, acute, moderately bent, with long basal lobe. Arolium present and big.

Wings (Figures 2(f) and 3(b)): membranes hyaline, venation tubular but with faint brown pigmentation, all cells closed; costal cell wide; Sc lost; R nearly straight except slightly bending at origin of Rs; first abscissa of Rs much shorter than first abscissa of M, Rs-M (first abscissa) juncture strongly angled; first abscissa of Rs+M slightly arched; only 2r-rs present, positioned near mid-length of pterostigma. Pterostigma large, completely sclerotised. 1m-cu present and straight. Marginal cell minute, ending on pterostigma rather than on wing margin next to pterostigma. Cell 1M nearly pentagonal, broad. Cell 2M short and high; Cell 2Cu long and broad. M+ Cu slightly curved. A1 straight. Cross-veins 1cu-a and 2cu-a present, thus demarcating second cubital cell, 2cu-a smooth. A2+3 with severe arch midway before a cross-vein. Hind wing incomplete.

Abdominal terga wider than long, imbricate, widest at junction of fourth and fifth segments, then tapering posteriorly. Ovipositor closed, flat, thin, saw-like, nearly one-half abdominal length. Cercus length 0.27 mm, with two cercomeres, basal cercomere with several prominent, suberect, apically directed setae.

Paratype

♂, poorly preserved specimen. Body about 4.09 mm in length, antenna 1.94 mm and forewing 2.82 mm in length, maximum width 0.80 mm.

Body (Figure 2(g)) thin and long. Head 1.05 mm wide and 0.41 mm long, proximately inverted trapezoidal shape; Compound eyes large, ocelli displayed appreciably as a triangle. Mandibles scythe-like, flattened, and crossing scissor-like, apical tooth acute. Maxillary palpus and labial palps indistinct. Antenna with 13 flagellomeres, eight primary segments connected tightly to form the first flagellomere. Scape 0.44 mm long, maximum 0.13 mm in width; pedicel 0.11 mm long, maximum 0.08 mm wide; first flagellomere thickest, 0.10 mm wide, 0.65 mm long; remainder flagellum 0.74 mm in length, maximum 0.03 mm in width.

Thorax wide, width across tegulae 0.94 mm; pronotum large, triangular with long collar and medial line. Mesoscutum small with medial line; mesoscutellum tapering to acute apex. Legs slender, metafemur length 0.74 mm, metatibiae length 0.65 mm. Protibia, meso- and metatibiae with at least two preapical spurs and all tibiae with many additional spines. Basitarsi of foreleg long but shorter than remaining tarsomeres combined, fifth tarsomere elongate but shorter than basitarsi; basitarsi of hind leg with slender appendages.

Forewing with all cells closed; costal cell wide; Sc lost; first abscissa Rs much shorter than that of M, Rs-M juncture strongly angled; first abscissa Rs+M slightly arched; only 2r-rs present, inclined basally, positioned near middle point of pterostigma; Pterostigma large, completely sclerotised. M+ Cu bent smoothly and A1 straight; 1m-cu present. Cross-veins 1cu-a and 2cu-a present, thus demarcating second cubital cell; A2 + 3 with deep arch midway before a cross-vein. Hind wing invisible.

Abdomen slightly wider than mesothorax, the fourth segment widest. Genitalia visible but unclear, existing on the eighth tergum. Cercus distinctly divided into two segments, with slender setae, cercus length 0.28 mm.

Remarks

Deltoxyela engeli sp. nov. is erected based on eight primary segments connected tightly to form the first flagellomere; pronotum long and triangular; protibia with many spur-like spines and additional appendages; forewing with pterostigma large and completely sclerotised; Rs much shorter than M; juncture of Rs-M strongly angled, A2 + 3 sharply bent.

Genus ***Syspastoxyela*** Engel & Huang, 2016 (Figure 3–5, 6)

Diagnosis

Antenna with first flagellomere greatly elongate and thickened, composite resulting from fusion of seven primary segments to

form the first flagellomere, longer than remaining portion of flagellum; clypeus narrow, mandibles elongate, longer than scape, scythe-like, flattened; mesoscutum with well-delineated medial line and notauli; pronotum with short collar; forewing with pterostigma large; first abscissa Rs proclival, much shorter than first abscissa of M, Rs-M juncture slightly angled; Rs+M slightly arched; marginal cell exceedingly short; Rs apically not bifurcate; A2 + 3 with shallow arch midway before a-a cross-vein.

Type species

Syspastoxyela rhaphidia Engel & Huang, 2016

Syspastoxyela pinguis Wang, Shih, Ren & Gao, sp. nov. (Figure 3–4, 6)

Diagnosis

Antenna with 13 flagellomeres, first flagellomere longer than the remaining ones; pronotum wide, apex round in dorsal view; pterostigma slender, margin slightly sclerotised; costal cell narrow; 2r-rs positioned near one-third length of pterostigma; trochanter of foreleg long and ovipositor elongate, nearly abdominal length.

Derivation of name

The species name is derived from the Latin word 'pinguis', meaning broad, referring to the broad abdomen.

Remarks

The new species is assigned to *Syspastoxyela* Engel & Huang, 2016 based on several generic diagnostic characters, including seven primary segments connected tightly, body size small, mandibles elongate, scythe-like, mesoscutum with well-delineated medial line and notauli, weakly sclerotised pterostigma (Figure 3(a,c)). However, ***Syspastoxyela pinguis* sp. nov**. has many different features compared to *S. rhaphidia*: antenna with 13 flagellomeres, first flagellomere longer than the remaining ones; pterostigma slender; costal area narrow; 2r-rs positioned near one-third length of pterostigma; cell 1M broad and nearly pentagon-shaped; cell 2M short, cell 2Cu long and broad; Cross-vein 2cu-a smooth; trochanter of foreleg long and ovipositor nearly equal to abdomen in length.

Material

Holotype: No. CNU-HYM-MA2018013

Occurrence

Kachin (Hukawng Valley) of northern Myanmar. The lowermost Cenomanian (near Albian boundary); mid-Cretaceous.

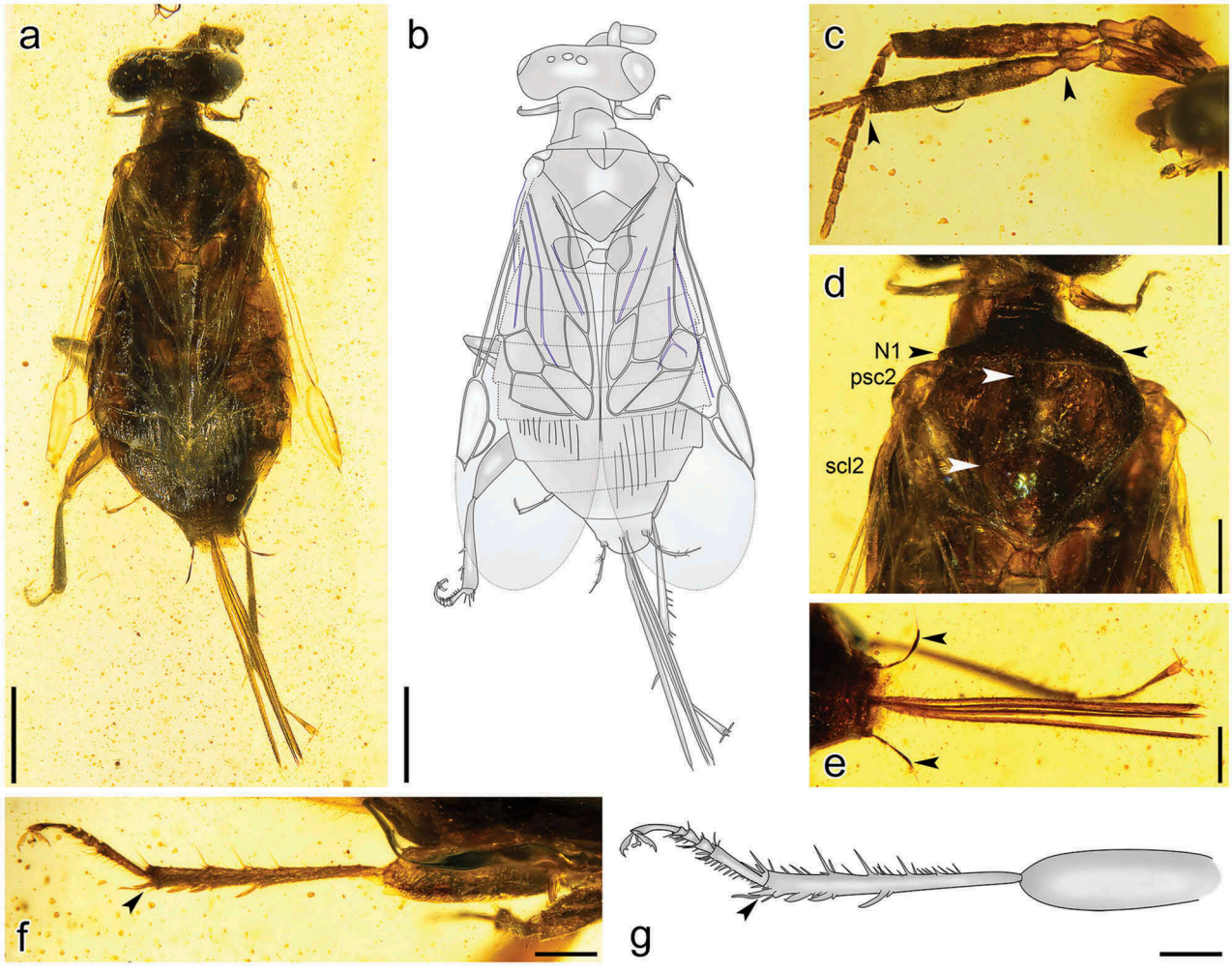

Figure 4. *Syspastoxyela pinguis* sp. nov. Holotype No. CNU-HYM-MA2018013. (a) Photograph of habitus in dorsal view. (b) Line drawing in dorsal view. (c) Photograph of antenna in lateral view. (d) Photograph of thorax in dorsal view. (e) Photograph of ovipositor in dorsal view. (f) Photograph of hind leg in lateral view. (g) Line drawing of hind leg in lateral view. Scale bars: A, B = 0.5 mm; C–G = 0.2 mm. Abbreviations: N1 = pronotum, psc2 = mesoscutum, scl2 = mesoscutellum.

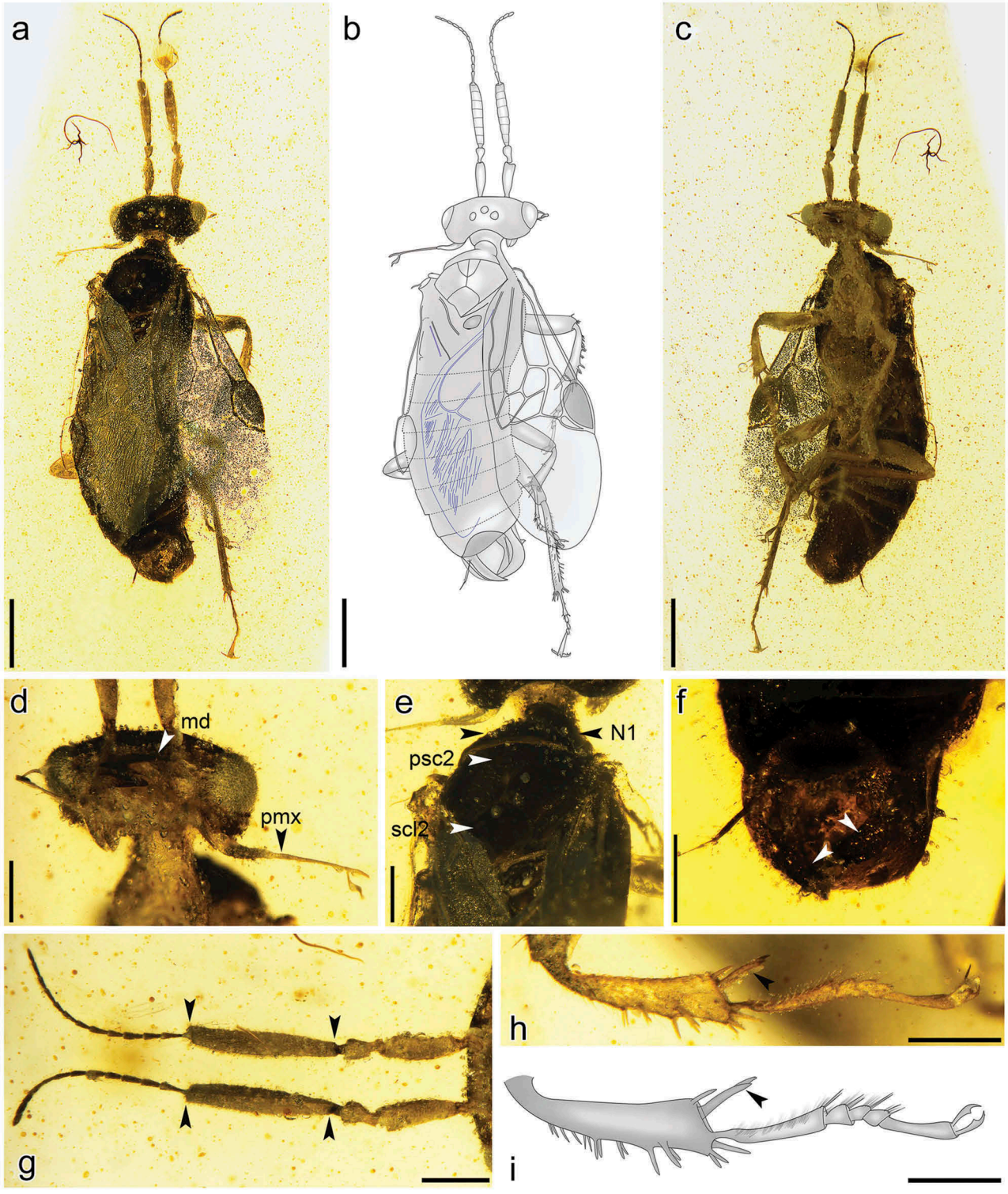

Figure 5. *Syspastoxyela simpla* sp. nov. Holotype No. CNU-HYM-MA2018014. (a) Photograph of habitus in dorsal view. (b) Line drawing in dorsal view. (c) Photograph of habitus in ventral view. (d) Photograph of mouthparts in ventral view. (e) Photograph of thorax in dorsal view. (f) Photograph of genital in dorsal view. (g) Photograph of antenna in ventral view. (h) Photograph of foreleg in ventral view. (i) Line drawing of foreleg in ventral view. Scale bars: A–C = 0.5 mm; D–I = 0.2 mm. Abbreviations: md = mandible, pmx = palpus maxillary, N1 = pronotum, psc2 = mesoscutum, scl2 = mesoscutellum.

Description

♀, well-preserved specimen. Body about 2.69 mm in length excluding ovipositor and antennae in dorsal view, antenna 1.46 mm and ovipositor about 1.33 mm; forewing 1.17 mm in length, maximum width 0.80 mm.

Integument generally brown to dark brown, without scattered setae (Figure 4(a,b)). Head about 0.81 mm wide and 0.22 mm long. Compound eyes oval, ocelli visible, in low triangle. Maxillary palpus, leg-like in form, but the last segment bifurcated. Labial palpus with three segments. Antenna (Figure 4(c)) with 13 flagellomeres,

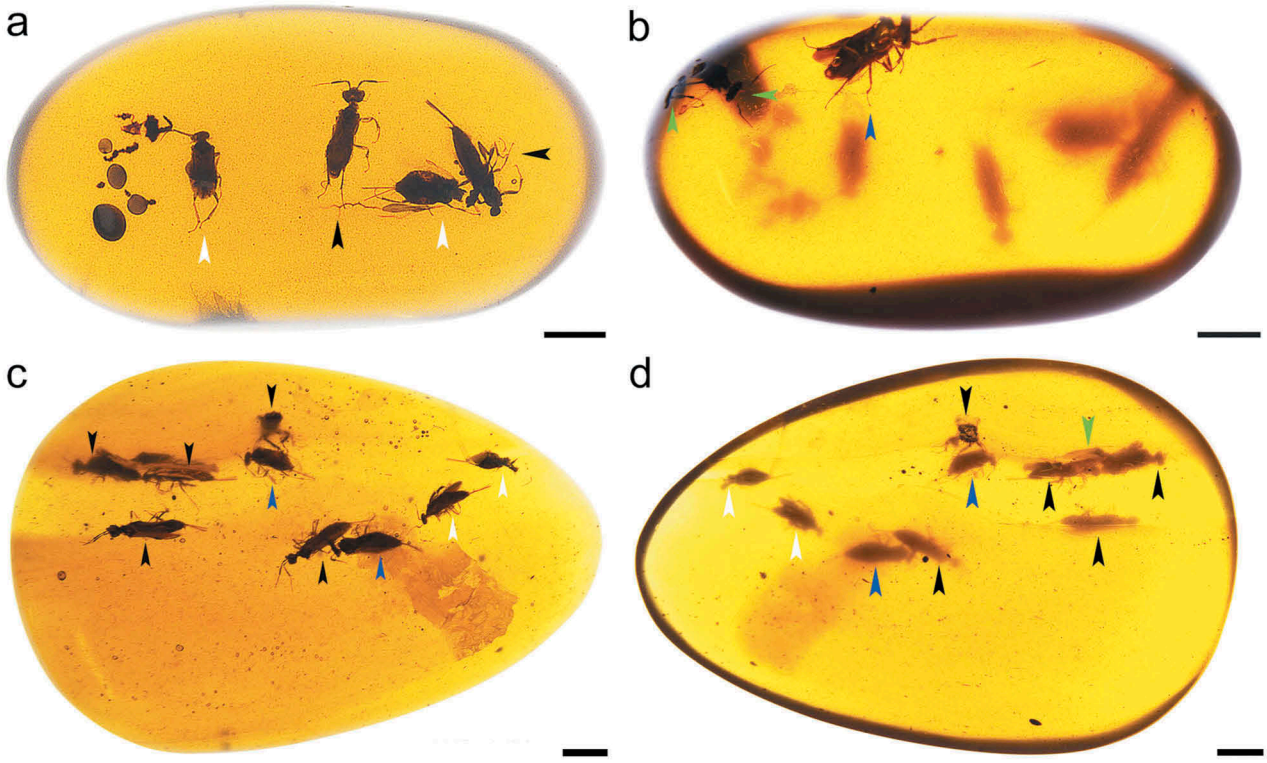

Figure 6. (a) Amber No. 1 in dorsal view. (b) Amber No. 1 in ventral view. (c) Amber No. 2 in dorsal view. (d) Amber No. 2 in ventral view. Scale bars: A–D = 2 mm. Black arrows indicate *Deltoxyela engeli* gen. et sp. nov., white arrows indicate *Syspastoxyela pinguis* sp. nov., blue arrows indicate *Syspastoxyela simpla* sp. nov. and green arrows indicate unknown.

first flagellomere thickened and long, apparently composite resulting from fusion of seven primary segments, longer than remaining portion of flagellum. Scape 0.28 mm long, maximum 0.09 mm in width; pedicel 0.10 mm long, maximum 0.05 mm wide; first flagellomere thickest, 0.09 mm wide, 0.56 mm long; remainder flagellum 0.52 mm in length, maximum 0.04 mm in width.

Thorax (Figure 4(d)) wide, width across tegulae 0.77 mm; pronotum wide, apex round in dorsal view. Pronotum with medial line. Mesoscutum with medial line and notauli strongly impressed, tapering to acutely rounded base; mesoscutum without line to mesoscutellum; mesoscutellum tapering to acutely sharp apex; mesoscutum without line to mesoscutellum; metascutum with cenchri present and large. Legs (Figure 4(f,g)) spindly, meso- and metafemur much shorter than tibia. Metafemur length 0.49 mm, metatibiae slender, 0.77 mm in length. Trochanter of foreleg long (0.11 mm). All tibiae with at least two preapical spurs (two on protibia, meso- and metatibiae with three spurs and additional spines; apical spur formula of tibiae 2-2-2, with protibial spurs of equal length, both simple; All tarsi with spur-like setae on outer anterior surface at position of inner preapical spurs. Basitarsi long but shorter than remaining tarsomeres combined, pretarsal claws long, with curved apices and minute subapical tooth.

Forewings (Figure 4(c)) with all cells closed; costal cell narrow; Sc lost; R straight except slightly bending at origin of Rs; first abscissa Rs much shorter than first abscissa of M, Rs-M juncture strongly angled; first abscissa Rs+M slightly arched; only 2r-rs present, positioned near one-third length of pterostigma. Pterostigma slender, marginal slightly sclerotised. 1m-cu present and slightly curved. Cell 1M broad and nearly pentagon-shaped. Cell 2M short and high, cell 2Cu long and broad. Marginal cell present and minute. M+ Cu slightly curved. A1 straight. Cross-veins 1cu-a and 2cu-a present, 2cu-a smooth. A2 + 3 with deep arch midway before a cross-vein. Hind wing incomplete. R straight, M+ Cu slightly bent. M and Cu present.

Abdominal terga wider than long, the first seven covered by wings, but the fourth segment widest (1.19 mm). Ovipositor (Figure 4(e)) opened, elongate, thin, needle-like, nearly abdominal length (1.33 mm in dorsal view), sheaths flattened. Cercus distinctly divided into two segments, 0.30 mm in length, with slender setae.

Syspastoxyela simpla Wang, Shih, Ren & Gao, sp. nov. (Fig 3, 5,6)

Diagnosis

Antenna with 13 flagellomeres, seven primary segments connected tightly to form the first flagellomere; pterostigma large, anterior border swollen, almost completely sclerotised; pronotum slightly wide, apex round in dorsal view.

Derivation of name

The species name is derived from the Latin word ‘simplex’, meaning simple, referring to the simple and ordinary morphologies.

Remarks

The new species is assigned to *Syspastoxyela* Engel & Huang, 2016 based on its relatively small body size, seven primary segments of the first flagellomere connected tightly, clypeus narrow, mandibles elongate, longer than scape, scythe-like, flattened, mesoscutum with well delineated medial line and notauli, costal area wide. However, *S. simpla* sp. nov. is distinctly differentiated from *S. rhaphidia* by the following characters: antenna with 13 flagellomeres; pterostigma completely sclerotised; the apex of pronotum round in dorsal view; cell 1M broad and nearly pentagon-shaped; cell 2M short, cell 2Cu long, broad; 2cu-a smooth. *Syspastoxyela simpla* sp. nov. is further distinguished from *S. pinguis* sp. nov. by the following

characters: pterostigma wide and completely sclerotised; costal cell wide; 2r-rs positioned near 1/2 length of pterostigma and foreleg trochanter short (Figure 3(a,c,d)).

Material

Holotype: No. CNU-HYM-MA2018014

Occurrence

Kachin (Hukawng Valley) of northern Myanmar. The lowermost Cenomanian (near Albian boundary); mid-Cretaceous.

Description

♂, well-preserved specimen. Body about 3.00 mm in length excluding antennae; antenna 1.47 mm and forewing about 2.05 mm, 0.79 mm at the widest point.

Body (Figure 5(a–c)) and appendages black to dark brown as preserved, covered with scattered setae. Body thin and long. Head broad and short, about 0.75 mm wide, 0.27 mm long. Compound eyes oval, ocelli visible, in low triangle. Maxillary palpus (Figure 5(d)) with five palpomeres, the last segment bifurcated. Antenna (Figure 5(g)) with 13 flagellomeres, seven primary segments connected tightly. Scape 0.29 mm long, maximum 0.08 mm in width; pedicel 0.13 mm long, maximum 0.07 mm wide; first flagellomere thickest, 0.07 mm wide, 0.47 mm long; remainder flagellum 0.58 mm length, maximum 0.02 mm in width.

Thorax (Figure 5(e)) narrow, width across tegulae 0.56 mm; pronotum slightly wide, apex round in dorsal view. Mesoscutum with medial line and notauli strongly impressed, tapering towards acutely sharp base; mesoscutellum tapering to acute apex; mesoscutum without line to mesoscutellum; metascutum with cenchri present and large (only one-half cenchri visible); Legs slender, meso- and metafemur (0.56 mm in length) much shorter than tibia, metatibiae slender, 0.72 mm in length. All tibiae with at least two preapical spurs (two on protibia, meso- and metatibiae with three and additional spur-like spines); apical spur formula of tibiae 2-2-2, with a longer and complicate preening spur and simple and shorter another; meso- and metatibiae with similar spurs as those of protibial but spur-like setae on outer anterior surface. All tarsi with spur-like setae on outer anterior surface, basitarsi long but shorter than remaining tarsomeres combined; fifth tarsomere elongate but shorter than basitarsus.

Forewing (Figure 4(d)) with all cells closed; costal cell slightly wide; Sc lost; R almost straight before Rs base; first abscissa Rs much shorter than that of M, Rs-M juncture slightly angled; first abscissa of Rs+M slightly arched; 2r-rs present, positioned near mid-length of pterostigma. Pterostigma broad, completely sclerotised. 1m-cu present and straight. Cell 1M broad and nearly pentagon-shaped. Cell 2M short and high, cell 2Cu long, broad. Marginal cell present and minute. M+Cu slightly curved. A1 straight. 1cu-a and 2cu-a present, 2cu-a smooth. A1 straight. Cross-veins 1cu-a and 2cu-a present, thus demarcating second cubital cell; A2 + 3 with shallow arch midway before a cross-vein. Hind wing with many folds. Veins a and cu-a present.

Abdominal terga wider than long, integument more distinctly, albeit still weakly, imbricate, widest at junction of fourth and fifth segments, then tapering posteriorly. Genitalia (Figure 5(f)) visible, existing on the eighth tergum. Gonocoxa and gonostylus visible, digitiform and possibly divided into two segments. Cercus minute, length 0.19 mm, with two cercomeres.

Discussion

Before this study, only two known species, *Syspastoxyela rhaphidia* and *Striaexyela longicornis*, have been described from the mid-Cretaceous Myanmar (Burmese) amber (Engel et al. 2016; Zheng et al. 2019). The three newly described species for Syspastoxyelidae in this study provide additional information on the variation of morphological characters of this family. For the first time, we document the males of Syspastoxyelidae. According to the new male specimens, *Deltoxyela* gen. nov. shows some sexual dimorphism in body size and antenna length. Male is slightly larger than female in average body size (3.74 mm n = 2 for males vs. 3.67 mm n = 5 for females), and equipped with longer antenna, about 1.25 times as long as that of the female.

Based on these new findings, it is confirmed that all the groups of Syspastoxyelidae possess the plesiomorphic character of xyelid-like antenna. As we know, the xyelid-like specimens often have the composite, thick and long first flagellomere, usually occurring in Xyelidae, Xyelotomidae, Xyelydidae and Mirolydidae, etc. The oldest Xyelidae in Hymenoptera has the composite, thick and long first flagellomere. Wang et al. (2017) proposed four hypothetical pathways about the antennal transformation within Hymenoptera based on one specimen, *Mirolyda hirta*, from the Middle Jurassic of China. Similar to *Syspastoxyela rhaphidia, Deltoxyela engeli* gen. et sp. nov. has the basalmost flagellomere inflexibly connected, with eight segments combined in a composite first flagellomere, and the boundary lines are weakly present. We suggest antenna of Syspatoxyelidae is similar to the third pathway: segmentation of the first flagellomere at once into seven or eight enlarged primary segments, except that flagellomeres after the first flagellomere became thin (Wang et al. 2017). However, *S. pinguis* sp. nov. has a composite first flagellomere with seven segments combined, which is longer than remaining portion of flagellum with distinct boundary lines. The length and width is reduced for the composite first flagellomere with seven combined segments in *S. simpla* sp. nov. The new material described here suggests that homonomous flagellum, several primary segments connected tightly forming a xyelid-like antenna, might be a very common feature among many groups of sawflies. Diversity in antennal morphology of Syspastoxyelidae shows clear transitions in its evolutionary process, which further indicate that the Mesozoic, especially from the Middle Jurassic to mid-Cretaceous, is an important evolutionary period for the diversification and radiation of living groups of hymenopterans.

Wing venation is one of the main characters used to identify and classify Hymenoptera, which have a comparatively simple wing pattern among many pterygote lineages. The venation has been simplified from basal to derived taxa within the Hymenoptera (Comstock and Needham 1899; Wheeler et al. 2001; Sharkey and Roy 2002; Trautwein et al. 2012; Perrard et al. 2016). In some basal taxa, e.g. *Abrotoxyela lepida* and *A. multiciliata*, the veins are relatively complex (Gao et al. 2009). Within the Apocrita, however, there is a much greater diversity of venational patterns than within the 'Symphyta' (Carpenter 1992). In many extant groups of Proctotrupoidea, the forewing veins are greatly reduced, and only a simple membrane covered with short setae. Interestingly, forewing venations of *Syspastoxyela* and *Deltoxyela* display two distinct parts, the basal part showing typical nearly complete venational characters within sawflies; however, the apical part, after pterostigma, losing all veins, and reflecting membrane structure forming many folds (Figures 2(f), 4(a) and 5(a)). More new fossil specimens are needed to further elucidate whether such specified wing pattern observed in Syspastoxyelidae represent a general trend in the group.

Different from other sawflies, all legs of the known species of Syspastoxyelidae are covered with hard setae besides the specialised spurs, varying in sizes and lengths. Such highly armed legs are commonly found among insects living in forest floor and other

Table 1. Measurements of specimens in Amber No. 1 and No. 2.

	No.	Species	Sex	Body (mm)	Antenna (mm)	Ovipositor (mm)
	CNU-HYM-MA 2018011	*Deltoxyela engeli*	Female	4.32	1.69	1.25
	CNU-HYM-MA 2018012	*Deltoxyela engeli*	Male	4.09	1.94	-
	CNU-HYM-MA 2018013	*Syspastoxyela pinguis*	Female	2.69	1.46	1.33
	CNU-HYM-MA 2018014	*Syspastoxyela simpla*	Male	3.00	1.47	-
	CNU-HYM-MA 2018015	*Syspastoxyela pinguis*	Male	2.15	1.24	-
	CNU-HYM-MA 2018016	*Deltoxyela engeli*	Male	3.39	1.43	-
	CNU-HYM-MA 2018017	*Syspastoxyela simpla*	Male	3.22	1.49	-
Amber 1	CNU-HYM-MA 2018018	*Syspastoxyela pinguis*	Female	?	-	1.07
	CNU-HYM-MA 2018019	*Deltoxyela engeli*	Female	?	-	1.07
	CNU-HYM-MA 2018020	*Syspastoxyela simpla* (?)	?	-	1.19	-
	CNU-HYM-MA 2018021	*Deltoxyela engeli* (?)	?	-	-	-
	CNU-HYM-MA 2018022	*Syspastoxyela pinguis*	Female	?	1.07	1.12
	CNU-HYM-MA 2018023	*Syspastoxyela pinguis*	Female	2.55	1.19	1.12
	CNU-HYM-MA 2018024	*Syspastoxyela simpla*	Female	3.14	1.62	1.07
	CNU-HYM-MA 2018025	*Deltoxyela engeli*	Female	3.61	1.27	1.26
Amber 2	CNU-HYM-MA 2018026	*Syspastoxyela simpla*	Female	2.54	1.49	1.24
	CNU-HYM-MA 2018027	*Deltoxyela engeli*	Female	3.59	-	1.11
	CNU-HYM-MA 2018028	*Deltoxyela engeli*	Female	3.52	-	1.22
	CNU-HYM-MA 2018029	*Deltoxyela engeli*	Female	3.30	-	1.01
	CNU-HYM-MA 2018030	*Syspastoxyela simpla* (?)	Female	2.70	-	0.89
	CNU-HYM-MA 2018031	*Deltoxyela engeli*	Male	-	-	-

more or less hidden places, such as cockroaches, where such traits are useful and helpful for crawling and warning. Furthermore, as observed in Hemiptera, burrower bugs (Cydnidae) have the specialised burrowing legs or grasping legs adapted for their particular way of life (Lis and Schaefer 2005). The inner spur of fore and hind tibia of Syspastoxyelidae may be devices for cleaning dust or soil particles from the antennae or labium. In addition, the abundant spines arming dorsal tibial surface in Syspastoxyelidae could help defending the insect and its moving through obstacles. It is suggested that the Syspastoxyelidae should have highly crawling ability, and such diverse and dense spines helped them quickly move on rough surfaces of flowers or trees.

In addition to all the specimens mentioned above, we found two pieces of amber with several specimens of Syspastoxyelidae preserved together (Figure 6). One is preserved with seven specimens including three males, two females and two gender – unknown. Another one is preserved with 10 sawflies, 1 male and 9 females. The taxonomy and measurements of these specimens are shown in Table 1. The new findings suggest that syspastoxyelids were speciose and prosperous in the ecosystem, even though only one family of sawflies, Syspastoxyelidae, is reported hitherto. Björkman *et al.* suggested the oviposition preferences of a monophagous pine sawfly (*Neodiprion sertifer*) seemed to prefer trees with high resin acid (diterpenoid) concentration (Björkman et al. 1997). Many syspastoxyelids of different genera and species in two amber pieces might be caused by insects' attraction to resins.

Conclusions

We have described here three new species of sawflies, *Deltoxyela engeli* gen. et sp. nov., *Syspastoxyela pinguis* sp. nov. and *Syspastoxyela simpla* sp. nov. from the mid-Cretaceous Myanmar amber. For the first time, we document the males of Syspastoxyelidae, which extend the fossil records and enhance our knowledge on morphological characters of Syspastoxyelidae. The new findings demonstrate a distinct evolutionary trend in antennal morphology and venational reduction of Syspastoxyelidae. Forewing venations of *Syspastoxyela* and *Deltoxyela* display two distinct parts, the basal part showing nearly complete venational characters of typical sawflies, but the apical part, after pterostigma, losing all the veins and the membrane structure having many folds. Although only one family of sawflies, Syspastoxyelidae, is reported in the mid-Cretaceous Myanmar amber, we believe syspastoxyelidswere speciose and prosperous in that ecosystem and there are more sawflies from Myanmar amber waiting to be discovered.

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Disclosure statement

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ORCID

Ren Dong http://orcid.org/0000-0001-8660-0901
Taiping Gao http://orcid.org/0000-0002-8118-8708

References

Björkman C, Larsson S, Bommarco R. 1997. Oviposition preferences in pine sawflies: a trade-off between larval growth and defence against natural enemies. Oikos. 79:45–52.

Carpenter FM. 1992. Superclass Hexapoda. Arthropoda 3–4 KAESLER RL, editor. Treatise on invertebrate paleontology, part R. Boulder (CO): Geological Society of America; 1–655, xxii + 655.

Chen S, Deng SW, Shih CK, Zhang WW, Zhang P, Ren D, Gao TP. 2018. The earliest timematids in Burmese amber reveal diverse tarsal pads of stick

insects in the mid-Cretaceous. Proceedings of the Royal Society B Biological Sciences. 285(1877):20180425.
Comstock JH, Needham JG. 1899. The wings of insects. American Naturalist. 33:845–860.
Cruickshank RD, Ko K. 2003. Geology of an amber locality in the Hukawng valley, northern Myanmar. Journal of Asian Earth Sciences. 21(5):441–455.
Engel MS, Huang DY, Alqarni AS, Cai CY. 2016. An unusual new lineage of sawflies (Hymenoptera) in Upper Cretaceous amber from northern Myanmar. Cretaceous Research. 60(60):281–286.
Gao TP, Ren D, Shih CK. 2009. *Abrotoxyela* gen. nov. (Insecta, Hymenoptera, Xyelidae) from the Middle Jurassic of Inner Mongolia, China. Zootaxa. 2094:52–59.
Grimaldi DA, Engel MS, Nascimbene PC. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates. 62(3361):1–71.
Huber JT, Sharkey MJ. 1993. Structure. In: Goulet H, Huber JT, editors. Hymenoptera of the world: an identification guide to families. Ottawa: Agriculture Canada; p. 13–59.
Li LF, Shih CK, Rasnitsyn AP, Li DQ, Ren D. 2018. A new wasp of Mynmarinidae (Hymenoptera: stephanoidea) from the mid-Cretaceous Myanmar amber. Cretaceous Research. 86:33–40.
Lin XD, Labandeira CC, Shih CK, Hotton CL, Ren D. 2019. Life habits and evolutionary biology of new two-winged long-proboscid scorpionflies from mid-Cretaceous Myanmar amber. Nat Commun. 10(1):1235.
Lis JA, Schaefer CW. 2005. Tibial combs in the Cydnidae (Hemiptera: heteroptera) and their functional, taxonomic and phylogenetic significance. Journal of Zoological Systematics and Evolutionary Research. 43(4):7.
Liu X, Shi G, Xia F, Lu X, Wang B, Engel MS. 2018. Liverwort mimesis in a Cretaceous lacewing larva. Current Biology. 28(9):1475–1481.
Perrard A, Lopez-Osorio F, Carpenter JM. 2016. Phylogeny, landmark analysis and the use of wing venation to study the evolution of social wasps (Hymenoptera: Vespidae: Vespinae). Cladistics. 32(4):406–425.
Rasnitsyn AP, Poinar JG, Brown AE. 2017. Bizzare wingless parasitic wasp from mid-Cretaceous Burmese amber (Hymenoptera, Ceraphronoidea, Aptenoperissidae fam. nov.). Cretaceous Research. 69:113–118.
Rasnitsyn AP, Quicke DL. 2002. History of insects. Dordrecht (Netherlands): Kluwer Academic Publisher.
Ren D, Shih CK, Gao TP, Wang YJ, Yao YZ. 2019. Rhythms of insect evolution – evidence from the Jurassic and Cretaceous in northern China. New York: Wiley Blackwell; p. 710.
Ronquist F, Klopfstein S, Vilhelmsen L, Schulmeister S, Murray DL, Rasnitsyn AP. 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. Syst Biol. 61(6):973–999.
Ross A 2019. Burmese (Myanmar) amber checklist and bibliography 2018. Palaeoentomology. 2(1):22–84.
Ross A, Mellish C, York PV, Crighton B. 2010. Chapter 12. Burmese amber. Penneyy D, editor. Biodiversity of fossils in amber from the major world deposits. Manchester: Siri Scientific Press; 208–235.
Sharkey MJ, Carpenter JM, Vilhelmsen L, Heraty J, Liljeblad J, Dowling APG, Schulmeister S, Murray D, Deans AR, Ronquist F, et al. 2012. Phylogenetic relationships among superfamilies of Hymenoptera. Cladistics. 28:80–112.
Sharkey MJ, Roy A. 2002. Phylogeny of the Hymenoptera: a reanalysis of the Ronquist *et al.* (1999) reanalysis, emphasizing wing venation and apocritan relationships. Zool Scr. 31:57–66.
Shi GH, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang MC, Lei WY, Li QL, Li XH. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research. 37:155–163.
Trautwein MD, Wiegmann BM, Beutel RG, Kjer KM, Yeates DK. 2012. Advances in insect phylogeny at the dawn of the postgenomic era. Annu Rev Entomol. 57:449–468.
Wang B, Xia FY, Wappler T, Simon E, Zhang HC, Jarzembowski EA, Szwedo J. 2015a. Brood care in a 100-million-year-old scale insect. Elife. 4:e05447.
Wang M, Rasnitsyn AP, Li H, Shih CK, Sharkey MJ, Ren D. 2015b. Phylogenetic analyses elucidate the inter-relationships of Pamphilioidea (Hymenoptera, Symphyta). Cladistics. 32(3):407–411.
Wang M, Rasnitsyn AP, Yang ZQ, Shih CK, Wang HA, Ren D. 2017. Mirolydidae, a new family of Jurassic pamphilioid sawfly (Hymenoptera) highlighting mosaic evolution of lower Hymenoptera. Sci Rep. 7:43944.
Wheeler WC, Whiting M, Wheeler QD, Carpenter JM. 2001. The phylogeny of the extant hexapod orders. Cladistics. 17:113–169.
Yang HR, Yin XC, Lin XD, Wang C, Shih CK, Zhang WW, Ren D, Gao TP. 2019. Cretaceous winged stick insects clarify the early evolution of Phasmatodea. Proceedings of the Royal Society B. 286(1909):20191085.
Zhang HC, Zhang JF. 2000. Xyelid sawflies (Insecta, Hymenoptera) from the Upper Jurassic Yixian formation of western Liaoning, China. Acta Palaeontologica Sinica. 39(4):476–492.
Zhang Q, Rasnitsyn AP, Wang B, Zhang HC 2018. Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: A review of the fauna. *Proceedings of the Geologists' Association*, 129, 736–747.
Zhang WT, Li H, Shih CK, Zhang AB, Ren D. 2017. Phylogenetic analyses with four new Cretaceous bristletails reveal inter-relationships of Archaeognatha and Gondwana origin of Meinertellidae. Cladistics. 34:384–406.
Zhao ZP, Yin XC, Shih CK, Gao TP, Ren D. 2019. Termite colonies from mid-Cretaceous Myanmar demonstrate their early eusocial lifestyle in damp wood. National Science Review. nwz141. doi:10.1093/nsr/nwz141.
Zheng Y, Zhang Q, Chen J, Zhang H. 2019. A remarkably new basal wasp with uniquely transformed forewing in mid-Cretaceous Burmese amber (Hymenoptera, Syspastoxyelidae). Cretaceous Research. 104:104172.