

Short communication

New genus and species of syspastoxyelid sawflies (Insecta, Hymenoptera) from the mid-Cretaceous Kachin amber with a review of the family Syspastoxyelidae

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ABSTRACT

Burmoxyla lii gen. et sp. nov. is described and illustrated based on a male collected from mid-Cretaceous Kachin (Burmese) amber. *Pinguixyela* gen. nov. is described for *Syspastoxyela pinguis* Wang, Shih, Ren & Gao, 2019, and *Syspastoxyela simpla* Wang, Shih, Ren & Gao, 2019 is transferred to the genus *Striaxyela* Zheng et al., 2019 as *Striaxyela simpla* (Wang, Shih, Ren & Gao, 2019), comb. nov., both from Kachin amber. This results in 5 genera and 6 species comprising the family thus far. A key to genera and species of Syspastoxyelidae is provided. The family is considered as the most basal branch of Hymenoptera sister to Xyelidae. Biologically Syspastoxyelidae are hypothesized to develop within male cones of conifer trees and to feed on pollen grains both as adult and immature. Our discovery supports the hypothesis that the mid-Cretaceous Kachin biota was highly endemic.

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1. Introduction

Kachin amber of the Kachin Province of Myanmar (Burma) is widely famous for exquisite preservation of Hymenoptera, provided an important contextual information on palaeoenvironment and amber formation as well as the most abundant biota

(Rasnitsyn, 1996; Rasnitsyn & Ross, 2000; Rasnitsyn et al., 2016; Ross, 2018, 2021; Zheng et al., 2019). Hymenoptera are generally divided into two grades, Symphyta and Apocrita; with the basal Symphyta being of exceptionally importance in evolution of the order (Rasnitsyn, 1988; Grimaldi & Engel, 2005). However, Symphyta fossils are scanty in Cretaceous amber (Ortega-Blanco et al., 2008; Engel et al., 2016; Wang et al., 2019, 2020; Zheng et al., 2019, 2020), as well as generally in ambers. This makes a painful loss in our knowledge of their morphology because we miss a wealth of their tiny details that otherwise might be preserved in the incomparable amber record. Up to now, only three families are recorded there trustfully, Syspastoxyelidae (erroneously called Xyelidae), Cephidae and Anaxyelidae (Zhang et al., 2018, tab. 2),

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with only six species in five genera described in two families thus far (Engel et al., 2016; Wang et al., 2019; Zheng et al., 2019, 2020).

The family Syspastroxyelidae has been erected by Engel et al. (2016) based on a unique female. The record was supplemented soon by Wang et al. (2019) and Zheng et al. (2019), resulted in three genera and five species established, *Syspastroxyela raphidia* Engel & Huang, 2016, *S. pinguis* Wang, Shih, Ren & Gao, 2019, *S. simpla* Wang, Shih, Ren & Gao, 2019, *Striaxyela longicornis* Zheng et al., 2019, *Daltoxyela engeli* Wang, Shih, Ren & Gao, 2019, all from the Kachin amber.

As a result, Syspastroxyelidae appears as an extinct basal family of Symphyta endemic to the Kachin amber that combines a unique plesiomorphy (segmented cerci) with striking synapomorphies (spinose legs and deeply modified wing venation) and so seems to take the sister position in respect to all other Hymenoptera (Wang et al., 2019; Zheng et al., 2019). At the same time, Syspastroxyelidae show distinct similarity to the living and, simultaneously, the oldest family Xyelidae and particularly to the genus *Xyela* Dalman, the most diverse living genus in the family, in its general appearance and in some morphological details. Important among them are exaggerated leg-like maxillary palps used for extracting pollens as a food from anthers (Rasnitsyn, 1965). *Xyela* females deposit eggs inside the male cones of the pine trees where their larvae develop, and the similarity in general appearance between *Xyela* and syspastroxyelids, including similar shape and size of ovipositor suggests a possibly similar biology. There are important differences: (i) both *Xyela* and *Pinus* L. are mainly extratropical in distribution in contrast to the tropical Kachin biota, (ii) Pinaceae are not particularly characteristic of Kachin flora, as well as the minor contribution from Cupressaceae cannot be completely ruled out (Dutta et al., 2011), (iii) *Xyela* was not extremely rare at least from about the Eocene/Oligocene boundary to the end of the Oligocene, and yet it has never been recorded in amber in spite of the abundance of pine trees in the late Eocene Baltic flora (Zherikhin et al., 2009). In contrast, Syspastroxyelidae are not very rare in the Kachin amber and sometimes form mass burials there (Wang et al., 2019). Interestingly as well is the observation that Syspastroxyelidae form a rather diverse group which is still recorded exclusively from Kachin amber. All of this makes important exploration of diversity of that unusual group of insects.

Our new discovery of a new genus and species, *Burmaxyela lii* gen. et sp. nov., as well as other finds concerning taxonomy, morphology and biology of Syspastroxyelidae, are described and illustrated in the present paper. These include description of a new species and two new genera, transfer of two species to different genera, and new hypotheses concerning biology of the family and possible functions of some structures of its component species.

2. Material and methods

The type specimen is contained in a small piece of amber collected from the Hukawng Valley, near Tannai, Kachin State, northern Myanmar. The age of Kachin amber has been assigned to the earliest Cenomanian (about 98.79 ± 0.62 Ma) based on the radiometric analyses of zircons (Shi et al., 2012). A late Albian – early Cenomanian age has also been suggested based on ammonites (Yu et al., 2019). Age of the Kachin amber was debated based on other palaeontological data as well (Smith & Ross, 2018).

The holotype of *Burmaxyela lii* gen. et sp. nov. is preserved in a rectangular piece of amber measuring $8.13 \times 4.86 \times 1.12$ mm, and housed in the Linyi University, under the collection number XCAM-HY-2002. The studied specimen piece shows pale yellow. The

preservation state is moderate because of lost antennae and distinct depression of the fossil that hinder visibility of some details. In order to reach better visibility of morphological details, the piece was cut as thin as possible and polished manually using the emery paper (grit sizes of 5000–1000) and rotary polisher (Mecattech 33, France). This specimen was checked by stereomicroscope and a Nikon D800 and examined by VHX 5000 digital microscope. Line drawings were prepared using CorelDraw X7 and Adobe Photoshop CC graphics software. The measurements were made with Image J software.

The wing venation terminology of Syspastroxyelidae follows Zheng et al. (2019) with the abbreviations as follow (Fig. 1): 1A, 2+3A, anal veins; C, costal vein; Cu, cubital vein; h, humeral vein; M, median vein; R, radial vein; Rs, radial sector; SC, subcostal vein; 1-Cu, 3-Cu, 1-M, 2-M, etc., succeeding sections of respective longitudinal veins; 1a-2a, interanal crossvein; r-m, crossvein between R and RS and M; 2r-rs, second radial crossvein; 1cu-a and 2cu-a, crossveins between Cu and A; 1m-cu and 2m-cu, crossvein between M and Cu; 1a, 2a, 1cua, 2cua, 1mcu, 2mcu, etc., respective cells; r+rm, fused cells 1r, 2r, 2rm and possibly 3rm.

This published work and the nomenclatural acts it contains have been registered in ZooBank (<http://www.zoobank.org/>, last access: June 28, 2021), with the following LSID (reference): urn:lsid:zoobank.org:pub:EEC343F0-3F7A-4636-860E-8DD9EE4DAA42.

3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Family Syspastroxyelidae Engel et al., 2016

Type genus: *Syspastroxyela* Engel et al., 2016

Diagnosis. Similar to Xyelidae and particularly Xyelinae except that pronotum elongate anteriorly, medially (vs. simple transverse plate in Xyelidae), fore wing with venation shifted basal leaving distal 0.4 of wing veinless and densely longitudinally corrugated, and venation strongly modified: SC lost at least as longitudinal vein, 1-RS much shorter than 1-M, cells 1r, 2r, 2rm and 3rm fused in one cell, RS ending at pterostigma or at wing margin close to pterostigma, M and Cu lacking free apices, hind wing lacking venation in its distal third and with no free vein ending visible, with r cell short triangular and 1r-m meeting R far basally of RS base. Tibiae and tarsi strongly spinose (vs. weakly armed in Xyelidae), with preapical spurs placed far more distal than in Xyelidae. Cerci long, 3-segmented (vs. simple in other Hymenoptera including Xyelidae). **Genera included.** *Syspastroxyela* Engel et al., 2016 (Fig. 1A), *Daltoxyela* Wang, Shih, Ren & Gao, 2019 (Fig. 1B), *Striaxyela* Zheng et al., 2019 (Fig. 1C, D), *Pinguixyela* gen. nov. (Fig. 1E), and *Burmaxyela* gen. nov. (Fig. 1F), all from the mid-Cretaceous Kachin amber.

Remarks. All the above characters are forming synapomorphies of Syspastroxyelidae except for 3-segmented cerci that represent a striking plesiomorphy of the family in respect to all other Hymenoptera and so qualify Syspastroxyelidae as the most basal lineage sister to remaining Hymenoptera.

Genus *Syspastroxyela* Engel et al., 2016

Syspastroxyela: Engel et al., 2016, p. 283.

Type species: *Syspastroxyela raphidia* Engel et al., 2016

Emended diagnosis. Antennal thread (flagellar segments behind composite first segment) 8-segmented and distinctly shorter than first (composite) flagellomere. Pronotum shorter than wide. Notauli meeting before mesoscutellum. Pterostigma wide, not sclerotised. 1-RS not dot-like. RS distal of 2r-rs gently curved, ending to wing

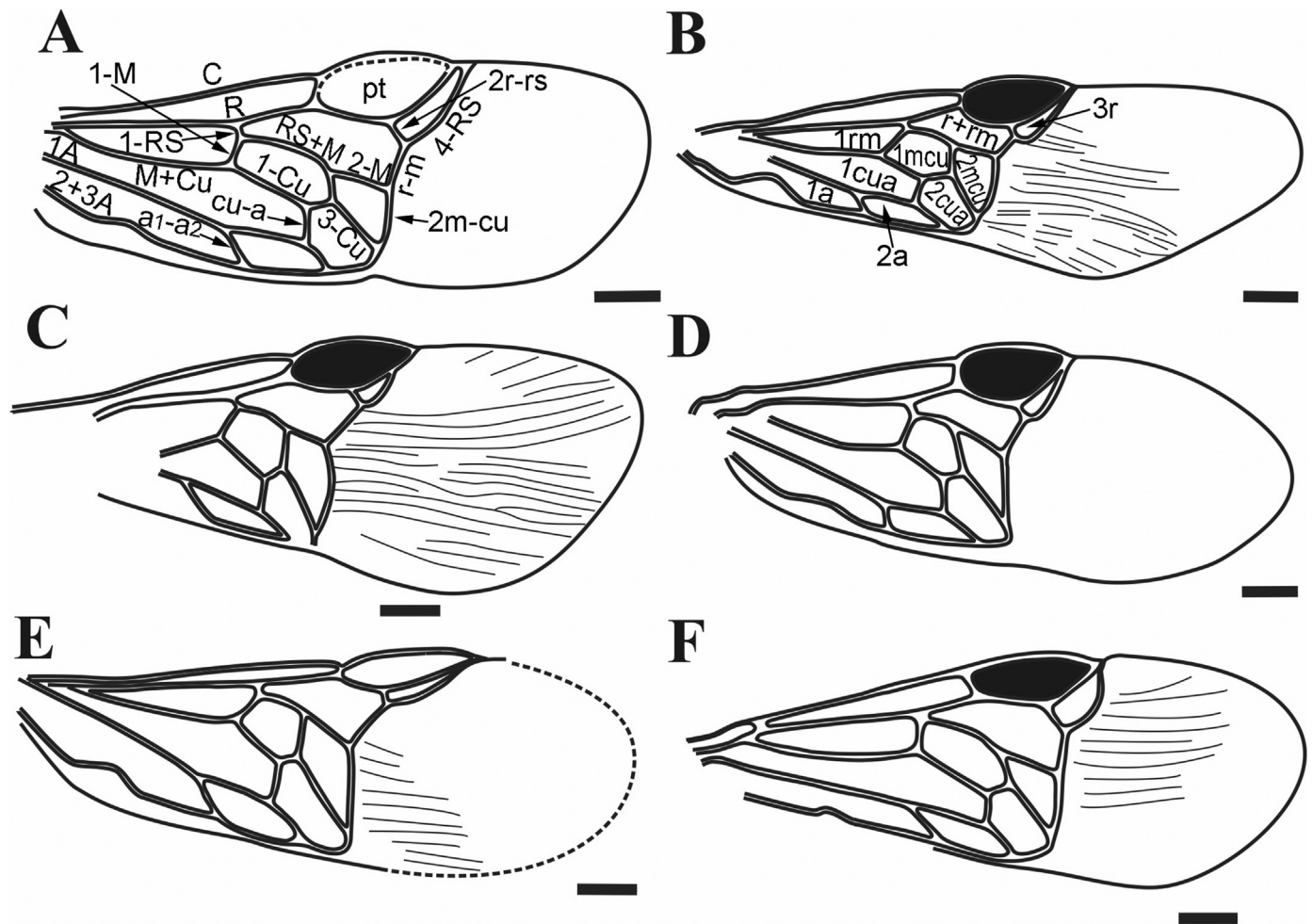


Fig. 1. Wings line drawings of all described species of Systastoxylidae. A, *Systastoxyla raphidia* Engel et al., 2016, with vein names shown; B, *Deltoxyela engeli* Wang, Shih, Ren & Gao, 2019, with cell names shown; C, *Striaexyela longicornis* Zheng et al., 2019; D, *Striaexyela simpla* (Wang, Shih, Ren & Gao, 2019); E, *Pinguixyela pinguis* (Wang, Shih, Ren & Gao, 2019); F, *Burmoxyla lii* gen et sp. nov. For abbreviations, see [Material and methods](#). Scale bars, 0.2 mm.

margin distinctly away pterostigmal apex. Cell 1mcu twice as long as high. Crossveins r-m and 2cu-a aligned. Fore tibia lacking row of short thick setae at flexor surface. Femora not particularly swollen. *Species included.* Type only (Fig. 1A).

Remarks. For comparison to other genera see key below. For *S. pinguis* Wang et al., 2019 and *S. simpla* Wang et al., 2019 originally attributed here, see below (genera *Pinguixyela* and *Striaexyela*, respectively). Number of primary segments fused as the composite first flagellomere is not used here to diagnose genera because the primary segmentation is not always clear enough from photographs and needs examination of the type material to get sufficient certainty. Among the diagnostic characters listed above, putatively synapomorphic of the genus is the short and oligosegment antennal thread.

Genus *Deltoxyela* Wang, Shih, Ren & Gao, 2019

Deltoxyela: Wang et al., 2019, p. 2.

Type species: *Deltoxyela engeli* Wang, Shih, Ren & Gao, 2019

Emended diagnosis. Antennal thread 12-segmented and distinctly longer than first flagellomere. Pronotum longer than wide. Notauli meeting before mesoscutellum. Pterostigma wide, sclerotised. 1-RS not dot-like. RS distal of 2r-rs gently curved, ending to pterostigma before its apex. Cell 1mcu slightly longer than high. Crossveins 3r-m

and 2cu-a meeting at distinct angle. Fore tibia with row of short thick setae at flexor surface. Femora not particularly swollen.

Species included. Type only (Fig. 1B).

Remarks. For comparison to other genera see key below. Form of the pronotum was apparently misinterpreted originally: photographs (Wang et al., 2019, figs 1a and 2c) suggest that the anterior oval plate is a part of pronotum and that the triangular structure behind it probably represents relief on pronotal collar. Among the diagnostic characters listed above, putatively synapomorphic of the genus are very long pronotum and setose flexor surface of fore tibia.

Genus *Striaexyela* Zheng et al., 2019

Type species: *Striaexyela longicornis* Zheng et al., 2019

Striaexyela: Zheng et al., 2019, p. 2.

Systastoxyla (partim, quoad *S. simpla*): Wang et al., 2019, p. 7.

Emended diagnosis. Antennal thread 12-segmented and distinctly longer than first flagellomere. Pronotum shorter than wide. Notauli meeting before mesoscutellum. Pterostigma wide, sclerotised. 1-RS not dot-like. RS distal of 2r-rs gently curved, ending to pterostigma before its apex. Cell 1mcu scarcely longer than high. Crossveins r-m and 2cu-a meeting at distinct angle. Fore tibia with no thick setae at flexor surface. Femora not particularly swollen.

Species included. Type species (Fig. 1C) and *Striaexyela simpla* (Wang, Shih, Ren & Gao, 2019), comb. nov. (Fig. 1D).

Remarks. For comparison to other genera see key below. No unique synapomorphy is known for the genus thus far.

Striaxyela simpla is treated here as belonging to the genus *Sypastoxyela* because its type specimen as described and illustrated (Wang et al., 2019, figs 3, 5, 6) fits the diagnosis of the former and not the latter as defined above. Particularly, it has long 12-segmented flagellar thread behind the composite first flagellomere, sclerotized pterostigma receiving apex of RS, short cell 1mcu and angularly joined r-m and 2m-cu.

A possibility that *S. longicornis* and *S. simpla* represent a female and male of the same species, respectively, cannot be ruled out for the present. However until the putative (undescribed) females of the latter found synincluded with the putative males of the same species (Wang et al., 2019) are not re-examined, we prefer to consider these species as distinct.

Genus ***Pinguixyela*** Zheng & Rasnitsyn, gen. nov.

Type species: *Sypastoxyela pinguis* Wang, Shih, Ren & Gao, 2019

Sypastoxyela (partim, quoad *S. pinguis*): Wang et al., 2019, p. 5.

urn:lsid:zoobank.org:act:267DEFCA-C397-4B1A-9171-0024A10FC3B2

Diagnosis. Antennal thread 12-segmented and distinctly longer than first flagellomere. Pronotum shorter than wide. Notauli meeting before mesoscutellum. Pterostigma narrow, not sclerotised. 1-RS not dot-like. RS distal of 2r-rs gently curved, ending to pterostigma before its apex. Cell 1mcu slightly longer than high. Crossveins r-m and 2cu-a meeting at distinct angle. Fore tibia lacking row of short thick setae at flexor surface. Femora not particularly swollen.

Etymology. The generic name combines the type species name *pinguis*, the Latin for fatty, and the generic name *Xyela*. The gender is feminine.

Species included. Type only (Fig. 1E).

Remarks. For comparison to other genera see key below. The new genus is created here for *Sypastoxyela pinguis* because it does not fit diagnoses of other genera and demonstrate a unique feature, a narrow pterostigma that supposedly forms a synapomorphy of the genus.

Genus ***Burmoxyela*** Zheng & Rasnitsyn, gen. nov.

urn:lsid:zoobank.org:act:290690A0-B122-474C-A69B-CE360636ADEB

Type species: *Burmoxyela lii* Zheng & Rasnitsyn, gen. et sp. nov.

Diagnosis. Antennal thread 12-segmented and distinctly longer than first flagellomere. Pronotum shorter than wide. Notauli widely separated at mesoscutellum. Pterostigma wide, sclerotised. 1-RS dot-like short. RS distal of 2r-rs strongly curved, ending to pterostigma before its apex. Cell 1mcu twice as long as high. Crossveins r-m and 2cu-a aligned. Fore tibia lacking row of short thick setae at flexor surface. Mid femur unusually swollen (less than 1.5 times as long as wide).

Etymology. The generic name is from Burma, the old name of Myanmar, and the generic name *Xyela*. The gender is feminine.

Species included. Type only (Fig. 1F).

Remarks. For comparison to other genera see key below. Putative synapomorphic of the genus are notauli separated at mesoscutellum, 1-RS dot-like short, RS distal of 2r-rs strongly curved, and particularly almost disk-like wide mid femur (in contrast to slim mid tibia and tarsus).

Burmoxyela lii Zheng & Rasnitsyn, gen. et sp. nov.

Figs. 1F; 2A-B; 3A-F; 4A-D

urn:lsid:zoobank.org:act:77AD5CB1-620A-4DD4-9E84-778F4933E9B3.

Etymology. The species is named in honor to Mr. Bo Li, who has provided the holotype material.

Holotype. Male, XCAM-HY-2002, housed in Linyi University, Linyi, China.

Locality and Horizon. Hukawng Valley, Kachin State, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Diagnosis. As for genus.

Description. Male (female unknown). Body large by sypastoxyelid standard, length 3.71 mm (second only to *D. engeli* which is above 4 mm long without antenna and ovipositor), almost dark as preserved, especially in head, metasoma, tibiae and tarsi, wing venation other than pterostigma yellow and with yellow close longitudinal corrugation, pterostigma brown, mid femora more dark brown. Integument apparently smooth (no distinct micro-sculpture visible).

Head thin in hind view (apparently because of postburial depression), slightly wider than thorax, 1.13 mm wide and 0.33 mm high; head with anterior margin smoothly angled; compound eyes broad and nearly oval, strongly bulging; three ocelli distinct and close to each other on frons; mouthparts not discernible; antenna not preserved; maxillary palp leg-like, with six segments 0.13, 0.39, 0.31, 0.06, 0.05 and 0.05 mm, respectively, with segment 2 thick, fusiform, segment 5 pedunculate and segment 6 apparently cup-like; labial palp 4-segmented, segments 1, 2, 4 slightly elongate, segment 3 subquadrate, at least segments 1–3 each with strong seta.

Mesosoma 1.30 mm long and 1.07 mm wide across tegulae. Pronotum smooth, with elongate collar, 0.48 mm long and 0.67 mm wide basally; propleura large (0.52 mm long), almost abut in middle third; prosternum very large (0.42 mm long and 0.29 mm wide); mesonotum with notauli reaching scutellum at a distance from midscutal line, well diverging forward; mesoscutellum roundly obtusely angular anteriorly; structure of mesoventropleuron not clear except for very long postepisternal condyli (according to size of midcoxa); metascutellum well defined, cenchri developed but not well visible. Legs short, all tibiae armed with strong spines dorsally, even though less heavy so than in other Sypastoxyelidae, mid and hind tibiae with 2 spurs each, one preapical spur visible close to apical ones in mid tibiae only; fore leg ordinary with coxa ca. 0.43, trochanter 0.21, femur 0.65 and tibia 0.60 mm long, tarsal segments 1–4 0.56 mm long, with basitarsus slightly shorter than segments 2–4 combined. Mid coxae and femora disproportionally increased, coxa 0.56 mm long and 0.29 mm wide, femur almost disk-like, 0.59 mm long and 0.42 mm wide, mid trochanter short, transverse; in contrast, mid tibia ordinary, 0.68 mm long and 0.10 mm wide; mid tarsus length 0.79 mm, with tarsomere ratio: 0.3: 0.08: 0.07: 0.06: 0.21, with basitarsus longer than tarsomeres 2–4 combined; pretarsal claws long, with small basal tooth and thinner, curved apex; arolium small. Hind leg ordinary, with coxa 0.34 mm long and 0.24 mm wide, trochanter 0.18 mm long, trochantellus 0.09 mm long (other trochantelli not distinct), femur spindle-like, 0.86 mm long and 0.30 mm wide, hind tibia 0.68 mm long and 0.10 mm wide.

Forewing 3.22 mm long and 1.20 mm wide; pterostigma large, longer than wide, completely sclerotized, 0.57 mm long and 0.31 mm wide. SC present as crossvein just behind M+Cu base, C lost between Sc and humeral vein, C and R connected with sclerotized bridge next to pterostigma (as in Xyelidae: Macroxyelinae); 1-RS dot-like short, RS+M arching midway; 1r-rs and 2+3-RS lost; 2r-rs less than half as long as pterostigma wide, reaching pterostigma slightly before its midlength; 4-RS strongly curved, meeting wing margin just at apex of pterostigma; 2r-m lost, 3r-m and 2m-cu aligned to form line vertical to wing hind margin at 0.60 wing length; rudimentary base of Cu apparently present at very wing base, M+Cu arching, angled with 1-Cu, 1-Cu straight, about as long as RS+M, 1m-cu distinctly longer than 2-Cu, almost aligned

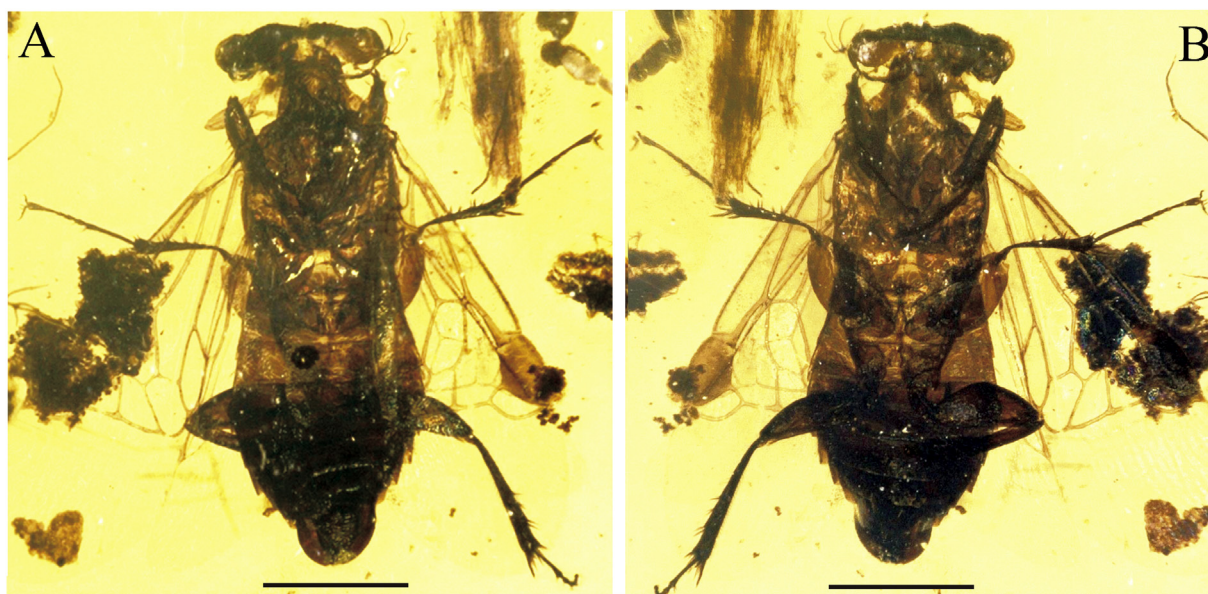


Fig. 2. *Burmoxyela lii* Zheng & Rasnitsyn, gen. et sp. nov., holotype (XCAM-HY-2002). A, dorsal view, B, ventral view. Scale bar, 1 mm.

with RS+M and 3-Cu (cell 2mcu triangular); cu-a 0.30 times as long as 1-Cu; apical 0.40 of wing veinless, densely and regularly corrugated parallel to wing axis. Hind wing incompletely preserved, with RS forming short and high triangular cell distal of wing midlength, 1r-m vertical to wing fore margin near wing midlength (well basal of RS), 2r-m aligned with 2-RS and almost so with m-cu, RS+M 3 times as long as 1r-m, slightly longer than 1-M and slightly shorter than m-cu; M+Cu straight; cu-a not preserved.

Metasoma length 2.12 mm, width 1.29 mm (segmnt 4 is the widest), with 7 terga and 8 sterna visible (supposedly sternum 8 hidden), tergum 1 split, with halves distant basally, each half with oblique groove, tergum 2 longest, with wide V-like groove, following terga more or less uniform, with no distinct sculpture. Sternum 1 absent, sterna 2–6 more or less uniform belt-like, sternum 7 with rounded hind margin, sternum 9 longest, wide crescent-like. Genitalia not distinct, apparently gonocoxa and gonostilus narrow, elongate. Cerci not preserved.

Remarks. Incrassate mid coxae and femora imply a specific function of mid legs, particularly a saltatory one, in parallel to, for instance, chalcidoid wasps Encyrtidae. However, ordinary structure of mid tibia question the saltatory hypothesis.

A key to known genera and species of *Sypastoxyelidae*.

1. Antennal thread 8-segmented, shorter than 1st flagellomere. RS ending wing margin at distance from pterostigma. Cell 1mcu twice as long as high..... *Sypastoxyela raphidia* Engel & Huang, 2016
 - Antennal thread 12-segmented, not shorter than 1st flagellomere. RS ending at or before pterostigmal apex. Cell 1mcu usually shorter..... 2
2. Pronotum strongly elongate (longer than wide basally). Body length 4 mm or more. *Deltoxyela engeli* Wang, Shih, Ren & Gao, 2019
 - Pronotum less elongate. Body length less than 4 mm 3
3. Notauli reaching mesoscutellum separately. 1-RS dot-like short, 4-RS strongly curved, meeting pterostigmal apex. Mid femur almost disk-like wide ... *Burmoxyela lii* Zheng & Rasnitsyn, gen. et sp. nov.
 - Notauli meeting before mesoscutellum. 1-RS longer. 4-RS gently curved, meeting pterostigma before its apex..... 3
4. Pterostigma narrow, not sclerotised.....
 *Pinguixyela pinguis* (Wang, Shih, Ren & Gao, 2019)

- Pterostigma wide, completely sclerotized. *Striaxyela* Zheng et al., 2019..... 5
- 5. 2r-rs about half as long as 4-RS. 2m-cu convex, more than twice as long as 2+3-M..... *Striaxyela longicornis* Zheng et al., 2019
 - 2r-rs at most 0.30 times as long as 4-RS. 2m-cu straight, about 1.50 times as long as 2+3-M *Striaxyela simpla* (Wang, Shih, Ren & Gao, 2019).

4. Discussion

Until now the family Sypastoxyelidae was known exclusively in mid-Cretaceous Kachin amber and represented there by three genera and five species (Engel et al., 2016; Wang et al., 2019; Zheng et al., 2019). The present work adds one new species and two new genera from the same source resulting in five genera (*Sypastoxyela* Engel et al., 2016, *Striaxyela* Zheng et al., 2019, *Deltoxyela* Wang, Shih, Ren & Gao, 2019, *Pinguixyela* gen. nov. and *Burmoxyela* gen. nov.) with six species (*Sypastoxyela raphidia* Engel & Huang, 2016, *Deltoxyela engeli* Wang, Shih, Ren & Gao, 2019, *Pinguixyela pinguis* (Wang, Shih, Ren & Gao, 2019), *Striaxyela longicornis* Zheng et al., 2019, *S. simpla* (Wang, Shih, Ren & Gao, 2019) and *Burmoxyela lii* sp. nov.). This attests the family as a diverse group endemic to the mid-Cretaceous Kachin biota which is generally famous for its incomparably richness and unique composition (Ross, 2018, 2019; Zhang et al., 2018; Rasnitsyn & Öhm-Kühnle, 2018). The very presence of Sypastoxyelidae in the Kachin biota is more than noteworthy, because it is a basal and by inference ancient group sister to all other Hymenoptera (see introduction), and additionally it is apparently the only group of Symphyta well represented in any amber (with the only possibly rival Anaxyelidae; cf. Zhang et al., 2018).

Burmoxyela lii gen. et sp. nov. is a fascinating discovery among mid-Cretaceous symphytan wasps. It makes an addition to diversity of the family and of Symphyta in general and demonstrates some problems in taxonomy of Sypastoxyelidae. This helps to reorganize system of the family in a somewhat more logic way by creating two new genera and transfer of two earlier described species to a supposedly more natural position.

At the same time the new fossil reveal characters, both described earlier and new ones, which are suggestive in respect of their possible function, both expectable and unexpected. Particularly

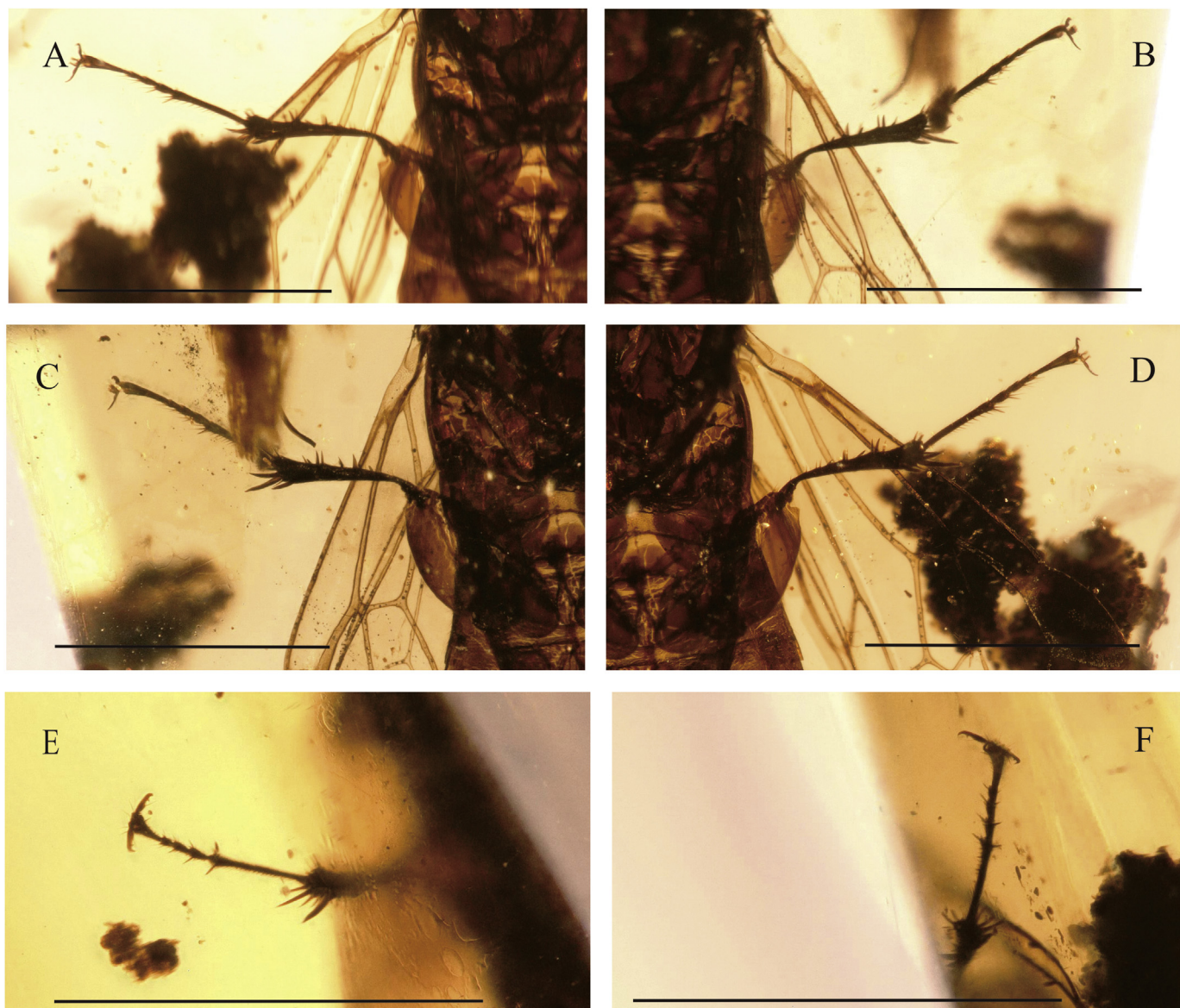


Fig. 3. *Burmoxyela lii* Zheng & Rasnitsyn, gen. et sp. nov., holotype (XCAM-HY-2002), midlegs in different views. A-B, dorsal view; C-D, ventral view; E-F, side view. Scale bar, 1 mm.

enigmatic is the sypstoxyelid wing venation which is not so much reduced as pushed basal, leaving the outer 0.40 of the wing veinless and neatly corrugated. Modifications of that sort are not exceptional *per se*: they are characteristic of such hymenopteran taxa as Siricidae s.str. (living horntails and their close fossil kins, cf. Archibald & Rasnitsyn, 2016), modern Scolidae and some Bradynobaenidae aculeate wasps. The problem is that all these examples are comparatively large insects with characteristic wing length 1 cm or more. The corrugation replaces lost veins there in their function to support outer wing membrane that suffers of strong deformation at flight. The deformation range is size dependent, and that is why the corrugation of outer wing membrane is characteristic of larger insects. Regular corrugation in small (up to 3 mm) wings of Sypstoxyelidae, if serving to the same goal, would indicate an extremely high wing beat frequency that would provide extreme wing deformation. However, an adaptation of this kind would correlate with hypertrophy of the flight musculature and respective enlargement of the pterothorax in a manner characteristic of many smaller Diptera and Hymenoptera Microprocta (cf. Rasnitsyn & Öhm-Kühnle, 2020). Unlike this, Sypstoxyelidae have their pterothorax as ordinary as in

Xyelidae. Another even though a more remote parallel can be found in Heteroptera with their hemelytra, that is, the wings being variously incrassate basally and weakened distally. The hemelytra are a tool combined both defensive and locomotory function of the fore wing, that permits it to protect body when dwelling in close spaces and to fulfil a sophisticated flight when on wings. The similarity between the sypstoxyelid and heteropteran fore wing is not profound but nevertheless striking and might suggest similar evolutionary reasons of their origin and hence a partially secretive behavior of adult Sypstoxyelidae.

The above inference apparently contradicts to the general appearance of Sypstoxyelidae similar to that of living *Xyela* including not only small size and weak integument but also characteristic form of ovipositor and leg-like maxillary palps. Taking together this imply similar biology and particularly development within staminate cones of conifers and feeding, both as adult and immature, on pollen grains (Burdick, 1961; Rasnitsyn, 1965). These features do not imply secretive behavior of adults. However, another unique character of Sypstoxyelidae so much contrasting with all known Xyelidae and Symphyta in general, their tibiae

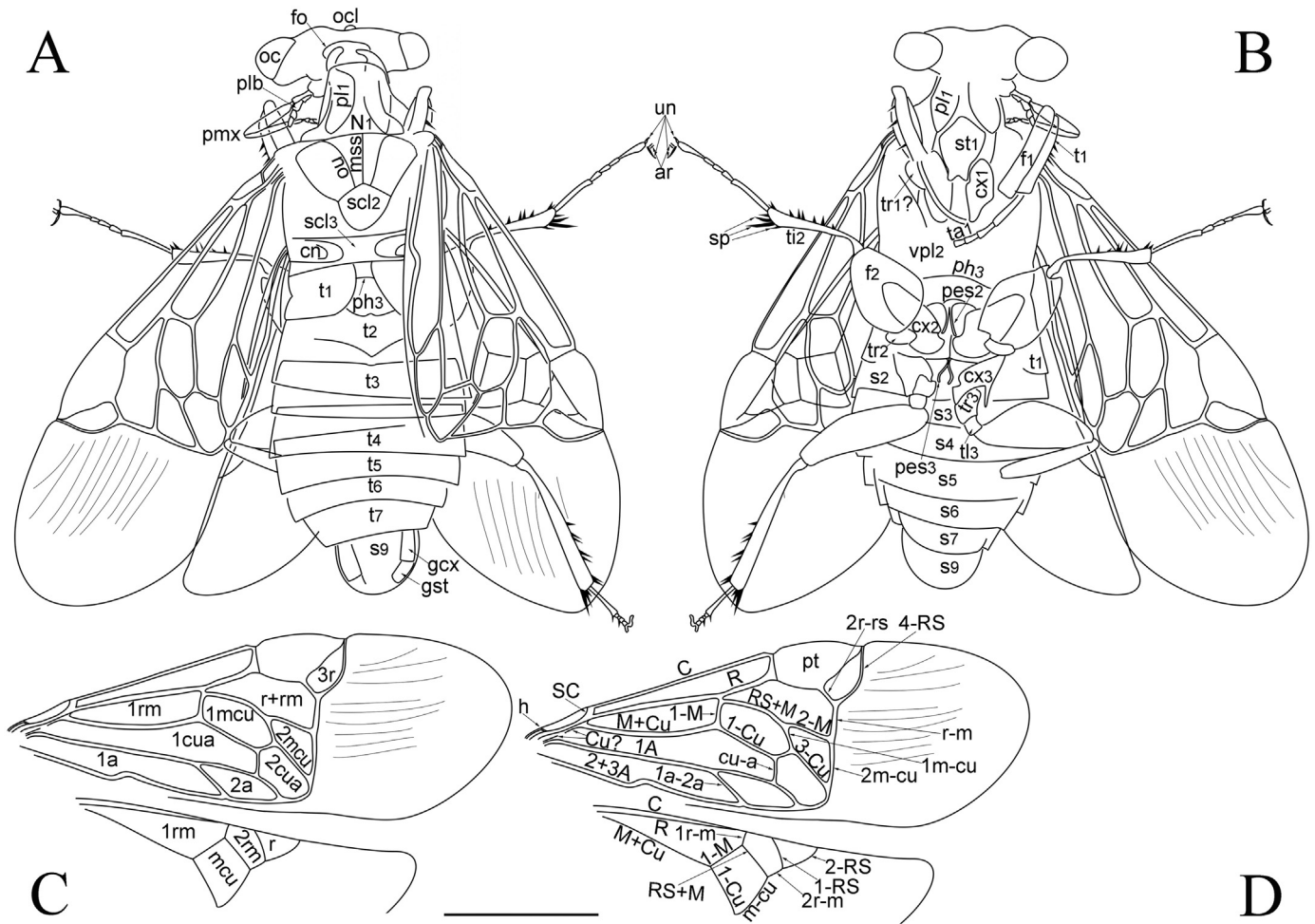


Fig. 4. *Burmoxyela lii* Zheng & Rasnitsyn, gen. et sp. nov., holotype (XCAM-HY-2002), interpretation. A, dorsal view; B, ventral view; C, wings, cell names indicated; D, wings, vein names indicated. Scale bar, 1 mm. Symbols: ar, arolium; cn, cenchrus; cx₁, cx₂, cx₃, pro-, meso-, and metacoxa; f₁, f₂, pro- and mesofemur; fo, occipital foramen; gcx, gonocoxa; gst, gonostyles; oc, eye; ocl, ocellus; ph₃, hind (metathoracic) phragma; pl₁, propleuron; plb, labial palp; pmx, maxillary palp; mss, mid mesoscutal suture; N₁, pronotum; no, notaulus; scl₂, mesosutellum; scl₃, metascutellum; s₁, prosternum; s₂, s₃, etc., abdominal sterna (s₉, hypopygium); sp, spurs; t₁, t₂, etc., abdominal terga; ta₁, protarsus; ti₁, ti₂, pro- and mesotibia; tl₃, metatrochantellus; tr₁, tr₂, tr₃, pro-, meso-, and metatrochanter; un, claw; vpl₂, mesoventropleuron. Venational symbols standard (see [Material and methods](#)).

heavily armed with strong spines, finds its parallel in cockroaches and cockroach-like *Notiothauma* McLahlan 1877 (Mecoptera) which are characteristic of a cryptic fauna of leaf litter, underbark spaces and so on. Taking into account the observations by [Wang et al. \(2019\)](#) about mass burial of diverse Sypastoxylidae in the Kachin amber, it is logic to imply that they spend much of their time on the source tree of the Kachin amber, possibly visiting crevices and underbark space there. This suggests as well that the amber source tree was also the host tree of the sypastoxylid wasps. Unfortunately, evidence of the botanical attribution of the amber is still circumstantial; for instance, [Grimaldi & Ross \(2017\)](#) tentatively name Cupressaceae and particularly *Metasequoia* as a possible source tree because their “leafy shoots ... are not uncommon in Burmese amber” (id., p. 289). Preliminary Cupressaceae could be considered as a possible host plant of Sypastoxylidae.

The uniquely incrassated mid coxae and femora of *B. lii* are left unexplained. They would suggest a saltatory function unless this contradicted to their ordinary tibiae lacking any saltatory adaptation. In general, jumping adaptations are not particularly characteristic of Symphyta. Future discoveries of more Sypastoxylidae will hopefully resolve this puzzle.

5. Conclusions

Burmoxyela lii gen. et sp. nov. is described herein from the mid-Cretaceous Kachin amber as the fifth genus and sixth species of the archaic family Sypastoxylidae that forms a basal clade within the hymenopteran grade Symphyta. Examination of this unique fossil made possible to reorganize system of the family and provide a new key to its genera and species. New hypotheses are proposed as well about biology and functional morphology of these wasps. It is supposed that sypastoxylid sawflies fed on plant pollen both as adults and immatures and developed in staminate cones of a conifer tree that produced the amber. It is further hypothesized that these sawflies developed adaptations toward dwelling within refuges rendered by the host tree (crevices in and under its bark), particularly a wing modification similar to hemelytron of true bugs (Heteroptera) and heavy armament of their tibia of the sort characteristic of cockroaches and some other crevice dwellers. High diversity of Sypastoxylidae and their unique adaptations additionally confirm the famous uniqueness of composition of the mid-Cretaceous Kachin biota ([Zhang et al., 2018](#); [Rasnitsyn & Öhm-Kühnle, 2018](#)).

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