

A new genus of anaxyelid wood wasps from the mid-Cretaceous and the phylogeny of Anaxyelidae (Hymenoptera)

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Abstract

Two new species of wood wasps (Anaxyelidae), *Orthosyntexis elegans* **gen. et sp. nov.** and *Orthosyntexis thanti* **sp. nov.**, are described from mid-Cretaceous Kachin amber. *Orthosyntexis* **gen. nov.** exhibits characters and character combinations unique to the family, such as the combination of two mesotibial spurs, a length ratio of forewing 1Rs to 1M < 1, a length to width ratio of forewing cell 1mcu ≥ 2, and the presence of 2M+Cu in the hind wing. The new species and morphological characters allow for an exploration of anaxyelid phylogeny. The phylogenetic results indicate that Anaxyelidae are monophyletic and it is suggested to classify the genera in two subfamilies, Syntexinae and Anaxyelinae, the latter including Kempendajinae and Dolichostigmatinae.

Keywords

Apomorphy, Kachin amber, morphological characters, phylogenetic analysis, Syntexinae, wing venation

Introduction

Anaxyelidae are a small family of wood wasps, comprising a single extant species, *Syntexis libocedrii* Rohwer, 1915, commonly called the incense cedar wood wasp, which occurs in western North America (Rohwer 1915; Wickman 1967). *Syntexis libocedrii* lays eggs in the sapwood of coniferous trees, e.g., yellow juniper, giant red cedar, incense cedar, and probably Douglas fir, preferring recently burnt timber. The larvae bore through the wood, sometimes wreaking economically significant levels of damage (Wickman 1967; Smith 1979; Grimaldi and Engel 2005). While the family today consists of a single species, during the Cretaceous, particularly the Early Cretaceous, a significant diversity of anaxyelids has been documented. This diversity has been arranged into four subfamilies: Syntexinae Benson, 1935 including *S. libocedrii* and several fossil species, and three other subfamilies, i.e., Dolichostigmatinae, Kempendajinae and Anaxyelinae, known exclusively from fossils (Rasnitsyn 1968, 1969, 1980, 1990; Zhang and Rasnitsyn 2006). To date, 18 genera and 44 species of Anaxyelidae have been described (Rasnitsyn et al. 1998; Rasnitsyn and Martínez-Delclòs 2000; Zhang and Rasnitsyn 2006; Ortega-Blanco et al. 2008; Kopylov 2018, 2019; Wang et al. 2018; Kopylov et al. 2020; Wang et al. 2020: listed in Suppl. material 1). Despite this considerable compression fossil diversity, only two specimens have been described in amber, one from the Early Cretaceous of Spain (*Eosyntexis parva* Ortega-Blanco, Rasnitsyn & Delclòs, 2008) and the other from the Late Cretaceous of northern Myanmar (*Sclerosyntexis hirsuta* Wang, Ren, Kopylov & Gao, 2020). In addition, seven undescribed specimens were recorded in Zhang et al. (2018).

Most morphological studies have recovered Anaxyelidae as basal among Siricoidea (Rasnitsyn 1988; Ronquist et al. 1999). The molecular analysis of Schulmeister et al. (2002) recovered a clade Anaxyelidae + Siricidae, while Vilhelmsen et al. (2010) found the same in their analysis using implied weights. Similarly, Heraty et al. (2011) recovered Anaxyelidae as sister to Siricidae with strong support in all analyses. Most work has supported Anaxyelidae as comprising a superfamily, Siricoidea, with Siricidae, and together as the sister group to Xiphydrioidae + Euhymenoptera (i.e., Orussoidea + Apocrita) (Sharkey et al. 2012). However, all of these studies concerned only extant taxa and there have been no reports concerning the phylogenetic relationships of the many fossil anaxyelids.

Herein, we describe a new genus, with two new species, of Anaxyelidae from Kachin amber, which have a single rs-m in the fore- and hind wings and a long pedicel. *Orthosyntexis* gen. nov. is attributed to the subfamily Syntexinae based on the wider pterostigma, 1r-rs longer than 2r-rs in the forewing, and 1m-cu lacking in the hind wing. More importantly, 2M+Cu is present in the hind wing and two apical mesotibial spurs are also present in these fossils, representing new morphological features for Anaxyelidae. In addition to providing formal descriptions of the species, we present a phylogenetic analysis of living and fossil Anaxyelidae to document the placement of the fossils, explore relationships among the various fossil species and *S. libocedrii*, clarify the suprageneric classification, and explore the early evolution of the family.

Material and methods

Taxonomy

All type specimens described herein are housed in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Beijing, China (CNUB; Curator, Dong Ren). Specimens were examined under a Leica M205C dissecting microscope, and photographed using a Nikon SMZ 25 microscope with an attached Nikon DS-Ri2 digital camera system. Line drawings were prepared in Adobe Illustrator CC and Adobe Photoshop CC. Wing venation nomenclature was modified after Rasnitsyn (1969, 1980), with the following abbreviations: A, anal vein; C, costal vein; Cu, cubital vein; M, median vein; R, radial vein; R1, first radial; Rs, radial sector; 1cu-a, crossvein between 1Cu and A; 2rs-m and 3rs-m, crossveins between Rs and M; 1m-cu and 2m-cu, crossveins between M and 1Cu.

Phylogenetic analyses

A phylogenetic analysis was undertaken using morphological characters to determine the position of the new genus *Orthosyntexis* and to clarify relationships among the subfamilies Syntexinae, Anaxyelinae, Dolichostigmatinae and Kempendajinae. Seven extant species and 19 fossil species were used in these analyses. The phylogenetic analyses include 27 taxa, with 20 ingroups and seven outgroups – *Macroxyela ferruginea* (Say 1824) (Xyelidae), *Acantholyda erythrocephala* (Linnaeus 1758) (Pamphiliidae), *Cephus nigrinus* (Thomson 1871) (Cephidae), *Sirex nigricornis* (Fabricius 1781) and *Urocerus gigas* (Linnaeus 1758) (both Siricidae), *Xiphydria camelus* (Linnaeus 1758) (Xiphydriidae), and *Orussus abietinus* (Scopoli, 1763) (Orussidae). Some of the body characters are attributable to Vilhelmsen (2001), while a subset of the wing characters is referenced in Wang et al. (2016). In addition, we made some changes to the character states based on published data and new findings, and we added new characters from the antennae and wing venation. For instance, compared with Wang et al. (2016), we designated the characters of the length ratios of forewing 1Rs to 1M as '0' for '<1', '1' for '≥ 1, < 3' and '2' for '≥ 3'; the length ratios of forewing 1m-cu to 3Cu as '0' for '≤ 1', '1' for '>1'; and the length ratios of forewing 1Cu to 1M as '0' for 'apparently<1', '1' for '≥ 1'. To make the characters of ingroups as broad as possible, we also defined forewing 1r-rs as '0' for 'always present', '1' for 'partly reduced', and '2' for 'completely reduced', and hind wing cell r as '0' for 'closed' and '1' for 'open'. A total of 63 morphological characters and their character states are presented in the Suppl. material 2. Some are clearly present in the two new species, and others are important features of representative ingroups. A character-state data matrix consisting of 27 taxa and 63 morphological characters is provided in the Suppl. material 3.

Parsimony analysis was performed using WinClada v.1.00.08 (Nixon 2002) and NONA v.2.0 (Goloboff 1997). Tree search implemented a heuristic search method,

and the options were set to hold 10,000 trees, 1000 replications, 100 starting tree replications, and a multiple TBR+TBR search strategy. All characters were treated as unordered and weighted equally. Bootstrap support values were determined in NONA with 1000 replications and are represented as numbers under the branches (in blue).

Results

Systematics

Order Hymenoptera Linnaeus, 1758

Family Anaxyelidae Martynov, 1925

Subfamily Syntexinae Benson, 1935

Genus *Orthosyntexis* J. Gao, Engel, Shih, & T. Gao, gen. nov.

<http://zoobank.org/9C41FD02-F175-44C8-B69A-64D8D951E62A>

Type species. *Orthosyntexis elegans* sp. nov.

Etymology. The new genus-group name is a combination of the Ancient Greek *orthós* (ὀρθός, meaning, “upright” or “erect”, and geometrically “right angle”), and the genus *Syntexis* (itself from Ancient Greek *súntēxis* (σύντηξις, meaning, “colliquescence”, “emaciating”, or “wasting away”)), type genus of the subfamily Syntexinae. Gender feminine.

Diagnosis. Female: Antenna with 16 flagellomeres, scape almost 3× as long as width and twice as long as flagellomere I, flagellomere I nearly 1.5× as long as flagellomere II. Forewing with pterostigma not enlarged, uniformly sclerotized and of normal width; 1Rs shorter than 1M; cell 1mcu length to width ratio slightly more than 2; 1r-rs and 2rs-m absent; 1Cu obviously shorter than 2Cu; 3Cu shorter than 4Cu; 2m-cu 1.5× shorter than 1m-cu in forewing; 3rs-m 2× shorter than 4M. Hind wing with abscissa 2M+Cu; 1M shorter than 2M; m-cu absent, cell r closed. Mesotibia with two apical spurs. Male: Unknown. Immatures: Unknown.

Included species. *Orthosyntexis elegans* sp. nov. and *O. thanti* sp. nov.

Remarks. *Orthosyntexis* may be differentiated from *Curiosyntexis*, in which the forewing pterostigma is desclerotized and 1r-rs is partly reduced (Kopylov 2019), and from *Dolichosyntexis*, which has an enlarged pterostigma and forewing 1Cu not obviously shorter than 2Cu (Kopylov 2019). The new genus can be separated from *Parasyntexis* by the latter's narrower pterostigma, narrower than the length of 2r-rs, and 1M longer than 2M in the hind wing (Kopylov 2019). *Orthosyntexis* can be distinguished from *Sclerosyntexis* by the latter's elongate scape, which is 3× longer than wide, and the open cell r in the hind wing (Wang et al. 2020). *Orthosyntexis* differs from the extant genus *Syntexis*, which has 3Cu longer than 4Cu and 2m-cu 1.5× longer than 1m-cu in the forewing (Rohwer 1915), and from *Daosyntexis* by 1Rs 3× being longer than 1M and 3rs-m 2× longer than 4M in the forewing (Kopylov et al. 2020). The new genus

differs from *Cretosyntexis* by 2r-rs meeting the pterostigma beyond midlength and Rs+M longer than 2M (Rasnitsyn and Martínez-Delclòs 2000), and from *Eosyntexis* in which 1RS is not shorter than 1M (Rasnitsyn and Martínez-Delclòs 2000).

***Orthosyntexis elegans* J. Gao, Engel, Shih, & T. Gao, sp. nov.**

<http://zoobank.org/0A3E4C6A-DB65-4FCA-83D5-E109FEAB9743>

Figs 1, 2 and 3

Etymology. The specific epithet is derived from the Latin word *elegans*, meaning elegant.

Diagnosis. Antennal scape length to width ratio slightly less than 3. Forewing 1Rs subvertical to R. Meso- and metafemur shorter than associated tibiae; mesotibial apical spurs elongate and distinctly narrowed apically.

Holotype. Female, no. CNU-HYM-MA2015101 (Figs 1–3).

Type locality and horizon. The amber specimen was collected from Kachin (Hukawng Valley) in northern Myanmar, and is dated at 98.79 ± 0.62 Mya (Cruickshank and Ko 2003; Shi et al. 2012).

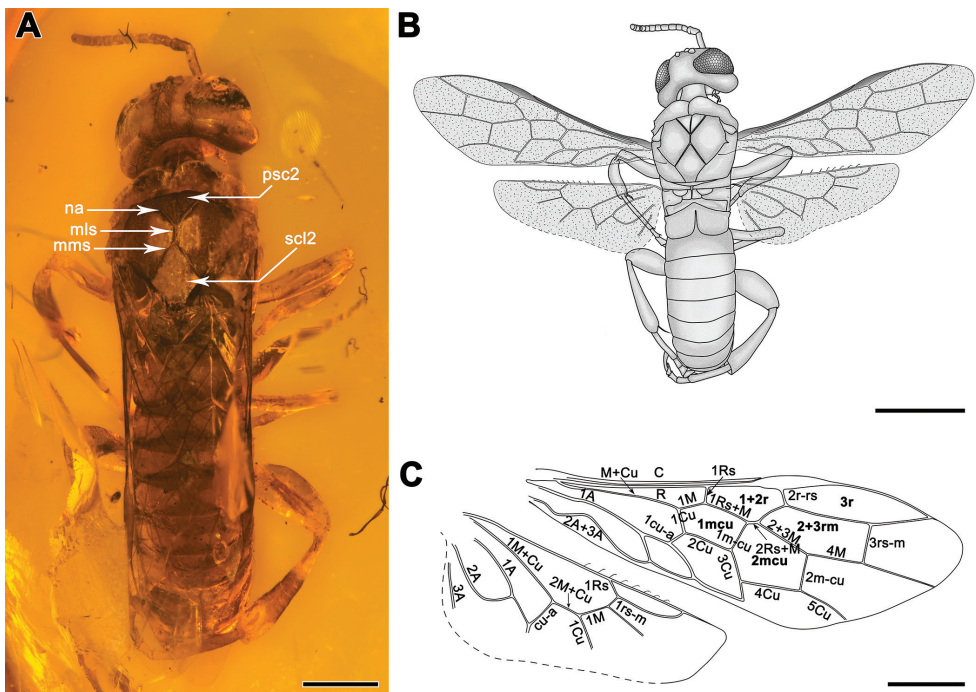


Figure 1. One photograph and two line drawings of *Orthosyntexis elegans* gen. et sp. nov., holotype (specimen CNU-HYM-MA2015101) female **A** dorsal view as preserved **B** line drawing of dorsal view with forewings and hind wings artificially extended from body **C** line drawing of forewing and hind wing. Scale bars: 1 mm (**A**, **C**); 2 mm (**B**). Abbreviations: mms, mesoscuto-mesoscutellar sulcus; mls, median longitudinal sulcus; na, notaulus; psc2, mesoprescutum; scl2, mesoscutellum.

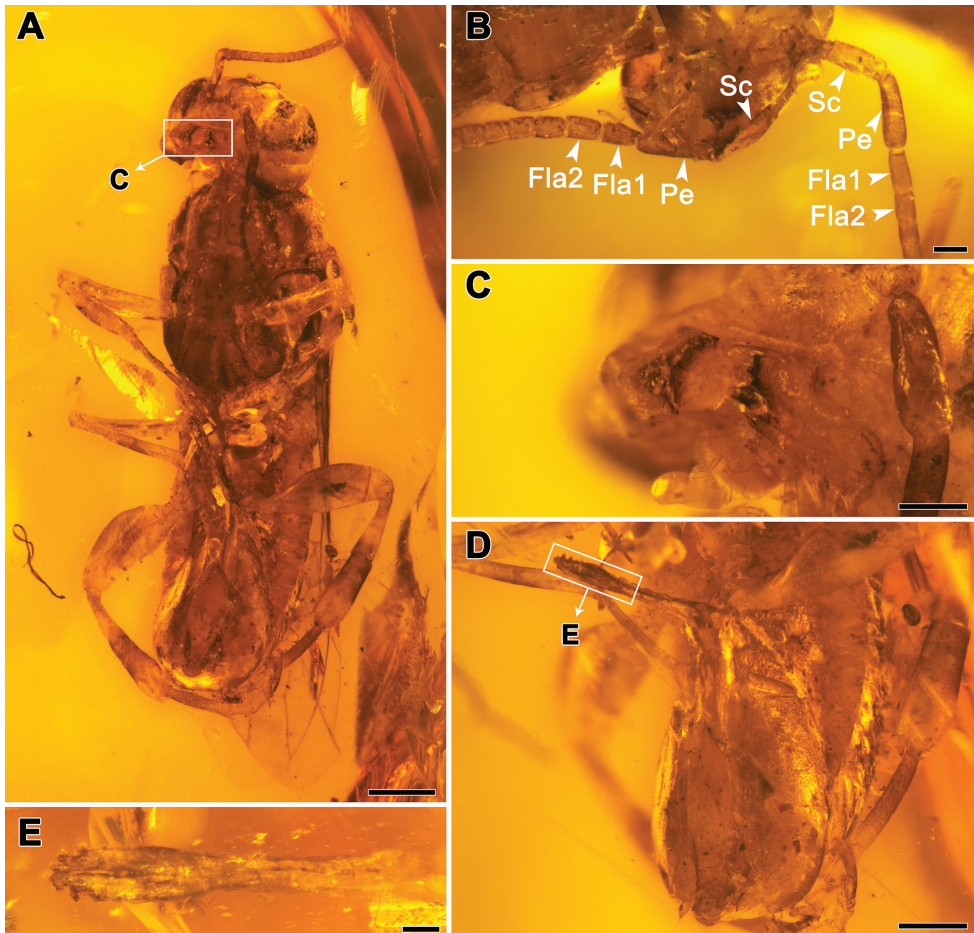


Figure 2. Photographs of *Orthosyntexis elegans* gen. et sp. nov. **A** habitus in ventral view **B** antenna in lateral view **C** mandible in ventral view **D** part of abdomen in lateral view **E** apical ovipositor in lateral view. Scale bars: 1 mm (**A**); 0.2 mm (**B**, **C**); 0.5 mm (**D**); 0.1 mm (**E**). Abbreviations: Fla1 and Fla2, flagellomeres I and II; Pe, pedicel; Sc, scape.

Description. Body about 8.25 mm long in dorsal view, antenna 2.73 mm long in ventral view; forewing about 5.69 mm in length, maximum width 1.74 mm; hind wing about 4.57 mm in length.

Head moderately large, narrower than thorax. Head 1.85 mm wide and 1.23 mm long, nearly quadrate. Compound eyes large and hemispherical; mandible straight, orthogonal with apical margin vertical (parallel to mandibular base) and with lowest tooth not that elongate (Fig. 2C); labial palpus with three palpomeres; maxillary palpus with at least five palpomeres; antenna with 16 flagellomeres, scape 0.40 mm long, maximum width 0.14 mm; pedicel 0.39 mm long, maximum width 0.12 mm; flagellomere I shorter than scape, 0.11 mm wide, 0.22 mm long, flagellomere II 0.10 mm wide, 0.19 mm long, as long as individual lengths of remaining flagellomeres (Fig. 2B).

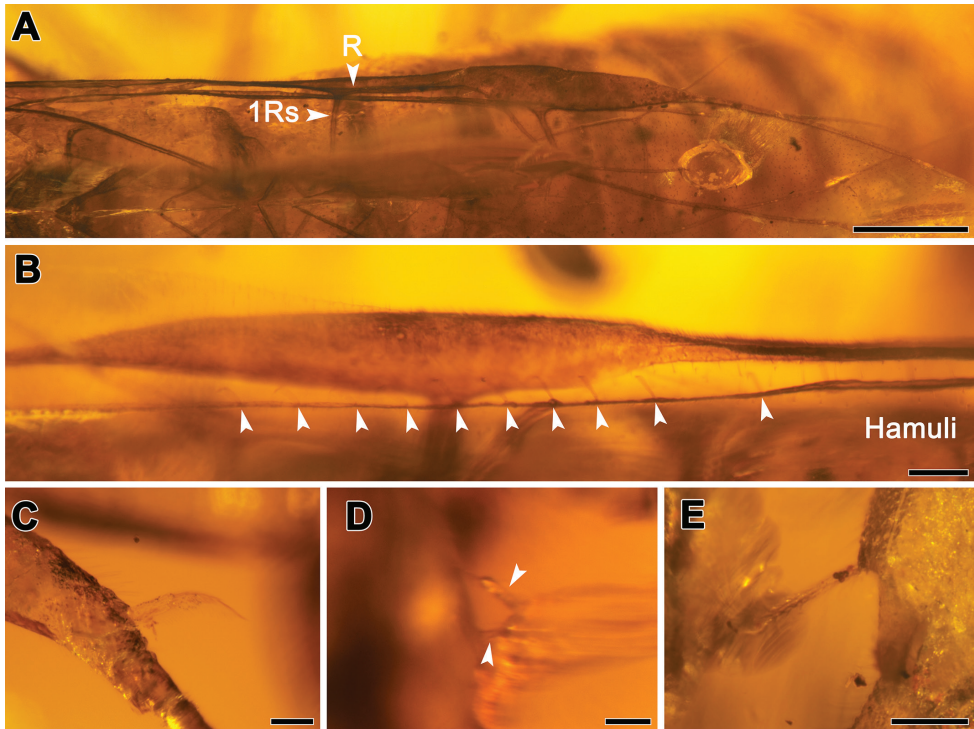


Figure 3. Photographs of *Orthosyntexis elegans* gen. et sp. nov. **A** part of left forewing **B** hind wing hamuli (white arrows) **C** right protibial spur **D** right mesotibial spurs **E** left metatibial spur. Scale bars: 0.5 mm (**A**); 0.1 mm (**B–E**).

Thorax wide, width across tegulae 1.56 mm; pronotum short, having prominent anterior notch and hind margin, with median longitudinal furrow dorsally. Mesoscutum with median longitudinal sulcus and notauli strongly impressed; mesoscutellum tapering to acute apex; ratio of lengths of prescutum, median longitudinal sulcus between notauli, and mesoscutum-mesoscutellar sulcus and mesoscutellum 2.5/1/4.5, notauli terminating close to mesoscutellum (Fig. 1A). Legs spindly, meso- and metafemora shorter than associated tibiae. Metafemur length 1.30 mm, metatibia thick subapically, length 1.65 mm. Protibia and metatibia with only one apical spur visible, mesotibia with two apical spurs (Fig. 3C, D and E); all tarsomeres with stiff apical setae; basitarsi long but shorter than remaining tarsomeres combined; tarsomere V elongate but shorter than basitarsus; pretarsal claws long, with curved apices and each with a single preapical tooth.

Abdomen only slightly narrower than mesothorax; abdominal tergum I split medially. Segments I and II slightly longer than remaining abdominal segments; ovipositor length 1.86 mm, not protruding beyond abdominal tip, strongly serrated apically (Fig. 2D and 2E)

Forewing with dense microtrichia but no coloration pattern except slightly darkened costal area. C and R thick, costal area narrower than C and R widths. Pterostigma completely sclerotized; Sc absent; 1r-rs and 2rs-m absent; 2r-rs issuing from pterostigma

at its basal $1/3$; 1Rs short and subvertical to R (Fig. 3A), about $0.6\times$ as long as 1M, meeting 1M at right angle. 2Rs+M distinct but short, $0.3\times$ as long as 1Rs+M. 2r-rs slightly proclival. 2+3M $1.1\times$ as long as 4M. Cell 1mcu pentagonal, about $1.9\times$ as long as wide; cell 2mcu hexagonal, about $1.3\times$ as long as wide. 2Cu $1.7\times$ as long as 1Cu. 1cu-a strongly reclival, nearly $0.7\times$ as long as 1Cu. 1m-cu nearly as long as 3Cu, 3Cu shorter than 4Cu. 2m-cu nearly $0.7\times$ as long as 4M and $1.2\times$ as long as 1m-cu.

Hind wing Sc absent. Cell r closed. 1Rs (about 0.28 mm in length) shorter than 1M (about 0.35 mm in length). 1rs-m (about 0.27 mm in length) reclival, nearly in line with 1M and as long as 1Rs. 1M straight; m-cu absent; 2M+Cu present (about 0.39 mm in length), free abscissa of Cu and cu-a (about 0.48 mm in length) developed, 1Cu and cu-a straight.

***Orthosyntexis thanti* J. Gao, Engel, Shih, & T. Gao, sp. nov.**

<http://zoobank.org/58143DF9-65BE-49C5-A832-FAD0BFA991E2>

Figs 4, 5, 6 and 7

Etymology. The specific epithet honours 3rd Secretary General of the United Nations and Burmese diplomat U Thant (1909–1974) and his dedication to seeking peace within and between nations.

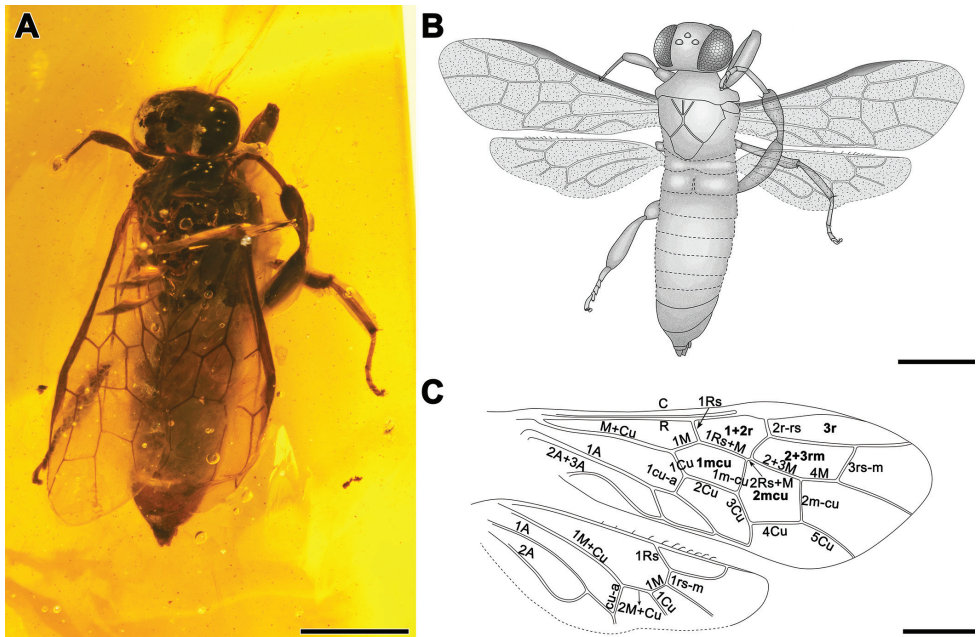


Figure 4. One photograph and two line drawings of *Orthosyntexis thanti* sp. nov., holotype (specimen CNU-HYM-MA2015102) female **A** dorsal view as preserved **B** line drawing of dorsal view with forewings and hind wings artificially extended from body **C** line drawing of forewing and hind wing. Scale bars: 2 mm (**A**, **B**); 1 mm (**C**).

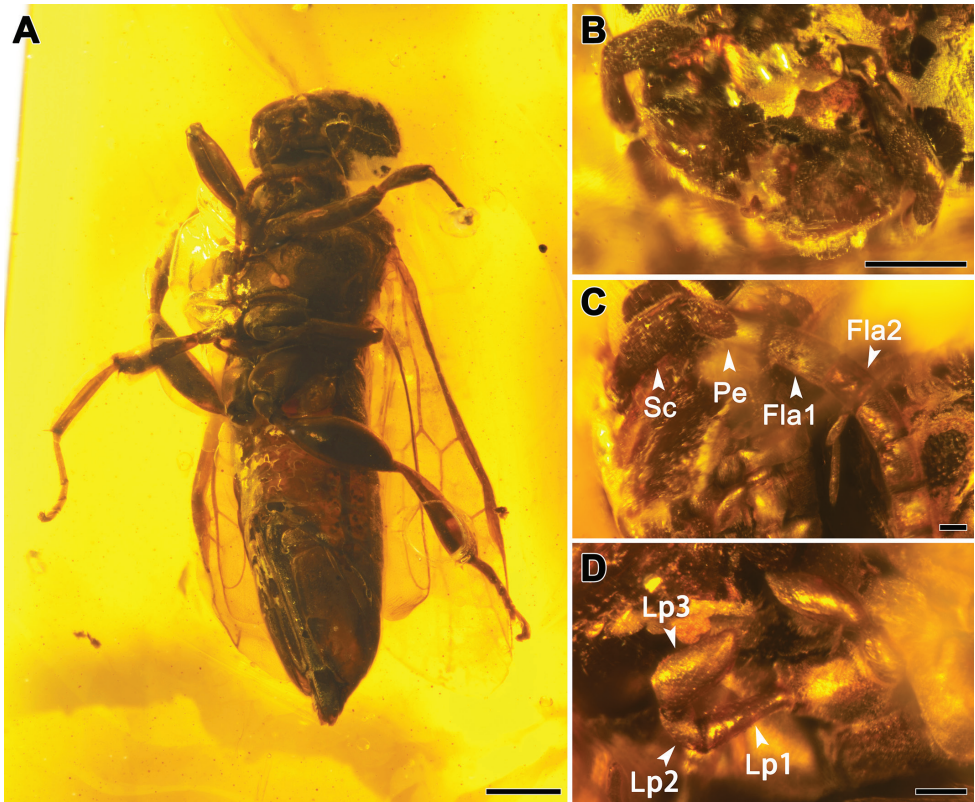


Figure 5. Photographs of *Orthosyntexis thanti* sp. nov. **A** habitus in ventral view **B** mandible in frontal view **C** part of antenna **D** labial palpus. Abbreviations: Fla1 and Fla2, flagellomeres I and II; Lp1, Lp2 and Lp3, labial palpomeres I, II and III; Pe, pedicel; Sc, scape.

Diagnosis. Antennal scape length to width ratio more than 3. Forewing 1Rs proclinal to R. Mesofemur longer than mesotibia, metafemur nearly as long as metatibia; mesotibial apical spurs somewhat shortened and not narrowed apically.

Holotype. Female, no. CNU-HYM-MA2015102 (Figs 4, 5 and 6).

Paratype. Female, no. CNU-HYM-MA2015103 (Fig. 7).

Description. *Holotype* [paratype measurements given in parentheses]: Body about 8.61 [8.42] mm long in dorsal view, antenna 2.85 [2.62] mm long in ventral view; forewing about 5.64 [5.48] mm in length, maximum width 2.09 [1.67] mm; hind wing about 4.21 [4.42] mm in length.

Head moderately large, slightly narrower than thorax. Head 1.98 [1.77] mm wide and 1.22 [1.31] mm long, nearly quadrate. Compound eyes large and hemispherical; mandible weakly bent, with apical margin vertical (parallel to mandibular base) and with lowest tooth not that elongate (Figs 5B and 7D); labial palpus with three palpomeres (Fig. 5D); antenna with 16 flagellomeres, scape 0.55 [0.46] mm long, maximum width 0.17 [0.14] mm; pedicel 0.37 [0.41] mm long, maximum width 0.13 [0.13] mm; flagellomere I shorter than scape, 0.15 [0.11] mm wide, 0.25 [0.21] mm

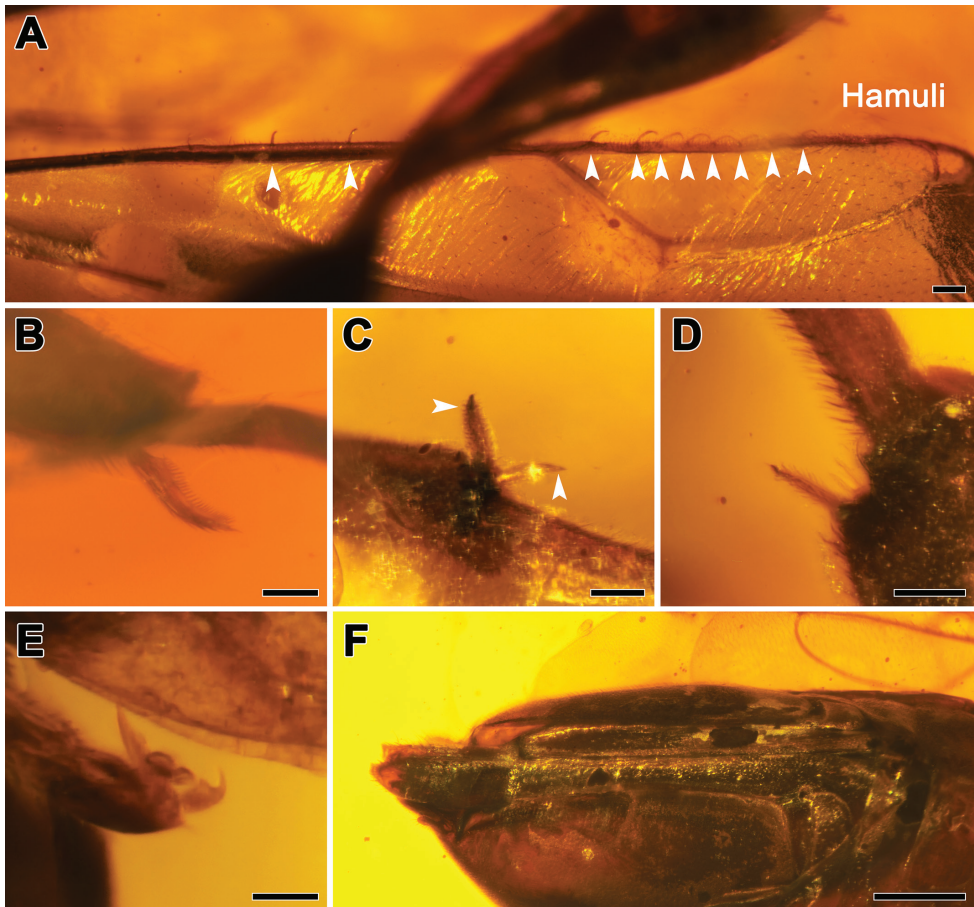


Figure 6. Photographs of *Orthosyntexis thanti* sp. nov. **A** hind wing hamuli (white arrows) **B** left protibial spur **C** right mesotibial spurs **D** left metatibial spur **E** right mesotarsal pretarsal claw **F** ovipositor sheath in lateroventral view. Scale bars: 0.1 mm (**A–E**); 0.5 mm (**F**).

long; flagellomere II 0.15 [0.12] mm wide, 0.17 [0.15] mm long, as long as individual lengths of remaining flagellomeres (Figs 5C and 7C).

Thorax wide, width across tegulae 1.59 [1.54] mm; pronotum short, with slightly developed anterior notch and prominent hind margin, and with mediolongitudinal furrow dorsally. Mesoscutum with longitudinal sulcus and notauli strongly impressed; mesoscutellum tapering to acute apex; ratio of lengths of prescutum, median longitudinal sulcus between notauli, and mesoscutum-mesoscutellar sulcus and mesoscutellum 2.3/1/5.3 [2.2/1/4.9], notauli close to mesoscutellum. Legs spindly, mesofemur longer than mesotibia. Metafemur length 1.69 [1.43] mm, nearly as long as metatibia (length 1.68 [1.50] mm), thick subapically, narrowed apically. Protibia and metatibia with only one apical spur (Figs 6B, D and 7G), mesotibia with two apical spurs (Figs 6C and 7H); all tarsomeres with stiff apical setae; basitarsi long but

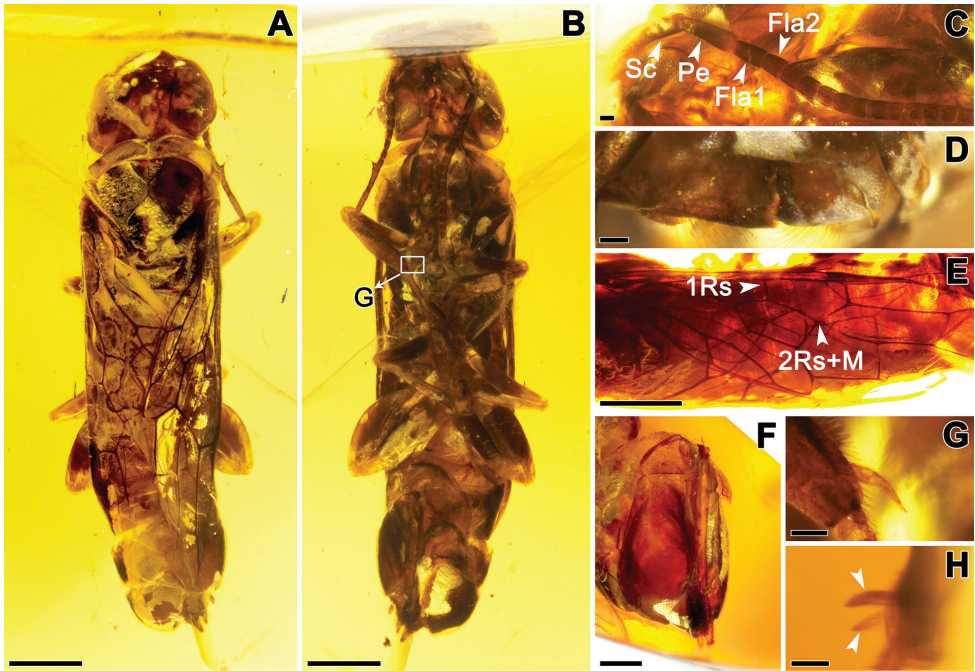


Figure 7. Photographs of *Orthosyntexis thanti* sp. nov., paratype (specimen CNU-HYM-MA2015103) female **A** habitus in dorsal view **B** habitus in ventral view **C** part of antenna **D** mandible in frontal view **E** left forewing **F** ovipositor in lateroventral view **G** protibial spur **H** mesotibial spurs. Scale bars: 1 mm (**A**, **B**); 0.2 mm (**C**); 0.1 mm (**D**–**H**). Abbreviations: Fla1 and Fla2, flagellomeres I and II; Pe, pedicel; Sc, scape.

shorter than remaining tarsomeres combined; tarsomere V elongate but shorter than basitarsus; pretarsal claws long, with curved apices and each with a single preapical tooth (Fig. 6E).

Abdomen only slightly narrower than mesothorax. Ovipositor strongly serrate apically, short, not protruding beyond abdominal tip, full length 2.67 [2.51] mm (Figs 6F and 7F).

Forewing with dense microtrichia but no coloration pattern, except for slightly darkened costal area. C and R thick, costal area narrower than C and R widths. Pterostigma completely sclerotized; Sc absent; 1r-rs and 2rs-m absent; 2r-rs issuing from pterostigma at its basal 1/3; 1Rs short and slightly proclival to R, about 0.7× as long as 1M, meeting 1M at right angle (Fig. 7E). 2Rs+M distinct but short, 0.1× as long as 1Rs+M (Fig. 7E). 2r-rs slightly proclival. 2+3M 1.6× [1.2×] as long as 4M. Cell 1mcu pentagonal, about 2.0× [2.1×] as long as wide; cell 2mcu hexagonal, about 1.1× [1.4×] as long as wide. 2Cu 2.1× [1.6×] as long as 1Cu. 1cu-a reclival, nearly 0.8× as long as 1Cu. 1m-cu nearly as long as 3Cu, 3Cu shorter than 4Cu. 2m-cu nearly 0.8× [0.6×] as long as 4M and 1.2× [1.1×] as long as 1m-cu.

Hind wing Sc absent. Cell r closed. 1Rs (about 0.36 [0.32] mm in length) longer than 1M (about 0.26 [0.30] mm in length). 1rs-m (about 0.23 [0.20] mm in length),

with an angle at 2Rs and shorter than 1Rs. 1M straight; m-cu absent; 2M+Cu present (about 0.40 [0.33] mm in length), free abscissa of Cu and cu-a (about 0.40 [0.43] mm in length) developed, 1Cu and cu-a straight.

Phylogenetic analyses

Our morphological phylogenetic analysis, based on 63 morphological characters coded in Winclada (Suppl. materials 2, 3), recovered 18 equally parsimonious topologies (consistency index, 0.40; retention index, 0.56), the strict consensus of which is presented in Figure 8. Anaxyelidae were recovered as monophyletic, supported by seven synapomorphies, e.g.: pedicel length to width ratio ≥ 2 (character 4), 2rs-m of forewing absent (character 28), length ratio of forewing 1Rs to 1M < 1 (character 36), forewing cell 1mcu length to width ratio apparently < 2 (character 42), and 3rs-m of hind wing absent (character 59).

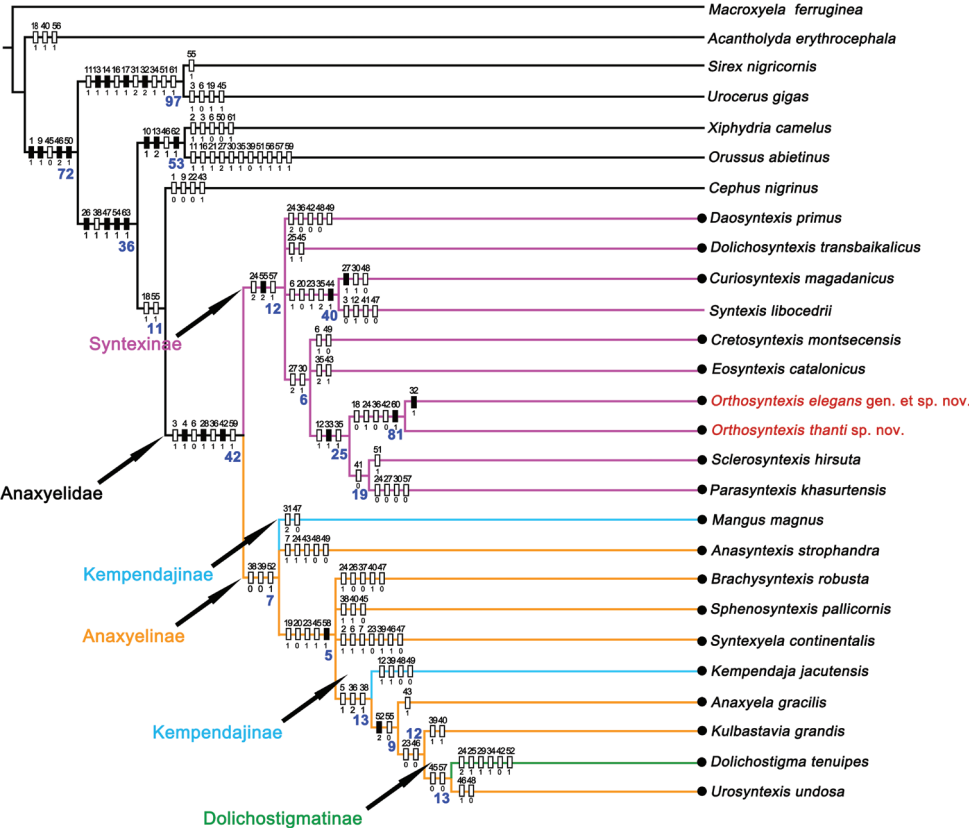


Figure 8. Phylogeny of Anaxyelidae based on 63 morphological characters (Suppl. material 1: File S1 matrix). Strict consensus of 18 trees of length = 195 steps, consistency index = 0.40, and retention index = 0.56. Numbers under branches are bootstrap support values (in blue). Small black bars = unambiguous unique characters; small white bars = homoplasious characters.

The monophyly of *Orthosyntexis* is supported by a unique combination of five homoplasious characters: mesotibia with two apical spurs (character 18), length ratio of the maximum width of pterostigma to 2r-rs nearly = 1 (character 24), length ratio of forewing 1Rs to 1M < 1 (character 36); forewing cell 1mcu length to width ratio ≥ 2 (character 42), and 2M+Cu of hind wing present (character 60). Furthermore, *Orthosyntexis* was recovered as sister to *Sclerosyntexis* + *Parasyntexis* based on: notauli close to mesoscutellum (character 12) and Rs+M bifurcating beyond 1m-cu = 1 (2Rs+M) (character 33).

Regarding the intrafamilial relationships of Anaxyelidae, two principle branches are supported in the consensus topology (Fig. 8), one equivalent to the subfamily Syntexinae, and the other composed of Dolichostigmatinae, Kempendajinae, and Anaxyelinae, and with the dolichostigmatines and kempendajines rendering anaxyelines paraphyletic. While support values of the two main branches are not great, there are convincing apomorphies supporting these clades. For example, the monophyly of Syntexinae is supported by the ratio of the maximum width of the pterostigma to the length of 2r-rs of forewing nearly = 1 (character 24 length of 2Cu to the length of 1Cu in the hind wing ≥ 5 (character 55), and crossvein m-cu of hind wing absent (character 57). At the same time, the monophyly of Anaxyelinae + Dolichostigmatinae + Kempendajinae is supported by length of 1r-rs to 2Rs of forewing < 1 (character 38), length of Rs+M to 2M of forewing < 1 (character 39), and hind wing crossvein 1rs-m at or quite close to Rs midlength (character 52).

Discussion

The placement of *Orthosyntexis* in Anaxyelidae is well-supported, most notably by the fore- and hind wings each with a single rs-m and the pedicel length to width ratio ≥ 2 . Moreover, the genus can be attributed to Syntexinae mainly based on the following combination of characters: forewing with the maximum width of pterostigma not shorter than 2r-rs, 1r-rs absent and hind wing m-cu absent. Given that most of the available fossil anaxyelids are preserved as compressions, often with body structures poorly discernible, there is a natural reliance on wing traits and so most characters currently supporting nodes are derived from the venation. Naturally, as more amber fossils become available, it is hoped that a finer comparison of body structures can be made across living and fossil taxa in the future.

Hitherto, no attempt has been made to explore relationships among anaxyelids in a cladistic framework, likely owing to the fact that there is only one extant species and that many of the known fossils are quite incomplete. Recent phylogenetic treatments of the families of Hymenoptera (e.g., Vilhelmsen 2000, 2001; Sharkey et al. 2012), identified a single putative apomorphy for the family, specifically the longitudinal subdivision of the pronotum, easily observed in our amber fossils. Our analysis recovered a monophyletic Anaxyelidae, even when including the considerable fossil diversity and the lack of critical information from many compression fossils. In addition, our

analysis indicated the pedicel length to width ratio ≥ 2 and the loss of forewing 2rs-m and hind wing 3rs-m to be additional putative apomorphies for the family (Fig. 8).

Zhang and Rasnitsyn (2006) and Kopylov (2019) organized the diversity of Anaxyelidae into four subfamilies. The establishment of Dolichostigmatinae and Kempendajinae was based on four fossil specimens from three species: *Dolichostigma tenuipes* Rasnitsyn 1968, *Kempendaja jacutensis* Rasnitsyn 1968 and *Mangus magnus* Kopylov 2019. The diagnosis of the subfamily Kempendajinae (Rasnitsyn 1980) focused generally on characters of the body and hind wing, which are plesiomorphies; for example, desclerotized pterostigma in the forewing and rs-m located in the distal third of hind wing cell r. Desclerotized pterostigma is also observed in two anaxyelids, *Anaxyela gracilis* Martynov 1925 and *Sphenosyntexis pallicornis* Rasnitsyn 1968. In addition, rs-m in the hind wing is also located in the distal third of cell r in *U. undosa*. Thus, the features used to justify the subfamily Kempendajinae are unreliable and our analysis robustly placed the group within Anaxyelinae. Similarly, the feature used to differentiate Dolichostigmatinae, i.e., large forewing pterostigma also exists in *Dolichosyntexis transbaikalicus* Kopylov 2019. Again, our analysis indicated that the subfamily Dolichostigmatinae is merely a subgroup of Anaxyelinae. Accordingly, we recognize only two monophyletic subfamilies in Anaxyelidae: Syntexinae and Anaxyelinae. Of course, this is only an analysis based on our phylogenetic results, and many fossil specimens provide few useful features due to preservation reasons. Therefore, it is hoped that more fossils of Anaxyelidae will provide more favorable evidence for our analysis in the future.

Recently, the anaxyelid *Sclerosyntexis hirsuta* was described from a single specimen in Kachin amber (Wang et al. 2020). Here, we add two new species, *O. elegans* and *O. thanti*, from the same deposit, based on three specimens. They have thick legs, particularly inflated metatibiae, and a pattern of forewing venation similar to *Sclerosyntexis*, such as 2r-rs joining the pterostigma proximal to pterostigmal midlength, 1r-rs absent, and 2Rs+M present. Furthermore, *Sclerosyntexis* + *Parasyntexis* was recovered as the sister group to *Orthosyntexis* in our phylogenetic estimate for the family.

Although *Orthosyntexis* belongs to the same clade as the modern *Syntexis*, these genera are relatively distantly related within the subfamily, and many features differ significantly between them, e.g., flagellomere I length to width ratio < 3 , mesotibia with two apical spurs, 1r-rs absent, 2Rs+M present, hind wing cell r closed, and hind wing 2M+Cu present. However, they do share some similar morphological traits, such as notauli close to the mesoscutellum and 1rs-m at the base of Rs in the hind wing. In addition, the new genus, like extant Anaxyelidae, has the ovipositor apically modified with marginal serrations. Extant Siricoidea use their ovipositor to insert their eggs and spores of a symbiotic fungus into dead or dying trees (Goulet 1993; Grimaldi and Engel 2005). However, there has been no evidence of fungal spores in extinct Anaxyelidae, so a symbiotic relationship between extinct Anaxyelidae and fungi has not been conclusively established, although the distribution of this trait across wood wasps tends to suggest that the extinct diversity had a similar association (e.g., Morgan 1968; Kajimura 2000; Grimaldi and Engel 2005). Nonetheless, conclusive evidence

of a fungal symbiosis in the fossils is lacking and requires further study as more fossil Anaxyelidae are discovered. Indeed, μ CT scans of amber-preserved anaxyelids would be critical to look for potential fungal spores carried on adult females or the presence of distinct mycangia. To date, only seven symphytan species have been described in Kachin amber, of which five are sypstoxyelids, one is an anaxyelid, and one is an orussid (Engel et al. 2016; Zhang et al. 2018, 2020; Zheng et al. 2019; Wang et al. 2020, 2021). And eight symphytan specimens have not been described in Kachin amber, of which seven are anaxyelids and one is an orussid (Zhang et al. 2018). Compared with Mesozoic fossil deposits of China and Russia, the number of Symphyta in Kachin amber is quite small. The reason for such a low diversity and abundance may be that the mid-Cretaceous fauna of Kachin amber is characterized by high levels of endemism indicative of an insular biota (Grimaldi et al. 2002; Rasnitsyn and Öhm-Kühnle 2018; Lin et al. 2019; Zhao et al. 2020), as well as its high thermophilic (tropical) nature (Grimaldi et al. 2002; Zhang et al. 2018).

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Supplementary material I

File S1

Authors: Jia Gao, Michael S. Engel, Chungkun Shih, Dong Ren, Taiping Gao

Data type: Distribution (Word file (.docx))

Explanation note: File S1. List of distribution of living and fossil Anaxyelidae.

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Link: <https://doi.org/10.3897/jhr.86.73161.suppl1>

Supplementary material 2

File S2

Authors: Jia Gao, Michael S. Engel, Chungkun Shih, Dong Ren, Taiping Gao

Data type: Morphological characters (Word file (.docx))

Explanation note: File S2. List of morphological characters and character states for the phylogenetic analyses.

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Link: <https://doi.org/10.3897/jhr.86.73161.suppl2>

Supplementary material 3

File S3

Authors: Jia Gao, Michael S. Engel, Chungkun Shih, Dong Ren, Taiping Gao

Data type: Matrix (Excel file (.xls))

Explanation note: Data matrix of characters used in the phylogenetic analyses.

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Supplementary material 4

Nex File

Authors: Jia Gao, Michael S. Engel, Chungkun Shih, Dong Ren, Taiping Gao

Data type: Data matrix in nexus file

Explanation note: Data matrix in nexus file of Suppl. material 3: File S3.

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