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A new anaxyelid wood wasp (Hymenoptera, 'Symphyta', Anaxyelidae) from the mid-Cretaceous Kachin amber of Myanmar [New anaxyelid woodwasps (Hymenoptera: 'Symphyta': Anaxyelidae) from Mid-Cretaceous Kachin amber]

Left running head: Z. WANG *et al.*

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Abstract

A new species of anaxyelid wood wasp genus *Orthosyntexis* (Syntexinae) is described from mid-Cretaceous (lower Cenomanian) amber found in the Kachin State of northern Myanmar. The new taxon can be distinguished by: antenna with swollen scape; 14 flagellomeres; forewing with Sc, 1r-rs and 2rs-m absent; 1-Rs shorter than 1-M and proclival; 2Rs + M present but short; and 3r-m being remarkably curved. This evidences a second anaxyelid species (represented by a male individual) in Kachin amber insect assemblage, and adds to the morphological diversity of the family. A key to the species of *Orthosyntexis* is provided.

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KEYWORDS

Anaxyelidae, taxonomy, Myanmar, Mesozoic

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THE MID-CRETACEOUS Kachin amber deposits of northern Myanmar constitute one of the most significant fossil insect Lagerstätte worldwide (~~Ross, 2015, 2021~~). Hymenoptera are particularly abundant in the assemblage (second only to beetles), with 70 families, 202 genera and 350 species documented to date (Ross, 2024). Modern hymenopterans are likewise diverse, and serve as indicators of arthropod ecological complexity (Zherikhin *et al.* 2009, Peters *et al.* 2017, Morrison *et al.* 2018). The order is divided into two grades—Apocrita and ‘Symphyta’—with basal symphytans being important for understanding the evolution of the group (Rasnitsyn 1988, Grimaldi & Engel 2005). The majority of hymenopteran taxa reported from the Kachin amber deposits are apocritans, while only 15 symphytan species have been recognized to date. These comprise: six genera and seven species of Syspastroxyelidae; four genera and five species of Anaxyelidae; and single genera and species each for Burmorussidae, Orussidae and Sepilicidae (Engel *et al.* 2016, Zheng *et al.* 2019, 2021a, 2021b, Zhang *et al.* 2020, Gao *et al.* 2021, Wang *et al.* 2021, Jouault *et al.* 2022).

Today, Anaxyelidae, or incense-cedar wood wasps, are a distinctive lineage of usually mid-sized basal Siricoidea considered to be putative ancestors of Vespina (Rasnitsyn, 1980, Ronquist *et al.*

2012, Sharkey *et al.* 2012, Kopylov, 2018). Among anaxyelids, *Syntexis libocedrii* Rohwer, 1915 is the only extant taxon known from western North America (Rohwer 1915; but occasionally imported to Spain—Franco *et al.* 2020), and is associated with conifer trees (Wickman 1967, Smith 1979, Zhang & Rasnitsyn 2026). The fossil record of anaxyelids dates back to the Middle–Late Jurassic of Karatau in Kazakhstan (Martynov 1925), and later Jurassic of Khoutiym-Khotgor in Mongolia (Kopylov, 2018). The geologically oldest occurrence comes from the Middle Jurassic of Daohugou in China, and is represented by 41 recognized specimens (Rasnitsyn & Zhang 2004, Kopylov *et al.* 2020). Anaxyelidae has been subdivided into four subfamilies: the extant Syntexinae, and extinct Dolichostigmatinae, Kempendajinae and Anaxyelinae (Rasnitsyn, 1968, 1969, 1980, 1990, Zhang & (Benson, 1935) Rasnitsyn, 2006, Kopylov, 2019). However, a recent phylogenetic analysis (Gao *et al.* 2021) proposed division of the monophyletic Anaxyelidae into only two subfamilies; Syntexinae and Anaxyelinae (integrating taxa previously assigned to Kempendajinae and Dolichostigmatinae).

Fossil anaxyelids preserved in amber have all been described from Cretaceous deposits, with *Eosyntexis parva* Ortega-Blanco, Rasnitsyn & Delclòs, 2008 reported from the Lower Cretaceous of Spain, and *Sclerosyntexis hirsuta* Wang, Ren, Kopylov & Gao, 2020, *Orthosyntexis elegans* Gao, Engel, Shih & Gao, 2021, *Orthosyntexis thanti* Gao, Engel, Shih & Gao, 2021, *Curvitexis kopylovi* Jouault, Nam & Rasnitsyn, 2022 and *Paraxiphydira resinata* Gao, Engel & Gao, 2022, from the mid-Cretaceous of Myanmar (Ortega-Blanco *et al.* 2008, Wang *et al.* 2020, Gao *et al.* 2021, Jouault *et al.* 2022).

Here, we describe another new anaxyelid wood wasp from the mid-Cretaceous amber of Myanmar. This specimen is represented by a well-preserved male individual identified as a previously unrecognized species of Syntexinae.

Institutional abbreviation

LYU, Institute of Geology and Paleontology, Linyi University, Linyi, China.

Materials and methods

The holotype, LYU-HY-ZD013, is preserved within a yellow quadrilateral piece of Kachin amber

measuring $10.7 \times 8.13 \times 1.32$ mm. LYU-HY-ZD013 was collected prior to 2015, and acquired in full compliance with the laws of Myanmar. It is permanently stored in the Beijing Xiachong Amber Museum. The amber containing LYU-HY-ZD013 was re-cut and polished flat using a precision diamond-wire saw (Geotome Dual [AQ1](#), Eybens, France) and rotary polisher (Mecatech 33 [AQ2](#), Eybens, France). LYU-HY-ZD013 was imaged with simultaneous incident and transmitted light on a Nikon SMZ-10R stereo-microscope [AQ3](#) (Tokyo, Japan) and VHX 5000 digital microscope platform (Itasca, USA). Approximately 40 images were digitally superimposed using Helicon Focus Pro-64 [AQ4](#) (Kharkiv, Ukraine) for optimal depth of field. Our line drawings were prepared with CorelDraw X9 [AQ5](#) (<https://www.coreldraw.com/en/>) and Adobe Photoshop CS6 [AQ6](#) (<https://www.adobe.com/>). Measurements were taken with ImageJ software (National Institutes of Health, Bethesda, MD, USA). Anatomical [AQ7](#) terminology for anaxyelids follows Rasnitsyn (1980).

Systematic palaeontology

Order HYMENOPTERA Linnaeus, 1758

Superfamily SIRICOIDEA Billberg, 1820

Family ANAXYELIDAE Martynov, 1925

Subfamily SYNTEXINAE Benson, 1935

Orthosyntexis Gao, Engel, Shih & Gao, 2021

Type species

Orthosyntexis elegans (Gao *et al.* 2021). Other species include *Orthosyntexis thanti* (Gao *et al.* 2021) and *Orthosyntexis cretacicus* Zheng, sp. nov.

Diagnosis

Antenna with 14–16 flagellomeres. Forewing with pterostigma completely sclerotized; 1-Rs straight and shorter than 1-M; 1-R1 shorter than pterostigma; Sc absent; 1r-rs absent; 2r-rs inclined and

issuing from the pterostigma near its mid-length; 2Rs + M present but short; 1-Cu shorter than 2-Cu; Rs + M bifurcated beyond 1m-cu; 3r-rm 0.67× as long as 4-M. Cell 1mcu pentagonal, with length/width ratio ≥ 2 ; cell 2mcu as long or shorter than cell 1mcu. Hind wing with cell 3r closed.

***Orthosyntexis cretacicus* Zheng sp. nov.**

(Figs 1–3)

Figure 1. *Orthosyntexis cretacicus* (LYU-HY-ZD013). **A**, Habitus in dorsal view showing head tubercles (blue arrows) and transverse tooth-structures on the pronotum (white arrows); **B**, habitus in lateral view; Scale bars = 1 mm.

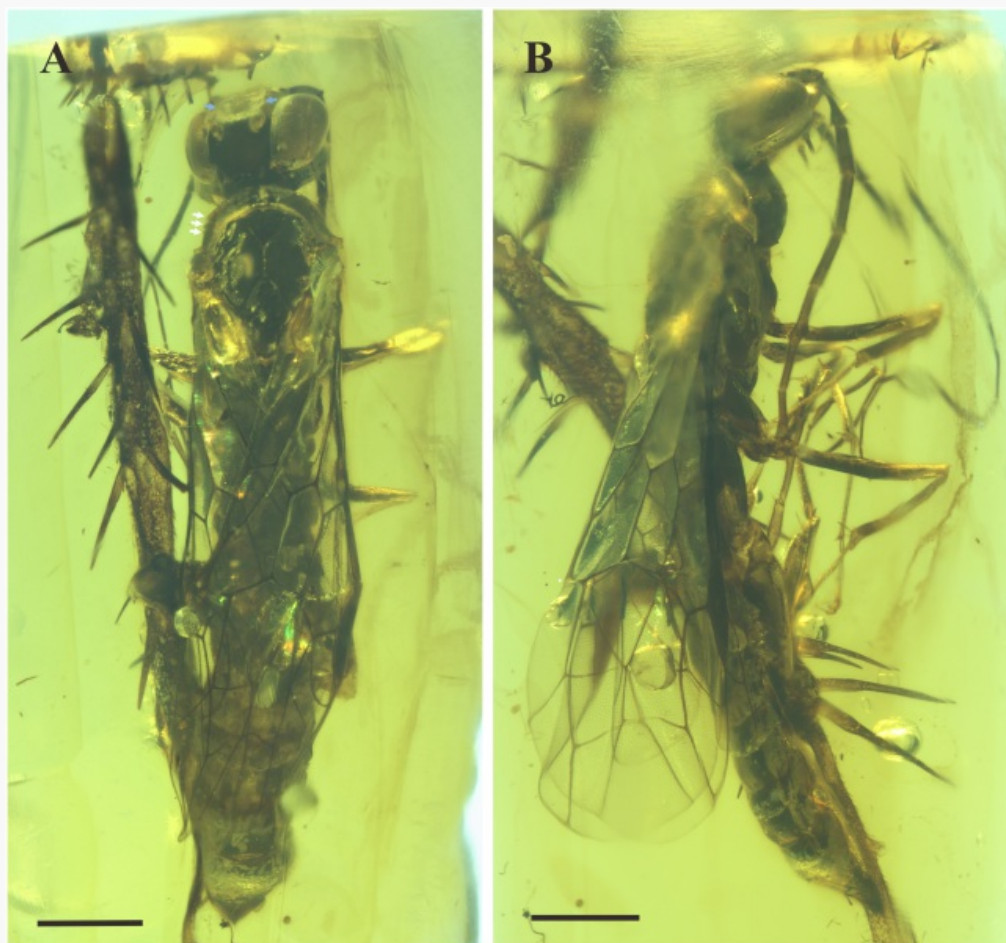


Figure 2. *Orthosyntexis cretacicus* (LYU-HY-ZD013). **A**, Mandible and maxillary palp; **B**, pronotum, mesoscutum and mesoscutellum showing transverse tooth-structures on the pronotum (white arrows); **C**, antenna; **D**, genitalia and cerci (white arrows); **E**, spur of the protibial (white arrows); **F**, spurs of the mesotibia (white arrows) and metatibia (blue arrows); **G**, forewing. Scale bars = 0.2 mm in A, B, D–F; 0.5 mm in C; 1 mm in G.

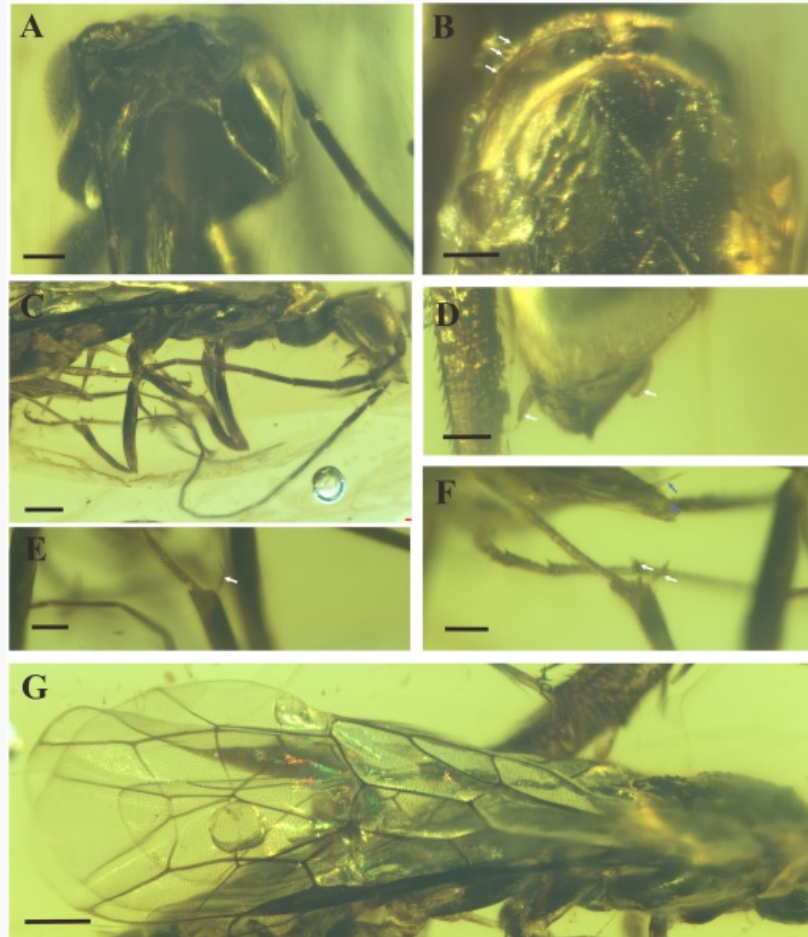


Figure 3. Line drawing of *Orthosyntexis cretacicus*. Scale bar = 1 mm.



Diagnosis

Antenna with 16 antennomeres, scape swollen with length to width ratio <2 , and shorter than the pedicel; pedicel as long as flagellomere I and narrowing basally. Forewing 1-Rs proclival; cell 1mcu with parallel sides and length/width ratio >4 ; 3r-m with acutely curved mid-length. Fore and mid-femora and tibiae long and thin; hind ones thick.

Etymology

Species is named after the Cretaceous Period.

Holotype

LYU-HY-ZD013, a complete individual preserved beneath a cockroach leg.

Type locality, unit and age

Amber recovered from the Hukawng Valley of Kachin State in northern Myanmar (26°20' N, 96°36' E). Age of the Kachin amber volcanoclastic matrix is earliest Cenomanian, 98.79 ± 0.62 Ma based on U-Pb zircon dating (Shi *et al.* 2012). However, biostratigraphy (Smith & Ross 2018) and possible redeposition of zircons (Rasnitsyn & Öhm-Kühnle 2021) has made this estimate ambiguous.

Description

Male individual with body length of 8.09 mm excluding antennae. Colour pattern is dark as preserved. Head massive and flat in lateral view (0.87/1.37 mm high/wide), with length greater than height and width narrower than the thorax. Compound eyes large, sub-hemispherical and bulging (occupying almost half the length of the head). Three large ocelli are situated posteriorly near the eyes, and anteriorly at the mid-length of the shallowly impressed subquadrate basin; they are bordered laterally by four small tubercles.

The mandible is sickle-shaped and covered with long setae; the apical tooth is long, sharp and slanting. The maxillary palp is slender and elongate, with five palpomeres: 0.17, 0.24, 0.25, 0.22 and 0.33 mm in length. The antenna has 16 swollen antennomeres with a large scape (0.26/0.13 mm in length/width). The pedicel is clavate and basally tapering: 0.47 mm long; 0.08/0.04 mm in minimum height/width. The first flagellomere is 1.88 times the scape length (= 0.49/0.07 mm long/wide). The remaining antennomeres are almost equal in length and taper distally.

The mesosoma measures 1.41 mm across the tegulae. The short pronotum is 1.23/0.17 mm long/wide across its base, with a series of transverse tooth-like structures on the lateral side, and the pronotal collar being sub-rounded anteriorly. The mesoscutum has a straight longitudinal sulcus and a strongly impressed, V-shaped notauli. The mesoscutellum is also acutely angular anteriorly. Prescutum length = 0.37 mm; length of the longitudinal sulcus between the notauli and mesoscutum-mesoscutellar sulcus = 0.21 mm; mesoscutellum length = 0.61 mm. The metanotum has a well-defined metascutellum covered by membranous wings. The pro- and meso-legs are slender and elongate; the tibiae and tarsus are armed with dense setae. The pro-leg has elongate cylindrical

coxa *ca* 0.48 mm in length; the trochanter = 0.26 mm in length; femur = 1.24/0.17 mm in length/width. The tibiae are short and only about half the length of the femora. In addition, the tibiae each have one long and strong preapical spur with a 'hook-like' apical bend; two tarsal segments are visible. The meso-coxa are 0.53 mm long with narrow trochanters that are less than half the width of the coxa. The femora are femur *ca* 1.24/0.17 mm in length/width. The tibiae are 0.7 times the femoral length with two straight preapical spurs. The tarsus is 1.87 mm long with tarsomere ratios of: 0.92, 0.42, 0.22, 0.12 and 0.19. The basitarsus is longer than the combined tarsomeres 2–5. The meta-legs are robust with swollen femora and tibiae; the tibiae are less than twice the width of the pro-and meso-tibia, and bear two apical spurs. The tarsus is *ca* 2.06 mm long; the meta-basitarsus is distinctly wider than the pro-and meso-basitarsi. Segment 1–5 lengths are: 0.82, 0.39, 0.30, 0.28 and 0.27 mm. The claws are simple, elongate, acute, and apically hooked with a distinct arolium.

The forewing is 5.78/1.81 mm in length/width when measured in lateral view. The wing membrane is hyaline except for a darkened costal space that is covered by abundant microtrichia. The pterostigma is sclerotized throughout, and 1.08/0.19 mm in length/width; it does not reach the middle of cell 3r. Veins C and R are thickened with costal areas that are narrower than C and R in width. 1-R1 is short, at *ca* 0.7 times the length of the pterostigma. Sc and 1r-rs are absent. 2r-rs attaches near the mid-length of the pterostigma. M + Cu are straight; 1-Rs is straight and short, being *ca* 0.8 times the length of 1-M. Rs + M bifurcate beyond 1m-cu. 2-Rs + M is distinct but exceptionally short, being only *ca* 0.14 times the length of 1-Rs + M. 2 + 3-Rs is half the length of 1-Rs + M, and about *ca* 0.3 the length of 4 + 5-Rs; 4 + 5-Rs is shallowly bent, being *ca* 1.5 times the length of 6-Rs. 2 + 3-M is *ca* 1.6 times the length of 4-M, and *ca* 0.91 times the length of 5-M. 2r-m is absent. 3r-m is angularly curved at its basal mid-point. 1-Cu is *ca* 0.3 times the length of 2-Cu. 1cu-a is strongly proclival, meeting 1-A slightly distal to 1a-2a; it is also longer than 1a-2a and almost the same length as 1-Cu. 2m-cu is apically arched and *ca* 2.25 times the length of 1m-cu. Cell 1 + 2r is *ca* 2.78 times as long as wide. Cell 1mcu is pentagonal, narrow and elongate in shape, and both shorter and narrower than cell 1 + 2r. Cell 2mcu is equal in length and twice as wide as cell 1mcu. The hind wings are present but obscured except for cell r, which is closed.

The metasoma has nine segments: 5.37/1.06 mm in length/width (segment IV is widest). The

genitalia visible but their structures are not discernible. Cerci are also visible.

Remarks

Orthosyntexis cretacicus differs from other species in the genus (see Gao *et al.* 2021) by possessing antenna with 14 flagellomeres, a scape that is shorter than flagellomere I (16 flagellomeres and elongated scapes are present in *Orthosyntexis elegans* and *Orthosyntexis thanti*), and forewing venation with 3r-m curved and 2m-cu *ca* 1.5 times the length of 1m-cu (3r-m is straight and 2m-cu is *ca* 1.2 times the length of 1m-cu in *O. elegans* and *O. thanti*). *v* additionally differs from *O. elegans* in its proclival 1-Rs (versus 1-Rs being sub-vertical to R), and from *O. thanti* by the scape length/width ratio being <3 (versus scape length/width ratio >3). Lastly, the 1-Rs/1-M ratio in *O. cretacicus* = 0.84, versus 0.6 in *O. elegans* and 0.78 in *O. thanti*.

Key for species of *Orthosyntexis*

1. Forewing vein cu-a longer than 1-Cu and very close to cu-a. Pro- and meso-femora and tibiae long and narrow—*Orthosyntexis cretacicus*.
Forewing vein cu-a shorter than 1-Cu and distant from cu-a. Pro- and meso-femora and tibiae thick and short—2.
2. 1-Rs sub-vertical to R—*Orthosyntexis elegans*.
1-Rs proclival—*Orthosyntexis thanti*.

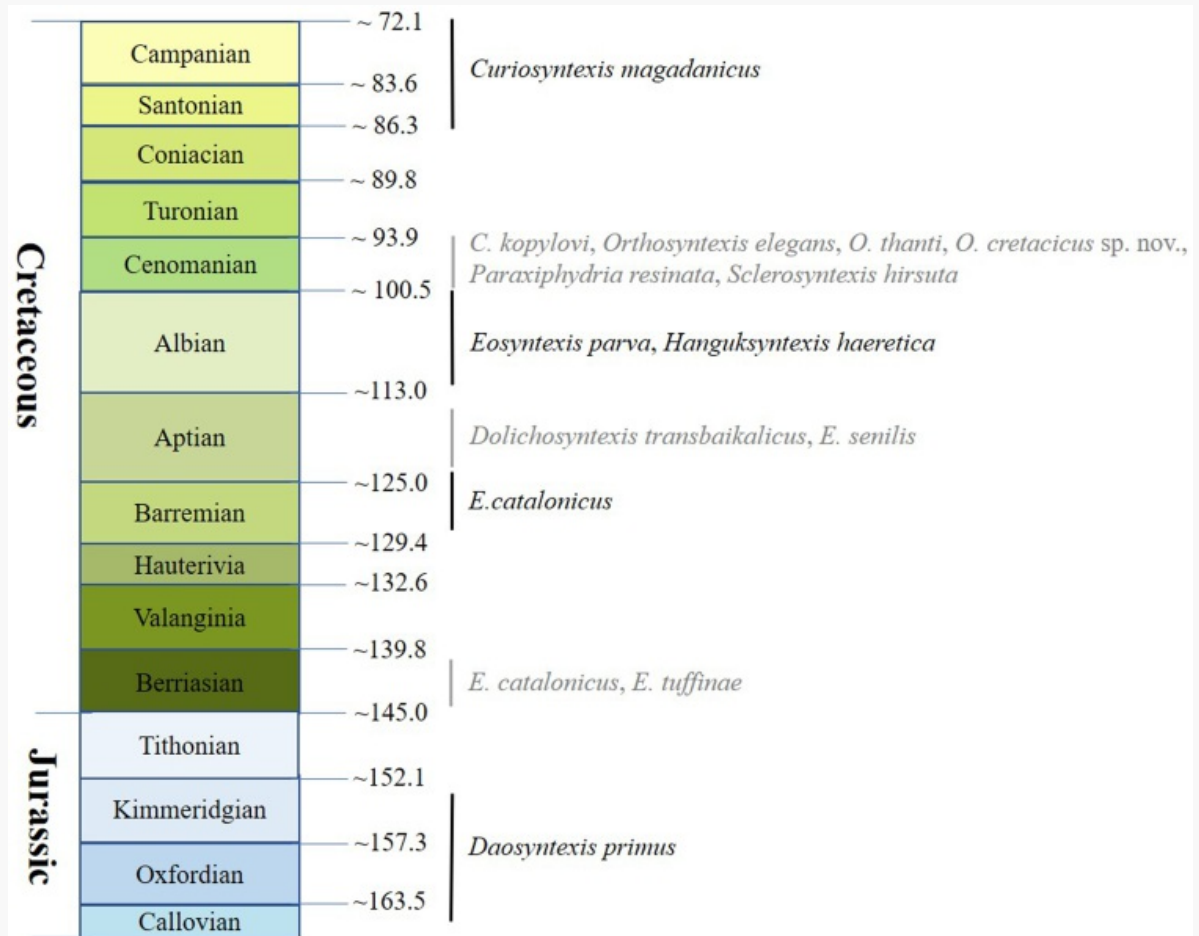
Discussion

The majority of Jurassic–Cretaceous ‘Symphyta’ are known from compression fossils, with occurrences in amber being comparatively under-represented (Ross 2024). For example, of the over 1200 species of arthropods thus far described from mid-Cretaceous Kachin amber, only 15 are currently assigned to ‘Symphyta’ (Ross 2024), which suggests a substantially underestimated diversity (Zherikhin *et al.* 2009, Vilhelmsen *et al.* 2024). Our identification of *Orthosyntexis cretacicus* is therefore an important addition to this existing assemblage (Wang *et al.* 2020, Gao *et al.* 2021, 2022, Jouault *et al.* 2022).

Orthosyntexis cretacicus can be unambiguously placed within Anaxyelidae (see Gao *et al.* 2021) based on its wing venation lacking 2r-m, the presence of 3r-m, absence of a transscutal suture, and

the pedicel being twice as long as wide (although this last feature also occurs in Xiphydriidae). Further, the absence of 1r-rs and presence of 2-Rs + M are undoubtedly consistent with Syntexinae (Rosse-Guillevic *et al.* 2023; Fig. 4). *Orthosyntexis cretacicus* can be distinguished amongst *Orthosyntexis* spp. (Table 1) by the presence of antennae with 14 flagellomeres, forewings with the 3r-m curved, the 2m-cu being longer than 1m-cu, and slim fore and mid-legs. The venation features are rarely sexually dimorphic, making *O. cretacicus* unlikely to be conspecific with either *Orthosyntexis elegans* or *Orthosyntexis thanti*.

Figure 4. Diversity and timescale of known fossil Syntexinae (Anaxyelidae).



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Table 1. The diversity and character distribution of known fossil species of Anaxyelidae (Syntexinae).

Taxon	Country/age	Characters													Reference
		Bd	Co	Pt	1r-rs	2r-rs	Rs + M-1m-cu	Rs + M-2-M	2-Rs + M	1-Rs-1-M	1-Rs	3r-m	cu-a-1-Cu	1m-cu	
<i>Curiosyntexis magadanicus</i>	Russia/Upper Cretaceous	1	1	1	1	1	0	2	1	1	0	1	2	0	Kopylov (2019)
<i>C. kopylovi</i>	Myanmar/Upper Cretaceous	–	1	0	2	1	1	1	0	0	1	0	1	0	Jouault <i>et al.</i> (2022)
<i>Daosyntexis primus</i>	China/Middle Jurassic	1	1	0	0	1	1	1	0	1	1	1	2	1	Kopylov <i>et al.</i> (2020)
<i>Dolichosyntexis transbaikalicus</i>	Transbaikalia/Lower Cretaceous	1	0	0	2	1	1	2	0	1	0	1	0	1	Kopylov (2019)
<i>Eosyntexis parva</i>	Spain/Lower Cretaceous	0	1	0	1	1	1	2	0	0	0	0	2	0	Ortega-Blanco <i>et al.</i> (2008)
<i>E. catalonicus</i>	Spain/Lower Cretaceous	1	1	0	2	1	0	2	1	0	0	0	2	0	Rasnitsyn & Delclòs (2000)
<i>E. senilis</i>	Transbaikalia/Lower Cretaceous	1	0	0	1	1	2	2	0	0	1	0	1	0	Rasnitsyn (1990)
<i>E. tuffinae</i>	England/Lower Cretaceous	–	0	0	2	1	2	2	0	0	0	0	1	0	Rasnitsyn <i>et al.</i> (1998)
<i>Hanguksyntexis haeretica</i>	Korea/Lower Cretaceous	1	1	1	1	1	0	2	1	0	0	0	0	0	Rosse-Guillevic <i>et al.</i> (2023)
<i>Orthosyntexis elegans</i>	Myanmar/Upper Cretaceous	1	1	0	2	0	2	0	0	1	0	0	2	0	Gao <i>et al.</i> (2021)
<i>O. thanti</i>	Myanmar/Upper Cretaceous	1	1	0	2	0	2	0	0	1	0	0	2	0	Gao <i>et al.</i> (2021)
<i>O. cretacicus</i>	Myanmar/Upper Cretaceous	1	1	0	2	0	2	0	0	1	0	1	1	0	This study
<i>Parasyntexis khasurtensis</i>	Russia/Lower Cretaceous	1	0	0	0	2	2	1	0	0	1	1	1	0	Kopylov (2019)
<i>Paraxiphydira resinata</i>	Myanmar/Upper Cretaceous	0	0	2	1	1	1	1	1	1	0	0	2	1	Gao <i>et al.</i> (2022)
<i>Sclerosyntexis hirsuta</i>	Myanmar/Upper Cretaceous	0	1	0	2	0	2	2	0	0	0	0	1	0	Wang <i>et al.</i> (2020)

Abbreviations: Bd = body type, small and fusiform (0) or medium and elongate (1); Co = costal area wide (0) or narrow or almost absent (1); Pt = pterostigma type, sclerotized (0) or desclerotized (1); 1r-rs, completely (0), reduced partly (1) or absent (2); 2r-rs = meeting with pterostigma at its basal (0) or middle (1) or apical (2); Rs + M-1m-cu = Rs + M furcating just at 1m-cu (0) or before (1) or beyond (2); Rs + M-2-M = Rs + M as long as 2-M (0) or longer (1) or shorter (2); 2-Rs + M = present (0) or absent (1); 1-Rs-1-M = 1-Rs longer than 1-M (0) or shorter (1); 1-Rs = straight (0) or curve (1); 3r-m = straight (0) or curve (1); cu-a-1-Cu = cu-a as long as 1-Cu (0) or longer (1) or shorter (2); 1m-cu = pentagonal (0) or hexagonal (1).

Most of the anaxyelid specimens previously described from Kachin amber are females, and range in size from 4.90–8.61 mm; the only exception is the small-bodied male holotype of *Sclerosyntexis hirsute*, which is 4.11 mm long (Wang *et al.* 2020). *Eosyntexis parva* was also documented from a small male individual 4.4 mm in length. *Orthosyntexis cretacicus* is otherwise the second known male fossil anaxyelid found in amber, and is one of the smallest at 8.09 mm, thereby demonstrating probably sexual dimorphism with females being generally larger (up to 11.13 mm: Engel *et al.* 2016, Zheng *et al.* 2019, 2021a, 2021b, Zhang *et al.* 2020, Gao *et al.* 2021, Wang *et al.* 2021, Jouault *et al.* 2022).

Hymenopterans that live in wood use specialized structures to anchor the body inside bore holes in ~~wood-living~~ living wood [AQ8](#). These include ocellar coronae in members of Burmorussidae, Orussidae, Ohlhoffiidae, Stephanidae and some Gasteruptiidae (Rasnitsyn & Martínez-Delclòs 2000, Vilhelmsen & Turrisi, 2011, Kopylov & Rasnitsyn, 2017, Jouault *et al.* 2020, Zhang *et al.* 2020, Wang *et al.* 2024), transverse ridges in Siricidae, Sepulcidae and Ichneumonidae (Vilhelmsen & Turrisi, 2011, Kopylov & Rasnitsyn, 2017), parascobal crests in some Pteromalidae (Krogmann & Burks, 2009), and head sculptures in Andreneliidae (Rasnitsyn & Martínez-Delclòs, 2000). The paired rows of tubercles adjacent to the posterior ocellus in *O. cretacicus* (Fig. 1A) probably evidence a xylophagous orussid-like head adaptation (Vilhelmsen & Turrisi 2011). Together with the elongate sub-cylindrical body, numerous teeth on the mesonotum (Fig. 2B), and mobile head preserved in a prognathous position, we posit that a wood-boring lifestyle was also likely for *O. cretacicus*.

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1.

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