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New fossil Anaxyelidae (Insecta: Hymenoptera: Siricoidea) from the Lower Cretaceous Yixian Formation of northeastern China

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Abstract

One new genus and two new species, *Hemisyntexis lepida* **gen. et sp. nov.**, *Eosyntexis conflata* **sp. nov.**, and new material of *Parasyntexis khasurtensis* Kopylov, 2019 are respectively described and illustrated based on three well-preserved compression fossils from the Lower Cretaceous Yixian Formation of northeastern China. *Eosyntexis conflata* **sp. nov.**, placed in the genus *Eosyntexis* Rasnitsyn, together with *H. lepida,* belongs to the subfamily Syntexinae of Anaxyelidae. The new species provide important morphological characters to enhance our understanding of the subfamily Syntexinae, and to revise the diagnostic characters of *Eosyntexis* as well. Moreover, we carried out a comprehensive survey of all currently published extant and extinct species of Anaxyelidae to gain a better understanding of the trend of change for the forewing and body length. Furthermore, we formally documented that the Anaxyelidae had four different color patterns for the wings simultaneously in the Jehol Biota of the Lower Cretaceous.

Key words: *Eosyntexis*, *Hemisyntexis*, wasp, Huangbanjigou, Syntexinae, new species

Introduction

Siricoidea are a large group of wood-boring insects with unique characters (Huber & Sharkey 1993). The siricoid family Anaxyelidae are the earliest diverged family of Siricoidea (Heraty *et al*. 2011; Sharkey *et al*. 2012). Anaxyelidae, a relict group of wood wasps with abundant fossil records, which flourished in the Mesozoic, were comparatively much more diverse than today. The diversity of Anaxyelidae reached its apex from the Middle Jurassic to the Early Cretaceous, but declined sharply in the Late Cretaceous (Jouault *et al*. 2022a).

The first fossil species of Anaxyelidae, *Anaxyela gracilis* Martynov, 1925, was described from the Middle-Upper Jurassic of Karatau (Kazakhstan) (Martynov 1925). Anaxyelidae have been arranged into four subfamilies: Anaxyelinae Martynov, 1925, Syntexinae Benson, 1935, Dolichostigmatinae Rasnitsyn, 1968 and Kempendajinae Rasnitsyn, 1980 (Martynov 1925; Benson 1935; Rasnitsyn 1968, 1980; Zhang & Rasnitsyn 2006; Kopylov 2019). Gao *et al*. (2021) provided a phylogenetic analysis of Anaxyelidae, and suggested to classify this family into two subfamilies, Syntexinae and Anaxyelinae. So far, there are 22 genera and 49 species assigned to Anaxyelidae, mostly distributed in Kazakhstan, China, and Russia (Martynov 1925; Rasnitsyn 1968, 1980; Kopylov 2019; Rosse-Guillevic *et al*. 2023).

The only living species of Anaxyelidae, *Syntexis libocedrii* Rohwer, 1915, inhabits coniferous forests in western North America (Wickman 1967; Smith 1978), attracted to forest burnt areas soon after late summer or early fall

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forest fires (Middlekauff, 1964), and lays eggs in the sapwood of coniferous trees, yellow juniper, giant red cedar, and probably Douglas fir and its larvae bore in the wood (Smith 1979; Zhang & Rasnitsyn 2006). It was reported that *S. libocedrii* specimens have been found in California (Rohwer 1915; Middlekauff 1974; Smith 1979), Idaho (Smith 1979), Oregon (Middlekauff 1974; Smith 1979), and British Columbia (Goulet & Huber, 1993). *Syntexis libocedrii* used to be assigned to the family of its own, the Syntexidae, by Benson (1935). And later it was downgraded under Anaxyelidae as a subfamily Syntexinae by Rasnitsyn (1969). Syntexinae are unique among anaxyelid wasps because of the forewing with the Rs+M typically bifurcating right next to or slightly distally from 1m-cu, and 2r-rs being commonly shifted towards the base and connecting with the pterostigma near its midpoint (Rosse-Guillevic *et al*. 2023). In addition, 10 other fossil genera with 14 species of Syntexinae have been recorded (Table 1). It is worth mentioning that the genus *Cretosyntexis* Rasnitsyn & Martínez-Delclòs, 2000, originally placed in the Syntexinae, has been transferred into the Anaxyelinae (Rosse-Guillevic *et al*. 2023).

TABLE 1. The lengths of the bodies, forewings and ovipositors for all known anaxyelids.

Tribe	Taxon	Locality and horizon	Body length (mm)	Forewing length (mm)	Ovipositor length (mm)
Anaxyelinae	*Anasyntexis strophandra* Rasnitsyn, 1968	Kazakhstan, J_{2-3}	10	6.3	
Anaxyelinae	*Anaxyela destructa* Rasnitsyn, 1969	Kazakhstan, J_{2-3}	8.5	4.5	6.3
Anaxyelinae	*Anaxyela gracilis* Martynov, 1925	Kazakhstan, J_{2-3}	11.8–14.5	6.2–10.5	17.3
Anaxyelinae	*Anaxyela parvula* Rasnitsyn, 1968	Kazakhstan, J_{2-3}	4.2	3.5	
Anaxyelinae	*Anaxyela nana* Rasnitsyn, 1963	Kazakhstan, J_{2-3}	4.8	3.2	2.9
Anaxyelinae	*Brachysyntexis robusta* Zhang & Rasnitsyn, 2006	China, K_1	11.5	6.5	2.6
Anaxyelinae	*Brachysyntexis brachyura* Rasnitsyn, 1968	Kazakhstan, J_{2-3}	8–14	5–8.2	2.8–4.7
Anaxyelinae	*Brachysyntexis micrura* Rasnitsyn, 1969	Kazakhstan, J_{2-3}	20	10.3	5
Anaxyelinae	*Brachysyntexis nova* Rasnitsyn, 1969	Kazakhstan, J_{2-3}	11	5.7	2.4
Anaxyelinae	*Brachysyntexis tenebrosa* Kopylov, 2018	Kazakhstan, J_{2-3}	17	11.5	
Anaxyelinae	*Brachysyntexis tigris* Kopylov, 2018	Kazakhstan, J_{2-3}	15	8.4	
Anaxyelinae	*Brachysyntexis minuta* Kopylov *et al*., 2020a	China, J_2	7.7	5.2	
Anaxyelinae	*Brachysyntexis sinensis* Kopylov *et al*., 2020a	China, J_2	13.7	9.8	4.3
Anaxyelinae	*Brachysyntexis rohweri* Kopylov *et al*., 2020a	China, J_2	9.2	4.5	2.3
Anaxyelinae	*Brachysyntexis brevicornis* Kopylov *et al*., 2020a	China, J_2	7.2	5.5	
Anaxyelinae	*Brachysyntexis laticella* Kopylov *et al*., 2020a	China, J_2	11.4	9.1	3
Anaxyelinae	*Brachysyntexis acuta* Kopylov *et al*., 2020a	China, J_2	12.8	8.5	3
Anaxyelinae	*Kulbastavia macrura* Rasnitsyn, 1963	Kazakhstan, J_{2-3}	14.2	8.6	28.3
Anaxyelinae	*Kulbastavia grandis* Kopylov, 2018	Kazakhstan, J_{2-3}	21.1	13.6	
Anaxyelinae	*Sphenosyntexis antonovi* Rasnitsyn, 1963	Kazakhstan, J_{2-3}	7.9	5.6	10
Anaxyelinae	*Sphenosyntexis pallicornis* Rasnitsyn, 1969	Kazakhstan, J_{2-3}	9	7	5
Anaxyelinae	*Syntexyela asiatica* Rasnitsyn, 1968	Kazakhstan, J_{2-3}	15–16	8.6	

......continued on the next page

TABLE 1. (Continued)

Tribe	Taxon	Locality and horizon	Body length (mm)	Forewing length (mm)	Ovipositor length (mm)
Anaxyelinae	*Syntexyela continentalis* Zhang & Rasnitsyn, 2006	China, K_1	15	8.4	12.1
Anaxyelinae	*Syntexyela gracilicornis* Rasnitsyn, 1968	Kazakhstan, $J_{2\text{-}3}$	10	7	
Anaxyelinae	*Syntexyela inversa* Rasnitsyn, 1968	Kazakhstan, $J_{2\text{-}3}$	11.5	7.5	
Anaxyelinae	*Syntexyela media* Rasnitsyn, 1963	Kazakhstan, $J_{2\text{-}3}$	9.2	6.8	5.8
Anaxyelinae	*Urosyntexis depressa* Rasnitsyn, 1969	Kazakhstan, $J_{2\text{-}3}$	13	6	5.8
Anaxyelinae	*Urosyntexis drepanura* Rasnitsyn, 1968	Kazakhstan, $J_{2\text{-}3}$	9.5	6	7.8
Anaxyelinae	*Urosyntexis magna* Rasnitsyn, 1968	Kazakhstan, $J_{2\text{-}3}$	13	9.2	10
Anaxyelinae	*Urosyntexis undosa* Kopylov, 2019	Russia, K_1	9.5	7.9	3.8
Anaxyelinae	*Cretosyntexis montsecensis* Rasnitsyn & Martínez-Delclòs, 2000	Spain, K_1		3	
Syntexinae	*Daosyntexis primus* Kopylov *et al*., 2020a	China, J_2	11.7	7.5	2.9
Syntexinae	*Curiosyntexis magadanicus* Kopylov, 2019	Russia, K_2	11.7	4.2	4.8
Syntexinae	*Dolichosyntexis transbaikalicus* Kopylov, 2019	Russia, K_1		9.8	
Syntexinae	*Parasyntexis khasurtensis* Kopylov, 2019	Russia, K_1		11.3	9.4
Syntexinae	*Eosyntexis catalonicus* Rasnitsyn & Martínez-Delclòs, 2000	Spain, K_1	12.5	8.5	
Syntexinae	*Eosyntexis parva* Ortego-Blanco *et al*., 2008	Spain, K_1	4.4	2.7	
Syntexinae	*Eosyntexis senilis* Rasnitsyn, 1990	Russia, K_1	15	7	7
Syntexinae	*Eosyntexis tuffinae* Rasnitsyn & Jarzembowski, 1998	England, K_1		5.5	
Syntexinae	*Eosyntexis conflata* **sp. nov.**	China, K_1	10.81	6.49	4.85
Syntexinae	*Hanguksyntexis haeretica* Guillevic *et al*., 2023	Republic of Korea, K_1	7.8	7.1	
Syntexinae	*Sclerosyntexis hirsuta* Wang *et al*., 2020	Myanmar, K_2	4.11	2.7	
Syntexinae	*Paraxiphydria resinata* Gao *et al*., 2022	Myanmar, K_2	4.9	4	
Syntexinae	*Orthosyntexis elegans* Gao *et al*., 2021	Myanmar, K_2	8.25	5.7	
Syntexinae	*Orthosyntexis thanti* Gao *et al*., 2021	Myanmar, K_2	8.61	5.6	
Syntexinae	*Curvitexis kopylovi* Jouault *et al*., 2022a	Myanmar, K_2		5.3	
Syntexinae	*Hemisyntexis lepida* **gen. et sp. nov.**	China, K_1	16.90	10.2	8.94
Dolichostigmatinae (transferred to Anaxyelinae)	*Dolichostigma tenuipes* Rasnitsyn, 1968	Russia, K_1	11.5	9	
Dolichostigmatinae (transferred to Anaxyelinae)	*Sclerostigma trimaculata* Kopylov & Rasnitsyn,2020b	Russia, K_1	4.6	5.3–6.0	
Kempendajinae (transferred to Anaxyelinae)	*Kempendaja jacutensis* Rasnitsyn, 1968	Russia, J_3/K_1	5.5		
Kempendajinae (transferred to Anaxyelinae)	*Mangus magnus* Kopylov, 2019	Mongolia, K_1		19.3	

Recently, we collected a new genus and species as well as a new species of fossil Anaxyelidae from the Yixian Formation. After detailed examinations, we consider these specimens belonging to the subfamily Syntexinae Benson, 1935, which enhance our knowledge of the Syntexinae in the Mesozoic of northeastern China. The newly described *Hemisyntexis lepida* **gen. et sp. nov.** and one new material of *Eosyntexis,* re-description of *Parasyntexis khasurtensis,* increased the diversity of anaxyelid wasps during the Early Cretaceous.

Material and methods

The fossil specimens were collected from the Yixian Formation, Huangbanjigou, Beipiao City, Liaoning Province, China (Figs. 1–3). The type materials (two holotypes and one new material) described herein are housed at the fossil collection of the Key Lab of Insect Evolution and Environmental Changes, at the College of Life Sciences, Capital Normal University (CNUB; Dong Ren, Curator), in Beijing, China.

The specimens were examined and photographed using Nikon SMZ 25 dissecting microscope with an attached Nikon DS-Ri2 digital camera system. The line drawings were prepared using Affinity Designer V1. The wing venation nomenclature used in this study is modified from Huber and Sharkey (1993), with the following abbreviations: Additionally, p/c means part and counterpart fossils.

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Suborder Symphyta Gerstaecker, 1867

Superfamily Siricoidea, Billberg, 1820

Family Anaxyelidae Martynov, 1925

Subfamily Syntexinae Benson, 1935

Genus *Hemisyntexis* Li, Wang, Rasnitsyn & Shih, gen. nov.
urn:lsid:zoobank.org:act:DF01EA9F-051E-4115-8BB2-3B749CE51B9F

Type Species. *Hemisyntexis lepida* Li, Wang, Rasnitsyn & Shih, **sp. nov.**

Etymology. The generic name is a combination of Greek "*Hemi-*", meaning half and referring to the pterostigma without sclerotized part basally, and the generic name *Syntexis*.

Diagnosis. Mesonotum with scuto-scutellar sulci 1.5 times as long as notauli. Forewing with costal area narrow uniformly; pterostigma wedge, desclerotized basally, the rest part completely sclerotized, 0.6 times as long as 2r-rs; Sc absent; 2r-rs issuing from pterostigma at its mid-length; cell 2r darkened; 1-Rs proclival, twice as long as 1-M; 2-Rs front of 1m-cu, 2-M less than half 2-Rs length; 5-M (section between 3r-m and wing margin) as long as 2m-cu; cell 3r 1.3 times as long as cells 1r and 2r together; cell 1mcu hexagonal.

Remarks. The new genus is unique within Syntexinae in having pterostigma not sclerotized basally. It belongs to the basal group of genera which retain 1r-rs and long and proclival 1-Rs. This group also includes *Syntexis* Rohwer, 1915, *Dolichosyntexis* Kopylov, 2019, *Daosyntexis* Kopylov, 2020, *Parasyntexis* Kopylov, 2020 and *Hanguksyntexis* Rosse-Guillevic *et al*., 2023. Within this group, *Hemisyntexis* is additionally unique in having pterostigma not reaching the middle 3r cell (*vs*., pterostigma reaching the middle 3r cell in *Dolichosyntexis*) and narrow (at 2r-rs, much narrower than length of 2r-rs, *vs.* at most as wide there as 2r-rs long).

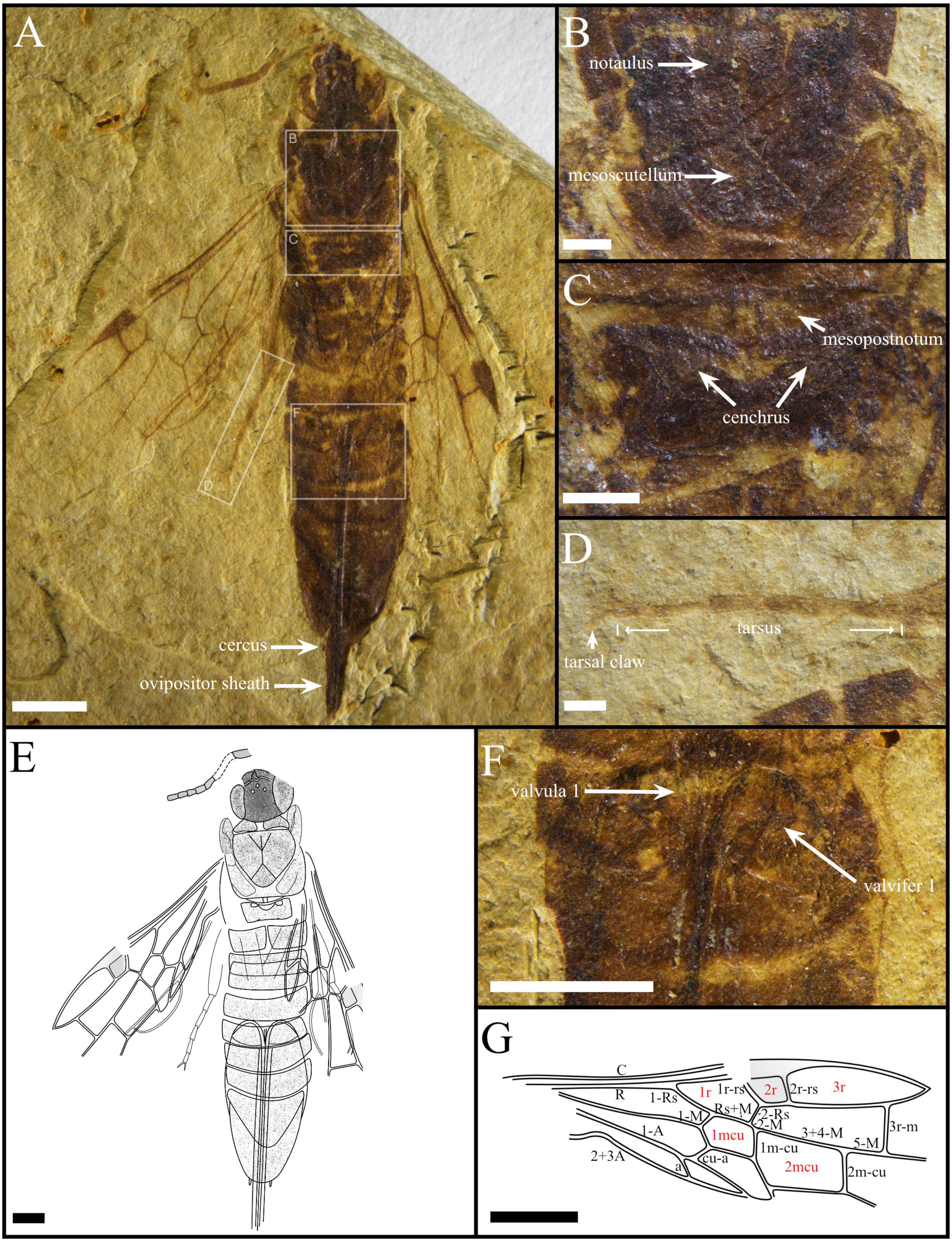

FIGURE 1. Photographs of *Hemisyntexis lepida* **gen. et sp. nov.**, holotype (specimen CNU-HYM-LB2024501), female. **A**, Dorsal view as preserved. **B**, Photo of mesoscutum. **C**, Photo of mesoscutum and metanotum. **D**, Photo of part hind leg. **E**, Line drawing of dorsal view. **F**, Photo of basal ovipositor. **G**, Line drawing of forewing. Scale bars: 2 mm in (**A**, **E**, **G**); 0.5 mm in (**B**–**D**); 1 mm in (**F**).

Hemisyntexis lepida **Li, Wang, Rasnitsyn & Shih, sp. nov.**
urn:lsid:zoobank.org:act:CE39453F-60D6-4BDD-9850-3B70BC411AD2

Material. Only the holotype, CNU-HYM-LB2024501.

Etymology. The specific name is from Latin "lepidus", meaning exceptional and referring to the well-preserved fossil specimen.

Horizon and locality. Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China; Lower Cretaceous (Barremiane–Aptian), Yixian Formation.

Diagnosis. As for the genus.

Description. Female. Head entirely dark, slightly darker than thorax and abdomen, with ovipositor slightly darker; legs lightly colored; wing veins dark (Fig. 1).

Head: Moderately large, narrower than thorax, nearly round shaped. Eye elongate ovoid, occupying all head side; ocelli small, in wide triangle at level before eye midlength (Fig. 1A). Antenna thin, with almost uniform width, flagellomeres partly preserved and almost equal in lengths, maximum 0.39 mm in length and 0.25 mm in width (Fig. 1E).

Thorax: Pronotum short and trapezoid, at least four times as wide as long; pronotum posterior border slightly curved in dorsal view. Mesoscutum large, with anterior margin nearly straight, with longitudinal sulcus and notauli strongly impressed (Fig. 1B); mesoscutellum tapering to acutely sharp apex; ratio of lengths of prescutum, longitudinal sulcus between notauli and scuto-scutellar sulcus and scutellum 3.3/2.1/4.0. Mesopostnotum trapezoid (Fig. 1C), slightly narrower than metascutellum; metascutum with metascutellum small, rounded quadrangularly, transverse; cenchri present and small.

Leg: Legs spindly. Tarsi pentamerous, basitarsi long but shorter than remaining tarsomeres combined; tarsomeres (Fig. 1D) about twice as long as wide; pretarsal claws more than half length of fifth tarsomere, with curved apices.

Wing: Forewing three times as long as wide (Fig. 1G); vein C and R slightly bent, 1r-rs 1.2 times as long as 2r-rs; 1-Rs long and proclival, about twice as long as 1-M; 2-M distinct, 0.2 times as long as Rs+M; M+Cu slightly bent basally; 3+4-M 2.4 times as long as 5-M; 5-M 1.2 times as long as 3r-m; 3r-m and 2m-cu vertical; 2-Cu twice as long as 1-Cu; 1cu-a straight, lying basally of cell a, as long as 1-Cu; 2+3A with distinct subbasal loop; cell 2+3rm long and pentagonal, about 3.4 times as long as wide. Cell 1r about 2.1 times as long as wide; cell 2r short, as long as wide; cell 3r 3.4 times as long as wide; cell 1mcu about 1.7 times as long as wide.

Abdomen: Abdomen only slightly narrower than mesothorax, first abdominal tergite split medially (Figs. 1A, E). Ovipositor straight, prominent significantly behind abdomen, incompletely preserved (Fig. 1E). First valvifer small, subhemicircular as visible (Fig. 1F); second valvifer large narrowing up to single thickening before meeting with valvula 3 (saw sheath), six times as long as the first valvifer; valvula 2 (dorsal stylet) visible only basally at its thickened base; ovipositor sheaths almost straight, prominent significantly behind abdomen.

Measurements (in mm). Body length at least 19.21, excluding ovipositor 16.90; head length 2.54, width 2.71; antenna 4.50 long as preserved; thorax length 4.06; abdomen length 10.51; forewing 10.24 long as preserved, maximum width 2.69; ovipositor length 8.94 as preserved.

Genus *Eosyntexis* Rasnitsyn, 1990

Type species. *Eosyntexis senilis* Rasnitsyn, 1990.

Species included. *Eosyntexis senilis* Rasnitsyn, 1990; *Eosyntexis tuffinae* Rasnitsyn, 1998; *Eosyntexis catalonicus* Rasnitsyn and Martínez-Delclòs, 2000; *Eosyntexis parva* Ortega-Blanco, Rasnitsyn and Delclòs, 2008.

Revised diagnosis. Forewing with pterostigma sclerotized, not reaching midlength of cell 3r; crossvein 2r-rs at midlength of pterostigma (not near apex); 1r-rs lost; Rs+M typically bifurcating right next to or slightly distally 1m-cu; vein 1-Rs proclival, issuing before the 1-M and 1-Cu bifurcation, more than twice as long as 1-M; section 3-Cu shorter than 4-Cu. Ovipositor short, its apical section less than basal section.

Remarks. *Eosyntexis* is the most diverse genus in Syntexinae that differs from all other genera in having a combination of the crossvein 1r-rs completely lost and 1-Rs long (more than twice as long as 1-M) and proclival (1-Rs issuing before the 1-M and 1-Cu bifurcation).

Eosyntexis conflata **Li, Wang, Rasnitsyn & Shih, sp. nov.**
urn:lsid:zoobank.org:act:56FED6DF-2AF1-49DC-A9AA-F99656013D50

Material. Only the holotype, CNU-HYM-LB2024502.

Etymology. The species name is from the Latin "conflatus", meaning expanded and referring to the expanded scape of the antenna.

Locality and horizon. Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China; Lower Cretaceous (Barremiane–Aptian), Yixian Formation.

Diagnosis. Forewing with costal area narrower than veins C and R; pterostigma as wide as the length of 2r-rs; Rs+M bifurcated before 1m-cu; 2-M as long as Rs+M; cell 3r 1.6 times as long as cell 1+2r; 3r-m 1.3 times as long as 5-M, 2m-cu 1.1 times as long as 5-M. Ovipositor short, its apical section less than half of basal section.

Description. Female. Head and thorax entirely dark, slightly darker than abdomen; ovipositor slightly darker; wing veins dark (Fig. 2).

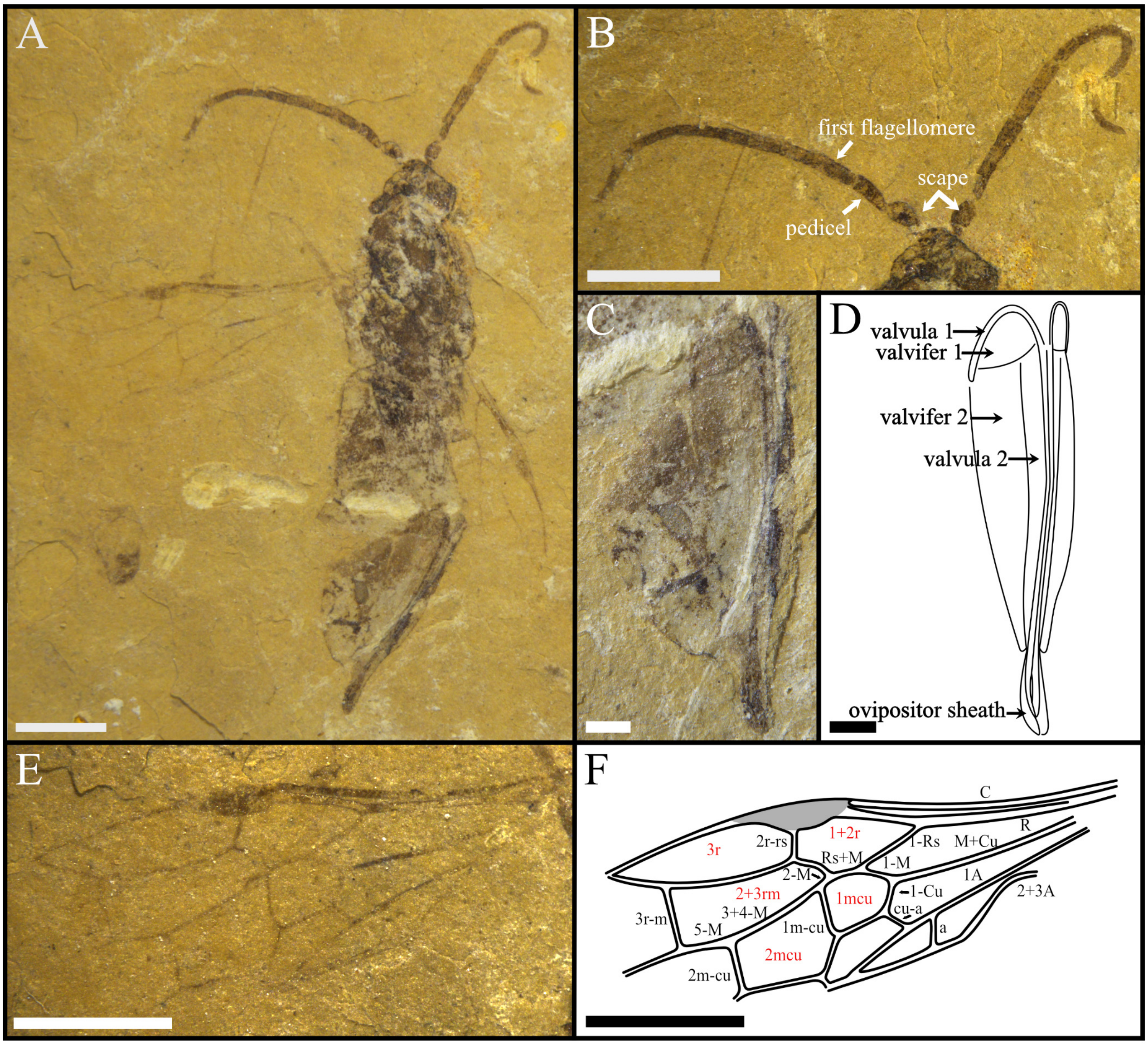

FIGURE 2. Photographs of *Eosyntexis conflata* **sp. nov.**, holotype (specimen CNU-HYM-LB2024502), female. **A**, Dorsal view as preserved. **B**, Photo of antenna. **C**, Photo of ovipositor. **D**, Line drawing of ovipositor. **E**, Photo of forewing. **F**, Line drawing of forewing. Scale bars: 2 mm in (**A**, **B**, **E**, **F**); 0.5 mm in (**C**, **D**).

Head: Head moderately small, narrower than thorax. Head 5.51 mm wide and 0.74 mm long, nearly quadrate (Fig. 3A). Antenna with 16 flagellomeres visible; scape slightly expanded; scape 0.50 mm long, maximum width 0.27 mm; pedicel 0.52 mm long, maximum width 0.21 mm; flagellomere I longer than scape, 0.19 mm wide, 0.76 mm long; flagellomere II 0.18 mm wide, 0.56 mm long, the visible parts of flagellomeres gradually shortened and their length-width ratio (excluding the first and second flagellomeres) from twice to 1.5 times toward the apex (Fig. 2B).

Thorax: Mesoscutum large, with anterior margin almost angular, the sculpture of the thorax almost not preserved (Fig. 2A).

Leg: Legs poorly preserved, hind tarsi thin, rather short (Fig. 2A).

Wing: Forewing 2.8 times as long as wide (Fig. 2E, F). C and R bent; 1-Rs twice as long as 1-M; 2-M short, 0.2 times as long as Rs+M; 2r-rs slightly proclival; 3+4-M 2.1 times as long as 5-M; 1m-cu slightly bent, as long as 2m-cu; cell 1+2r 2.3 times as long as wide; cell 3r long and large, 3.6 times as long as wide; cell 1mcu pentagonal, 1.3 times as long as wide; cell 2mcu 1.6 times as long as wide; 2-Cu 1.7 times as long as 1-Cu; 1-Cu 1.5 times as long as cu-a, located at the base of cell a.

Abdomen: Abdomen slightly distorted and incompletely preserved (Fig. 2A). Ovipositor with first valvifer small, subhemicircular as visible; second valvifer large, with thickening medially and basally, narrowing up to single thickening before meeting with ovipositor sheath (valvula 3); valvula 2 visible only basally at its thickened base; ovipositor straight, sword-shaped, 0.74 times as long as forewing length (Figs. 2C, D); ovipositor sheaths slightly bent, elongated and narrowly rounded apically, prominent significantly behind abdomen (Fig. 2A), 0.2 times as long as forewing length.

Measurements (in mm). Body excluding ovipositor about 10.81 in length; head about 0.74 in length, 5.51 in width; thorax about 3.66 in length; abdomen about 6.25 in length; forewing (incompletely preserved) about 6.49 in length, maximum width 2.31; ovipositor about 4.85 in length.

Remarks. The new species can be assigned to the genus *Eosyntexis* based on the forewing with pterostigma completely sclerotized and not reaching the midlength of cell 3r; vein 1r-rs absent; crossvein 2r-rs arising from the mid-part of pterostigma (not from near apex); vein 1-Rs more than twice as long as 1-M, Rs+M ending near 1m-cu. By the presence of 2-M, the new species is most similar to *E. senilis*, but differs from it in having pterostigma as wide as 2r-rs, 1-M nearly as long as Rs+M.

Genus *Parasyntexis* Kopylov, 2019

Type species. *Parasyntexis khasurtensis* Kopylov, 2019.

Parasyntexis khasurtensis Kopylov, 2019

Material. CNU-HYM-LB2024503(P/C).

Locality and horizon. Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China; Lower Cretaceous (Barremiane–Aptian), Yixian Formation.

Description. Female. Head and thorax predominantly dark, slightly darker than abdomen; ovipositor slightly darker; legs lightly colored; forewing with pterostigma completely sclerotized; cell 1r darkened and H-shaped pattern around veins 1-Cu, 2-Cu, 3-Cu, 1m-cu and 1cu-a dark (Fig. 3).

Head: Head moderately large, nearly oval, narrower than thorax. Compound eye large and ovate (Fig. 3A, C). Antenna thick, strongly tapering to sharp apex, apparently short, with fifteen flagellomeres visible; scape slightly expanded (Fig. 3B); scape 0.68 mm long, maximum width 0.45 mm; pedicel 0.82 mm long, maximum width 0.19 mm; flagellomere I shorter than scape, 0.21 mm wide, 0.91 mm long; flagellomere II 0.17 mm wide, 0.65 mm long; the visible parts of flagellomeres gradually shortened and their length-width ratio (excluding the first and second flagellomeres) from 3.2 times to one times toward the apex, except for the last flagellomere slender and twice as long as wide.

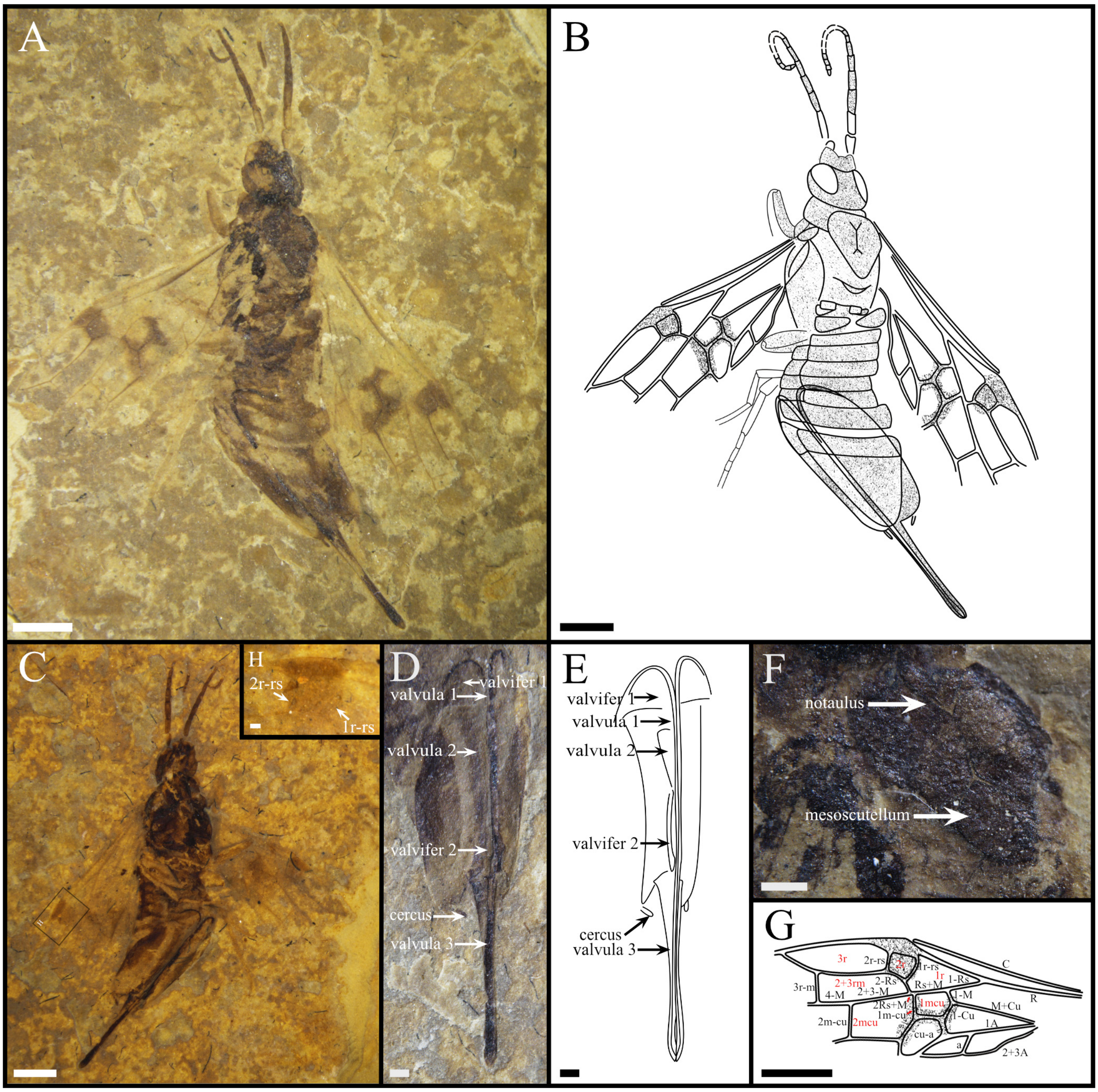

FIGURE 3. Photographs of *Parasyntexis khasurtensis* Kopylov, 2019, new specimen (CNU-HYM-LB2024503 P/C), female. **A**, Dorsal view as preserved. **B**, Line drawing of dorsal view. **C**, Ventral view as preserved was taken wetted with 95% ethanol. **D**, Photo of ovipositor. **E**, Line drawing of ovipositor. **F**, Photo of mesoscutum. **G**, Line drawing of forewing. **H**, Photo of forewing cell 2r was taken wetted with 95% ethanol. Scale bars: 2 mm in (**A**–**C**, **G**); 0.5 mm in (**D**–**F**); 0.1 mm in (**H**).

Thorax: Pronotum trapezoid (Fig. 3A). Mesoscutum large, with anterior margin nearly straight, median longitudinal sulcus and notauli strongly impressed; mesoscutellum tapering to acute apex; ratio of lengths of prescutum, median longitudinal sulcus between notauli and mesoscuto-mesoscutellar sulcus, and mesoscutellum 3.7/4.5/4.1 (Fig. 3B), mesoscutellum triangular, tapering to acutely sharp apex (Fig. 3F).

Leg: Leg with pro- and metafemur shorter than tibia; profemur length 2.01 mm, metafemur length 1.78 mm, thick subapically, narrowed apically. Tarsi long and thin (Fig. 3B, C).

Wing: Forewing three times as long as wide (Fig. 3G). Vein C and R thick, costal area wide medially. 1r-rs 1.5 times as long as 2r-rs (Fig. 3H), 2r-rs issuing from pterostigma at its one-third of apex, as long as pterostigma wide; 1-Rs long, aligned with Rs+M, about 3.2 times as long as 1-M; 2-Rs+M short, 0.2 times as long as 1-Rs+M; 2r-rs slightly proclival; 2+3-M 1.8 times as long as 4-M; 4-M slightly longer than 3r-m and 2m-cu. Cell 1mcu pentagonal, about 1.7 times as long as wide; cell 2mcu about 0.2 times as long as wide; 2-Cu 0.8 times as long as 1-Cu; 1cu-a straight, shorter than 1-Cu; 2A+3A with long subbasal loop; cell 2+3rm long and pentagonal, about 3.2 times as long as wide; cell 1+2r 2.4 times as long as wide; cell 3r about 3.3 times as long as wide; cell 3r as long as 1+2r.

Abdomen: Abdomen slightly distorted, wider than the mesothorax, parallel-sided before ovipositor base. First abdominal tergite split medially (Fig. 3A, C). Ovipositor with first valvifer small, subhemicircular as visible; second valvifer large, with thickening medially and distally, narrowing up to single thickening before meeting with valvula 3 (saw sheath), 1.2 times as long as valvula 3, valvula 2 (dorsal stylet) visible only basally at its thickened base (Fig. 3D, E); ovipositor straight, sword-shaped (Fig. 3A, D); ovipositor full length equal to 1.1 times forewing length; ovipositor elongated and narrowly rounded apically, prominent significantly behind abdomen, valvula 3 0.4 times as long as forewing length.

Measurements (in mm). Body excluding ovipositor about 14.81 in length; head about 2.42 in length, 2.51 in width; thorax about 4.02 in length; abdomen about 8.28 in length; forewing (incompletely preserved) at least 9.72 in length, maximum width 3.61; ovipositor about 4.41 in length.

Remarks. The new specimen can be assigned to the genus *Parasyntexis* based on the forewing characters: costal area wide; pterostigma as wide as vein 2r-rs long; 1-Rs as long as pterostigma; both 1r-rs and 2r-rs developed, 1r-rs 1.3 times as long as 2r-rs; cell 2r wider than pterostigma; Rs+M furcating after 1m-cu, 2Rs+M present, cell 1mcu pentagonal. Kopylov (2019) described the type species *P. khasurtensis* based on one specimen; however, the antennae, thorax and ovipositor were not described due to the lack of preservation of these structures. Our well-preserved new specimen (CNU-HYM-LB2024503(P/C)) reported herein can supplement some new body characters for further study.

Discussion

Taxonomic position

Comparative morphological analysis of the new genus revealed some crucial phenotypic similarities with the subfamily Syntexinae in the forewing: Rs+M typically bifurcated close to 1m-cu (*vs*., Anaxyelinae with the forewing Rs+M bifurcated well before 1m-cu, usually at or before reaching the midlength of the cell 1mcu), the length of cell 2r is less than 1.5 times its width (*vs*. Anaxyelinae with the length of cell 2r typically more than 1.5 times its width), 2r-rs is commonly shifted towards the base and connects with the pterostigma near its midpoint (*vs*., Anaxyelinae with 2r-rs typically displaced towards the distal quarter of the pterostigma), 6-Rs remains usually straight along its entire length (*vs*., Anaxyelinae with the subterminal section of 6-Rs strongly curved forward, forming a right-angle junction with C), and resulting in a sharp apex for cell 3r (*vs*., Anaxyelinae with the apex of cell 3r typically rounded). As a result, assigning the new fossils to Syntexinae would be appropriate.

According to the key for the genera of Syntexinae (Rosse-Guillevic *et al*. 2023), the new genus *Hemisyntexis* is most similar to *Parasyntexis,* because of the following characters: forewing with 1r-rs complete; tubular veins developed in the apical third of the wing; pterostigma not reaching the middle 3r cell, 2r-rs originating from behind the middle of pterostigma and about as long as pterostigma wide; and 1-M distinctly longer than half 1-Cu. The new genus *Hemisyntexis* differs from the genus *Parasyntexis* in having pterostigma narrow and wedge, not sclerotized basally, costal area not wider than C and R width, Rs+M bifurcated before 1m-cu (*vs*., pterostigma pentagonal and distinctly wider, sclerotized entirely, costal area wider than C and R, Rs+M bifurcated behind 1m-cu). Therefore, we believe that the new genus can be established in the subfamily Syntexinae based on the above-mentioned comparisons.

As the number of the reported species increases, based on the summary of Rosse-Guillevic *et al.* in 2023, we re-evaluated the distinctive features of *Eosyntexis* and defined the morphological gap with other genera. *Eosyntexis* is similar to *Orthosyntexis*, *Sclerosyntexis, Paraxiphydria* and *Curvitexis* but differs from all other genera of Syntexinae in having 1r-rs entirely lost. At the same time, 1-Rs long (more than twice as long as 1-M) and proclival (1-Rs issuing before the 1-M and 1-Cu bifurcation) differs *Eosyntexis* from all the above genera.

Range changes of forewing, ovipositor and body length

We carried out a comprehensive survey to examine all currently published extant and extinct species by comparing forewing venations and body lengths, to gain better understanding of the trend of change for the forewing and body lengths in the subfamily Syntexinae, and the family Anaxyelidae as a whole. The lengths of the body and forewing for all known anaxyelids are summarized in Table 1. In the Jurassic, the body lengths ranged from 4.20 to 21.10 mm, and wing lengths 3.2 to 13.7 mm, while in the Early Cretaceous they varied between 4.4 and 16.9 mm and between 2.7 and 19.3 mm, respectively. This implies no striking differences between the Jurassic and Early Cretaceous Anaxyelidae. In contrast, the data in Table 1 show a different pattern for the amber species that are generally of much smaller sizes. Their body lengths varied from 4.11 to 8.61 mm and forewing lengths from 2.7 to 5.7 mm, which are at the low end of the size range of the family. Apparently, these results were caused by selectivity of the amber traps that are known to gives a preference to smaller objects to be glued and then buried there (Zherikhin 2002). The only living species *Syntexis libocedrii* fits well to the body length ranges of the Mesozoic compression fossils of Anaxyelidae, with its females ranging from 8 to 16 mm and males from 8 to 12 mm long (Wickman 1967). Otherwise, the lengths of the ovipositor varied greatly, ranging from 2.3 mm to 28.3 mm in the Jurassic and from 2.6 mm to 9.4 mm in the Early Cretaceous.

Wing coloration patterns among the fossil Anaxyelidae

Wing coloration was a very ancient feature among insects (Jouault *et al*. 2022b). Color patterns play central roles in the behavior of insects and are important traits for taxonomic studies (Shevtsova *et al.*, 2011). Many fossil insects showed monochromatic color patterns, scanning electron microscopy reveals that melanin-rich cuticles were more resistant to degradation than melanin-poor cuticles. These preserved color patterns can thus be plausibly explained as melanin-based patterning (Wang *et al*. 2023).

It has been reported that a spectacular variety of color patterns on the wings of the ‘giant’ Palaeodictyoptera, Megasecoptera, Archaeorthoptera, Dictyoptera, ‘Grylloblattodea’, and Hemiptera in the Paleozoic and the Triassic. During the Middle Jurassic to the Early Cretaceous, some Odonata formed color patterns on their wings and became more and more frequent. Through bibliographic studies and the discovery of new Syntexinae specimens, we found that some of anaxyelids in Siricoidea developed color patterns on their wings during the Lower Cretaceous. In the Lower Cretaceous Jehol Biota, a total of eight species were reported in the Anaxyelidae, of which four species had three different color patterns in phylogenetically distant clades. However, in other periods and localities, we found no Anaxyelidae with color patterns so far (perhaps the coloration was lost due to taphonomical reasons). Up to now, we can distinguish four forewing patterns of coloration in the Anaxyelidae (Fig. 4):

1) The first type with color patterns along cell 2r and vein 1-M, 1-Cu, cu-a, 2-Cu, m-cu, 3-Cu, like an H (*Parasyntexis khasurtensis* Kopylov, 2019) (Fig. 4A);

2) The second type with darkened cell 2r (*Hemisyntexis lepida* Li, Wang, Rasnitsyn & Shih, **gen. et sp. nov.**) (Fig. 4B);

3) The third type with color patterns along the apex of cell 1r, cell 2r, cell 1mcu, the basal of cell 2+3rm, 2mcu, and cell 2a (*Syntexyela continentalis* Zhang & Rasnitsyn, 2006) (Fig. 4C);

4) The fourth type with a completely hyaline wing (all other anaxyelid species) (Fig. 4D).

Such differences in colorations are generally characteristic of different species in the same genus. Hence, we recommend considering the color patterns as a supplementary diagnostic character for the classification of Anaxyelidae. It is interesting that the color patterns are only registered in female species of Anaxyelidae thus far. Yet we cannot infer for the present whether the color pattern is related to sexual dimorphism due to limited small number of available fossils. It is worth noting that among various Mesozoic xylophilous Symphyta, we have managed to observe a sophisticated wing color pattern (in form of spots and lines) only in the genus *Ghilarella* Rasnitsyn, 1988 (Sepulcidae, Cephoidea), in all its species except *G. kopylovi* Li *et al.*, 2024 (Li *et al*. 2024). Similar to the Anaxyelidae, the color patterns appeared there predominately as a line around 1r-rs, base of 2rm cell, and 3-Cu. A simple pattern like the basal wing part shaded widely is found in another sepulcid genus *Thoracotrema* Rasnitsyn, 1988 (Rasnitsyn 1993).

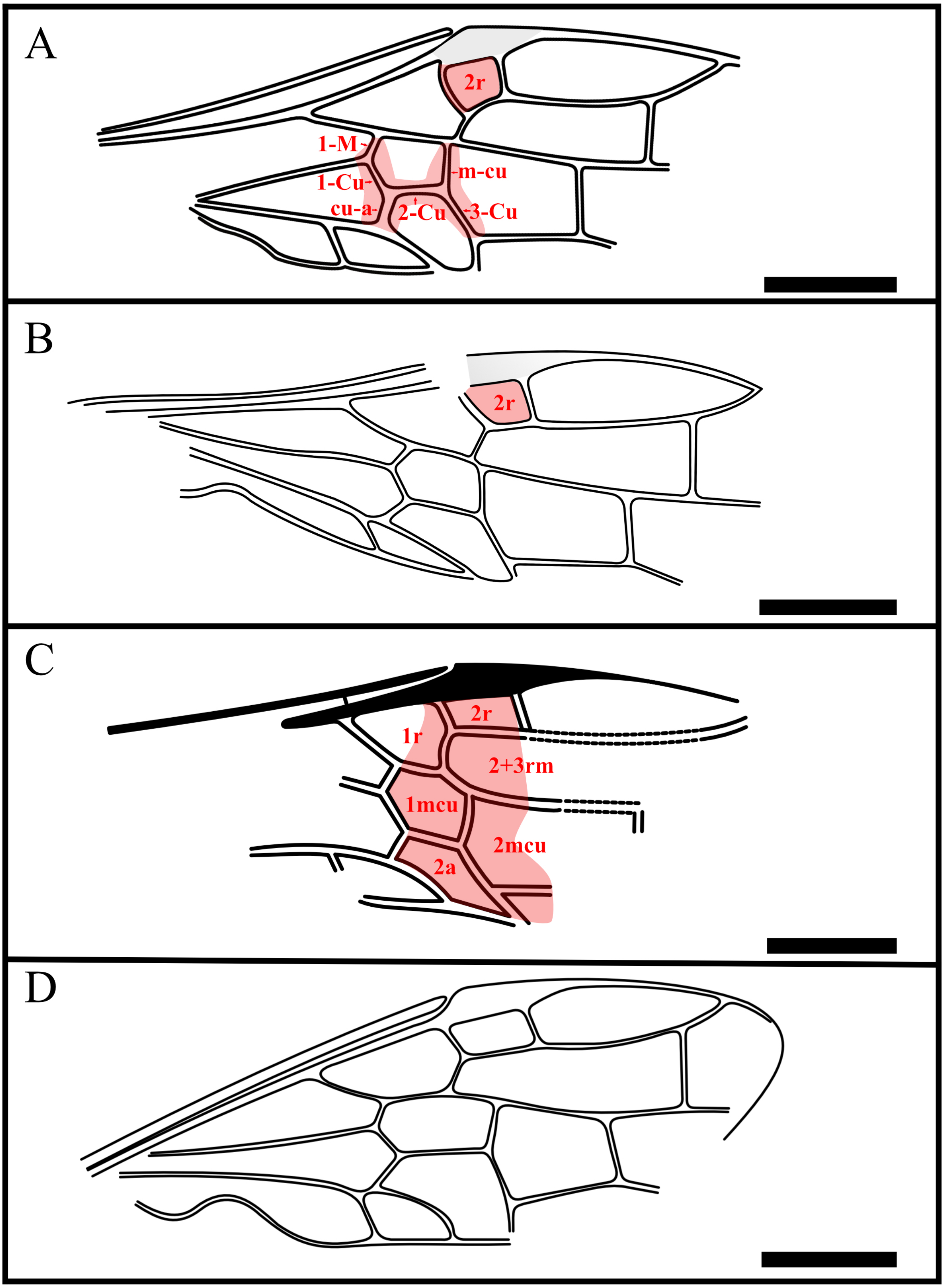

FIGURE 4. Different patterns of forewing coloration. **A**, The first type (*Parasyntexis khasurtensis* Kopylov, 2019). **B**, The second type (*Hemisyntexis lepida* Li, Wang, Rasnitsyn & Shih, **gen. et sp. nov.**). **C**, The third type (*Syntexyela continentalis* Zhang and Rasnitsyn, 2006). **D**, The fourth type (*Brachysyntexis acuta* Kopylov & Rasnitsyn *et al*., 2020). Scale bars: 2 mm.

Previous studies have shown that color patterns among insects are primarily involved in anti-predation strategies or mating behaviors (Eberhard 1991, 1994; Ruxton *et al*. 2004a). We speculate that the forewing patterns of coloration in the Anaxyelidae were involved in the process of avoiding predators, reducing the probability to be captured (Ruxton *et al*. 2004b; Pinheiro *et al*. 2016), or just avoiding a potential attack by warning/scaring predators, *i.e*., aposematism (Hill & Vaca 2004; Crees *et al*. 2021; Xu *et al*. 2022).

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References

Benson, R.B. (1935) On the genera of the Cephidae, and the erection of a new family Syntexidae (Hymenoptera: Symphyta). *Annals and Magazine of Natural History (Ser. 10)*, 16, 534–553.
https://doi.org/10.1080/00222933508655081

Crees, L.D., DeVries, P. & Penz, C.M. (2021) Do hind wing eyespots of *Caligo* butterflies function in both mating behavior and antipredator defense? (Lepidoptera, Nymphalidae). *Annals of the Entomological Society of America*, 114, 329–337.
https://doi.org/10.1093/aesa/saaa050

Eberhard, W.G. (1991) Copulatory courtship and cryptic female choice in insects. *Biological Review*, 66, 1–31.
https://doi.org/10.1111/j.1469-185X.1991.tb01133.x

Eberhard, W.G. (1994) Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. *Evolution*, 48, 711–733.
https://doi.org/10.1111/j.1558-5646.1994.tb01356.x

Gao, J., Engel, M.S., Shih, C.K., Ren, D. & Gao, T.P. (2021) A new genus of anaxyelid wood wasps from the mid-Cretaceous and the phylogeny of Anaxyelidae (Hymenoptera). *Journal of Hymenoptera Research*, 86, 151–169.
https://doi.org/10.3897/jhr.86.73161

Gao, J., Engel, M.S., Grímsson, F., Gu, L., Ren, D. & Gao, T.P. (2022) The first xiphydriid wood wasp in Cretaceous amber (Hymenoptera: Xiphydriidae) and a potential association with Cycadales. *Fossil Record*, 24, 445–453.
https://doi.org/10.5194/fr-24-445-2022

Heraty, J., Ronquist, F., Carpenter, J.M., Hawks, D., Schulmeister, S., Dowling, A.P., Murray, D., Munro, J., Wheeler, W.C., Schiff, N. & Sharkey, M.J. (2011) Evolution of the hymenopteran megaradiation. *Molecular Phylogenetics and Evolution*, 60, 73–88.
https://doi.org/10.1016/j.ympev.2011.04.003

Hill, R.I. & Vaca, J.F. (2004) Differential wing strength of Pierella butterflies (Nymphalidae, Satyrinae) supports the deflection hypothesis. *Biotropica*, 36, 362–370.
https://doi.org/10.1111/j.1744-7429.2004.tb00328.x

Huber, T.H. & Sharkey, M.J. (1993) Structure. *In*: Goulet, H. & Huber, T.H. (Eds), Hymenoptera of the world: An identification guide to families. Centre for Land and Biological Resources Research, Ottawa, Ontario, pp. 13–59.

Jouault, C., Nam, G.S. & Rasnitsyn, A.P. (2022a) A new anaxyelid wood wasp (Hymenoptera: 'Symphyta') from the mid Cretaceous Burmese amber. *Annales de Paléontologie*, 108, 102568.
https://doi.org/10.1016/j.annpal.2022.102568

Jouault, C., Tischlinger, H., Henrotay, M. & Nel, A. (2022b) Wing coloration patterns in the Early Jurassic dragonflies as potential indicator of increasing predation pressure from insectivorous reptiles. *Palaeoentomology*, 5 (4), 305–318.
https://doi.org/10.11646/palaeoentomology.5.4.3

Kopylov, D.S. (2018) Forgotten giants: new Anaxyelidae (Hymenoptera) from the Jurassic of Karatau. *Zootaxa*, 4514 (3), 332–340.
https://doi.org/10.11646/zootaxa.4514.3.2

Kopylov, D.S. (2019) New anaxyelids (Hymenoptera: Anaxyelidae) from the Cretaceous of Asia. *Zootaxa*, 4603 (2), 341–353.
https://doi.org/10.11646/zootaxa.4603.2.7

Kopylov, D.S., Rasnitsyn, A.P., Zhang, H.C. & Zhang, Q. (2020a) Anaxyelidae of Daohugou: oldest occurrences of the relict family in the fossil record. Part 1: Daosyntexis and Brachysyntexis. *Alcheringa*, 44, 104–114.

https://doi.org/10.1080/03115518.2019.1697753
Kopylov, D.S., Rasnitsyn, A.P., Aristov, D.S., Bashkuev, A.S., Bazhenova, N.V., Dmitriev, V.Yu., Gorochov, A.V., Ignatov, M.S., Ivanov, V.D., Khramov, A.V., Legalov, A.A., Lukashevich, E.D., Mamontov, Yu.S., Melnitsky, S.I., Ogłaza, B., Ponomarenko, A.G., Prokin, A.A., Ryzhkova, O.V., Shmakov, A.S., Sinitshenkova, N.D., Solodovnikov, A.Yu., Strelnikova, O.D., Sukacheva, I.D., Uliakhin, A.V., Vasilenko, D.V., Wegierek, P., Yan, E.V. & Zmarzły, M. (2020b) The Khasurty fossil insect Lagerstätte. *Paleontological Journal*, 54, 1221–1394.
https://doi.org/10.1134/S0031030120110027
Li, Y., Wang, M., Rasnitsyn, A.P., Shih, C.K., Zhuang, J.L. & Ren, D. (2024) Two new species of Ghilarellinae (Hymenoptera, Cephoidea, Sepulcidae) from the Lower Cretaceous. *Cretaceous Research*, 159, 105875.
https://doi.org/10.1016/j.cretres.2024.105875
Martynov, A.V. (1925) To the knowledge of fossil insects from Jurassic beds in Turkestan. *Bulletin de L'Academie des Sciences de l'URSS*, 19, 753–762.
Middlekauff, W.W. (1964) Notes and description of the previously unknown male of *Syntexis libocedrii*. *The Pan-Pacific Entomologist*, 40, 255–258.
Middlekauff, W.W. (1974) Larva of the Wood-boring Sawfly *Syntexis libocedrii* Rohwer (Hymenoptera: Syntexidae). *The Pan-Pacific Entomologist*, 50, 288–290.
Ortega-Blanco, J., Rasnitsyn, A.P. & Delclos, X. (2008) First record of anaxyelid woodwasps (Hymenoptera: Anaxyelidae) in Lower Cretaceous Spanish amber. *Zootaxa*, 1937 (1), 39–50.
https://doi.org/10.11646/zootaxa.1937.1.3
Pinheiro, C.E.G., Freitas, A.V.L., Campos, V.C., DeVries, P.J. & Penz, C.M. (2016) Both palatable and unpalatable butterflies use bright colors to signal difficulty of capture to predators. *Neotropical Entomology*, 45, 107–113.
https://doi.org/10.1007/s13744-015-0359-5
Rasnitsyn, A.P. (1963) Pozdneyurskiye pereponchatokrylye Karatau. *Paleontologicheskii Zhurnal*, 86–99.
Rasnitsyn, A.P. (1968) New Mesozoic sawflies (Hymenoptera, Symphyta). *In*: Rohdendorf, B.B. (Ed.), *Jurassic Insects of Karatau*. Nauka Press, Moscow, pp. 190–236. [in Russian].
Rasnitsyn, A.P. (1969) Origin and evolution of the lower Hymenoptera. Transactions of the Paleontological Institute. *Academy of Sciences of the USSR*, 123, 1–196. [in Russian].
Rasnitsyn, A.P. (1980) Origin and evolution of the Hymenoptera. Transactions of the Paleontological Institute. *Academy of Sciences of the USSR*, 174, 1–192. [in Russian].
Rasnitsyn, A.P. (1990) Hymenoptera. *In*: Rasnitsyn, A.P. (Ed.), Late Mesozoic insects of Eastern Transbailalia. *Transactions of the Paleontological Institute, Academy of Sciences of the USSR*, 239, 177–205. [in Russian].
Rasnitsyn, A.P., Jarzembowski, E.A. & Ross, A.J. (1998) Wasp (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. *Cretaceous Research*, 19, 329–391.
https://doi.org/10.1006/cres.1997.0114
Rasnitsyn, A.P. & Martínez-Delclòs, X. (2000) Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain. *Acta Geologica Hispanica*, 35, 65–95.
Rasnitsyn, A.P. & Zhang, H.C. (2004) Composition and age of the Daohugou hymenopteran (Insecta, Hymenoptera = Vespida) assemblage from Inner Mongolia, China. *Palaeontology*, 47, 1507–1517.
https://doi.org/10.1111/j.0031-0239.2004.00416.x
Rohwer, S.A. (1915) A remarkable new genus of Cephidae. *Proceedings of the Entomological Society of Washington*, 17, 114–117.
Rosse-Guillevic, S., Kopylov, D.S., Rasnitsyn, A.P., Nam, G.S., Kwon, S.H. & Jouault, C. (2023) Blurring the limits of anaxyelid subfamilies: a new genus and species (Hymenoptera: Anaxyelidae) from the Albian of the Republic of Korea. *Palaeoentomology*, 6 (4), 424–434.
https://doi.org/10.11646/palaeoentomology.6.4.13
Ruxton, G.D., Sherratt, T.N. & Speed, M.P. (2004a) Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. Oxford University Press, Oxford, 264 pp.
https://doi.org/10.1093/acprof:oso/9780198528609.001.0001
Ruxton, G.D., Speed, M. & Sherratt, T.N. (2004b) Evasive mimicry: when (if ever) could mimicry based on difficulty of capture evolve? *Proceedings of the Royal Society B*, 271, 2135–2142.
https://doi.org/10.1098/rspb.2004.2816
Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P.G., Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L. & Wheeler, W.C. (2012) Phylogenetic relationships among superfamilies of hymenoptera. *Cladistics*, 28 (1), 80–112.
https://doi.org/10.1111/j.1096-0031.2011.00366.x
Shevtsova, E., Hansson, C., Janzen, D.H. & Kjaerandsen, J. (2011) Stable structural color patterns displayed on transparent insect wings. *Proceedings of the National Academy of Sciences*, 108 (2), 668–673.
https://doi.org/10.1073/pnas.1017393108
Smith, D.R. (1978) Suborder Symphyta. (Xyelidae, Pararchexyelidae, Parapamphiliidae, Xyelydidae, Karatavitidae, Gigasiricidae, Sepulcidae, Pseudosiricidae, Anaxyelidae, Siricidae, Xiphydriidae, Paroryssidae, Xyelotomidae, Blasticotomidae, Pergidae).

In: Hymenopterorum Catalogus. Nova Editio. The Hague, W. Junk Publishers, pp. 1–193.
Smith, D.R. (1979) Symphyta. *In*: Krombein, K.V., Hurd, P.J., Smith, D.R. & Burks, B.D. (Eds), Catalog of Hymenoptera in America North of Mexico. Smithsonian Institution Press, Washington DC, pp. 3–137.
Wang, S.Y., McNamara, M.E., Wang, B., Hui, H.J. & Jiang, B.Y. (2023) The origins of colour patterns in fossil insects revealed by maturation experiments. *Proceedings of the Royal Society B*, 29020231333.
https://doi.org/10.1098/rspb.2023.1333
Wang, Y.M., Wang, M., Rasnitsyn, A.P., Shih, C.K., Ren, D., Kopylov, D.S. & Gao, T.P. (2020) A new anaxyelid sawfly (Insecta, Hymenoptera, Siricoidea) in mid-Cretaceous Myanmar amber. *Cretaceous Research*, 109, 104372.
https://doi.org/10.1016/j.cretres.2020.104372
Wickman, B.E. (1967) Life History of the Incense-Cedar Wood Wasp, *Syntexis libocedrii* (Hymenoptera: Syntexidae). *Annals of the Entomological Society of America*, 60 (6), 1291–1295.
https://doi.org/10.1093/aesa/60.6.1291
Xu, C., Luo, C., Jarzembowski, E.A., Fang, Y. & Wang, B. (2022) Aposematic coloration from Mid-Cretaceous Kachin amber. *Philosophical Transactions of the Royal Society B*, 377, 20210039.
https://doi.org/10.1098/rstb.2021.0039
Zhang, H.C. & Rasnitsyn, A.P. (2006) Two new anaxyelid sawflies (Insecta, Hymenoptera, Siricoidea) from the Yixian Formation of western Liaoning, China. *Cretaceous Research*, 27 (2), 279–284.
https://doi.org/10.1016/j.cretres.2005.11.001
Zherikhin, V.V. (2002) Ecological history of the terrestrial insects. *In*: Rasnitsyn, A.P. & Quicke, D.L.J. (Eds), *History of Insects*. Kluwer Academic Publishers, Dordrecht, pp. 331–386.