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Anaxyelidae of Daohugou: oldest occurrences of the relict family in the fossil record. Part 1: *Daosyntexis* and *Brachysyntexis*

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One new genus and seven species of Anaxyelidae are described from the Middle Jurassic of Daohugou, Inner Mongolia, China, including *Daosyntexis primus* gen. et sp. nov. (Syntexinae), *Brachysyntexis sinensis* sp. nov., *B. rohweri* sp. nov., *B. laticella* sp. nov., *B. brevicornis* sp. nov., *B. acuta* sp. nov. and *B. minuta* sp. nov. (Anaxyelinae). They are the most ancient representatives of the relict family Anaxyelidae. The anaxyelid complex at Daohugou is more diverse than at Karatau, Kazakhstan, and includes not only Anaxyelinae, but also Syntexinae and probably Kempendajinae. Syntexinae and Kempendajinae are recorded in Jurassic strata for the first time.

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ANAXYELIDAE is a relict group of sawflies, represented in the extant fauna by the single species *Syntexis libocedrii* Rohwer, 1915 (Wickman 1967, Smith 1978). Although modern representatives are very rare, this was one of the most diverse and abundant families of Symphyta in the Mesozoic. It includes four subfamilies, over 10 genera and over 30 species described from Jurassic and Cretaceous deposits (Martynov 1925, Rasnitsyn 1963, 1968, 1969, 1980, Rasnitsyn *et al.* 1998, Zhang & Rasnitsyn 2006, Ortega-Blanco *et al.* 2008, Taeger *et al.* 2010, Kopylov 2018, 2019).

Thus far, Jurassic anaxyelids have been described only from Karatau (Middle–Late Jurassic of Kazakhstan). One poorly preserved specimen was also noted from Khoutiyn-Khotgor (Late Jurassic of Mongolia; Kopylov 2018). All anaxyelids from Karatau are represented by Anaxyelinae, and so it was considered that only this subfamily existed in the Jurassic, whereas Syntexinae, Kempendajinae and Dolichostigmatinae appeared only in the Cretaceous (Rasnitsyn 1963, 1968, 1969, 1980, Kopylov 2018).

Anaxyelids have been noted previously from the famous Middle Jurassic Daohugou Lagerstätte. Rasnitsyn & Zhang (2004) reported 17 specimens of Anaxyelidae from the collections of the Nanjing

Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). All of these were preliminarily referred to Anaxyelinae, but not identified or described in detail.

Our careful examination of the NIGPAS collections revealed 41 anaxyelid specimens from the Middle Jurassic strata at Daohugou. These specimens are the most ancient anaxyelids known to date. Surprisingly, the Anaxyelidae complex from Daohugou is even more diverse than at Karatau, including not only Anaxyelinae, but also Syntexinae and probably Kempendajinae.

Materials and methods

The specimens were collected from Daohugou, Ningcheng County, Inner Mongolia, China (41°18'N, 119°13'E), and preserved in a layer of grey-yellow siltstone in the Jiulongshan Formation. The age of the fossiliferous beds at Daohugou is still controversial, but various researchers have dated the overlying ignimbrite radiometrically to Middle Jurassic or early Late Jurassic: 164–152 Ma (He *et al.* 2004, Liu *et al.* 2006). The palaeoclimate at Daohugou is interpreted to have been warm during the Middle Jurassic (Wang *et al.* 2013).

Photographs of the specimens were acquired using a Leica M205C stereo microscope equipped with a Leica

Description. Head and thorax black, abdomen dark, wing veins very dark, membrane without coloration. Antenna $0.6\times$ length of forewing, nearly filiform, slightly tapering apically; scape robust, $1.3\times$ wider than the first flagellomere; pedicel having the same shape as the first flagellomere, $2.7\times$ longer than wide; flagellum with 14 flagellomeres; flagellomeres cylindrical; first flagellomere $2.6\times$ longer than wide; posterior flagellomeres gradually decreasing in width and length, the ratio of lengths of flagellomeres is 100/88/71/62/58/55/50/50/50/48/46/44/35/54; subapical flagellomere $1.3\times$ longer than wide and $0.8\times$ length of the

first; terminal flagellomere rounded apically. Mesonotum with well-developed notauli, longitudinal and scuto-scutellar sulci. Mesoscutellum with pointed front edge, narrow and long, $1.2\times$ longer than wide. Forewing with costal area twice as wide as R vein before furcation; 1-Rs $2.7\times$ longer than 1-M; Rs + M $8\times$ longer than 2-M; 1-rs $1.2\times$ longer than 2r-rs; 3r-m inclined; 5-M $0.17\times$ length of 2 m-cu; 1-Cu $0.7\times$ length of 2-Cu; cell 1m-cu $2.2\times$ longer than wide; 1 m-cu arched; 2-1 A $0.4\times$ length of 3-1 A. Hind wing with cell r $2.9\times$ longer than wide; 1-Rs almost straight, 2-Rs strongly arched, meeting R at right angle; 1-M smoothly arched; 1-Cu very short, $0.2\times$ length of cu-a; 2-1 A $1.1\times$ longer than cu-a. Ovipositor strongly serrate apically, short, not protruding beyond abdominal tip.

Body length 11.7 mm, antenna length 4.8 mm, ovipositor length 2.9 mm, forewing length 7.5 mm.

Remarks. The holotype bears a transverse vein inside the costal area next to the R furcation in the left forewing but lacks such a vein in the right forewing. The costal area in both wings is perfectly preserved, so there is no doubt that it represents the natural condition. The paratype has both forewings damaged near the R furcation and it is impossible to discern the presence or absence of a transverse vein there. The SC vein is not characteristic of Syntexinae. The position of SC immediately adjacent to the R furcation is very unusual for sawflies (it is usually placed well basad of the R furcation). Hence, we presume that this cross-vein is not a real SC, but an individual aberration.

Subfamily ANAXYELINAE Martynov, 1925

Brachysyntexis Rasnitsyn, 1969

Type species. *Brachysyntexis* (*Syntexyela*) *brachyura* Rasnitsyn, 1968. By original designation. South Kazakhstan, Upper Jurassic.

Identification key to species

1. Forewing with cell 3r more than $2.1\times$ longer than pterostigma; SC absent; Rs + M as long as 2-M; 5-M as long as 3r-m. *B. tigris* Kopylov, 2018
Forewing with cell 3r less than $1.8\times$ longer than pterostigma 2
2. Forewing with cell 1m-cu $1.2\times$ longer than wide; SC present; hind wing with 1-Rs more than twice as long as 2-Rs *B. laticella* sp. nov.
Forewing with cell 1m-cu more than $1.5\times$ longer than wide; hind wing with 1-Rs less than $1.5\times$ longer than 2-Rs 3
3. Rs + M shorter than 2-M; 5-M shorter than 3r-m; costal area usually wider than R width; SC usually present 4
Rs + M as long as or longer than 2-M; 5-M as

- long as or longer than 3r-m; costal area narrower than R width; SC absent 10
4. Forewing with 4 + 5-M subequal 6-M; cell 3r subequal 1r *B. brevicornis* sp. nov.
Forewing with 4 + 5-M at least $1.5\times$ longer than 6-M; cell 3r at least $1.5\times$ longer than 1r. 5
5. Forewing with cell 1r twice as long as 2r; costal area vanishingly narrow; SC absent. *B. minuta* sp. nov.
Forewing with cell 1r as long as, or shorter than 2r; costal area usually wider than R vein; SC present 6
6. Forewing with 1r-rs shorter than 2-Rs and 2r-rs. 7
Forewing with 1r-rs longer than 2-Rs and as long as 2r-rs 8
7. Forewing with 1r-rs $0.3\times$ longer than 2-Rs; cell 3r $3\times$ longer than 2r *B. micrura* Rasnitsyn, 1969
Forewing with 1r-rs $0.7\times$ longer than 2-Rs; cell 3r $1.5\times$ longer than 2r *B. robusta* Zhang & Rasnitsyn, 2006
8. Forewing with cell 1r shorter than wide and shorter than cells 2r and 1m-cu; costal area narrower than vein R width. *B. nova* Rasnitsyn, 1969
Forewing with cell 1r longer than or as long as cells 2r and 1m-cu; costal area wider than vein R width 10
9. Forewing with cell 2 + 3rm widened apically, 3r-m longer than 2m-cu; R bifurcates in the middle between SC and pterostigma . . *B. rohweri* sp. nov.
Forewing with cell 2 + 3rm not widened apically, 3r-m shorter than 2m-cu; R bifurcates next to SC *B. brachyura* Rasnitsyn, 1968
10. Forewing with 1r-rs as long as 2-Rs; 2-Cu twice as long as 1-Cu; hind wing with m-cu joining M beyond r-m; 1-M sharply bent. . . . *B. acuta* sp. nov.
Forewing with 1r-rs longer than 2-Rs; 2-Cu as long as 1-Cu; hind wing with m-cu joining M before r-m; 1-M curved 11
11. Forewing with cell 1r as long as 2r; 3r-m proclined. *B. tenebrosa* Kopylov, 2018
Forewing with cell 1r $1.5\times$ longer than 2r; 3r-m vertical *B. sinensis* sp. nov.

Brachysyntexis sinensis sp. nov. (Fig. 2)
(urn:lsid:zoobank.org:act:8A4778CB-39A0-4746-BC73-6F63A0B5CF25)

Etymology. The species name is derived from Latin *Sina*—China.

Material. Holotype NIGP169522, part and counterpart impression in mudstone; imago, female; well-preserved body with both forewings and one hind wing; mesonotum not preserved, antenna incomplete.

Description. Head and thorax very dark, abdomen lighter, antennae and wing veins dark, membrane

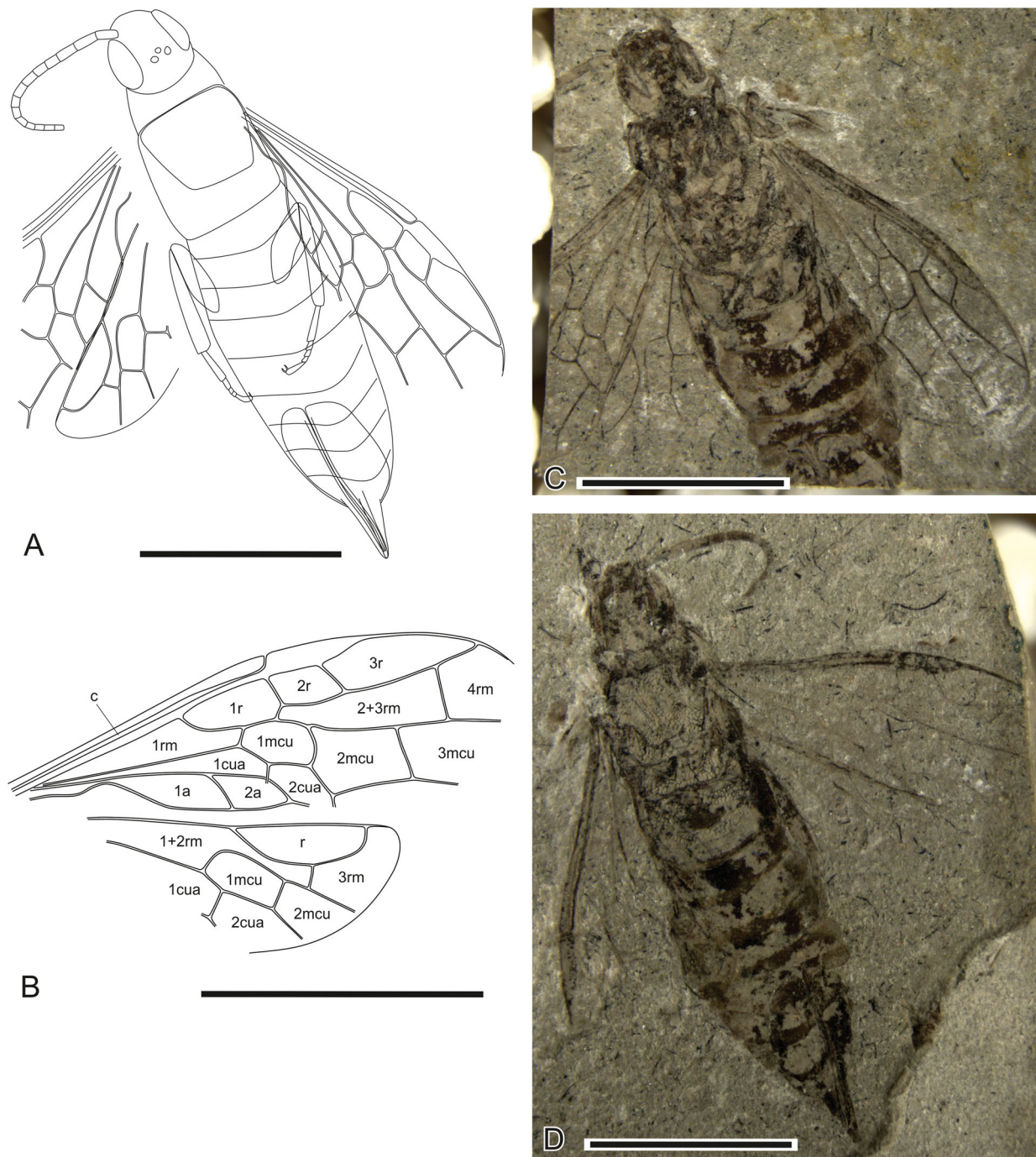


Fig. 2. *Brachysyntexis sinensis* sp. nov., holotype NIGP169522; A, Habitus drawing; B, Fore- and hind wings with cell names; C, Part photo; D, Counterpart photo. Scale bars = 5 mm.

without coloration. Antennae setaceous; flagellum with more than 12 flagellomeres; flagellomeres cylindrical, first flagellomere $2.2\times$ longer than wide; flagellomeres 2–5 $0.70\text{--}0.75\times$ length of the first; flagellomeres 6–12 $0.45\text{--}0.52\times$ length of the first; the width decreasing gradually; the last preserved flagellomere (12th) $0.55\times$ width of the first. Forewing with costal area $0.7\times$ length of R vein; SC absent; pterostigma $4.2\times$ longer than wide, reaching 0.28 of cell 3r length; 1-Rs strongly arched, $3.5\times$ longer than 1-M; Rs + M as long

as 2-M; 2-R $0.4\times$ length of 1r-rs; 1r-rs $0.9\times$ length of 2r-rs; the ratio of lengths of cells 1r/2r/3r is 33/19/48; 3r-m vertical; 5-M as long as 2m-cu; cell 1mcu $1.7\times$ longer than wide; 1-Cu $0.9\times$ length of 2-Cu; 2-1A $1.2\times$ longer than 3-1A. Hind wing with cell r $3.2\times$ longer than wide; 1-Rs and 2-Rs arched, 1-Rs $1.3\times$ longer than 2-Rs; r-m vertical, far beyond m-cu, 2-M $1.1\times$ longer than r-m; 1-M strongly arched; cell 1mcu $1.9\times$ longer than wide; 1-Cu $0.5\times$ length of 2-Cu. Ovipositor protrudes slightly beyond abdomen apex.

Body length 13.7 mm, ovipositor length 4.3 mm (from base to tip), 1.4 mm (from abdomen apex to tip); forewing length 9.8 mm.

Comparison. Based on the absence of SC, narrow costal area, arched 1-Rs, cell 3r as long as cells 1r and 2r together, long 5-M and long 1r-rs in the forewing, the new species is most similar to *B. tenebrosa* Kopylov, 2018. It differs from *B. tenebrosa* in having a long cell 1r and vertical 3r-m in the forewing, longer 2-M in the hind wing, a smaller wing size and a much lighter coloration.

***Brachysyntexis rohweri* sp. nov.** (Fig. 3A–C) (urn:lsid:zoobank.org:act:B9829FAF-47F6-426F-88DA-4BD119970D81)

Etymology. The species is named after American entomologist S.A. Rohwer (1887–1951), who described *Syntexis libocedrii*—the only extant species of Anaxyelidae.

Material. Holotype NIGP169523, part, without counterpart impression in mudstone; imago, female; well-preserved body with complete antennae; one forewing well preserved, another forewing and hind wings incomplete. Specimen NIGP169524 also possibly belongs to this species (see remarks below).

Description. Head and thorax dark, abdomen lighter, antennae dark and wing veins light, membrane without coloration. Antennae filiform, with 13 flagellomeres; scape and pedicel of the same width with flagellomere 1; the ratio of lengths of scape/pedicel/flagellomeres is 66/49/100/66/59/57/52/42/33/32/28/26/24/22/30; subapical flagellomere $0.8\times$ width of flagellomere 1; terminal flagellomere fusiform, pointed apically. Forewing with costal area $2.4\times$ width of R vein; SC transverse; pterostigma $3.4\times$ longer than, reaching 0.16 of cell 3r length; 1-Rs slightly s-shaped, $3.3\times$ longer than 1-M; Rs + M $0.47\times$ length of 2-M; 2-R $0.8\times$ length of 1r-rs; 1r-rs $0.8\times$ length of 2r-rs; the ratio of lengths of cells 1r/2r/3r is 28/24/48; 3r-m slightly proclined; 5-M $0.43\times$ length of 2m-cu; cell 1mcu $1.9\times$ longer than wide; 1-Cu $0.6\times$ length of 2-Cu; 2-1A $0.7\times$ length of 3-1A. Hind wing with cell r $4.8\times$ longer than wide; 1-Rs arched, 2-Rs strongly curved, 1-Rs $1.6\times$ longer than 2-Rs; r-m vertical, joining M beyond m-cu, 2-M $0.5\times$ length of r-m. Ovipositor does not protrude beyond abdomen apex. Body length 9.2 mm, antenna 3.6 mm, ovipositor 2.3 mm; forewing length 4.5 mm (preserved), 6.0 (estimated).

Comparison. Based on the wide costal area, presence of SC, 1r and 2r of subequal length, shape of cell 1mcu, short 5-M in the forewing and a similar size, the

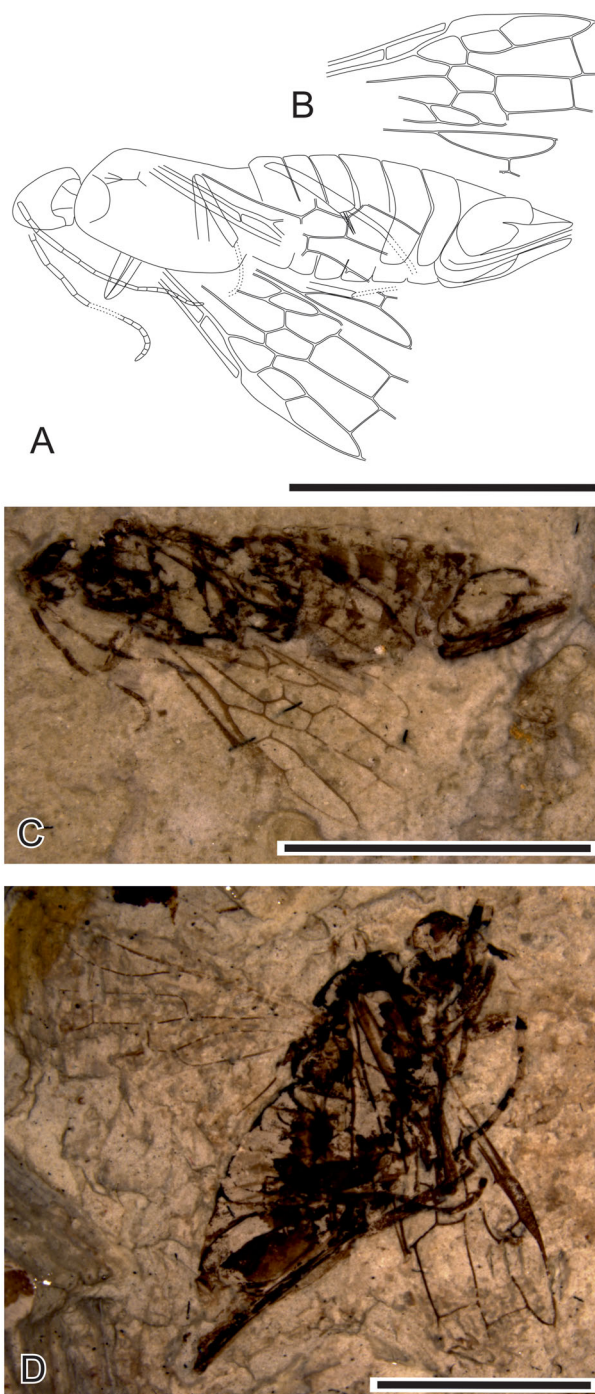


Fig. 3. A–C, *Brachysyntexis rohweri* sp. nov., holotype NIGP169523; A, Habitus drawing; B, Fore- and hind wings (scale bar is the same for A and B); C, Photo. D, *B. rohweri* (?), specimen NIGP169524. Scale bars = 5 mm.

new species is most similar to *B. brachyura*. It differs from *B. brachyura* in the filiform shape of the antennae, shorter ovipositor and r-m joining M beyond m-cu in the hind wing.

Remarks. Specimen NIGP169524 (Fig. 3D) has a similar venation and antennae, but differs in its significantly larger size: forewing length 9.5 mm. The reliable assignment of this specimen requires additional

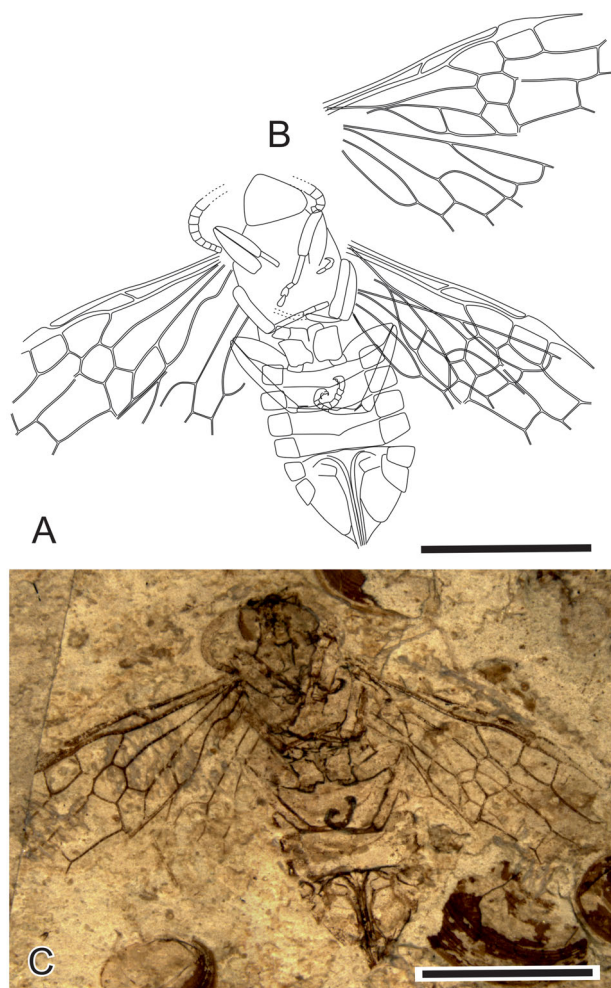


Fig. 4. *Brachysyntexis laticella* sp. nov., holotype NIGP169525; A, Habitus drawing; B, Fore- and hind wings; C, Photo. Scale bars = 5 mm.

material from Daohugou. Here we preliminarily assign it to *B. rohweri* (?).

***Brachysyntexis laticella* sp. nov.** (Fig. 4) (urn:lsid:zoobank.org:act:BB79F088-330C-4136-BF02-EEA56B29047A)

Etymology. The species name is derived from Latin *lata* (wide) and *cella* (cell), referring to the wide costal area and cell 1mcu in the forewing.

Material. Holotype NIGP169525, part, without counterpart impression in mudstone; imago, female; well-preserved body with fore- and hind wings complete; mesonotum not preserved, antennae incomplete.

Description. Head and thorax dark, abdomen lighter, antennae and wing veins dark, membrane without coloration, legs light, excepting dark tarsi. Antennae short, setaceous; flagellomeres cylindrical, very short: 0.9–1.1× longer than wide, strongly decreasing in length and width apically. Forewing with costal area 2.3×

wider than R vein; SC transverse; pterostigma 3.7× longer than wide; 1-Rs slightly s-shaped, 2.6× longer than 1-M; Rs + M 1.8× longer than 2-M; 2-R 0.7× length of 1r-rs; 1r-rs 0.8× length of 2r-rs; cell 1r 1.3× longer than 2r; 3r-m slightly inclined; 5-M as long as 2m-cu; cell 1mcu 1.1× longer than wide; 1-Cu as long as 2-Cu; 2-1A 1.3× longer than 3-1A. Hind wing with cell r 3.7× longer than wide; 1-Rs arched, 2-Rs strongly curved, 1-Rs 2.3× longer than 2-Rs; r-m arched, joining M beyond m-cu, 2-M 0.34× length of r-m; 1-M curved; cell 1mcu 2.0× longer than wide; 1-Cu 0.8× length of 2-Cu; 2-1A as long as 1-Cu. Ovipositor slightly protruding beyond abdomen apex. Body length 11.4 mm, ovipositor length 3.0 mm; forewing length 9.1 mm.

Comparison. Based on the wide costal area and presence of SC in the forewing, the new species is most similar to *B. brachyura* and *B. rohweri*. It differs from *B. brachyura* in its shorter ovipositor and r-m joining M beyond m-cu in the hind wing. It is distinguished from *B. rohweri* by the shape of the antennae. It is differentiated from both species in having a long Rs+M, short and wide cell 1mcu in the forewing and a much larger wing size. The new species is unique within *Brachysyntexis* in vein 1-Rs being more than twice as long as 2-Rs in the hind wing.

***Brachysyntexis brevicornis* sp. nov.** (Fig. 5) (urn:lsid:zoobank.org:act:87E5877A-B4DF-41DE-8E61-7071AB7A3974)

Etymology. The species name is derived from the Latin *brevis*—short and *cornu*—wing.

Material. Holotype NIGP169526, part, without counterpart impression in mudstone; imago, male; well-preserved body with complete antennae, fore- and hind wings; mesonotum not preserved.

Description. Head and thorax dark, abdomen lighter, antennae, legs and wing veins light, membrane without coloration. Antennae filiform, 0.9× length of forewing; scape, pedicel and flagellomeres cylindrical, scape 2.7× longer than wide and 1.2× longer than flagellomere 1; pedicel 3.1× longer than wide and 1.1× wider than flagellomere 1; the ratio of lengths of scape/pedicel/flagellomeres is 83/89/100/79/75/68/62/60/52/49/42/38/37/38. Forewing with costal area 1.1× wider than R vein; SC transverse; pterostigma 2.7× longer than wide, reaching 0.36 of cell 3r length; 1-Rs s-shaped, 2.8× longer than 1-M; Rs+M 0.6× length of 2-M; 2-R 1.5× longer than 1r-rs; 1r-rs 0.7× length of 2r-rs; the ratio of lengths of cells 1r/2r/3r is 34/22/44; 4 + 5-Rs 1.1× longer than 6-Rs; 3r-m vertical; 5-M 0.6× length of 2m-cu; cell 1mcu 1.8× longer than wide; 1-Cu 0.4× length of 2-Cu; cell 2mcu 1.3× longer than 1mcu; 2-1A 0.30× length of 3-1A. Hind wing with 1-Rs slightly arched; r-m vertical, joining M beyond

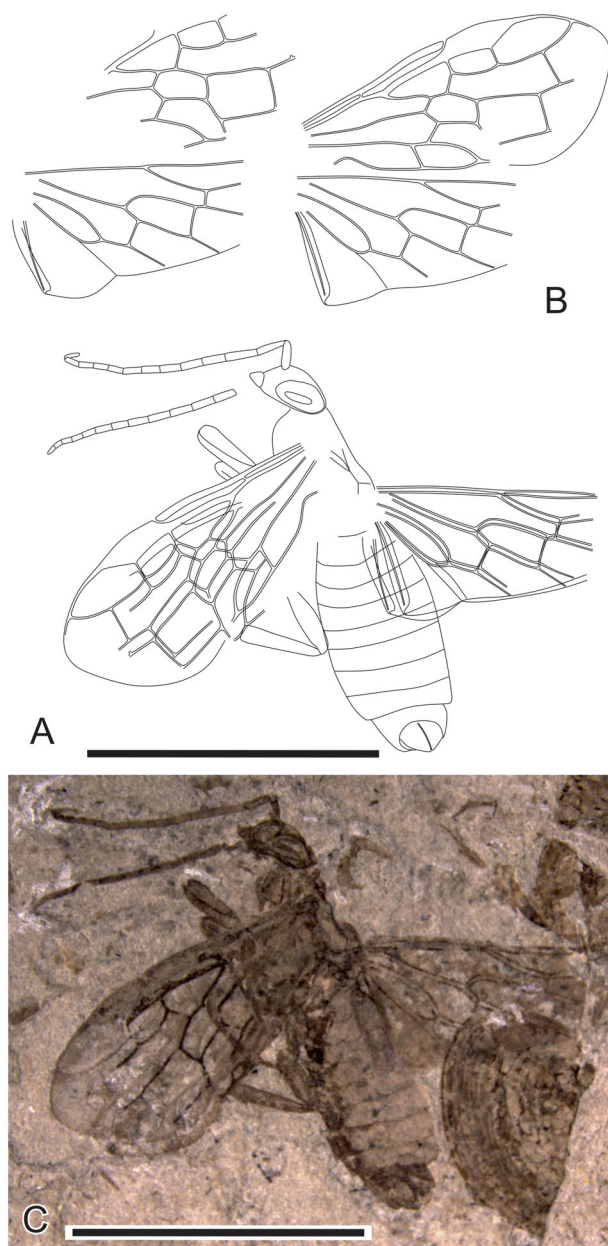


Fig. 5. *Brachysyntexis brevicornis* sp. nov., holotype NIGP169526; A, Habitus drawing; B, Fore- and hindwings (scale bar is the same for A and B); C, Photo. Scale bars = 5 mm.

m-cu, 2-M $0.5\times$ length of r-m; 1-M curved; cell 1mcu $2.3\times$ longer than wide; 1-Cu $0.4\times$ length of 2-Cu; 2-1 A $1.5\times$ longer than 1-Cu. Body length 7.2 mm, antennae 4.8 mm; forewing length 5.5 mm.

Comparison. The new species is unique within *Brachysyntexis* in having 4 + 5-Rs subequal to 6-Rs and much longer antennae. It also differs from other species, except *B. acuta* described below, in having a short 2-1 A in the forewing.

Brachysyntexis acuta sp. nov. (Fig. 6) (urn:lsid:zoobank.org:act:C637C01D-9E19-4394-B83D-65D7AD9F12AA)

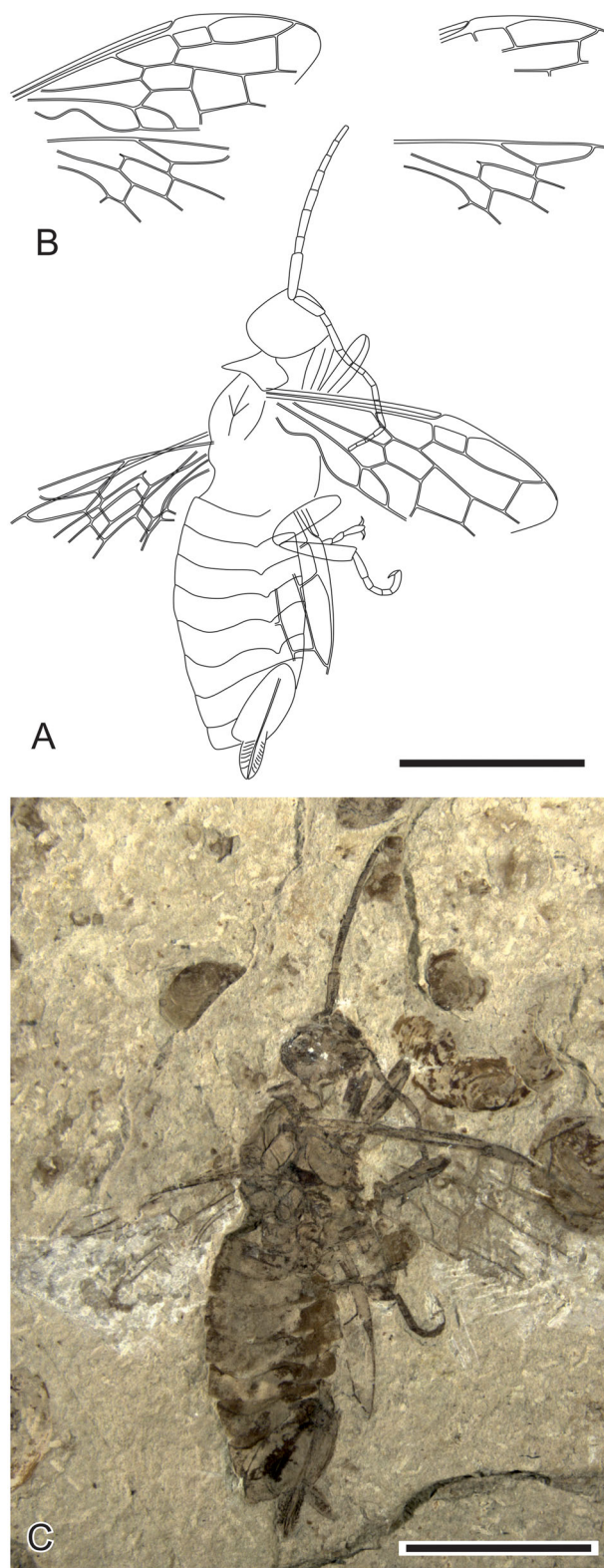


Fig. 6. *Brachysyntexis acuta* sp. nov., holotype NIGP169527; A, Habitus drawing; B, Fore- and hind wings (scale bar is the same for A and B); C, Photo. Scale bars = 5 mm.

Etymology. The species name is derived from the Latin *acutus*—sharp, referring to the peculiar shape of cell 1mcu in the hind wing.

Material. Holotype NIGP169527, part, without counterpart impression in mudstone; imago, female; well-preserved body with one fore- and both hind wings complete; mesonotum not preserved, antennae incomplete.

Description. Head and thorax very dark, abdomen lighter, antennae and wing veins dark, membrane without coloration. Antennae setaceous; scape robust, $4\times$ as long as wide and $1.7\times$ wider than as flagellomere 1; pedicel small, $1.9\times$ longer than wide and as wide as flagellomere 1; flagellomeres cylindrical, strongly decreasing in length and width apically; the last preserved flagellomere (11) $0.27\times$ length of and $0.32\times$ width of flagellomere 1. Forewing with costal area $1.2\times$ wider than R vein; SC absent; pterostigma $3.7\times$ longer than wide, reaching 0.21 of cell 3r length; 1-Rs almost straight, $3.2\times$ longer than 1-M; Rs+M $1.4\times$ longer than 2-M; 2-R $1.1\times$ longer than 1r-rs; 1r-rs as long as 2r-rs; the ratio of lengths of cells 1r/2r/3r is 34/19/47; 3r-m slightly inclined; 5-M $1.4\times$ longer than 2m-cu; cell 1mcu $2.0\times$ longer than wide; 1-Cu $0.4\times$ length of 2-Cu; 2-1 A $0.18\times$ length of 3-1 A. Hind wing with cell r $4.4\times$ longer than wide; 1-Rs straight, 2-Rs arched, 1-Rs $0.7\times$ length of 2-Rs; r-m vertical, joining M before m-cu, 2-M $0.4\times$ length of r-m; 1-M sharply bent, with a short extra vein stub; cell 1mcu $2.5\times$ longer than wide; 1-Cu $0.4\times$ length of 2-Cu; 2-1 A as long as 1-Cu. Ovipositor serrate, not protruding beyond abdomen apex. Body length 12.8 mm, ovipositor length 3.0 mm; forewing length 8.5 mm, hind wing length 6.0 mm.

Comparison. The new species is unique within *Brachysyntexis* in having a sharply bent M with an extra vein stub in the hind wing (hind wings are not preserved or very incomplete in *B. micrura*, *B. robusta*, *B. tigris* and *B. rohweri*). It also differs from other congeners in having a very short 2-1 A in the forewing (except *B. brevicornis*), and r-m joining M before m-cu in the hind wing (except *B. robusta*).

***Brachysyntexis minuta* sp. nov.** (Fig. 7) (urn:lsid:zoobank.org:act:1B849FDE-48B6-4C76-8324-05963E79D087)

Etymology. The species name is derived from the Latin *minus*—small.

Material. Holotype NIGP169528, part, without counterpart impression in mudstone; imago, female; mesonotum not preserved, antennae and ovipositor indistinct, wing veins barely discernible, hind wings incomplete.

Description. Body very dark, wing veins dark, membrane lacking coloration. Forewing with costal area very narrow; SC absent; pterostigma $3.9\times$ longer than wide, reaching 0.37 of cell 3r length; 1-Rs curved basally,

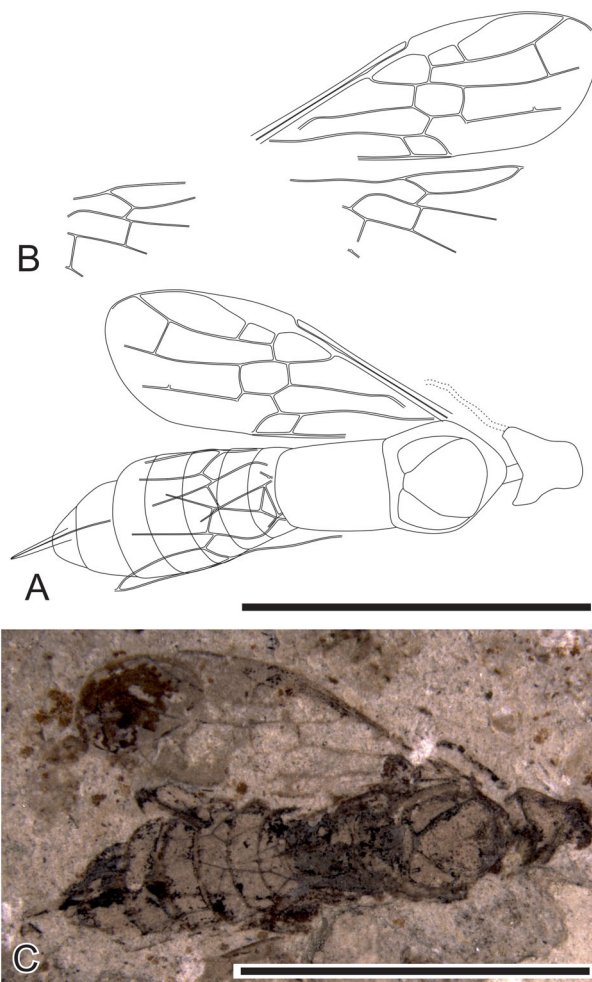


Fig. 7. *Brachysyntexis minuta* sp. nov., holotype NIGP169528; A, Habitus drawing; B, Fore- and hind wings (scale bar is the same for A and B); C, Photo. Scale bars = 5 mm.

$2.3\times$ longer than 1-M; Rs+M $0.4\times$ length of 2-M; 2-R $1.4\times$ longer than 1r-rs; 1r-rs $0.6\times$ length of 2r-rs; the ratio of lengths of cells 1r/2r/3r is 29/16/55; 4 + 5-Rs $1.8\times$ longer than 6-Rs; 3r-m vertical; cell 1mcu $1.4\times$ longer than wide; 1-Cu $0.7\times$ length of 2-Cu; 2 m-cu lost excepting a short stub on Cu; 2-1 A $0.66\times$ length of 3-1 A. Hind wing with cell r $5.3\times$ longer than wide; 1-Rs slightly arched forwards, 2-Rs arched backwards, 1-Rs $0.28\times$ length of 2-Rs; r-m strongly inclined, joining M before m-cu, 2-M $0.4\times$ length of r-m; 1-M curved; cell 1mcu $2.3\times$ longer than wide; 1-Cu $0.4\times$ length of 2-Cu. Body length 7.7 mm; forewing length 5.2 mm.

Comparison. The new species is unique within *Brachysyntexis* in having cell r more than $5\times$ longer than wide, 1-Rs very short and r-m strongly inclined in the hind wing.

***Brachysyntexis* spp. (incertae sedis; Fig. 8A–D)**

NIGP169529. *Brachysyntexis* sp. (Fig. 8A). Part, without counterpart impression in mudstone; imago,

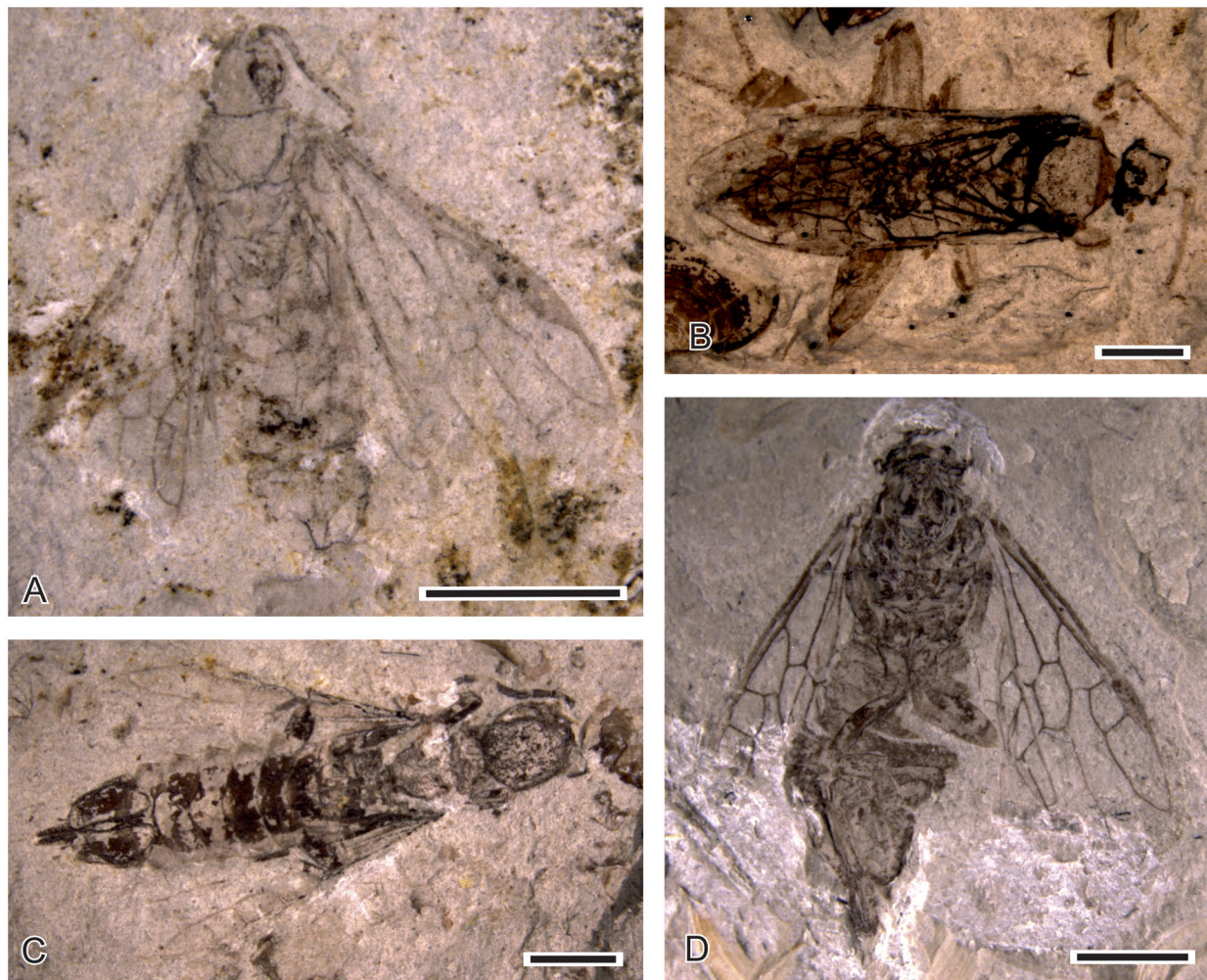


Fig. 8. **A**, *Brachysyntexis* sp., specimen NIGP169529. **B**, *Brachysyntexis* sp., specimen NIGP169530. **C**, *Brachysyntexis* sp. cf. *sinensis*, specimen NIGP169531. **D**, *Brachysyntexis* sp. cf. *brachyura*, specimen NIGP169532. Scale bars = 2 mm.

female; body and wings poorly preserved. With forewing 4.8 mm long, this is the smallest representative of *Brachysyntexis*. The state of preservation does not allow its assignment to any species.

NIGP169530. *Brachysyntexis* sp. (Fig. 8B). Part, without counterpart impression in mudstone; imago, female; body poorly preserved, wings badly damaged. Description is impossible owing to poor preservation. However, the preserved part of the forewing with extremely long cell 3r leaves no doubt that this specimen belongs to a new species.

NIGP169531. *Brachysyntexis* sp. cf. *B. sinensis*. (Fig. 8C). Part, without counterpart impression in mudstone; imago, female; wing venation almost completely lost. Owing to its poorly preserved venation, reliable specific identification is impossible. Based on its similar size, antennae and ovipositor structure, the specimen is most similar to *Brachysyntexis sinensis*.

NIGP169532. *Brachysyntexis* sp. cf. *B. brachyura*. (Fig. 8D). Part and counterpart impression in mudstone; imago, female; body and forewings well preserved, but hind wings and antennae missing. The absence of the hind wings and antennae prevents reliable specific

identification. Based on the size and forewing venation, the specimen is most similar to *B. brachyura* from Karatau.

Discussion

Thus far, Jurassic anaxyelids have been described only from the Middle–Late Jurassic of Karatau (Kazakhstan). At Karatau, Anaxyelidae is represented by 27 specimens, seven genera and 21 species. All Karatau anaxyelids belong to Anaxyelinae (Martynov 1925, Rasnitsyn 1963, 1968, 1969, Kopylov 2018). One specimen of Jurassic Anaxyelidae was also noted from Khoutiyn-Khotgor (Late Jurassic of Mongolia), but its generic, and even subfamily, identification is impossible owing to its poor preservation (Kopylov 2018).

During revision of the NIGPAS Daohugou collection, we found 41 specimens of Anaxyelidae, among which 34 specimens were identified as Anaxyelinae, two as Syntexinae and another five probably belonging to Kempendajinae. These specimens represent the oldest occurrences of Anaxyelidae in the fossil record.

Syntexinae and Kempendajinae are noted in Jurassic strata for the first time. Previously, they were known only from Cretaceous deposits.

Anaxyelinae is represented at Daohugou by *Brachysyntexis*, *Urosyntexis* and *Syntexyela*. The new discoveries of *Urosyntexis* and *Syntexyela* fill the morphological gap between these two closely related genera, such that a clear distinction between these genera is no longer possible. A detailed comparison of *Urosyntexis* and *Syntexyela* is needed to reveal any additional distinctive characters or to synonymize these genera. In this paper, 11 specimens attributed to *Brachysyntexis* are described including six as holotypes for new species and one tentatively assigned to *B. rohweri*. Another four specimens can not be reliably assigned to any established species.

Syntexinae from Daohugou is represented by a single species, *Daosyntexis primus*, which represents the first discovery of this subfamily in the Jurassic. Surprisingly, based on the fore- and hind wing venation (presence of both 1r-rs and 2r-rs, a rather short 3r cell in the forewing, arched 1-M and the absence of m-cu in the hind wing), the new Jurassic species is much more similar to the extant *S. libocedrii*, than to other fossil (Cretaceous) syntexines. However, the forewing venation of the majority of Cretaceous syntexines is highly apomorphic towards extant *Syntexis*. *Eosyntexis* and *Cretosyntexis* having lost 1r-rs from the forewing (Rasnitsyn 1990, Rasnitsyn *et al.* 1998, Rasnitsyn & Martynetz-Delclos 2000, Ortega-Blanco *et al.* 2008). Another two undescribed genera from Baissa (Lower Cretaceous of Transbaikalia) and Obeshchayushchiy (Upper Cretaceous of Magadan region) also have very distinctive venation. The first has an extremely elongated 3r cell, the second has the forewing venation strongly displaced basad and no tubular veins in the apical third of the wing (Kopylov 2019). Thus, extant *Syntexis* is a sister group to the majority of fossil Syntexinae. In contrast, *Daosyntexis* has very plesiomorphic forewing venation that is very similar to that of *Syntexis*, which can be treated as the bauplan for this subfamily. A similar forewing venation is also noted in one undescribed genus from Khasurti (Lower Cretaceous of Transbaikalia), but it differs from *Syntexis* and *Daosyntexis* in having m-cu present in the hind wing (Kopylov 2019).

Unidentified Kempendajinae (?) specimens need additional research and comparison with Cretaceous anaxyelids for reliable identification. Presently, this subfamily is represented by only one described species, *Kempendaja jacutensis*, from the Early Cretaceous of Kempenday, Yakutia (Rasnitsyn 1968) and one undescribed species from Bon-Tsagan, Mongolia (Kopylov 2019).

Daohugou and Karatau, two key Jurassic fossil insect Lagerstätten, host highly similar fossil Hymenoptera assemblages.

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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.
- HE, H.Y., WANG, X.L., ZHOU, Z.H., ZHU, R.X., JIN, F., WANG, F., DING, X. & BOVEN, A., 2004. ⁴⁰Ar/³⁹Ar dating of ignimbrite from Inner Mongolia, northeastern China, indicates a post-Middle Jurassic age for the overlying Daohugou Bed. *Geophysical Research Letters* 31, L20609.
- KOPYLOV, D.S., 2018. Forgotten giants: new Anaxyelidae (Hymenoptera) from the Jurassic of Karatau. *Zootaxa* 4514, 332–340.
- KOPYLOV, D.S., 2019. New anaxyelids (Hymenoptera: Anaxyelidae) from the Cretaceous of Asia. *Zootaxa* 4603, 341–353.
- LINNAEUS, C., 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Edition 10, Laurentius Salvius, Stockholm, 824 pp.
- LIU, Y., LIU, Y., JI, S. & YANG, Z., 2006. U–Pb zircon age for the Daohugou Biota at Ningcheng of Inner Mongolia and comments on related issues. *Chinese Science Bulletin* 51, 2634–2644.

- 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.
- ORTEGA-BLANCO, J., RASNITSYN, A.P. & DELCLÓS, X., 2008. First record of Anaxyelid woodwasps (Hymenoptera: Anaxyelidae) in Lower Cretaceous Spanish amber. *Zootaxa* 1937, 39–50.
- RASNITSYN, A.P., 1963. Pozdnezyurskie pereponchatokrylye Karatau [Late Jurassic Hymenoptera of Karatau]. *Paleontologicheskij Zhurnal [Paleontological Journal]* 1, 86–93. (Russian)
- RASNITSYN, A.P., 1968. Novye mezozoiskiye pilil'shiki [New Mesozoic sawflies (Hymenoptera, Symphyta)]. In *Yurskiye Nasekomye Karatau [Jurassic Insects of Karatau]*. ROHDENDORF, B.B., ed., Nauka, Moscow, 190–236. (Russian)
- RASNITSYN, A.P., 1969. Proiskhozhdenie i evoliutsiia nizshikh pereponchatokrylykh [Origin and Evolution of the Lower Hymenoptera]. Proceedings of the Paleontological Institute of the USSR Academy of Sciences, Nauka, Moscow, 196. (Russian)
- RASNITSYN, A.P., 1980. Proiskhozhdenie i evoliutsiia pereponchatokrylykh nasekomykh [The origin and evolution of Hymenoptera]. Proceedings of the Paleontological Institute of the USSR Academy of Sciences, Nauka, Moscow, 192 pp. (Russian)
- RASNITSYN, A.P., 1990. Hymenoptera = Vespida. In *Pozdne-Mezozojskie Nasekomye Vostochnogo Zabajkal'ya [Late Mesozoic Insects of Eastern Transbaikalia]*. RASNITSYN, A.P., ed., Proceedings of the Paleontological Institute, Academy of Sciences USSR 239. Nauka, Moscow, 177–205. (Russian)
- RASNITSYN, A.P. & MARTINEZ-DELCLÓS, X., 2000. Wasps (Insecta: Vespida = Hymenoptera) from the early Cretaceous of Spain. *Acta Geológica Hispánica* 35, 65–95.
- RASNITSYN, A.P. & ZHANG, H., 2004. Composition and age of the Daohugou hymenopteran (Insecta, Hymenoptera = Vespida) assemblage from Inner Mongolia, China. *Palaeontology* 47, 1507–1517.
- RASNITSYN, A.P., JARZEMBOWSKI, E.A. & ROSS, A.J., 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. *Cretaceous Research* 19, 329–391.
- ROHWER, S.A., 1915. A remarkable new genus of Cephidae. *Proceedings of the Entomological Society of Washington* 17, 114–117.
- SMITH, D.R., 1978. Suborder Symphyta. (Xyelidae, Pararchxyelidae, Parapamphiliidae, Xyelydidae, Karatavidae, Gigasiricidae, Sepulcidae, Pseudosiricidae, Anaxyelidae, Siricidae, Xiphydriidae, Paroryssidae, Xyelotomidae, Blasticotomidae, Pergidae). In *Hymenopterorum Catalogus (Nova Editio)*. VAN DER VECHT, J. & SHENEFELT, R.D., eds., W. Junk Publishers, The Hague, 1–193.
- TAEGER, A., BLANK, S.M. & LISTON, A.D., 2010. *World Catalog of Symphyta (Hymenoptera)*. Zootaxa, Magnolia Press, Auckland, New Zealand, 1064 pp.
- WANG, B., ZHANG, H., JARZEMBOWSKI, E.A., FANG, Y. & ZHENG, D., 2013. Taphonomic variability of fossil insects: a biostratigraphic study of Palaeontinidae and Tettigarctidae (Insecta: Hemiptera) from the Jurassic Daohugou Lagerstätte. *Palaios* 28, 233–242.
- WICKMAN, B.E., 1967. Life history of the incense-cedar wood wasp, *Syntexis libocedrii* (Hymenoptera: Syntexidae). *Annals of the Entomological Society of America* 60, 1291–1295.
- ZHANG, H. & RASNITSYN, A.P., 2006. Two new anaxyelid sawflies (Insecta, Hymenoptera, Siricoidea) from the Yixian Formation of western Liaoning, China. *Cretaceous Research* 27, 279–284.