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Revision of *Anomopterella* Rasnitsyn, 1975 (Insecta, Hymenoptera, Anomopterellidae) with two new Middle Jurassic species from northeastern China

LONGFENG LI, CHUNGKUN SHIH and DONG REN✉

College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, 100048 Beijing, China; ✉ rendong@mail.cnu.edu.cn

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Abstract: New *Anomopterella* Rasnitsyn, 1975, wasps from the Jiulongshan Formation (Bathonian/Callovian) at Daohugou (Inner Mongolia of China), with well-preserved wings, body, antennae and tarsi, document relationship among species and enhance our understanding of the morphology of the extinct family Anomopterellidae Rasnitsyn, 1975. Based on eight well-preserved specimens, we describe, *A. pygmea* sp. n. and *A. brevis* sp. n., describe new materials of *A. ovalis* Li, Rasnitsyn, Shih & Ren, 2013, and *A. ampla* Li, Rasnitsyn, Shih & Ren, 2013, emend the genus in Anomopterellidae (*A. pygmea* sp. n. with toruli and eyes), and provide a determination key to species of the genus, including four specimens outside the formal classification.

Key words: Fossil insect assemblage, new species, extinct parasitoids, Middle Jurassic, Jiulongshan Formation, Daohugou, China.

Introduction

Anomopterellidae, a Mesozoic family of wasps, was originally classified as a family of the superfamily Evanioidea, and later as a subfamily of the family Praeaulacidae (Rasnitsyn 1975). In 2013, Anomopterellidae was restored as a family with three genera: *Anomopterella* Rasnitsyn, 1975, *Synaphopterella* Li, Rasnitsyn, Shih & Ren, 2013 and *Choristopterella* Li, Rasnitsyn, Shih & Ren, 2013, on the basis of new fossil specimens from Daohugou and phylogenetic analysis of the superfamily Evanioidea (Li et al. 2013a). These analyses also suggest that the extinct family Praeaulacidae is the most basal group of Evanioidea, and Anomopterellidae is the second family of Evanioidea present in the upper Middle Jurassic of China (Li et al. 2013a). *Anomopterella* Rasnitsyn, 1975 was erected with the type species *A. mirabilis* Rasnitsyn, 1975 from the Upper Jurassic of the Karabastau Formation in Kazakhstan (Rasnitsyn 1975).

In addition to the type species *A. mirabilis* from the Upper Jurassic Kazakhstan, *A. gobi* Rasnitsyn, 2008 occurs in the Upper Jurassic of Mongolia, while *A. huangi* Zhang & Rasnitsyn, 2008, *A. coalita* Li, Rasnitsyn, Shih et Ren, 2013, *A. brachysteli* Li, Rasnitsyn, Shih & Ren, 2013, *A. ampla* Li, Rasnitsyn, Shih & Ren, 2013, *A. divergens* Li, Rasnitsyn, Shih & Ren, 2013 and *A. ovalis* Li, Rasnitsyn, Shih & Ren, 2013 occur in the Upper Middle Jurassic Jiulongshan Formation at Daohugou in northeastern China (Rasnitsyn 1975, 2008; Zhang & Rasnitsyn 2008; Li et al. 2013a). The species from Daohugou indicate that this genus varies in the wing venation (e.g. forewing with crossvein 1r-rs is absent or rudimentary like a stub; crossvein cu-a is interstitial or slightly postfurcal) and in the shape of the first metasomal segment (e.g. broad triangular, elongated triangular and particularly narrow with a short petiole).

In this study, we describe eight new well-preserved fossil specimens of *Anomopterella* from the Middle Jurassic Jiulongshan Formation at Daohugou Village in Inner Mongolia, China, which belongs to the Yanliao Biota (Ren et al. 2010, 2012). The Daohugou locality contains abundant and diverse insect assemblages, comprising complete specimens of Ephemeroptera (reference missing), Plecoptera (Liu et al. 2007), (Huang et al. 2008), Mantophasmatodea (Huang et al. 2008), Coleoptera (Chang et al. 2009), Trichoptera (Wang et al. 2009; Gao et al. 2013a,b), Megaloptera (Wang & Zhang 2010), Nakridletia (Vršanský et al. 2010), Lepidoptera (Huang et al. 2010; Zhang et al. 2013), Dermaptera (Shang et al. 2011; Zhao et al. 2011), Grylloblattodea (Cui et al. 2011, 2012), Orthoptera (Gu et al. 2012), Heteroptera (Dong et al. 2012), Odonata (Li et al. 2013d), Blattaria (e.g. Wei et al. 2013), Homoptera (Li et al. 2013c), Mecoptera (Wang et al. 2013), Neuroptera (Shi et al. 2013), Diptera (Shi et al. 2013) and Hymenoptera (Li et al. 2013a,b). According to the Ar-Ar and SHRIMP U-Pb dating, the Jiulongshan Formation corresponds to the upper parts of the Middle Jurassic (Bathonian/Callovian boundary, 165 Ma — Ren et al. 2012).

The specimens reported herein are from the Middle Jurassic Jiulongshan Formation of Daohugou Village, Shantou Township, Ningcheng County, Chifeng City, Inner Mongolia, China (Fig. 1). The age of the Daohugou fossil-bearing beds is likely older than or equal to 165 Ma (Chen et al. 2004).

On the basis of the new characters of four of the newly collected specimens, we established *A. pygmea* sp. n., *A. brevis* sp. n., and re-describe *A. ovalis*, and *A. ampla*. The additional four specimens remain outside the formal species-level classification within the genus *Anomopterella*. We emend the diagnosis of *Anomopterella* Rasnitsyn, 1975 and add a taxonomic key to all known species.

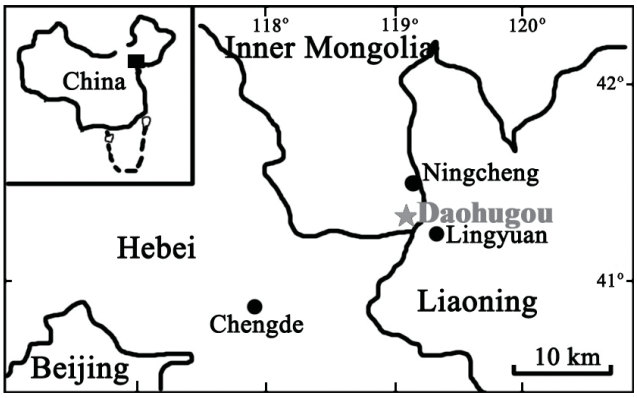

Fig. 1. Map showing the locality at Daohugou Village (Inner Mongolia, China) with the Middle Jurassic Jiulongshan Formation.

Materials and methods

This study is based on eight specimens collected near Daohugou Village and housed in the Key Lab of Insect Evolution and Environmental Changes, the College of Life Sciences, Capital Normal University in Beijing, China (CNUB; Dong Ren, Curator). The specimens were examined and photographed using a Leica MZ12.5 dissecting microscope with a Leica DFC 500 digital camera and illustrated with the aid of a camera lucida attached to the microscope. The line drawings were drawn by CorelDraw 12.0 and Adobe Photoshop CS5.

Wasp wing venation terminology is adapted from Rasnitsyn (1975), following the general concept of Comstock and Needham (1898): C — Costa, R — Radial, Rs — Radial sector, M — Media, Cu — Cubitus, 1A — the first Anal, 1r-rs — the first Radial crossvein, 2r-rs — the second Radial crossvein, 3r-m — the second Radiomedial crossvein, 1m-cu — the first Mediocubital crossvein, 2m-cu — the second Mediocubital crossvein, cu-a — the first Anal crossvein.

The Daohugou fossil-bearing beds consist of tuffaceous grand conglomerates, tuffaceous conglomerates, tuffaceous siltstones, tuffaceous mudstones, tuffaceous shales, and volcanic breccias. In these layers, the layer of a tuffaceous conglomerate contains abundant fossils. The paleoclimate of this area is usually interpreted as humid and warm-temperate (Ren et al. 2010, 2012).

Systematic paleontology

Order: **Hymenoptera** Linnaeus, 1758
Suborder: **Apocrita** Gerstaecker, 1867
Superfamily: **Evanioidea** Latreille, 1802
Family: **Anomopterellidae** Rasnitsyn, 1975
Genus: *Anomopterella* Rasnitsyn, 1975

Type species: *Anomopterella mirabilis* Rasnitsyn, 1975.

Type locality: Karatau, south Kazakhatan. Late Jurassic Karabastau Formation.

Differential diagnosis (improved after Rasnitsyn 1975): Body size under 8 mm. Head medium size, usually as wide as or narrower than thorax. Antenna with 18 or more segments. When preserved, legs long, tarsus with five segments. Mesosoma short and high. Propodeum high, strongly convex or quite short, with posterior margin subvertical in lateral view. Forewing venation with 1r-rs absent or rudimentary like a stub, M+Cu not aligned with RS+M, 1-M present, 2r-rs and 2m-cu basad of 3r-m. Vein cu-a interstitial or slightly postfurcal. Metasoma broadest beyond its midlength, with the first segment gradually broadening distally and longer than any other segments. Ovipositor short and only slightly extending beyond metasomal apex, with sheaths shorter than basal sclerite.

Composition: Type species: *A. huangi*, *A. gobi*, *A. coalita*, *A. brachysteli*, *A. ampla*, *A. divergens*, *A. ovalis*, *A. pygmea* sp. n. and *A. brevis* sp. n.

Stratigraphic and paleogeographic range: Upper Jurassic Karabastau Formation in south Kazakhstan (*A. mirabilis*), Upper Jurassic Shar-Teg Formation in southwestern Mongolia (*A. gobi*); upper Middle Jurassic Jiulongshan Formation at Daohugou in northeastern China (*A. huangi*, *A. coalita*, *A. brachysteli*, *A. ampla*, *A. divergens*, *A. ovalis*, *A. pygmea* and *A. brevis* sp. n.).

Remarks: *Anomopterella* was erected based on 2 specimens (Rasnitsyn 1975). After studying ten (six with part and counterpart) well-preserved fossil specimens attributed to *Anomopterella*, we added diagnostic characters of the head, body and forewings (Li et al. 2013a). In this paper, after studying an additional eight specimens (one with part and counterpart), we improve diagnostic characters with well-preserved body, complete antenna and tarsus of legs. *A. pygmea* sp. nov. is the first species of Anomopterellidae with clearly preserved toruli and eyes.

Anomopterella pygmea sp. n.
(Figs. 2, 4A)

Derivation of name: From the Latin word "*pygmea*" meaning "scrubby", referring to the small body size of this wasp.

Type material: CNU-HYM-NN-2012-045, a well-preserved complete female (Fig. 2A).

Type horizon and locality: Near Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. Jiulongshan, the late Middle Jurassic.

Differential diagnosis: Antenna with 23 segments. Propodeum short, slightly narrower than metanotum or metapostnotum. Forewing with 1-Rs originating more distal of pterostigma base, 1r-rs absent, 3-Rs longer than 3r-m, cu-a interstitial. Metasoma short with first metasomal segment particularly narrow like a distinct petiole, remaining part round.

Description: A female wasp preserved in dorsal view, body and wings well preserved and veins clearly discernible. Small body size (4.4 mm long, excluding antennae), 1.1 mm wide (Fig. 2A). Head and mesosoma mostly dark.

Head round, nearly as long as wide (length 0.8 mm, width 0.9 mm). Compound eyes large and symmetrically located on both sides of the head; two ocelli round with diameter of about 0.1 mm; antenna with 25 segments and gradually thinner from base to apical; two toruli present and in contact

with radicles; scape long and thickened apically, distinctly longer than radicle, but slightly longer than pedicel (scape length 0.25 mm; radicle length 0.12 mm, pedicel length 0.23 mm); flagellomeres with basal eleven segments nearly as long as wide, twelfth to apex gradually becoming shorter and narrower.

Mesosoma approximately 1.7 mm long and 1.1 mm wide, about 1.6 times as long as wide; mesonotum long and broad, but the boundary and shape of mesoscutum and scutellum unknown; metanotum nearly as wide as metapostnotum, both very short; propodeum longer than metanotum and metapostnotum combined, but nearly as wide.

Legs partly preserved, but hind legs complete; hind femur about 5.5 times as long as wide and nearly as wide as the maximal width of tibia; hind tibia thin basally and gradually swollen toward apex, nearly as long as hind femur; hind tarsus consisting of 5 segments, much narrower than hind tibia, first segment distinctly longer than any other segments of hind tarsus.

Wings well preserved, forewing 3.6 mm long and 1.5 mm wide, with 1-Rs (0.3 mm) longer than 1-M (0.2 mm) and much longer than its distance (0.1 mm) to pterostigma; pterostigma long, about 4.5 times as long as wide (length 0.9 mm, width 0.2 mm); 1r-rs absent; 2r-rs (0.4 mm) issuing from pterostigma nearly at the apex of it, about 2 times as long as the width of pterostigma; 3-Rs longer than 3r-m (3-Rs length 0.3 mm, 3r-m length 0.2 mm); cell 3r broad, 2.4 times as long as wide (length 1.2 mm, width 0.5 mm); cell 2+3rm wider than 2mcu, in contact with 1mcu by a point; cell 1mcu nearly rectangle, 2 times as long as wide (length 0.4 mm, width 0.2 mm); cu-a interstitial (0.3 mm long) and curved, nearly as long as 1-Rs; cell cua broad, 2 times as wide as 1mcu. Hind wing 1.8 mm long and 0.6 mm wide, with 1-Rs, 1-M and Rs+M forming "Y-shape", 1-Rs nearly as long as 1-M (both length about 0.1 mm), cu-a present and curved.

Metasomal short with 6 segments (excluding propodeum), first metasomal segment particularly narrow like a distinct petiole, elongate triangular, 1.5 times as long as wide (length 0.6 mm, maximum width 0.4 mm); remaining part round in dorsal view, the second segment transversally ellipse, distinctly shorter and wider than first; the third segment slightly shorter and wider than the second, the fourth to sixth segments gradually becoming shorter and narrower.

Dimensions (in mm): Body length 4.4; length of head 0.8, width 0.9; length of antenna 2.8; length of mesosoma 1.7, width 1.1; length of forewing 3.6, width 1.5; length of hind wing 1.8, width 0.6; length of first metasomal segment 0.6, width 0.4, length of second metasomal segment 0.4, width 1.1; length of remaining metasomal segments 1.1, maximal width 1.4; length of hind leg: femur 1.2, tibia 1.2, tarsomeres I–V: 0.24, 0.22, 0.17, 0.17, 0.15.

Anomopterella brevis sp. n.
(Figs. 3A–B, 4B)

Derivation of name: From the Latin word "brevis" meaning "short", referring to the forewing with 3-Cu very short.

Type material: CNU-HYM-NN-2012-043P/C (Fig. 3A–B).

Type horizon and locality: Near Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. Jiulongshan, the late Middle Jurassic.

Differential diagnosis: Forewing with 1-Rs origin quiet away from pterostigma base, 1r-rs rudimentary like a short stub, cu-a postfurcal, 3-Cu short, about 1/2 length of 1m-cu. First metasomal segment short, comparatively thin basally but broadened apically.

Description of new material: Body mostly dark. A wasp preserved in dorsal view, sex unknown, body and wings partly preserved but veins clearly discernible. Small body size (3.7 mm long as preserved, excluding antennae), 1.6 mm wide (Fig. 3A–B).

Head round, nearly 0.6 times as long as wide (length 0.5 mm, width 0.8 mm). Antenna with about 23 segments and gradually thickened from base to tenth; scape short and thick, distinctly longer and wider than radicle; flagellomeres with basal ten segments much longer than wide, the maximum length about 2.7 times as long as the maximum width, eleventh to apex gradually becoming shorter and narrower.

Mesosoma broad, nearly as long as wide. Legs partly preserved, fore tibia distinctly shorter and narrower than hind tibia, hind femur slightly wider than hind tibia, hind tibia thin basally and gradually swollen toward apex.

Wings well preserved, forewing 4.0 mm long and 1.6 mm wide, with 1-Rs (0.4 mm) distinctly longer than 1-M (0.1 mm); 1r-rs present, like a very short stub on Rs, Rs geniculate; 2r-rs (0.4 mm) issuing from pterostigma nearly at the apex, about 2 times as long as the width of pterostigma; 3-Rs nearly as long as 3r-m (lengths of both 0.2 mm); cell 3r broad, 2.3 times as long as wide (length 1.4 mm, width 0.6 mm); cell 2+3rm nearly as wide as 2mcu, in contact with 1mcu by a point; cell 1mcu nearly rectangle, about 2.5 times as long as wide (length 0.5 mm, width 0.2 mm); cu-a postfurcal (0.3 mm long) and curved. Hind wing with 1-Rs, 1-M and Rs+M forming "Y-shape", 1-Rs (0.2 mm) longer than 1-M (0.1 mm), cu-a present and curved.

Metasomal short with 5 segments as preserved (excluding propodeum), first metasomal segment short, comparatively thin basally but broadened apically (length 0.6 mm, maximum width 0.6 mm); remaining part round in dorsal view, the second segment transversally triangular, distinctly wider than first; the remaining segments distinctly shorter than the second.

Dimensions (in mm): Body length 3.7; length of head 0.5, width 0.8; length of antenna 3.4; length of mesosoma 1.6, width 1.6; length of forewing 4.0, width 1.6; length of first metasomal segment 0.7, maximum width 0.6.

Anomopterella ovalis Li, Rasnitsyn, Shih & Ren, 2013
(Figs. 3C, 4C)

2013 *Anomopterella ovalis* Li, Rasnitsyn, Shih & Ren, p. 12, fig. 8

New material: CNU-HYM-NN-2012-044, collected near Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China, the Middle Jurassic. The new material is considered as *A. ovalis* Li, Rasnitsyn, Shih & Ren, 2013 mainly due to the following characters: forewing with

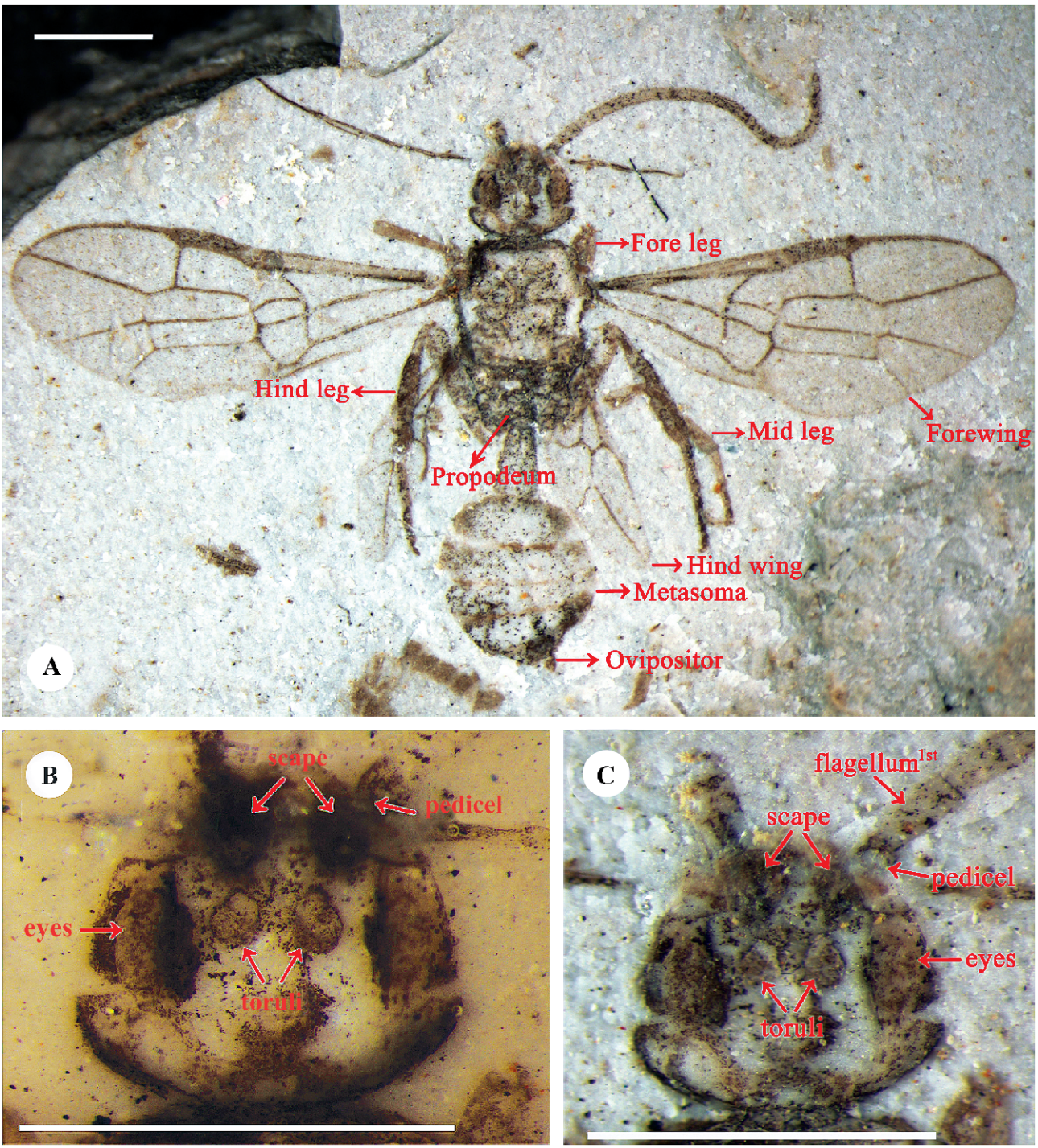

Fig. 2. *Anomopterella pygmea* sp. n., Holotype CNU-HYM-NN-2012-045. **A** — Habitus; **B** — Interpretation of head examined under alcohol; **C** — Interpretation of head examined in the absence of alcohol. Scale bars: 1 mm.

1r-rs rudimentary, like a very short stub on Rs, 3-Rs long, cu-a postfurcal and first metasomal segment elongate triangular.

Description of new material: A wasp preserved in dorsal view, body and wings partly preserved but veins clearly discernible. Small body size (5.2 mm long, excluding antennae), 1.1 mm wide (Fig. 3C).

Head round, 2/3 times as long as wide (length 0.6 mm, width 0.9 mm). Antenna with about 23 segments and gradually thickened from base to tenth; scape short and thick, nearly as long and wide as radicle; flagellomeres with basal ten segments with nearly equal width, eleventh to apex gradually becoming shorter and narrower.

Mesosoma long and narrow, approximately 2.0 mm long and 1.1 mm wide, about 1.8 times as long as wide. Legs partly preserved, hind femur slightly wider than hind tibia, hind tibia thin basally and gradually swollen toward apex.

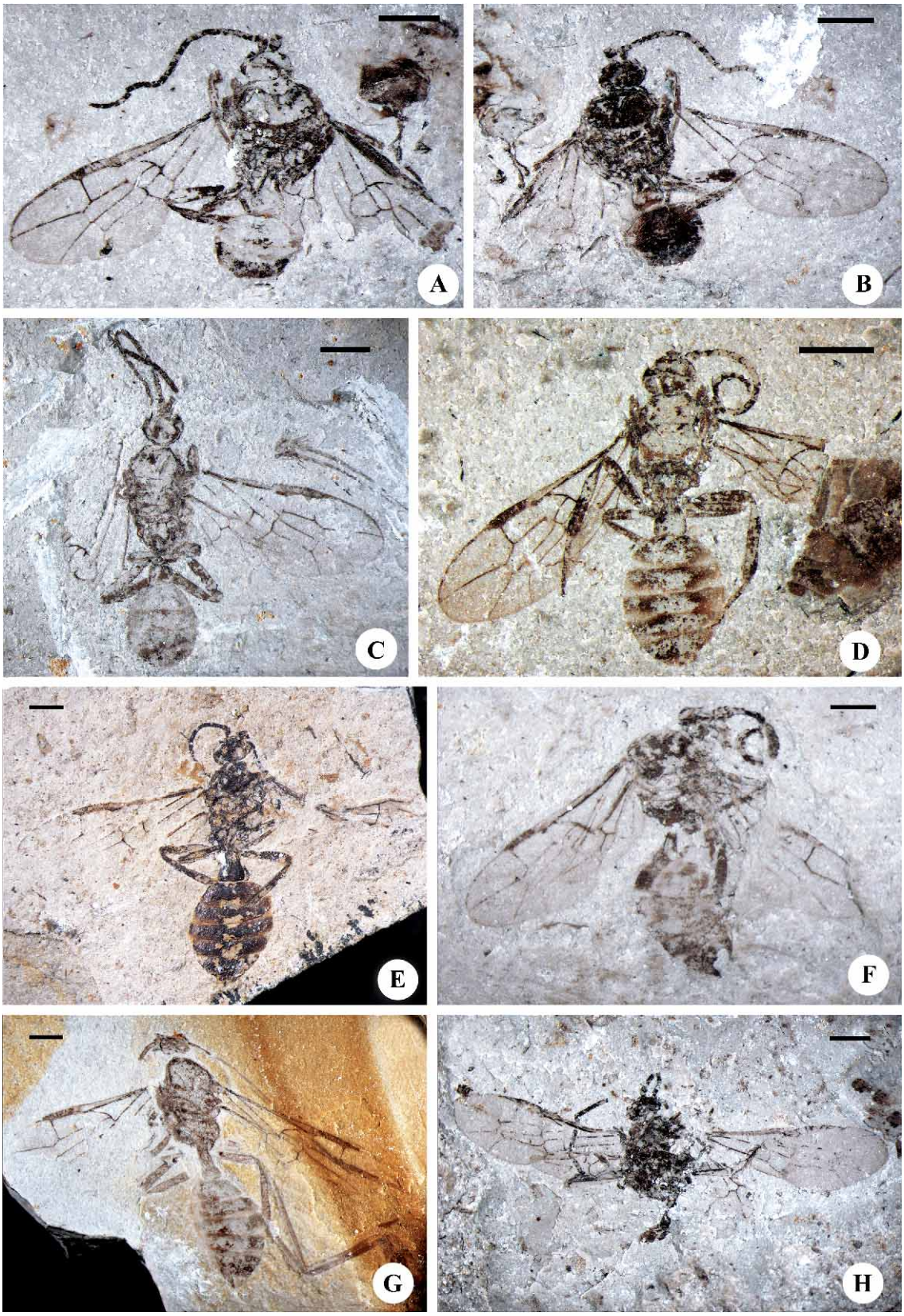

Fig. 3. *Anomopterella brevis* sp. n., Holotype, CNU-HYM-NN-2012-043P/C. **A** — Part; **B** — Countpart; **C** — *Anomopterella ovalis* Li, Rasnitsyn, Shih & Ren, 2013, CNU-HYM-NN-2012-044; **D** — *Anomopterella ampla* Li, Rasnitsyn, Shih & Ren, 2013, CNU-HYM-NN-2012-047. *Anomopterella* spp.; **E** — CNU-HYM-NN-2012-029; **F** — CNU-HYM-NN-2012-046; **G** — CNU-HYM-NN-2012-048; **H** — CNU-HYM-NN-2012-049. Scale bars: 1 mm.

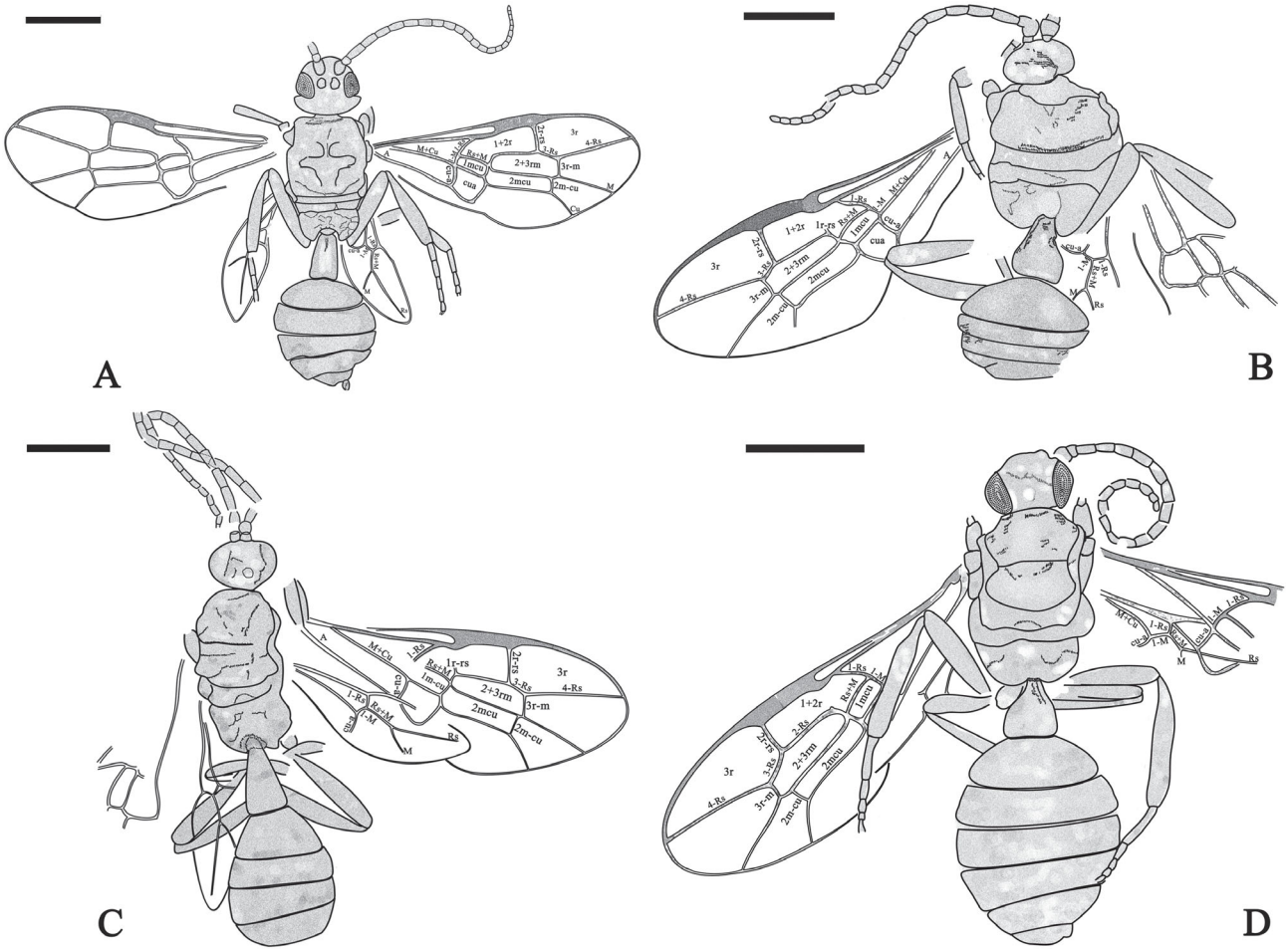

Fig. 4. A — *Anomopterella pygmea* sp. n. Line drawing of holotype, CNU-HYM-NN-2012-045; **B** — *Anomopterella brevis* sp. n. Line drawing of holotype, CNU-HYM-NN-2012-043P/C; **C** — *Anomopterella ovalis* Li, Rasnitsyn, Shih & Ren, 2013, Line drawing of CNU-HYM-NN-2012-044; **D** — *Anomopterella ampla* Li, Rasnitsyn, Shih & Ren, 2013, Line drawing of CNU-HYM-NN-2012-047; Scale bars: 1 mm.

Wings well preserved, forewing 4.0 mm long and 1.8 mm wide, with 1-Rs (0.4 mm) longer than 1-M (0.2 mm); 1r-rs rudimentary, like a very short stub on Rs; 2r-rs (0.4 mm) issuing from pterostigma nearly at the apex; 3-Rs nearly as long as 3r-m (both with lengths of about 0.3 mm); cell 3r broad, 2.3 times as long as wide (length 1.4 mm, width 0.6 mm); cell 2+3rm slightly wider than 2mcu, in contact with 1mcu by a point; cu-a postfurcal (0.3 mm) and curved. Hind wing 2.3 mm long and 0.8 mm wide, with 1-Rs, 1-M and Rs+M forming "Y-shape", 1-Rs nearly as long as 1-M (both about 0.1 mm long), cu-a present and curved.

Metasoma nearly as long as mesosoma, with 5 segments as preserved (excluding propodeum), first metasomal segment distinctly longer than other segments, comparatively thin basally and gradually broadened apically forming an elongate triangular (length 0.9 mm, maximum width 0.5 mm); remaining part oval in dorsal aspect, the second segment transversally trapezoid; the remaining segments distinct shorter than the second.

Dimensions (in mm): Body length 5.2; length of head 0.6, width 0.9; length of antenna 3.7; length of mesosoma 2.0, width 1.1; length of forewing 4.0, width 1.8; length of hind wing 2.3, width 0.8; length of first metasomal segment 0.8, width 0.5.

Anomopterella ampla Li, Rasnitsyn, Shih & Ren, 2013
(Figs. 3D, 4D)

2013 *Anomopterella ampla* Li, Rasnitsyn, Shih & Ren, p. 10, fig. 6

New material: CNU-HYM-NN-2012-047, collected near Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China, the Middle Jurassic. The new material is considered to be *A. ampla* Li, Rasnitsyn, Shih & Ren, 2013 mainly due to the following characters: forewing with 1r-rs absent, 3-Rs distinctly longer than 3r-m, cu-a interstitial, and first metasomal segment broad-triangular.

Description of new material: A wasp preserved in dorsal view, body and wings partly preserved but veins clearly discernible. Small body size (4.3 mm long, excluding antenna), 1.3 mm wide (Fig. 3D).

Head transversely ovate, distinctly wider than long (length 0.5 mm, width 0.8 mm). Compound eyes large and symmetrically located on both sides of the head. Antenna with about

21 segments as preserved, and gradually thickened from base to tenth; scape thick, wider than pedicel; flagellomeres with basal ten segments with nearly equal width, eleventh to the last gradually becoming shorter and narrower.

Mesosoma approximately 1.5 mm long and 1.0 mm wide, about 1.5 times as long as wide; pronotum short, covered by mesonotum; mesonotum long and broad, transscutal suture present; metanotum with small metascutellum and narrower than metapostnotum; metapostnotum very short; propodeum shorter and narrower than metapostnotum.

Legs partly preserved, but hind legs complete; hind femur (0.9 mm) shorter than hind tibia (1.1 mm); hind tibia thin basally and gradually swollen toward apex; hind tarsus consisting of 5 segments, much narrower than hind tibia, the first segment distinctly longer than any other segments of hind tarsus.

Wings well preserved, forewing 3.4 mm long and 1.3 mm wide, with 1-Rs (0.3 mm) longer than 1-M (0.2 mm); 1r-rs not distinct present and 2-Rs angular at its place; 2r-rs (0.3 mm) issuing from pterostigma nearly at the apex, about 2 times as long as the width of pterostigma; 3-Rs longer than 3r-m (3-Rs length 0.3 mm, 3r-m length 0.2 mm); cell 3r broad, 2.4 times as long as wide (length 1.2 mm, width 0.5 mm); cell 2+3rm wider than 2mcu, in contact with 1mcu by a point; cell 1mcu nearly rectangle, 2 times as long as wide (length 0.4 mm, width 0.2 mm); cu-a interstitial (0.2 mm long) and curved. Hind wing with 1-Rs, 1-M and Rs+M forming "Y-shape", 1-Rs shorter than 1-M (1-Rs length 0.1 mm; 1-M length 0.2 mm), cu-a present and curved.

Metasomal short with 6 segments (excluding propodeum), first metasomal segment short, comparatively thin basally but broadened apically (length 0.5 mm, maximum width 0.5 mm); remaining part ovate in dorsal view, the second segment transversally ellipse, distinctly wider than the first; the remaining segments distinctly shorter than the second.

Dimensions (in mm): Body length 4.3, width 1.3; length of head 0.5, width 0.8; length of antenna 2.8; length of mesosoma 1.5, width 1.0; length of forewing 3.4, width 1.3; length of first metasomal segment 0.5, maximum width 0.5; length of hind leg: femur 0.9, tibia 1.1, tarsomeres I–V: 0.37, 0.18, 0.12, 0.08, 0.10.

Key to species of *Anomopterella* Rasnitsyn, 1975, modified and improved according to Li et al. (2013a):

1. Forewing with cu-a interstitial.....2
— Forewing with cu-a postfurcal.....5
2. Forewing with Rs originating close to pterostigma, Rs very short between 2r-rs and 3r-m.....
.....*A. gobi* Rasnitsyn, 2008
— Forewing with Rs originating far from pterostigma, Rs (3-Rs) long between 2r-rs and 3r-m, 1r-rs absent 3
3. Both propodeum and metasoma short, first metasomal segment particularly narrow like a distinct petiole (length/width ratio 1.7), remaining part round.....
.....*A. pygmea* sp. n.
— Both propodeum and metasoma long, first metasomal segment triangular.....4
4. First metasomal segment elongate triangular (length/width ratio between 1.2 and 1.6).....
.....*A. coalita* Li, Rasnitsyn, Shih & Ren, 2013
— First metasomal segment broad triangular (length/width ratio 1.1).....
.....*A. ampla* Li, Rasnitsyn, Shih & Ren, 2013
5. 1-RS originating from pterostigma for a distance comparable with length of 1m-cu. Ovipositor long, far surpassing metasomal apex. First metasomal segment broad triangular (length/width ratio 1.0).....
.....*A. mirabilis* Rasnitsyn, 1975
— 1-RS originating far from pterostigma. Ovipositor short, weakly extending beyond metasomal apex.....6
6. Rudimentary 1r-rs about as long as 1m-cu. First metasomal segment particularly narrow with distinct petiole (length/width ratio 1.7).....
.....*A. brachystelis* Li, Rasnitsyn, Shih & Ren, 2013
— Rudimentary 1r-rs much shorter or lost. First metasomal segment elongate triangular.....7
7. Rudimentary 1r-rs absent.....
.....*A. divergens* Li, Rasnitsyn, Shih & Ren, 2013
— Rudimentary 1r-rs dot-like small.....8
8. First metasomal segment elongate triangular (length/width ratio between 1.4 and 1.6). Legs shorter and slightly wider.....
.....*A. ovalis* Li, Rasnitsyn, Shih & Ren, 2013
— First metasomal segment short (length/width ratio between 0.9 to 1.2).....9
9. Hind legs much longer and narrower, hind femur thin. Forewing with 3-Cu long, nearly as long as 1m-cu.....
.....*A. huangi* Zhang & Rasnitsyn, 2008
— Hind legs longer and thicker, hind femur thicker. Forewing with 3-Cu short, nearly 1/2 length of 1m-cu .....
.....*A. brevis* sp. n.

Discussion

Presently, nine species of *Anomopterella* are recorded (Table 1), suggesting (1) in total, 21 fossil specimens were found in the Jurassic sediments, with 2 specimens from the Upper Jurassic of Kazakhstan and Mongolia and 19 specimens from the upper Middle Jurassic of China. The rarity of *Anomopterella* specimens (only 19 specimens from a very large Daohugou fossil insect collection at the CNU of more than 250,000 specimens (Ren et al. 2010, 2012)) can imply that source area population sizes of species belonging to *Anomopterella* during the late Middle Jurassic were low relative to population sizes of other species. We did not find any species of *Anomopterella* in the CNU's similarly vast collection from the Lower Cretaceous Yixian Formation. These differences in species richness and abundance between the Middle Jurassic and Lower Cretaceous suggest that, *Anomopterella* was more diverse and abundant during the late Middle Jurassic than during the Early Cretaceous. (2) The 19 specimens from the late Middle Jurassic have a narrow range of body lengths from 3.7 to 7.8, forewing lengths from 3.4 to 6.3, and the ratios of wing length/body length ranging from 0.7 to 1.1. Compared to the large body size of female pelecinids (Shih et al. 2010) in the Middle Jurassic ranged between 9 and 27 mm, the small body size of *Anomopterella* highlighting that this group had a narrow range of these mor-

Table 1: A list of species of *Anomopterella* Rasnitsyn, 1975, with morphometric characters, and information about their sex, age, and locality.

Species/specimen ID number	BL.	FL.	FL./BL. ratio	S_1L.	S_1W.	S_1L./W. ratio	Sex	Formation	Age	Locality	Main wing venation and the shape of S_1
A. mirabilis Rasnitsyn, 1975 PIN No2239/2562	4.0	2.6	0.7	0.52	0.54	1.0	F	Karabastau	J_3	South Kazakhstan	2r-rs and 2m-cu basad of 3r-m; cu-a postfurcal; 1r-rs absent; 3-Rs long; S_1 wide triangular
A. gobi Rasnitsyn, 2008 PIN 4270/1549	NK	3.5	NK	NK	NK	NK	NK	Shar-Teg.	J_3	Southwestern Mongolia	2r-rs and 2m-cu basad of 3r-m; cu-a interstitial; 1r-rs absent; 3-Rs short ; S_1 NK
A. huangi Zhang & Rasnitsyn, 2008 NND2006/NIGP148228	NK	5.0	NK	0.65	0.76	0.9	NK	Jiulongshan	J_2	Inner Mongolia, China	2r-rs and 2m-cu basad of 3r-m; cu-a postfurcal; rudimentary 1r-rs dot-like small; 3-Rs long; S_1 short
A. brevis sp. n. CNU-HYM-NN-2012-043P/C	3.7	4.0	1.1	0.65	0.56	1.2	NK	Jiulongshan	J_2	Inner Mongolia, China	2r-rs and 2m-cu basad of 3r-m; cu-a postfurcal; rudimentary 1r-rs dot-like small; 3-Rs long; S_1 short
A. coalita Li, Rasnitsyn, Shih & Ren, 2013 CNU-HYM-NN-2012-023P/C CNU-HYM-NN-2012-030P/C CNU-HYM-NN-2012-028	 6.4 6.8 7.0	 5.0 5.0 5.4	 0.8 0.7 0.8	 0.81 0.90 0.60	 0.59 0.74 0.40	 1.4 1.2 1.5	 M F F	 Jiulongshan Jiulongshan Jiulongshan	 J_2 J_2 J_2	 Inner Mongolia, China Inner Mongolia, China Inner Mongolia, China	 2r-rs and 2m-cu basad of 3r-m; cu-a interstitial; 1r-rs absent; 3-Rs long; S_1 elongate triangular
A. ampla Li, Rasnitsyn, Shih & Ren, 2013 CNU-HYM-NN-2012-024P/C CNU-HYM-NN-2012-047	 7.3 4.3	 5.7 3.4	 0.9 0.8	 0.86 0.48	 0.82 0.45	 1.1 1.1	 F NK	 Jiulongshan Jiulongshan	 J_3 J_3	 Inner Mongolia, China Inner Mongolia, China	 2r-rs and 2m-cu basad of 3r-m; cu-a interstitial; 1r-rs absent; 3-Rs long; S_1 wide triangular
A. brachystelis Li, Rasnitsyn, Shih & Ren, 2013 CNU-HYM-NN-2012-025 CNU-HYM-NN-2012-020P/C	 6.4 6.9	 4.9 4.9	 0.8 0.7	 0.97 0.83	 0.56 0.48	 1.7 1.7	 NK NK	 Jiulongshan Jiulongshan	 J_2 J_2	 Inner Mongolia, China Inner Mongolia, China	 2r-rs and 2m-cu basad of 3r-m; cu-a postfurcal; rudimentary 1r-rs like a stub; 3-Rs long; S_1 particularly narrower with a distinct short petiole
A. divergens Li, Rasnitsyn, Shih & Ren, 2013 CNU-HYMNN-2012-026 CNU-HYMNN-2012-027	 5.1 NK	 4.6 4.5	 0.9 NK	 NK 0.73	 NK 0.45	 NK 1.6	 NK NK	 Jiulongshan Jiulongshan	 J_2 J_2	 Inner Mongolia, China Inner Mongolia, China	 2r-rs and 2m-cu basad of 3r-m; cu-a postfurcal; 1r-rs absent; 3-Rs long; S_1 elongate triangular
A. ovalis Li, Rasnitsyn, Shih & Ren, 2013 CNU-HYM-NN-2012-022P/C CNU-HYM-NN-2012-021P/C CNU-HYM-NN-2012-044	 5.8 7.1 5.2	 4.7 5.0 4.0	 0.8 0.7 0.8	 0.83 0.64 0.84	 0.61 0.45 0.52	 1.4 1.4 1.6	 F F NK	 Jiulongshan Jiulongshan Jiulongshan	 J_2 J_2 J_2	 Inner Mongolia, China Inner Mongolia, China Inner Mongolia, China	 2r-rs and 2m-cu basad of 3r-m; cu-a postfurcal; rudimentary 1r-rs dot-like small; 3-Rs long; S_1 elongate triangular
A. pygmea sp. n. CNU-HYM-NN-2012-045	4.4	3.6	0.8	0.63	0.37	1.7	F	Jiulongshan	J_2	Inner Mongolia, China	2r-rs and 2m-cu basad of 3r-m; cu-a interstitial; 1r-rs absent; 3-Rs long; S_1 like a distinct petiole
A. sp. 1. CNU-HYM-NN-2012-029	7.8	5.8	0.7	0.95	0.79	1.2	M	Jiulongshan	J_2	Inner Mongolia, China	2r-rs and 2m-cu basad of 3r-m; NK; S_1 wide triangular
A. sp. 2. CNU-HYM-NN-2012-046	5.7	4.8	0.8	0.78	NK	NK	F	Jiulongshan	J_2	Inner Mongolia, China	2r-rs and 2m-cu basad of 3r-m; NK; NK
A. sp. 3. CNU-HYM-NN-2012-048	7.7	6.3	0.8	0.95	0.59	1.6	NK	Jiulongshan	J_2	Inner Mongolia, China	2r-rs and 2m-cu basad of 3r-m; NK; S_1 particularly narrower with a distinct short petiole
A. sp. 4. CNU-HYM-NN-2012-049	NK	4.5	NK	NK	NK	NK	NK	Jiulongshan	J_2	Inner Mongolia, China	2r-rs and 2m-cu basad of 3r-m; NK; NK

Abbreviations of material ID numbers: CNU — Capital Normal University, Beijing, China; HYM-NN — Hymenoptera-Ningcheng, Inner Mongolia; BL. — Body length (mm); FL. — Forewing length (mm); S_1L. — First metasomal segment length (mm); S_1W. — First metasomal segment width (mm); F — female; M — male; J_2 — Middle Jurassic; J_3 — Late Jurassic; NK — unknown.

phological differences and smaller body size may have some advantages, such as agility, flexibility, stealth and energy conservation when they find and deposit eggs onto defenceless surface larval hosts (Shih et al. 2010).

New and complete specimens show that *Anomopterella* significantly varied in wing venation and in the shape of the first metasomal segment. Nearly complete wing venation, including C, Rs, M, Cu, 2r-rs, 3r-m and 2m-cu is always present. All species of *Anomopterella* have 2r-rs and 2m-cu basad of 3r-m, indicating that this vein character is very stable for this genus and can be considered diagnostic and conservative. On the other hand, veins of all species of *Anomopterella* show many differences, such as cu-a postfurcal (vs. cu-a interstitial), 1r-rs absent (vs. rudimentary 1r-rs, dot-like and small), 3-Rs long (vs. 3-Rs short), which can be considered as interspecific differences. In addition to the differences in veins, the first metasomal segment of *Anomopterella* is morphologically diverse, with a very broad range of the ratio of length/width from 0.9 to 1.7. Also, the first segment of the metasoma presents different shapes, such as broad triangular, elongate triangular and particularly narrow with a distinct short petiole.

We stress that toruli and compound eyes in Anomopterellidae are reported for the first time in our study, namely in *A. pygmea* sp. n. In general, insects have compound eyes and ocelli. Compound eyes are the most important visual organ of insects, which can mostly identify moving objects. However, ocelli do not have the imaging function, and are only used to sense the strength and direction of the light (Cai et al. 2001). The main function of ocelli is to control the swing and tilt in the process of flight, and sense the change of the light cycle associated with circadian behaviour (Cai et al. 2001). The central ocellus is known to recognize the position of insects, and is especially well-developed in predatory mantodeans and extinct cockroaches (Vršanský 2008). Deformities (Vršanský 2005) are rarely reported in hymenopteran wings at Daohugou, including a single deformed specimen of Anomopterellidae (CNU-HYM-NN-2012-022; Li et al. 2013a).

Conclusion

A. pygmea sp. n., *A. brevis* sp. n., and six other new fossils emend the records of the Mesozoic family Anomopterellidae, and enhance our understanding of the morphology of the extinct family Anomopterellidae. New and complete specimens show that *Anomopterella* significantly varied in wing venation and in the shape of the first metasomal segment. The differences in species richness and abundance between the Middle Jurassic and Lower Cretaceous suggest that, *Anomopterella* was more diverse and abundant during the late Middle Jurassic than during the Early Cretaceous.

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