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*Research Article*

# Quantitative Assessments and Taxonomic Revisions of the Genus *Urosyntexis* With New Species From Daohugou, China (Hymenoptera: Anaxyelidae)

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Three new species of *Urosyntexis*, *U. volita* sp. nov., *U. forta* sp. nov., and *U. ensia* sp. nov., belonging to the subfamily Anaxyelinae of Anaxyelidae were described and figured based on three well-preserved specimens from the Middle Jurassic Jiulongshan Formation of Northeastern China. We applied geometric morphometric analyses (GMA) to study 17 species with well-preserved forewings of easily confused genera *Syntexyela* and *Urosyntexis* and presented the results for the first time. The GMA results further confirmed the classification of our new species and shed light on the differences between the two genera are mainly in the length of 5-M and the emission position of 2r-rs.

## 1. Introduction

A single origin of the endophytic sawfly lineages (i.e., Siricoidea, Orussoidea, Cephoidea, and Xiphydrioidea) formed a paraphyletic grade [1–3], which made the first superfamily important to study the evolution of Hymenoptera. Siricoidea appears as a comparatively diverse group, both in the Mesozoic fossil records and in the present fauna. The superfamily comprises two extant families Anaxyelidae Martynov, 1925 with only one recent species, *Syntexis libocedrii* Rohwer, 1915, and Siricidae Billberg, 1820 with more than 10 extant genera widely distributed in Holarctic and Oriental Regions [4], and three extinct families †Protosiricidae [5], †Pseudosiricidae Handlirsch, 1908, and †Sinosiricidae Hong, 1975 [5–11].

Anaxyelidae is one of the few relict families in Siricoidea, existing from the Middle Jurassic to the present. Compared with the only living species, *Syntexis libocedrii* Rohwer, in western North America, Anaxyelidae had relatively high species diversity in the Mesozoic [12]. Hitherto, 52 species belonging to 23 genera of Mesozoic Anaxyelidae have been reported and classified into two subfamilies: Anaxyelinae Marytov, 1925, and Syntexinae Benson, 1935. The genus *Urosyntexis* was separated from *Syntexyela* based on notable findings from Karatau, Kazakhstan [13], and four species hitherto were described from the Middle Jurassic Kazakhstan and the Early Cretaceous Yixian Formation in China (Table 1) [13–15]. However, the clear boundaries between two genera *Urosyntexis* and *Syntexyela* were usually obscure and sometimes rather problematic, especially with persistent discoveries of new specimens challenging the diagnosis of these two genera [15, 16]. Therefore, we tried to use the method of geometric morphology to further verify the classifications of new specimens and the differences between two controversial genera of *Syntexyela* and *Urosyntexis*.

The Middle Jurassic strata in the Daohugou area of Inner Mongolia in China are well-developed and documented with

Table 1: Morphological differences in all reported *Urosyntexis* species.

| Taxa | Ratio of 5-M to 2m-cu in forewing | Ratio of 1-Rs to 1-M in forewing | Ratio of Rs+M to 2-M in forewing | Ratio of 1r-rs to 2r-rs in forewing | Ratio of valvifers to ovipositor sheaths |
|---|---|---|---|---|---|
| *Urosyntexis depressa* [13] | 0.5 | 2.4 | 1.6 | 1 | 1 |
| *Urosyntexis drepanura* [14] | – | 3.2 | 0.7 | 0.8 | 0.5 |
| *Urosyntexis magna* [14] | 0.5 | 2.8 | 1.3 | 1.4 | 1 |
| *Urosyntexis undosa* [15] | – | 3.1 | 0.4 | 0.7 | 1.1 |
| *Urosyntexis volita* sp. nov. | 0.6 | 4.5 | 0.6 | 1 | 0.9 |
| *Urosyntexis forta* sp. nov. | 0.4 | 5 | 0.4 | 0.5 | 1 |
| *Urosyntexis ensia* sp. nov. | 0.6 | 3 | 1.4 | 1 | 1 |

diverse and abundant fossil insects [17, 18]. Previously, six species of the *Brachysyntexis* Rasnitsyn, 1969 with the subfamily Anaxyelinae and one species of the *Daosyntexis* with the subfamily Syntexinae were documented in this area [19]. Herein, we described three new anaxyelids based on three well-preserved specimens from the same deposit assemblages. In addition to the morphological comparisons, we applied geometric morphometric analyses (GMA) to study well-preserved forewings of previously described fossil species and our new species, in order to confirm the differences between *Syntexyela* and *Urosyntexis* as well.

## 2. Material and Methods

*2.1. Material and Terminology.* The specimens were collected from the latest Middle Jurassic, Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Chifeng City, Inner Mongolia, China (41°180'N, 119°130'E) and preserved in a layer of gray–yellow siltstone in the Jiulongshan Formation.

All of the newly described species in the article are housed at the fossil collection of the Key Lab of Insect Evolution and Environmental Changes, the College of Life Sciences, Capital Normal University (CNUB; Dong Ren, Curator), Beijing, China.

The specimens were examined and photographed under Nikon SMZ 25 dissecting microscopes 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 [20], with the following abbreviations: A, anal vein; C, costal vein; Cu, cubital vein; M, median vein; R, radial vein; 1cu-a, crossvein between 1-Cu and 1A; 2r-m and 3r-m, crossveins between Rs and M; 1m-cu and 2m-cu, crossveins between M and 1-Cu; a, crossvein between 1A and 2A + 3A; succeeding sections of respective veins counted from base to apex of wing. Additionally, p/c means part and counterpart fossils.

## 3. GMA

*3.1. Softwares.* GMA softwares used in this study consist of the following: morphoj 1.06d [21], tpsutil 1.46 [22], and tpsdig 2.16 [23].

*3.2. Sample Collection.* To carry out the GMA, we chose 17 specimens of Anaxyelidae covering its two monophyletic lineages, including five described fossil species with five specimens from *Syntexyela* [12, 14, 24], seven species with 11 specimens from *Urosyntexis* [13–15], and one species with one specimen from *Daosyntexis* [19], all with well-preserved forewing venations. We selected 18 homology landmarks of forewing for Anaxyelidae species representing key points on the forewing veins.

*3.3. Data Acquisition.* Affinity designer V1 was used to process and redraw the venation of forewings used in the GMA based on new photos or previously published figures. The JPEG images were then exported to tpsutil 1.46 [22] and converted into TPS files. Cartesian coordinates of landmarks were digitized with tpsdig 2.16 software [23]. GMA were used to analyze the tps files produced in tpsdig 2.16. To examine the shape variation, we used MorphoJ software to analyze digital landmark data [21].

*3.4. Principal Component Analysis (PCA) and Canonical Variate Analysis (CVA).* Files from tpsdig 2.16 [23] were processed with morphoj 1.06d [21], which is based on the covariance matrix of landmark data in the tangent space, to analyze the shape variations of wing veins. The coordinates of the landmarks were used to perform PCA to assess the variability of each individual in the shape space. The relative similarity and discrimination of the three genera of Anaxyelidae were analyzed using CVA.

The CVA found shape values that maximize group means relative to variation within groups, by assuming that covariate matrices were identical [25]. Procrustes distances and Mahalanobis distances (the squareroot of the sum of squared differences between corresponding points) between each of the three genera were computed, and the matrix was produced by the MorphoJ software [21].

*3.4.1. Systematic Palaeontology.* Order Hymenoptera Linnaeus, 1758

Suborder "Symphyta" Gerstaecker, 1867

Superfamily Siricoidea, Billberg, 1820

Family Anaxyelidae Martynov, 1925

Subfamily Anaxyelinae Martynov, 1925

Genus *Urosyntexis* Rasnitsyn, 1969

Type species. *Urosyntexis magna* Rasnitsyn, 1968

Species included. *U. magna* [14], *U. drepanura* [14], *U. depressa* [13], *U. undosa* [15], *U. volita* Wang, Li, Shih and Ren, sp. nov., *U. forta* Wang, Li, Shih and Ren, sp. nov., and *U. ensia* Wang, Li, Shih and Ren, sp. nov.

Revised diagnosis of the genus. Antennae filiform, or setiform, gradually tapering apically. Forewing with pterostigma sclerotized, usually not reaching the midlength of cell 3r; Sc absent or present as a crossvein between C and R, before or near the orgin of 1-Rs; 2r-rs emitted from the one-third of the pterostigma; 5-M much shorter than 2m-cu, almost less than 0.6 times as long as the latter. Ovipositor significantly shorter than body, the length of valvifers more than half length of ovipositor sheaths.

*3.4.2. Urosyntexis volita Wang, Li, Shih and Ren, sp. nov.* Zoobank number: urn:lsid:zoobank.org:act:898AC086-D2F8-47AA-94D8-9F950DC62C1F.

Material: Only the holotype, CNU-HYM-NN2024004.

Etymology: The specific name is from Latin "*volitans*," meaning flying and referring to the taking-off body shape of the specimen.

Locality and horizon: Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (41°18.9790 N, 119°14.3180 E); latest Middle Jurassic of late Callovian age.

Diagnosis: Forewing with Sc crossvein-like present, merging into vein C at the origin of 1-Rs; 1r-rs parallel with and equal to 2r-rs in length; Rs+M 0.6 times as long as 2-M. Hind wing with r-m distal of m-cu and 0.8 times as long as the latter; 2-M shorter than m-cu; r-m issuing from cell r near its one-third apex.

Description: Female. Head, thorax, antennae and ovipositor uniform dark; legs slightly darker; abdomen with traces of color pattern; wing veins uniform dark (Figure 1A).

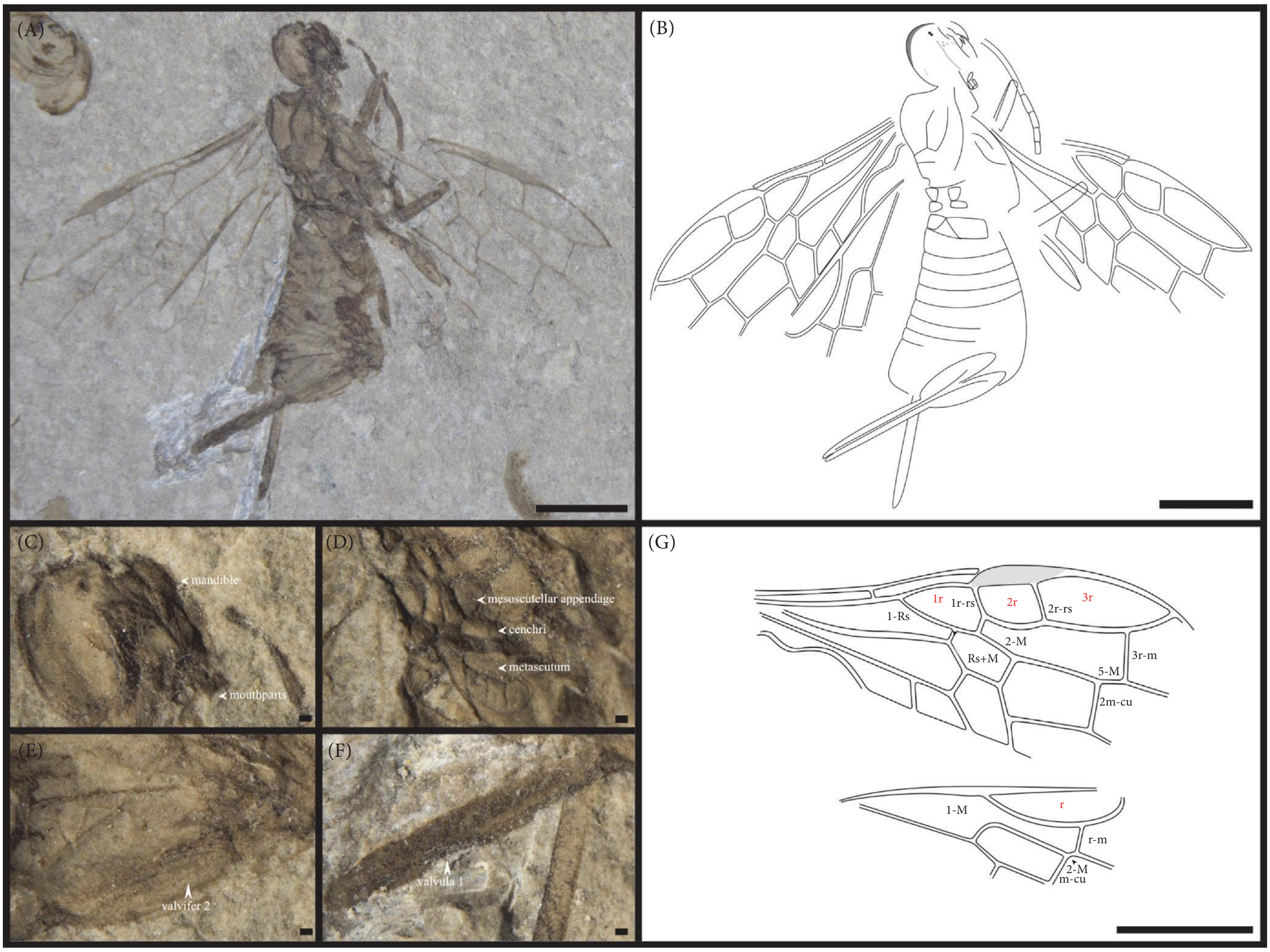


Figure 1: Photographs of *Urosyntexis volita* sp. nov., holotype (specimen CNU-HYM-NN2024004), female. (A) Dorsal view as preserved. (B) Line drawing of dorsal view. (C) Photo of head. (D) Photo of metanotum. (E) Photo of ovipositor basal section. (F) Photo of ovipositor apical section. (G) Line drawing of wing. Scale bars: 2 mm in Subparts (A, B, G); 0.1 mm in Subparts (C–F).

Head: Head moderately large, nearly round, narrower than thorax; mandible bent, sickle shaped (Figure 1C). Antenna filiform, with part of flagellomeres visible, rectangle, the maximum length three times as long as wide (Figure 1A).

Thorax: Mesoscutum with notauli strongly impressed; mesoscutellum triangular, ratio of lengths of prescutum, longitudinal sulcus between notauli and mesoscuto-mesoscutellar sulcus, and mesoscutellum 1:2.8:1.1 (Figure 1A); metascutum with metascutellum wide, metascutum trapezoid; metapostnotum rounded quadrangular (Figure 1D).

Legs: Legs poorly preserved, spindly, pro-, meso-, and metafemur wider and longer than tibia.

Wing: Forewing 2.5 times as long as wide (Figure 1G); vein Sc present, crossvein-like, merging into vein C at the origin of 1-Rs; 1-Rs long, slightly bend, about 4.5 times as long as 1-M, forming 90° angle with 1-M; 1r-rs as long as 2r-rs; 2r-rs emitted from the one-third of the pterostigma; Rs+M 0.6 times as long as 2-M; cell 1mcu hexagon, about twice as long as wide; 3 + 4-M 4 times as long as 5-M; 5-M 0.6 times as long as 2m-cu; cell 2 + 3rm long and pentagonal, about 3.5 times as long as wide; M + Cu bend basally, curved; 3r-m almost vertical; 2-Cu as long as 1-Cu; 1cu-a vertical and as long as 1-Cu, emitted from the middle of cell 2A; cell 2mcu hexagon, twice as long as wide. Hind wing with M + Cu straight, 2-M 0.4 times as long as r-m, and 0.3 times as long as m-cu.

Abdomen: Abdomen completely preserved but distorted.

Ovipositor: Ovipositor straight, sword-shaped, equal to 0.7 times as long as forewing length; second valvifer semicircular (Figure 1E); ovipositor sheaths elongated and narrowly rounded apically, prominent behind abdomen, length of valvifers together almost 0.9 times as long as sheaths (Figure 1F).

Measurements (in mm): Body about 10.5 in length, excluding ovipositor about 8.3 in length. Head about 1.4 in length, 1.5 in width; and antenna 2.8 long as visible. Thorax about 2.6 in length. Abdomen about 4.1 in length. The forewing (incompletely preserved) about 6.8 in length, maximum width 2.7. Ovipositor about 4.6 in length, ovipositor sheaths about 2.5 in length.

*3.4.3. Urosyntexis forta Wang, Li, Shih and Ren, sp. nov.* Zoobank number: urn:lsid:zoobank.org:act:4809EDFB-1CB1-4225-879A-524C5C316FBD.

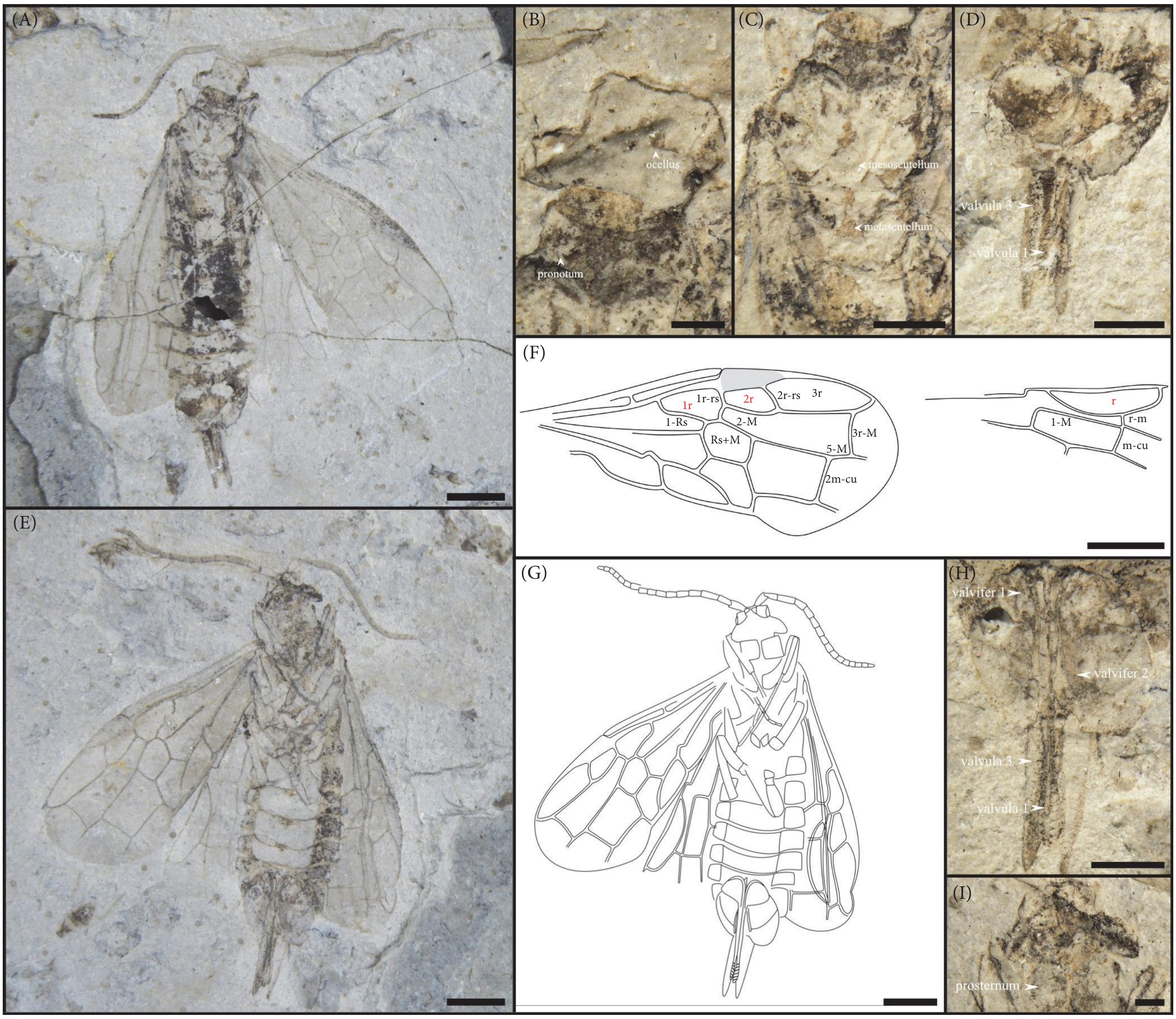


FIGURE 2: Photographs of *Urosyntexis forta* sp. nov., holotype (specimen CNU-HYM-NN2024005), female. (A) Dorsal view as preserved. (B) Photo of head. (C) Photo of metanotum. (D) Photo of ovipositor with dorsal view. (E) Ventral view as preserved. (F) Line drawing of wing. (G) Line drawing of ventral view. (H) Photo of ovipositor with ventral view. (I) Photo of head with ventral view. Scale bars: 2 mm in Subparts (A, E–G); 1 mm in Subparts (C, D, H); 0.5 mm in Subparts (B, I).

Material: Only the holotype, CNU-HYM-NN2024005 (P/C).

Etymology: The specific name is from Latin "*fortis*," meaning roborant and referring to the stout ovipositor.

Locality and horizon: Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (41°18.9790 N, 119°14.3180 E); latest Middle Jurassic of late Callovian age.

Diagnosis: Forewing with Sc crossvein-like present, merging into C before origin of 1-Rs; 1-Rs bend basally; Rs+M 0.4 times as long as 2-M; 1r-rs 0.5 times as long as 2r-rs. Hind wing with r-m aligned with m-cu and 0.4 times as long as the latter; 1-M arcuate basally almost forming a right angle; r-m issuing from cell r near its one-third apex.

Description: Female. As preserved, body moderately infuscated, pronotum and 3rd–5th abdominal segments slightly darker than remaining parts.

Head: Head nearly hemispherical, as wide as thorax. Ocelli small, in high-triangle (Figure 2B). Antenna with 16 flagellomeres, gradually tapering apically; scape slightly expanded, 0.6 mm long, maximum width 0.3 mm; pedicel 0.5 mm long, maximum width 0.2 mm; flagellomere I longer than scape, 0.2 mm wide, 0.7 mm long, flagellomere II 0.2 mm wide, 0.5 mm long (Figure 2A, E).

Thorax: Pronotum large and trapezoid, with medial line or furrow ventrally (Figure 2E), at least 1.6 times as wide as long; pronotum posterior border slightly curved in dorsal view (Figure 2I); mesoscutum large, with anterior margin nearly straight, notauli strongly impressed, converging to meet prior to mesoscutellum; mesoscutellum front circular, ratio of lengths of prescutum, longitudinal sulcus between notauli and mesoscuto-mesoscutellar sulcus, and mesoscutellum 1:1.5:1.1 (Figure 2C).

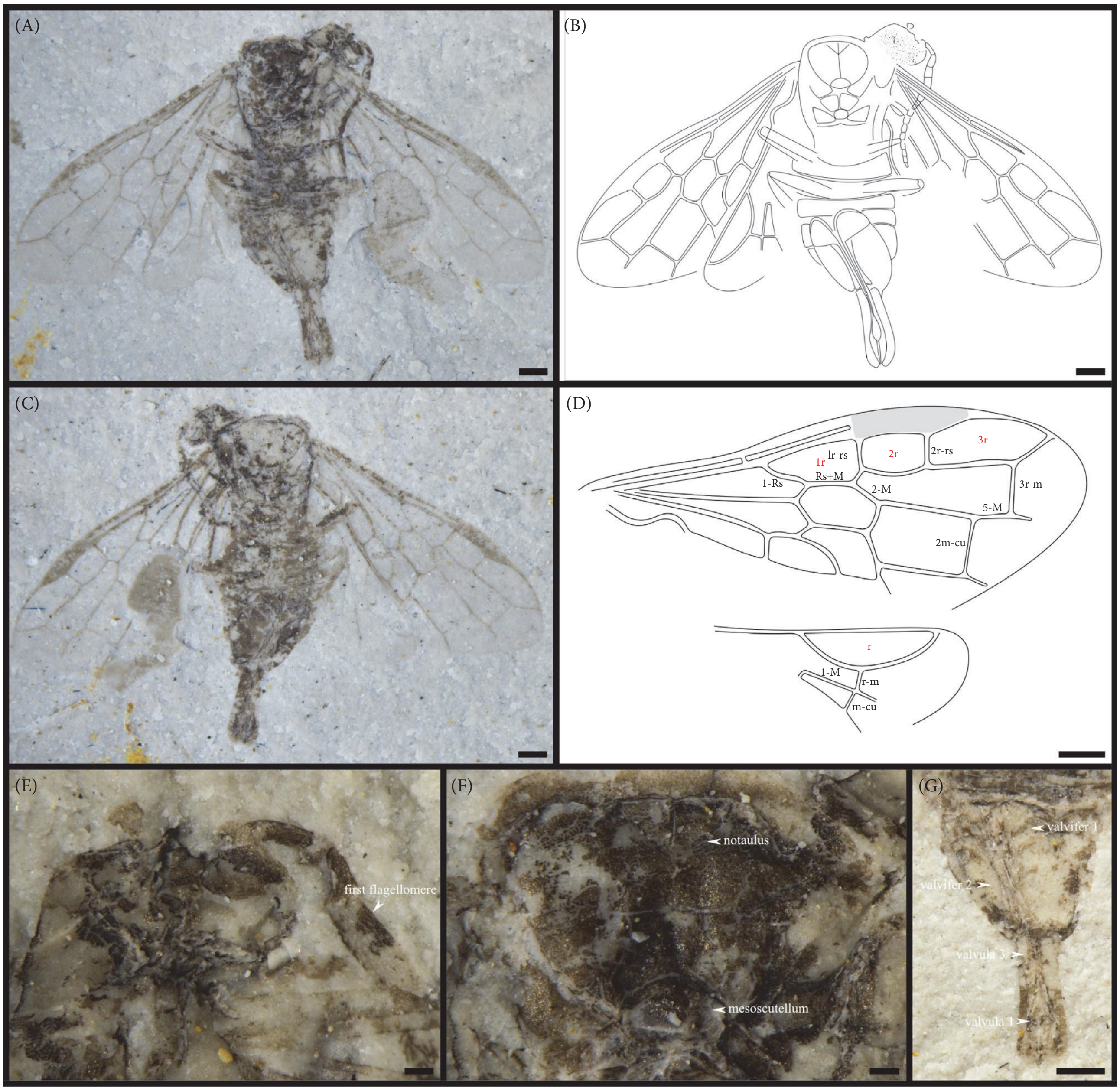


Figure 3: Photographs of *Urosyntexis ensia* sp. nov., holotype (specimen CNU-HYM-NN2024006), female. (A) Ventral view as preserved. (B) Line drawing of ventral view. (C) Dorsal view as preserved. (D) Line drawing of wing. (E) Photo of head. (F) Photo of metanotum. (G) Photo of ovipositor with ventral view. Scale bars: 0.5 mm in Subparts (A–D, G); 0.1 mm in Subparts (E, F).

Legs: Legs spindly, pro-, meso- and metafemur wider and longer than tibia. Metatibiae thick apically, narrowed subapically (Figure 2E, G).

Wing: Forewing 2.3 times as long as wide (Figure 2F); Sc present, crossvein-like, before origin of 1-Rs; 1-Rs about five times as long as 1-M, the angle with 1-M greater than 90°; Rs+M about 0.4 times as long as 2-M and as long as 2-Rs; 1r-rs 0.5 times as long as 2r-rs; 2r-rs emitted from the one-third of the pterostigma; cell 1mcu hexagon, about 1.3 times as long as wide; 3 + 4-M 3.7 times as long as 5-M; 5-M 0.4 times as long as 2m-cu; cell 2 + 3rm long and pentagonal, about 3.3 times as long as wide; M + Cu slightly downward basally; 3r-m slightly bend, 1-Cu 0.8 times as long as 2-Cu; cell 2mcu broad and pentagonal; 1cu-a vertical, emitted from the middle of the cell 2A, about 0.8 times as long as 1-Cu; 2A + 3A S-like bent basally. Hind wing with M + Cu straight; cell r extremely approaching to cell mcu in the middle, and r-m aligned with m-cu.

Abdomen: Abdomen with first tergum split medially, slightly wider than the mesothorax, parallel sided, with seven segments visible.

Ovipositor: Ovipositor sword shaped, 0.4 times as long as forewing length (Figure 2D); first valvifer small, subhemicircular as visible, first valvula with the remus basally; second valvifer large, with thickening medially, 0.6 times as long as ovipositor sheath (Figure 2H); ovipositor sheaths almost straight, elongated and narrowly rounded apically, prominent slightly behind abdomen; length of valvifers together as long as sheaths (Figure 2E).

Measurements (in mm): Body about 14.7 in length, excluding ovipositor about 12.9 in length. Head about 1.3 in length, 1.8 in width; and antenna 5.9 long visible. Thorax about 4.5 in length. Abdomen about 6.9 in length. The forewing (incompletely preserved) about 9.9 in length, maximum width 4.3. Ovipositor about 4.2 in length, ovipositor sheaths about 2.2 in length.

*3.4.4. Urosyntexis ensia Wang, Li, Shih and Ren, sp. nov.* Zoobank number: urn:lsid:zoobank.org:act:E534570A-EDEC-4A21-A757-C2B40D4DCC3F.

Material: Only the holotype, CNU-HYM-NN2024006 (P/C).

Etymology: The specific name is from Latin "*ensatus*", referring to the sword-like ovipositor of fossil specimen.

Locality and horizon: Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (41°18.9790 N, 119°14.3180 E); latest Middle Jurassic of late Callovian age.

Diagnosis: Forewing with Sc crossvein-like present, merging into C at origin of 1-Rs; 1r-rs as long as 2r-rs; Rs+M 1.4 times as long as 2-M. Hind wing with r-m aligned with m-cu and equal to it in length; r-m issuing from cell r slightly before its midlength.

Description: Body including head, thorax and ovipositor dark, abdomen and forewing vein slightly lighter (Figure 3A–C).

Head: Surface sculpture coarsely punctated, moderately small, narrower than thorax (Figure 3A). Antenna filiform, gradually tapering apically, and with 16 flagellomeres visible; scape slightly expanded, 0.5 times as wide as the first filagellomere (Figure 3E).

Thorax: Thorax slightly wider than head, incompletely preserved. Mesoscutum large, with anterior margin nearly straight, notauli strongly impressed, converging to meet prior to mesoscutellum; mesoscutellum semicircle, ratio of lengths of prescutum, longitudinal sulcus between notauli and mesoscuto-mesoscutellar sulcus, and mesoscutellum 1:2.3:1.1; anterior margin of mesoscutellum rounded; mesopostnotum trapezoid, slightly narrower than metascutellum (Figure 3F); metascutum with metascutellum small, rounded quadrangular, transverse.

Legs: Legs spindly, pro-, meso-, and metafemur wider and longer than tibia. Metatibiae thick apically, narrowed basally (Figure 3A).

Wing: Forewing 2.9 times as long as wide (Figure 3D). Sc present as an oblique crossvein just basad of Rs base; 1-Rs about 3 times as long as 1-M, the angle with 1-M less than 90°; Rs+M 1.4 times as long as 2-M and twice as long as 2-Rs; 1r-rs as long as 2r-rs, and 2r-rs emitted from the one-third of the pterostigma; cell 1mcu hexagon, about 1.7 times as long as wide; 3 + 4-M 2.5 times as long as 5-M; 5-M 0.6 times as long as 2 m-cu; cell 2 + 3rm long and pentagonal, about 3.3 times as long as wide; M + Cu straight; 2-Cu twice as long as 1-Cu; cell 2mcu broad, nearly hexagon, about 1.5 times as long as wide; 1cu-a strongly reclival, emitted from the one-third of the cell 2A; 1cu-a straight, about 0.7 times as long as 1-Cu; 2A + 3A strongly S-like bent basally. In hind wing, r-m aligned with m-cu.

Abdomen: Abdomen with first tergum split medially, slightly wider than the mesothorax, parallel sided, with seven segments visible, widest at the first three segments.

Ovipositor: Ovipositor straight and roundish in cross-section, sword-shaped, becoming widened toward apex, equal to 0.5 times as long as forewing length; length of valvifers together as long as sheaths; first valvifer small, subhemicircular as visible, first valvula with the remus basally; second valvifer large, with thickening medially (Figure 3G); ovipositor sheaths almost straight, elongated and narrowly rounded apically, prominent slightly behind abdomen, sheath 0.2 times as long as forewing length.

Measurements (in mm): Body about 6.4 in length, excluding ovipositor about 5.1 in length. Head about 0.4 in length, 0.9 in width; and antenna 2.3 long as visible. Thorax about 1.3 in length. Abdomen about 3.1 in length. Forewing (incompletely preserved) about 5.4 in length, maximum width 1.9. Ovipositor about 2.7 in length, ovipositor sheaths about 1.4 in length.

*3.5. Identification Key for Species of the Genus Urosyntexis (cf. Table 1)*

1. Forewing with Rs+M long, at least equal to 2-M in length……………………………………………2
   Forewing with Rs+M short, less than 0.6 times as long as 2-M………………………………………………4
2. Sc absent; 1r-rs longer than 2r-rs; length of valvifers half length of ovipositor sheaths…………………………………………………………*U. magna* [14]
   Sc short, crossvein-like, near the origin of 1-Rs; 1r-rs as long as 2r-rs; length of valvifers equal to ovipositor sheaths……………………………………………3
3. Mesoprescutum extremely short, length between mesoscutum and mesocutellum more than three times of the latter………………………………*U. depressa* [13]
   Mesoprescutum large, as long as mesocutellum, and the length between them almost twice as long as the latter………………………………*U. ensia* sp. nov.
4. 1r-rs as long as 2r-rs………………………………………………………………*U. volita* sp. nov.
   1r-rs shorter than 2r-rs…………………………………………………………………………5
5. Antennae filiform; length of valvifers almost equal to ovipositor sheaths……………………………………………………………*U. undosa* [15]
   Antennae setiform, gradually tapering apically………………………………………………………………6
6. 1-Rs long, three times as long as 1-M; length of valvifers half length of ovipositor sheaths……………………………………………………*U. drepanura* [14]
   1-Rs much longer, five times as long as 1-M; length of valvifers equal to ovipositor sheaths……………………………………………………*U. forta* sp. nov.

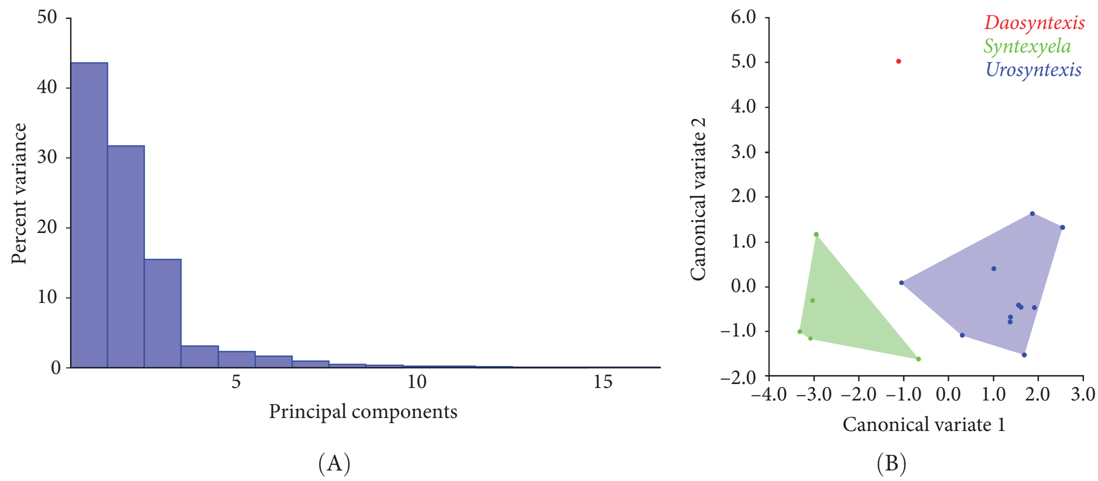


FIGURE 4: Result of GMA (A), Principal component analysis for the forewing with *Syntexyela*, *Urosyntexis*, and *Daosyntexis*. (B), The results of canonical variate (CV) analysis based on the forewing veins of the species within *Syntexyela*, *Urosyntexis*, and *Daosyntexis*.

## 4. Discussion

The genus *Urosyntexis* is one of the more diverse genera in family Anaxyelidae. With a few new specimens discovered from Karatau, Kazakhstan, two species *U. depressa* and *U. drepanura* were reported, and *Syntexyela magna* [14] was transferred from *Syntexyela* to *Urosyntexis* as its type species based on the filiform antenna, becoming gradually tapering to apical, the sclerotized pterostigma not reaching midpoint of the cell 3r, forewing with 5-M less than half of 2m-cu, hind wing r-m far from cu-a, and a thin and straight ovipositor. As the only Cretaceous species in the genus *Urosyntexis*, *U. undosa* [15] had significant morphological homology with the type species, that is, filiform antenna, gradually tapering apically, forewing with 5-M less than half-length of 2m-cu, 2r-rs emitted from the one-third of the pterostigma, which confirmed its genetic relationship with *Urosyntexis*, implying that *Urosyntexis* species retained their stable morphological features for ca. 20 million years.

However, the discriminations between *Urosyntexis* and *Syntexyela* are always encountered obstacles; some newfound specimens in CNU Anaxyelidae collections exhibited mosaic characters inducing the classification difficult. Traditional phenotypic taxonomy, by overemphasizing individual differences, may have led to an oversplitting of species. Whenever possible, objective and quantitative methods should serve as a complementary approach to verify these conventional classifications. In this study, we applied the GMA to review and validate the classification of our new species in *Urosyntexis*, including an objective confirmation of the two problematic genera.

In the PCA, we extracted the 16 principal components, of which the first principal component (PC1) accounted for 43.611% of the total variation, the second principal component (PC2) accounted for 31.796% of the total variation, and the third principal component (PC3) accounted for 15.450% of the total variation. The eigenvalues of the first three principal components accounted for 90.857% of the total variation (Figure 4A), which could explain the main differences among the samples and intuitively showed the main variation among the 13 species of Anaxyelidae (Figure 5A–L). The deformation grids show the deformation of the average shape of the sampled specimens within a species to the average shape of all 13 species (Figure 5M, N). The thin plate spline visualization presents some significant differences: in PC1, the maximum distortion is landmarks 8, 12, and 13 (the length of 5-M), landmarks 2 and 5 (the emission position of 2r-rs) have relatively large distortions (Figure 5M); in CV1, the maximum distortion is landmarks 12 and 13 (the length of 5-M), landmarks 6 and 10 (the bifurcation position of Rs+M), and landmark 2 (the emission position of 2r-rs) have relatively large distortions (Figure 5N). The distortion of landmarks suggests the existence of shape differences between species. The results showed that the length of 5-M, bifurcation position of Rs+M, and the emission position of 2r-rs were significantly different among the specimens. Since vein 4-Cu was not preserved in any of the species studied, landmarks 17 and 18, which also showed large distortions, could not be compared.

The CVA was used to explore the shape differences between genera, and the results further supported the view that there were significant differences between *Syntexyela* and *Urosyntexis*. The scatter plot is obtained by GMA, based on 10,000 repeated operations and confidence ellipse with a confidence level of 90%. The genera of *Daosyntexis*, *Syntexyela*, and *Urosyntexis* are clustered separately, and there is no overlap among these three genera (Figure 4B). It shows that the GMA based on the forewings can distinguish these three lineages well. The genera of *Urosyntexis* and *Syntexyela* are within the confidence ellipse of their respective genera, but the *Syntexyela* and *Urosyntexis* are closer in the distribution of scatter plots. *Syntexyela* and *Urosyntexis* are closely related genera, which are fully supported in CVA. They have a high overlap in geographical distribution and are distributed in the Daohugou, Karatau, Huangbanjigou, and Transbaikalia, which may be one of the reasons why the two genera are similar.

In summary, based on the comparisons of morphological characteristics and CVA results, we infer that the two genera are closely related genera, and the main differences between the

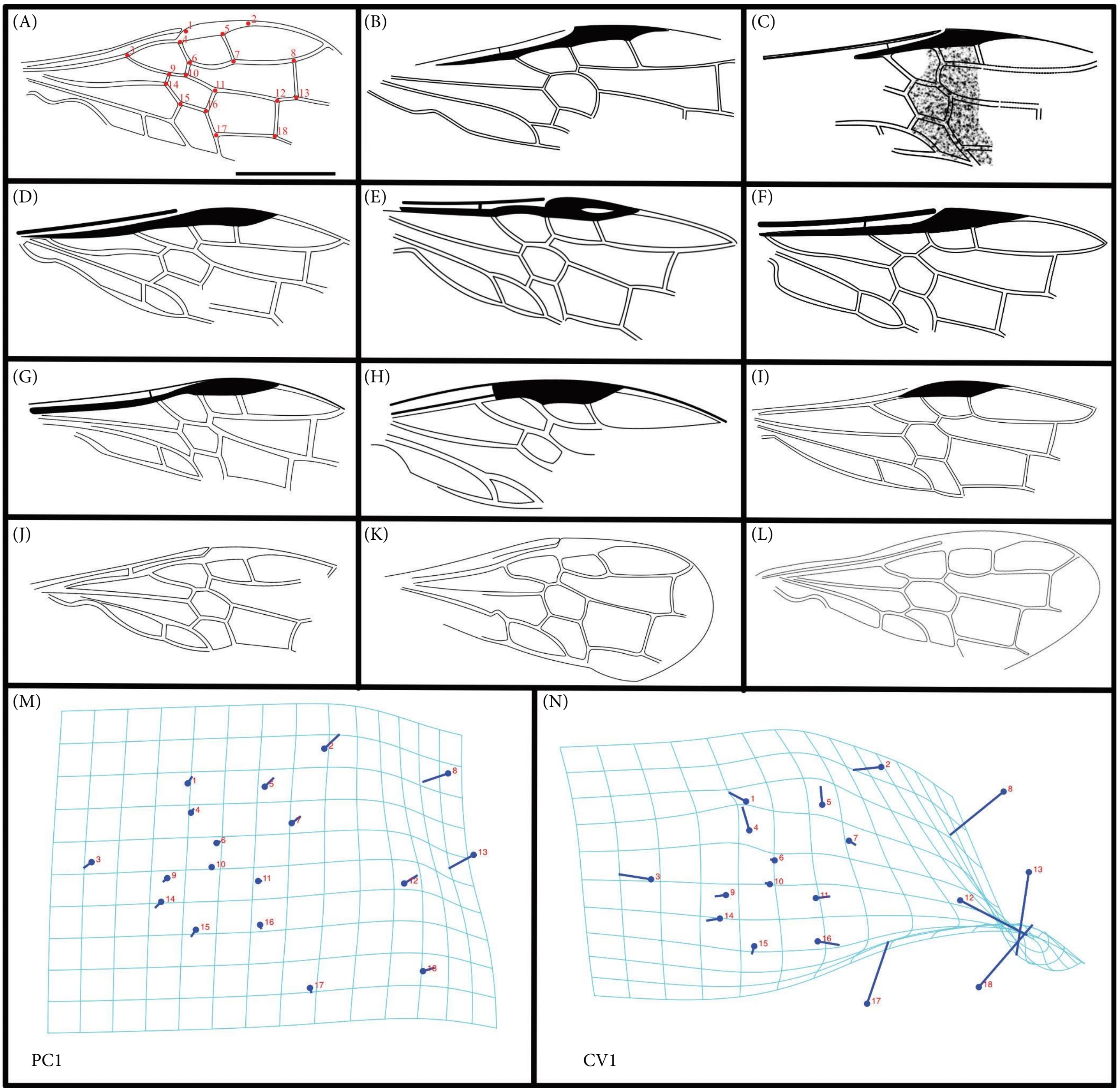


FIGURE 5: Landmark positions of the dozen forewing species of *Urosyntexis* and *Syntexyela* and thin plate spline of PC1 and CV1 for the wing veins. (A), *Urosyntexis volita* (B), *Syntexyela asiatica* (C), *S. continentalis* (D), *S. gracilicornis* (E), *S. inversa* (F), *S. meida* (G), *U. depressa* (H), *U. drepanura* (I), *U. magna* (J), *U. undosa* (K), *U. forta* (L), *U. ensia* (M), Thin plate spline of PC1 for the wing veins of *Syntexyela*, *Urosyntexis*, and *Daosyntexis* (N), Thin plate spline of CV1 for the wing veins of *Syntexyela*, *Urosyntexis*, and *Daosyntexis*.

two genera in the forewings are the length of 5-M and the emission position of 2r-rs. The genus *Syntexyela* has forewing with 5-M as long as or slightly shorter than 2m-cu, 2r-rs emanating from the midpoint of the pterostigma, while *Urosyntexis* possesses forewing with 5-M less than 0.6 times as long as 2m-cu, 2r-rs emitted from the one third of the pterostigma.

## Data Availability Statement

All data from this study are available in this paper and the associated papers.

## Conflicts of Interest

The authors declare no conflicts of interest.

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