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Blurring the limits of anaxyelid subfamilies: a new genus and species (Hymenoptera: Anaxyelidae) from the Albian of the Republic of Korea

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Abstract

Hanguksyntexis haeretica gen. et sp. nov. is the first Anaxyelidae described and illustrated from the early Albian Jinju Formation (Republic of Korea). This new taxon is attributed to the subfamily Syntexinae because of its forewing venation (*i.e.*, 1-Rs+M forking at 1m-cu level), but differs from all other syntexines genera because of its peculiar shape and length of 2r cell (*ca.* twice as long as wide, not distinctly widened apically nor basally) and by its vein 6-Rs strongly curved distally towards wing margin. The discovery of this new genus challenges the clear differentiation between Anaxyelinae and Syntexinae, prompting a thorough discussion on the diagnostic value of the wing venation characters that were previously used to distinguish the two subfamilies. Consequently, the genus *Cretosyntexis* Rasnitsyn & Martínez-Delclòs, 2000 is transferred to Anaxyelinae.

Keywords: Jinju Formation, Cretaceous, Korean Peninsula, new genus, new species

Introduction

The family Anaxyelidae is a relictual clade with a diverse fossil record but declining greatly, in terms of diversity,

during or after the Late Cretaceous (Kopylov, 2018, 2019; Gao *et al.*, 2021; Jouault *et al.*, 2022a). Today, this family is represented by only one species namely: *Syntexis libocedrii* Rohwer, 1915. This species, known as the ‘incense-cedar wood wasp’, occurs throughout diverse hosts (juniper—*Juniperus* L., 1753; giant red cedar—*Thuja plicata* Donn ex Don, 1824; incense cedar—*Calocedrus decurrens* (Torr.) Florin, 1956; and probably Douglas fir—*Pseudotsuga menziesii* (Mirb.) Franco, 1950) in western North America (Rohwer, 1915; Wickman, 1967). Its life cycle involves the laying of its eggs in the sapwood of the aforementioned gymnosperms, with a preference towards recently burnt and young trees (Wickman, 1967).

The oldest anaxyelids are known from the Middle Jurassic of Daohugou (Inner Mongolia, China) (Rasnitsyn & Zhang, 2004; Kopylov *et al.*, 2020a). These occurrences agree with age (*i.e.*, Early Jurassic–Late Triassic) estimated in time calibrated phylogenies (*e.g.*, Ronquist *et al.*, 2012; Malm & Nyman, 2014; Nyman *et al.*, 2019). The monophyly of the family Anaxyelidae is supported by molecular and morphological data (*e.g.*, Ronquist *et al.*, 2012; Malm & Nyman, 2014; Nyman *et al.*, 2019; Gao *et al.*, 2021). Herein, we describe a new genus and species of anaxyelid wasp from the Early Cretaceous

Jinju Formation. This new taxon further accentuates the difference of anaxyelid species diversity before and after the mid-Cretaceous.

Material and methods

The specimens were collected from the lower part of the Jinju Formation at the Jeongchon section (35°07'45"N, 128°06'02"E), 5.6 km south of the city of Jinju, Republic of Korea (see Park *et al.*, 2019). The most recent detrital zircon analysis shows that the age of the lower boundary of the Jinju Formation is 112.4 ± 1.3 Ma, while the upper boundary is 108.7 ± 0.5 Ma; hence the age of the formation can be considered early Albian (Lee *et al.*, 2018). The Jinju Formation is referred to as the latest stage of the famous Jehol Biota by Kopylov *et al.* (2020b: p. 1236–1237). The fossils are preserved as a reflective carbonaceous film on different slabs of dark grey shale. The specimens are housed in the Gongju National University of Education, with registration numbers GNUE218003, GNUE218004, GNUE218011, GNUE218012, GNUE218032, GNUE218038, and GNUE218044. The fossils were photographed with a Canon Eos 6D camera with an attached Canon EF 100 mm lens. Wing venation and cell nomenclature is adapted from Kopylov (2019).

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Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Superfamily Siricoidea Billberg, 1820
Family Anaxyelidae Martynov, 1925
Subfamily Syntexinae Benson, 1935

Genus *Hanguksyntexis* gen. nov.

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Type species. *Hanguksyntexis haeretica* sp. nov.

Etymology. The genus name is a combination of the Korean word “한국”, which means “Korea”, and the genus *Syntexis* (itself from Ancient Greek *syntēxis*—σύντηξις, meaning “colliquescence”, “emaciating”, or “wasting away”), type genus of the subfamily Syntexinae. Gender feminine.

Diagnosis. Forewing with 1r-rs complete; tubular veins developed in apical third of wing (R1, 6-Rs, free endings of M, Cu); pterostigma desclerotized, not

reaching midst 3r cell; 2r-rs arising from apical third of pterostigma; 1-R1 slightly shorter than pterostigma; 1-M of similar length as 1-Cu; cell 2r about twice as long as wide, not widened apically nor basally (nearly of the same width on all its length), beveled basally; cell 3r rounded apically (*i.e.*, vein 6-Rs strongly curved distally towards wing margin), about 1.8× longer than cell 2r, about as long as pterostigma, but distinctly wider than pterostigma; 1-Rs more than 2.3× as long as 1-M; ovipositor sheaths (♀) slender, short (about 0.6× metasomal length); ovipositor 0.73× forewing length.

Remarks. *Hanguksyntexis* gen. et sp. nov. differs from all other genera of the subfamily Syntexinae by its peculiar shape and length of 2r cell (*ca.* twice as long as wide, not distinctly widened apically nor basally) and by its vein 6-Rs strongly (~90°) curved upward towards wing margin.

By its forewing venation, *Hanguksyntexis* gen. nov. seems closer to *Syntexis* than to *Parasyntexis* Kopylov, 2019. However, the hind wings are missing in all studied specimens, precluding a comparison between these genera using the hind wing venation.

The wing venation of the new genus raises questions about the diagnostic value of previously used characters to distinguish between Syntexinae and Anaxyelinae, as it displays a combination of features from both subfamilies. The forking of vein 1-Rs+M right next to 1m-cu suggests its placement within Syntexinae. On the other hand, the elongated shape of cell 2r, being twice as long as wide, would rather support its placement in Anaxyelinae. However, the variable shape of cell 2r within Anaxyelidae prevents us from using it as a reliable diagnostic character. Similarly, the position of the 2r-rs vein joining the pterostigma also varies between Syntexinae and Anaxyelinae. While the general tendency in Anaxyelinae is to have 2r-rs displaced towards the pterostigma's distal quarter, suggesting a placement in Syntexinae, the rounded apex of cell 3r supports its placement in Anaxyelinae. Due to this combination of intermingled characters, we extensively discuss the value of each of them in the section ‘*Refining the limits and the wing venation diagnostic characters in the Anaxyelidae*’.

Hanguksyntexis haeretica sp. nov.

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(Figs 1–4)

Material. GNUE218038/GNUE218032 (holotype, ♀; part/counterpart), GNUE218003 (paratype, ♀), GNUE218004 (paratype, ♀), GNUE218011 (paratype, ♀), GNUE218012/GNUE218044 (paratype, ♀; part/counterpart), housed in the collection of the Gongju National University of Education, Gongju, Republic of Korea.

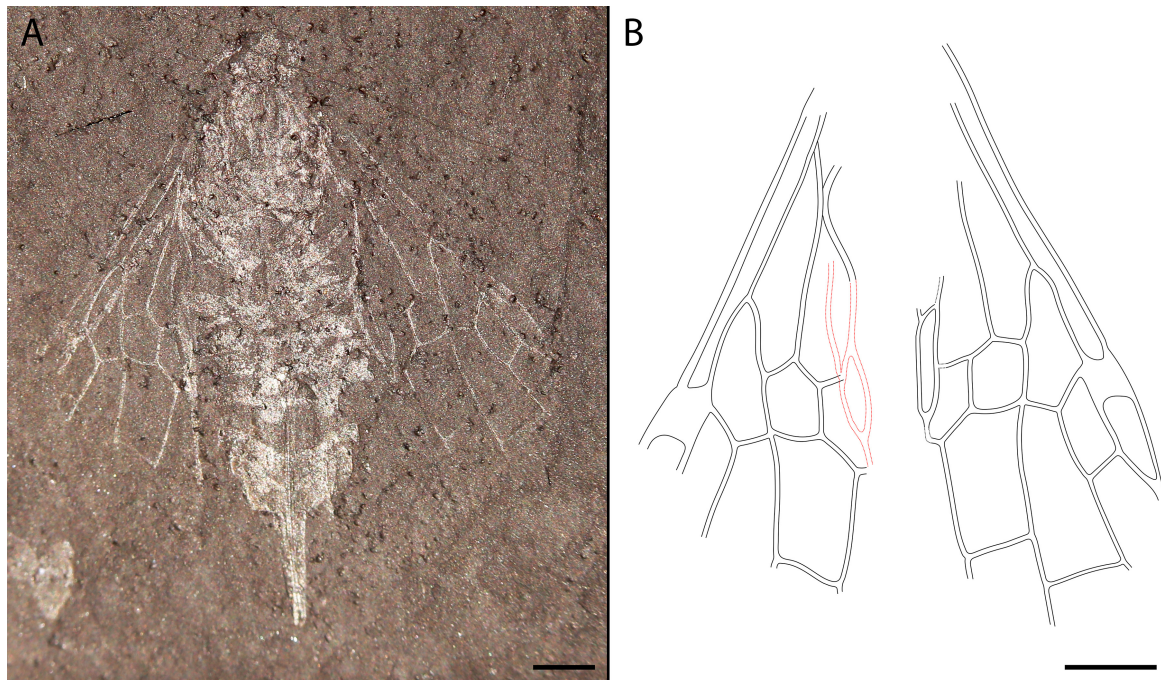


FIGURE 1. *Hanguksyntexis haeretica* gen. et sp. nov., holotype GNUE218038. A, Part. B, Interpretative drawing of forewing venation. Scale bars = 1 mm.

Etymology. The species name derives from the Latin word ‘*haeretica*’, which means ‘heretic’ or ‘heretical’ and refers to the unorthodox wing venation of the new species.

Locality and horizon. Jinju Formation, Jeongchon section, near the city of Jinju, Republic of Korea; early Albian, Early Cretaceous.

Diagnosis. As for the genus (*vide supra*).

Description. (mainly based on GNUE218038/GNUE218032). Body length (excluding ovipositor) *ca.* 7.8 mm. Wing veins and membrane not colored; body without distinctive coloration pattern.

Head *ca.* 0.9 mm long, 1.2 mm wide. Eyes large, occupying most of head lateral surface. Antennae (visible in GNUE218004) with scape longer than pedicel, wider distally; antennomeres (at least two preserved in GNUE218004) longer than wide with parallel sides.

Mesosoma *ca.* 2.8 mm long, *ca.* 2 mm wide (1.4× as long as wide). Mesofemur *ca.* 1.5 mm long, *ca.* 0.2 mm wide. Mesotibia *ca.* 1.4 mm long, *ca.* 0.18 mm wide, flared apically. Metafemur *ca.* 1.4 mm long, *ca.* 0.3 mm wide. Metatibia *ca.* 1.7 mm long, *ca.* 0.2 mm wide.

Forewing *ca.* 7.1 mm long, *ca.* 2.7 mm wide (2.63× as long as wide). Pterostigma *ca.* 1.5 mm long, *ca.* 0.4 mm wide (3.75× as long as wide). Cell 1r about 1.5 mm long and 0.7 mm wide (2.14× as long as wide). Cell 2r about 0.9 mm long and 0.43 mm wide (twice as long as wide). Cell 3r 2.3× as long as wide (no absolute measurements provided as it is incomplete in the holotype). Cell 2+3m about 2 mm long and 0.85 mm wide (2.35× as long as

wide), widening distally, widest along 3r-m. Cell 1mcu pentagonal, about 0.71 mm long, *ca.* 0.55 mm wide (1.29× as long as wide). Cell 2mcu trapezoidal, slightly wider basally (along 1m-cu and 3-Cu), about 1.43 mm long and 0.82 mm wide (1.74× as long as wide). Vein 1-Cu (*ca.* 0.27 mm long) about twice shorter than 2-Cu (*ca.* 0.54 mm long). 1r-rs (*ca.* 0.46 mm long) about 1.18× as long as 2r-rs (*ca.* 0.39 mm long). Vein 1-Rs+M trifurcating in 2-Rs, 2+3-M and 1m-cu (*i.e.*, cross-junction; 2-M absent). Vein 1-Rs curved basally, *ca.* 0.83 mm long, 2.37× as long as 1-M (*ca.* 0.35 mm long). Vein 1-Rs+M meets 1-Rs without significant bend. Vein 4+5-Rs (*ca.* 0.98 mm long) 1.25× as long as 3-Rs (*ca.* 0.78 mm long) and 1.23× as long as 6-Rs (no absolute measurements provided as it is incomplete in the holotype). Angle between 1-Cu and 1cu-a variable (likely due to preservation). Cell 2a triangular, longer than cell 1mcu. Crossvein a1-a2 present, inclined toward posterior wing margin, located well before M+Cu fork. Hindwing not preserved.

Abdomen (excluding ovipositor) about 4 mm long, 2.5 mm wide (1.6× as long as wide). Abdomen segments (visible in GNUE218004) wider than long, increasing in length distally (in ventral view). Ovipositor sheaths *ca.* 1.9 mm long, *ca.* 0.52 mm wide, slightly wider basally (protruding in GNUE218003: *ca.* 0.6× abdomen length), protruding beyond abdomen apex significantly. Ovipositor thin, about 4.13 mm long (probably incomplete), 0.73× forewing length (relative measures taken on GNUE218003).

Remarks. All absolute measurements used in the

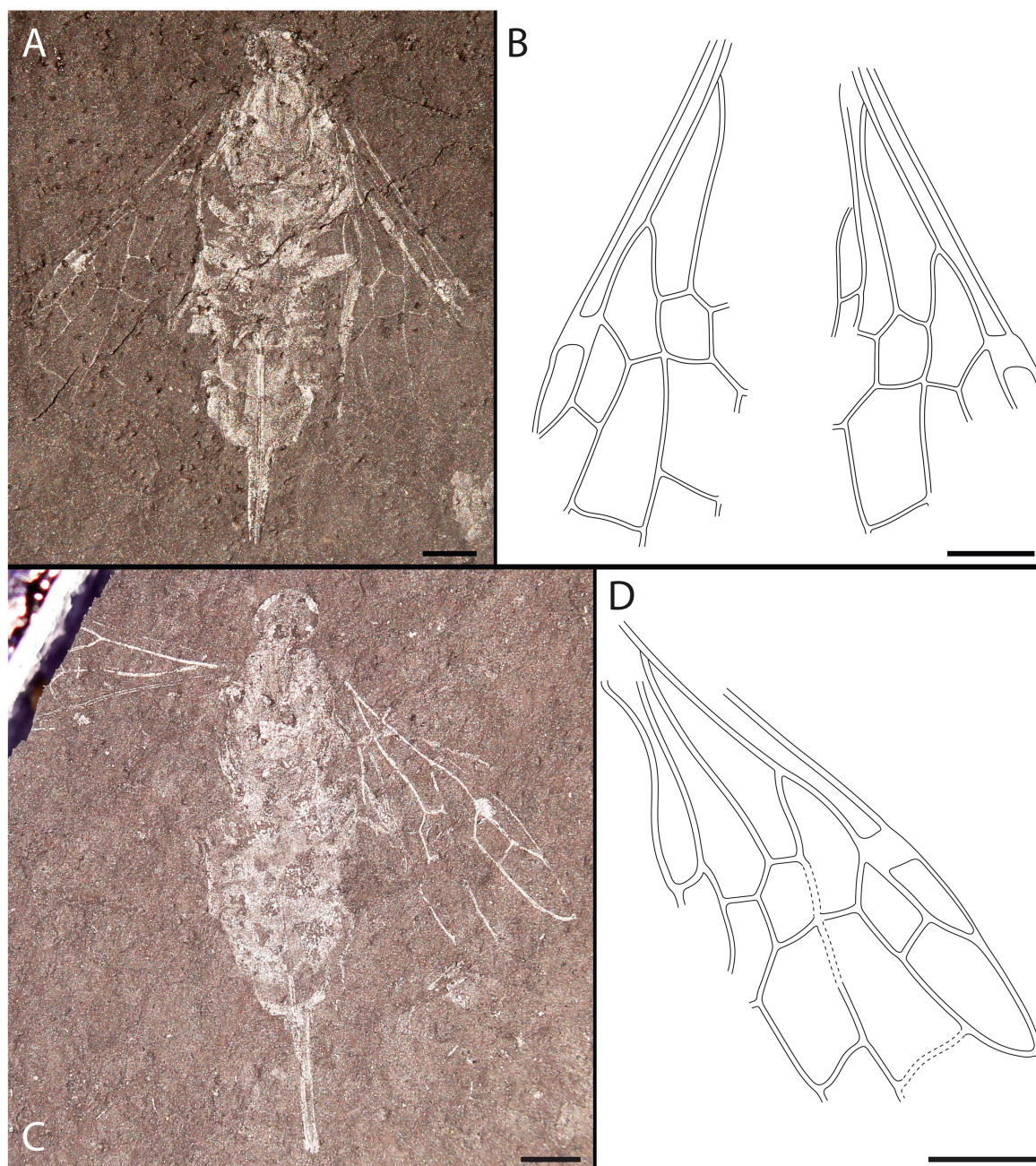


FIGURE 2. *Hanguksyntexis haeretica* gen. et sp. nov. **A**, Counterpart of holotype (GNUE218032). **B**, Interpretative drawing of forewing venation. **C**, Paratype (GNUE218003). **D**, Interpretative drawing of forewing venation. Scale bars = 1 mm.

description are taken on the holotype. For comparison purposes we also provide some key measurements of the paratypes: GNUE218003 body about 7.2 mm long (excluding ovipositor), forewing at least 6.4 mm long, ovipositor about 4.6 mm long; GNUE218004 body about 7.7 mm long (excluding ovipositor), forewing at least 6.5 mm long (as preserved), ovipositor at least 2.8 mm long (as preserved); GNUE218011 body at least 7 mm long (excluding ovipositor), forewing at least 7.1 mm long, ovipositor at least 3.8 mm long (as preserved); GNUE218044 body about 6.4 mm long (excluding ovipositor), at least 4.17 mm long, ovipositor at least 3.8 mm long (as preserved).

Identification key for genera of Syntexinae (updated from Kopylov, 2019 and Jouault *et al.*, 2022a):

1. Forewing with 1r-rs completely lost..... 2
- Forewing with 1r-rs at least partly developed 6
2. 1-Rs longer than 1-M (at least 1.1×); cell 2mcu longer than cell 1mcu 3
- 1-Rs shorter than 1-M (at most 0.9×); cell 2mcu as long as or shorter than cell 1mcu 5
3. Notauli almost reaching scutellum; 3r-m declined; 1cu-a joins A1 next to a1–a2 (2-A1 0.2× as long as 1cu-a) *Sclerosyntexis* Wang *et al.*, 2020
- Notauli meeting well before scutellum; 3r-m inclined or subvertical; 1cu-a displaced from a1–a2 (2-A1 at least 0.5× as long as 1cu-a) 4

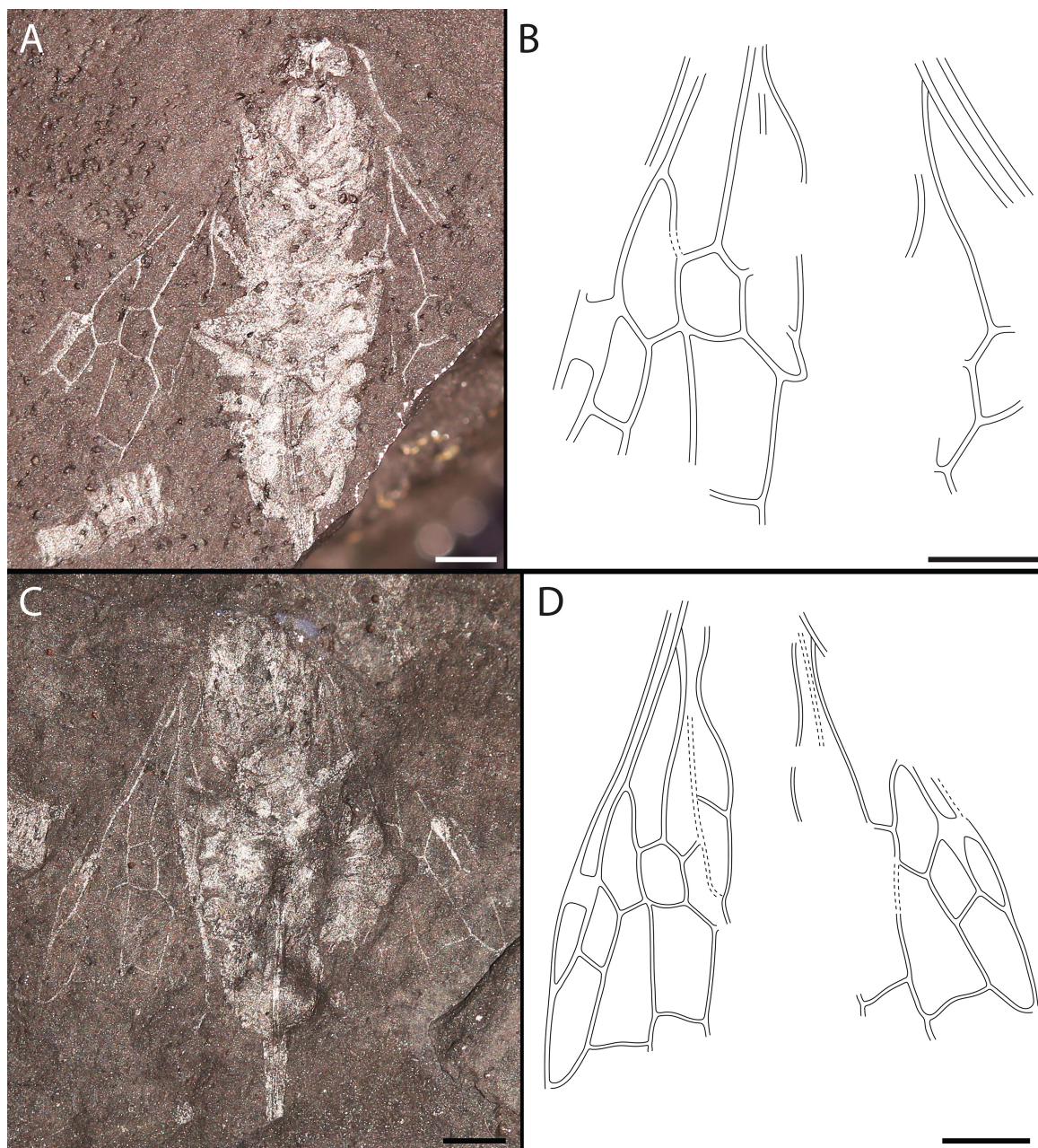


FIGURE 3. *Hanguksyntexis haeretica* **gen. et sp. nov.** **A**, Paratype (GNUE218004). **B**, Interpretative drawing of forewing venation. **C**, Paratype (GNUE218011). **D**, Interpretative drawing of forewing venation. Scale bars = 1 mm.

- | | | | | | |
|----|---|--|-----|---|--|
| 4. | 1-Rs at least 2.0× as long as 1-M; cell 1mcu at most 1.5× as long as wide..... | <i>Eosyntexis</i> Rasnitsyn, 1990 | - | Forewing with pterostigma not reaching middle of 3r cell; 2r-rs originating from middle of pterostigma..... | 8 |
| - | 1-Rs less than 1.6× as long as 1-M; cell 1mcu 2× as long as wide | <i>Curvitexis</i> Jouault <i>et al.</i> , 2022 | 8. | 1-M half as long as 1-Cu; 2-M half as long as 1m-cu..... | |
| 5. | 2m-cu closer to 3rs-m than to 1m-cu. Hind wing with cell 3r closed..... | <i>Orthosyntexis</i> Gao <i>et al.</i> , 2021 | - | 1-M much longer; 2-M absent or much shorter..... | 9 |
| - | 2m-cu closer to 1m-cu than to 3rs-m. Hind wing with cell 3r open | <i>Paraxiphidria</i> Gao <i>et al.</i> , 2022 | 9. | Forewing with 6-Rs strongly curved distally towards wing margin; cell 3r <i>ca.</i> 1.8× longer than cell 2r; cell 3r about same length as pterostigma..... | <i>Hanguksyntexis</i> gen. nov. |
| 6. | Forewing with 1r-rs incomplete and not reaching R; tubular veins not developed in apical third of the wing..... | <i>Curiosyntexis</i> Kopylov, 2019 | - | Forewing with 6-Rs <i>ca.</i> straight; cell 3r much longer than 1.8× cell 2r; cell 3r longer than pterostigma..... | 10 |
| - | Forewing with 1r-rs complete; tubular veins developed in apical third of the wing..... | 7 | 10. | Forewing with 2r-rs not shorter than pterostigma width. Hind wing with m-cu present; distal parts of Rs, M, Cu and A tubular | <i>Parasyntexis</i> Kopylov, 2019 |
| 7. | Forewing with pterostigma reaching middle of 3r cell; 2r-rs originating from basal third of pterostigma..... | <i>Dolichosyntexis</i> Kopylov, 2019 | - | Forewing with 2r-rs about half as long as pterostigma width. Hind wing with m-cu absent; distal parts of Rs, M, Cu and A nebulous..... | <i>Syntexis</i> Rohwer, 1915 |

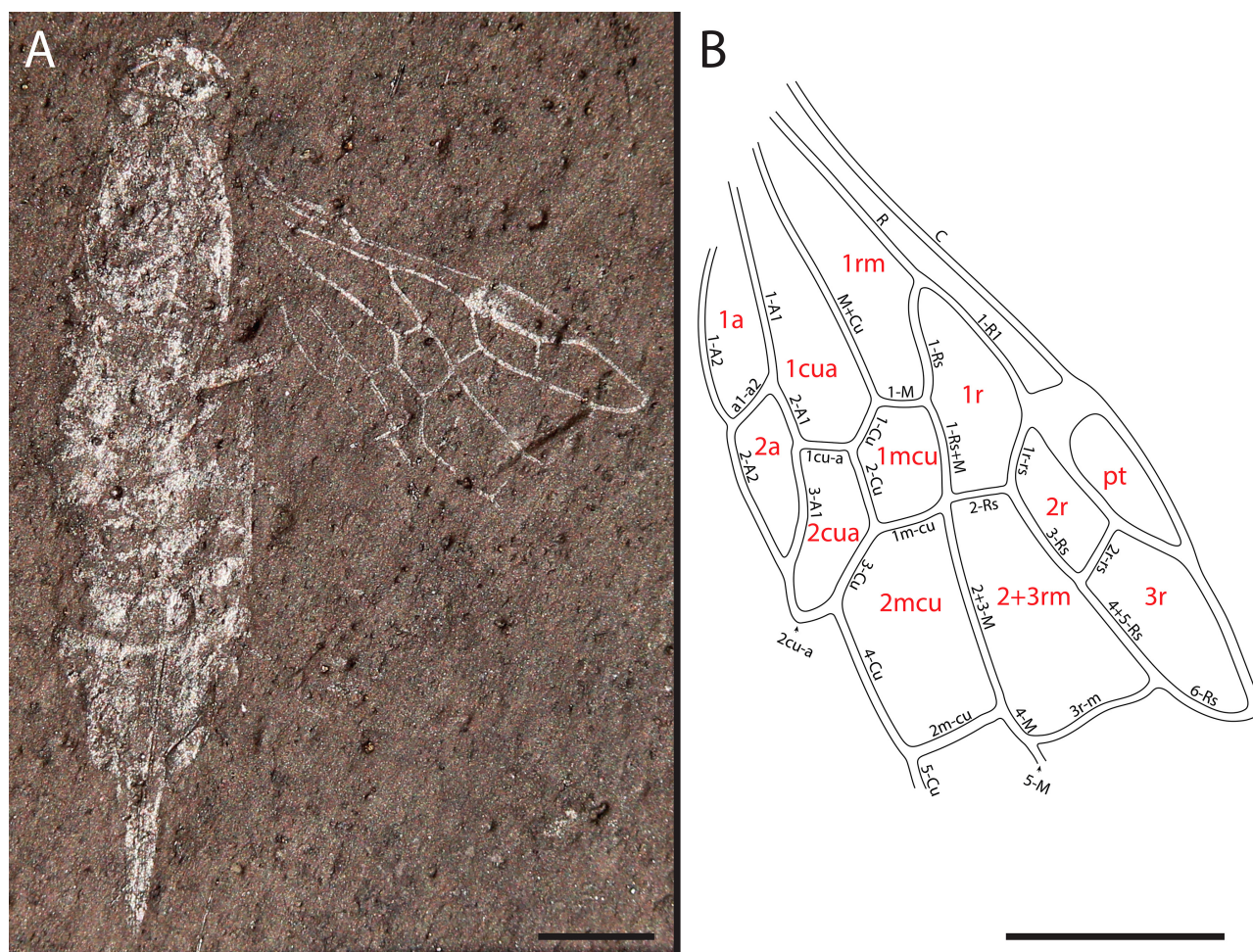


FIGURE 4. *Hanguksyntexis haeretica* gen. et sp. nov. **A**, Paratype (GNUE218044). **B**, Interpretative drawing of forewing venation. Scale bars = 1 mm.

Discussion

Systematic placement

The fossils cannot be placed within the families Xyelidae, Sypastoxyelidae, Blasticotomidae, and Xyelydidae because these lack an “enlarged first flagellomere succeeded by a series of thinner and shorter flagellomeres” (*i.e.*, a first flagellomere considered to be composite) (*e.g.*, Gao *et al.*, 2009, 2016; Engel *et al.*, 2016; Jouault *et al.*, 2021). Moreover, the Xyelidae have, most of the time, a well-developed longitudinal vein Sc between C and R (a character absent from the new fossils), and a different conformation of the distal part of the forewing with the cells 2rm and 3rm not fused and often a 1rs cell present (*i.e.*, Rs is forked distally with the exception of the Madygellinae: Mason, 1993; Jouault *et al.*, 2021; Dai *et al.*, 2022). The Sypastoxyelidae have reduced venation in the distal part of the forewing, while the forewing venation of the new fossils is normal (*e.g.*, Engel *et al.*, 2016; Wang *et al.*, 2021; Zheng *et al.*, 2021). Affinities with the Blasticotomidae are excluded because they have

a distinctly broader forewing cell 1mcu and a very short 1-Rs (*e.g.*, Gao *et al.*, 2009, 2016). The new fossils cannot be attributed to Pamphilioidea because of their forewings with a long 1-Rs nearly aligned with 1-Rs+M (*e.g.*, Rasnitsyn, 1977; Wang *et al.*, 2017; Jouault *et al.*, 2022b; Zhuang *et al.*, 2022). The absence of the crossvein 2r-m, and the long 1-Rs nearly aligned with 1Rs+M on the forewings of the new fossils preclude their placement in the Tenthredinoidea *s.l.* (*e.g.*, Vilhelmsen, 2001; Wappler *et al.*, 2005; Vilhelmsen *et al.*, 2010; Mendes *et al.*, 2015; Nel *et al.*, 2022). The Cephidae have a short vein 1-Rs on the forewings (*vs.* long in the new specimens) and a conformation of the cell under the pterostigma resembling that of the Tenthredinoidea (*e.g.*, Benson, 1946; Smith & Schmidt, 2009; Kopylov & Rasnitsyn, 2016).

The family Protosiricidae was created to accommodate the particular morphology of the species *Protosirex xyelopterus* Rasnitsyn, 1969 (*e.g.*, Rasnitsyn, 1969; Rasnitsyn & Zhang, 2004). However, the new specimens cannot be placed within this family, at least, because of their forewings with a partially desclerotized

pterostigma, a long and sigmoidal 1-Rs, and lacking the crossvein 2r-m.

The new fossils cannot be attributed to the Sinosiricidae because of their forewings with 1-Rs strongly inclined and originating well basad pterostigma (*vs.* subvertical to R and originating close to pterostigma in *Sinosirex* Hong, 1975), their 2-Rs vertical and nearly aligned with 1m-cu (*vs.* strongly inclined and originating well before 1m-cu, and because of the absence of the crossvein 2r-m (*vs.* present; Hong, 1975: fig. 3).

The forewings of the new specimens have large cells 1r and 2r (*vs.* small in Siricidae), a long, inclined and sigmoidal 1Rs (*vs.* short, vertical and straight), lack corrugation of the wing membrane (*vs.* often present), and show a particular configuration of the cubito-anal field. All these characters preclude affinities with the family Siricidae (*e.g.*, Archibald & Rasnitsyn, 2016; Wang *et al.*, 2018; Jouault *et al.*, 2020).

The limits of the family Myrmiciidae (= Pseudosiricidae) are unclear and often overlap the Sepulcidae. Carpenter (1992) proposed the following diagnostic characters: forewing with venation reduced; crossveins 3r-m and 2m-cu absent; vein Sc either present or obsolescent; basal section of Rs slanted toward wing apex or wing base (this diagnosis was initially proposed for Pseudosiricidae before its synonymization with Myrmiciidae). According to this diagnosis, the new specimens cannot be considered members of this family because of their 3r-m and 2m-cu present (note that *Myrmicium araripiterum* Freitas *et al.*, 2020 possesses 3r-m and 2m-cu crossveins). The most noticeable difference between the new genus and the Myrmiciidae lies in the absence of strong corrugations on the wing membrane, which typically extend from the level of 1r-rs and 1m-cu to the wing's apex.

To date, no fossil Xiphydriidae is described although one fossil resembling this family is known from the Cretaceous Kachin amber, although it is probably an Anaxyelidae (N. Oyama, pers. comm.). This family is recognizable among the Symphyta because of their unusually long propleuron, and typically display an elongate metasoma (Goulet & Huber, 1993). Besides, none of the described specimens displays the typical nearly straight, transverse groove between the base of the forewings associated with Xiphydriidae.

The family Sepulcidae is hardly discernible from the family Anaxyelidae because no forewing venation apomorphy allows a clear separation between the two families. In the Sepulcidae, 2r-m is present, or if it is lost, 3r-m is still present, the distinguishing feature lies in either having a very short 1-Rs (as observed in *Ghilarella* Rasnitsyn, 1988) or a centrally widely membranous mesonotum (this character may be difficult to observe on imprint/compression fossils). In the new fossils, the

vein 1-Rs is comparatively much longer. Nevertheless, the specimen GNUE218032 seems to bear the diagnostic longitudinal medial groove or articulation of the pronotum associated with Anaxyelidae. Therefore, affinities with the Sepulcidae are ruled out and we decide to place the new fossils within the Anaxyelidae.

Following the key provided in Kopylov (2019), our specimens key out either in the subfamily Syntexinae or Anaxyelidae: forewing with pterostigma not reaching the midlength of cell 3r; cell 2r less than $3 \times$ as long as wide, shorter than cell 1r; 1-Rs+M present (excluding Dolichostigmatinae); forewing with Sc absent or present as a crossvein (excluding Kempendajinae, in which all species also have a long 2-M vein, absent in GNUE218038).

We conclude that the new specimens can be placed in the subfamily Syntexinae because of the forking position of 1-Rs+M (see *Refining the limits and the wing venation diagnostic characters in the Anaxyelidae*). However, the shape of cell 2r (about twice as long as wide, not distinctively widened apically nor basally, and with 2r-rs arising from the apical third of the pterostigma) is unusual for Syntexinae, and would be more expected in Anaxyelinae (*e.g.*, *Anaxyela destructa* Rasnitsyn, 1969, *Sphenosyntexis pallicornis* Rasnitsyn, 1969, *Syntexyela nana* Rasnitsyn, 1968). Moreover, the presence of a cell 3r with a rounded apex supports a placement in Anaxyelinae rather than Syntexinae. As discussed below, we consider the forking of 1-Rs+M as the most diagnostic character supporting the placement of the new genus in Syntexinae, although it shares numerous characters with Anaxyelinae.

Following the key for genera of Syntexinae (Jouault *et al.*, 2022; updated from Kopylov, 2019), the new fossils key out close to *Syntexis* and *Parasyntexis* because of the following couplets and characters: forewing with 1r-rs at least partly developed (excluding *Cretosyntexis* Rasnitsyn & Martinez-Delclòs, 2000, *Eosyntexis* Rasnitsyn, 1990, *Curvitexis* Jouault *et al.*, 2022, *Sclerosyntexis* Wang *et al.*, 2020, *Orthosyntexis* Gao *et al.*, 2021 and *Paraxiphydria* Gao *et al.*, 2022); forewing with 1r-rs complete; tubular veins developed in the apical third of the wing (excluding *Curiosyntexis* Kopylov, 2019); forewing with pterostigma not reaching the middle of 3r cell; 2r-rs issuing from the apical third of pterostigma (excluding *Dolichosyntexis* Kopylov, 2019); 1-M of similar length as 1-Cu; 2-M absent (excluding *Daosyntexis* Kopylov *et al.*, 2020).

Affinities of the new species with the genus *Parasyntexis* can be excluded because of (most of the following forewing characters are diagnostic) the cells 2r and 3r conformations (most notably the 6-Rs curved distally) and relative sizes (most notably the cell 3r similar in length to the pterostigma), its widely desclerotized pterostigma, 1-R1 shorter than pterostigma, as well as

1Rs+M ‘trifurcating’ (i.e., 2-M absent). They can also be distinguished from *Syntexis* because of the cells 2r and 3r conformations (most notably the 6-Rs curved distally) and the relative sizes (most notably cell 3r similar in length to the pterostigma), and the size and shape of the ovipositor sheaths (longer than in *Syntexis*). Therefore, we consider that these specimens belong to a new genus.

Refining the limits and the wing venation diagnostic characters in the Anaxyelidae

As the number of described genera and species increases, distinguishing between Syntexinae and Anaxyelinae becomes an increasingly challenging endeavor. The newly described genus exhibits certain characteristics from both Syntexinae and Anaxyelinae, thus narrowing the morphological gap between these subfamilies. Consequently, a reevaluation of the distinguishing features for these subfamilies becomes imperative. In this context, we address the most significant characters proposed in previous studies (Rasnitsyn, 1969; Kopylov, 2019), along with introducing a novel one. Although most of these characters do not offer a clear-cut distinction between the two subfamilies independently, their combination allows us to lean towards one assumption or the other.

The first distinguishing character pertains to the position of the Rs+M bifurcation in regard to 1m-cu. In Anaxyelinae, Rs+M bifurcates at a considerable distance from the level of 1m-cu, usually at or before reaching the midlength of the 1m-cu cell. Although in some species, the bifurcation may be slightly shifted distally (e.g., *Anaxyela gracilis* Martynov, 1925, *Sphenosyntexis antonovi* Rasnitsyn, 1963), but 2-M is always at least 0.5 times longer than Rs+M. On the other hand, in Syntexinae, Rs+M typically bifurcates right next to or slightly distally from 1m-cu. In certain genera like *Daosyntexis*, *Dolichosyntexis*, and *Paraxiphydria*, the bifurcation occurs before 1m-cu but remains very close to it, with 2-M measuring less than 0.2 times the length of Rs+M. We consider this character to be the most reliable for identification purposes.

Cell 2r dimensions have been utilized as an identification character for the Anaxyelidae (Kopylov, 2019). In Anaxyelinae, the length of cell 2r is typically more than 1.5 times its width, while in Syntexinae, it is less than 1.5 times its width. Although this pattern is generally characteristic of the considered subfamilies, notable variations exist within each group. For instance, some species like *Anaxyela gracilis* Martynov, 1925, *A. destructa* Rasnitsyn, 1969, *Sphenosyntexis antonovi* Rasnitsyn, 1969, and *Urosyntexis depressa* Rasnitsyn, 1969 (Anaxyelinae) have the cell 2r with a length less than 1.5 times its width, while *Hanguksyntexis haeretica* **gen. et sp. nov.** (Syntexinae) exhibits cell 2r with a length twice its width. Furthermore, *Curiosyntexis magadanicus* Kopylov, 2019 has incomplete 1r-rs, but its position

suggests a relatively long cell 2r. Additionally, it is worth noting that the majority of syntexine species have entirely lost the trace of 1r-rs, rendering this character useful for identifying only four species in Syntexinae: *Daosyntexis primus* Kopylov *et al.*, 2020, *Dolichosyntexis transbaikalicus* Kopylov, 2019, *Parasyntexis khasurtensis* Kopylov, 2019, and *Syntexis libocedrii* Rohwer, 1915.

Cell 2r shape is a distinguishing feature between Syntexinae and Anaxyelinae. Typically, in Syntexinae, if the cell 2r is present, it tends to widen basally. However, the newly described species *Hanguksyntexis haeretica* **gen. et sp. nov.** deviates from this norm, displaying an almost parallel-sided cell 2r. On the other hand, in Anaxyelinae, cell 2r usually widens apically, but approximately 40% of species have parallel-sided cell 2r. Nonetheless, it is essential to note that the differences in shape can sometimes be indistinct, making this particular character useful only when clearly expressed.

The position of 2r-rs joining the pterostigma can differ among Syntexinae and Anaxyelinae. In Syntexinae, 2r-rs is commonly shifted towards the base and connects with the pterostigma near its midpoint. This trend is most pronounced in species with a missing 1r-rs, but it is still noticeable in species with complete venation. However, in the case of *Hanguksyntexis haeretica* **gen. et sp. nov.**, this characteristic is less pronounced, as 2r-rs emerges from the apical third of the pterostigma. On the other hand, in Anaxyelinae, 2r-rs is typically displaced towards the distal quarter of the pterostigma. Nevertheless, there are numerous exceptions to these observations found in *Anaxyela* Martynov, 1925, *Brachysyntexis* Rasnitsyn, 1969, and *Syntexyela* Rasnitsyn, 1968.

The shape of cell 3r, especially its apex, can offer valuable insights for a placement within the Syntexinae vs. Anaxyelinae. In Anaxyelinae, the apex of cell 3r is typically rounded, and the subterminal section of 6-Rs strongly curved forward, forming a right-angle junction with C. In contrast, in Syntexinae, 6-Rs remains usually straight along its entire length, resulting in a sharp apex for cell 3r. Nevertheless, there are exceptions to this pattern within both Anaxyelinae (approximately 30% of species) and Syntexinae (such as *Dolichosyntexis* and *Hanguksyntexis haeretica* **gen. et sp. nov.**). It is essential to acknowledge that assessing this particular characteristic might be subjective and biased due to the considerable variability in the “sharpness” of the cell apex. Additionally, the formal definition of this character might be imprecise or lacking in clarity.

Moreover, it should be emphasized that the polarity of the characters used to classify the subfamilies of Anaxyelidae remains uncertain. The recent cladistic analysis does not provide robust support for each anaxyelid subfamily and suggests that the Dolichostigmatinae and Kempendajinae could potentially be considered as

subgroups of Anaxyelinae (Gao *et al.*, 2021). This result could be attributed to the fact that there is only one extant anaxyelid species and to the incompleteness of many of the known fossils, which complicates our understanding of the evolution of the family.

Comments on the placement of Cretosyntexis montsecensis *Rasnitsyn & Martínez-Delclòs, 2000*

The patterns described above are contradicted by the species *C. montsecensis*, which was initially assigned to Syntexinae and described from the Early Cretaceous of Spain (Rasnitsyn & Martínez-Delclòs, 2000). This particular species exhibits unique characteristics, including the bifurcation of Rs+M near the midlength of cell 1mcu and the origin of 2r-rs near the apex of the pterostigma. Despite losing 1r-rs, the shape of 2+3-Rs in *C. montsecensis* more closely resembles that of Anaxyelinae rather than Syntexinae. In other words, if we reconstruct the lost vein based on the shape of 2+3-Rs, the “virtual cell” 2r would appear long and narrow, akin to the pattern observed in Anaxyelinae. Therefore, we propose transferring the genus *Cretosyntexis* to the subfamily Anaxyelinae.

Conclusion

The description of *Hanguksyntexis haeretica* **gen. et sp. nov.** contributes significantly to our understanding of the paleoentomofauna of the Jinju Formation. Notably, this new genus represents the first fossil record of the family Anaxyelidae on the Korean Peninsula. Of particular interest, this new genus exhibits a distinct combination of wing venation characters, challenging the boundaries between the subfamilies Anaxyelinae and Syntexinae. As a result, we have reevaluated the value of the characters typically employed to differentiate these two subfamilies, and we propose that the forking position of the vein Rs+M remains the most stable and useful character for distinguishing between them. Furthermore, we anticipate that further discoveries of fossil Hymenoptera from the Jinju Formation will greatly enhance our understanding of the diversity of this order during the Early Cretaceous.

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