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A new parapamphiliin wasp (Hymenoptera: Sepulcidae) from the Middle Jurassic Yan'an Formation, China

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Abstract

A new genus and species of Sepulcidae, *Yananphilius peizhuangensis* gen. et sp. nov., are described and illustrated from the Middle Jurassic Yan'an Formation of Yan'an City, China. The taxon is erected based on a forewing with key diagnostic preserved. The new taxon is easily distinguishable from the other Parapamphiliinae because its long Sc vein reaches R slightly distad 1r-rs. This discovery demonstrates the overall stability of the Parapamphiliinae diagnosis, which remained unchanged for decades, and shows that its slight emendation allows for a better understanding of sepulcid wasps diversity during the Jurassic. This new species is the first Sepulcidae described in a Jurassic deposit from China and the Yan'an Formation.

Key words: Mesozoic, wasp, stem group, Ordos Basin

Introduction

The superfamily Cephoidea currently includes one extant family, Cephidae, and one extinct family, Sepulcidae. Morphological evidence and some molecular analyses support Cephoidea as the sister group to Siricoidea + [Xiphydrioidea + (Orussoidea + Apocrita)] (Sharkey *et al.* 2012; Malm & Nyman 2015). However, this phylogenetic relationship remains debated. Recent molecular analyses propose an alternative topology, positioning Cephoidea as the sister lineage to (Orussoidea+Apocrita) (e.g., Peters *et al.* 2017; Blaimer *et al.* 2024; Wutke *et al.* 2024).

Sepulcidae is a diverse, though not particularly abundant, group of siricomorph wasps (Rasnitsyn & Martínez-Delclòs 2000). Fossils of the family have been documented in the Triassic strata of Germany and up to the Aptian (e.g., Barth *et al.* 2011; Kopylov & Rasnitsyn 2014, 2017a, b). This family was initially described from Jurassic deposits in Karatau, Kazakhstan, and subsequently assigned to Cephoidea based on their flat, saw-like ovipositor, establishing them as a stem group to Cephidae (Rasnitsyn 1968, 1988). Most of the family diversity comes from compression deposits of Asia with the highest number of species described from Cretaceous deposits of Russia (https://paleobiodb.org; accessed 19/12/2024). During the Jurassic the family is also diverse with records from Germany, India, Kazakhstan, Kyrgyzstan, and Mongolia (Kopylov & Rasnitsyn 2017a). To date, 58 species distributed across 15 genera have been documented from Mesozoic deposits (e.g., Darling & Sharkey 1990; Rasnitsyn 1993; Rasnitsyn & Ansorge 2000; Jattiot *et al.* 2011; Li *et al.* 2023).

Despite the relatively high number of species and the presence of Sepulcidae in most Jurassic Lagerstätten, the family has not yet been documented in Jurassic deposits from China. This absence is particularly surprising given the wealth of material recovered from the Daohugou Biota (Haifanggou Formation). In this study, I address this geographical gap by describing the first Sepulcidae specimen from China. Additionally, I encourage paleoentomologists to explore the Daohugou beds further, as they may yield additional fossils of this family.

Material and methods

A single specimen was collected from the grayish mudstones near the Peizhuang Village, Yan'an City, Shaanxi Province, China by Prof. Diying Huang on September 30th, 2023 (locality map see Xu *et al.*, 2023). The specimen was

carefully prepared using a sharp knife. Photographs were taken using a digital camera attached to a Zeiss AxioZoom V16 stereomicroscope, and a Canon EOS 5D Mark II camera with a Canon 100 mm macro lens attached. Line drawings were made using Adobe Illustrator 2019. The specimens are stored at the Nanjing Institute of Geology and Palaeotology, Chinese Academy of Sciences (China). Nomenclature is adapted from Rasnitsyn (1969: fig 1).

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758 Superfamily Cephoidea Newman 1834 Family Sepulcidae Rasnitsyn, 1968 Subfamily Parapamphiliinae Rasnitsyn, 1968

Included genera. *Micramphilius* Rasnitsyn, 1993, *Pamparaphilius* Rasnitsyn, 1993, *Parabakharius* Rasnitsyn, 1993, *Parapamphilius* Rasnitsyn, 1968, *Shurabisca* Rasnitsyn 1968, and *Yananphilius* gen. nov.

Emended diagnosis (modified from Rasnitsyn 1993: 81). Antennae with third antennomere enlarged. In forewing C normally developed, Sc either short or long, free, pressed to R, without anterior branch or, more often, absent. 1-Rs usually subvertical, less often oblique. M+Cu more or less S-shaped, sometimes distal bend weakly expressed, then dimensions are very small, 1r-rs of variable length (sometimes reduced or even absent). One crossvein mcu-a often developed before M+Cu fork. Cell 1mcu small, not sharply expanded to apex, always with distinct bend of Cu at level cu-a crossvein, the latter near middle, less often far distad middle of cell, in this case Cu is also curved basally or transverse. Ovipositor not or only slightly protruding beyond apex of abdomen.

Yananphilius gen. nov. (Fig. 1)

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Type species. Yananphilius peizhuangensis sp. nov.

Diagnosis. Forewing large, at least 2cm long; Sc developed, reaching R slightly distad 1r-rs; pterostigma sclerotized basally; 1-Rs subvertical to R; M+Cu distinctly curved in distal half; 1-M angled with M+Cu (but not as strongly as in *Shurabisca*); 2-M aligned with Rs+M; 2m-cu present; M with a free end; 2r-rs oblique, longer than 1r-rs and longer than pterostigma width; 2rs-m slightly proximal to 2r-rs; 1r-rs developed (i.e., not extremely short or reduced to a minute vein as in *Pamparaphilius vitimicus*); Cu distinctly angled at level of cu-a; cu-a located near middle of cell 1mcu; stem of mcu-a present.

Remarks. The new genus differs from *Micramphilius* in having a Sc well-developed (*vs.*, absent in *Micramphilius*), a subvertical 1-Rs (*vs.*, oblique), 1r-rs present (*vs.*, absent), a strong distal bend of M+Cu (*vs.*, weak), mcu-a present (*vs.*, absent), cu-a not at right angle with Cu (*vs.*, often at or nearly at right angle with Cu), 2m-cu present (*vs.*, Cu+A smoothly passing to M, and M lacking a free end) (Rasnitsyn 1993: 85). It differs from *Pamparaphilius* because of its larger size (forewing more than 20 mm long vs. about 6–8 mm long in *Pamparaphilius*), partially sclerotized pterostigma (*vs.*, not sclerotized), cu-a located near the middle of the cell 1mcu (vs. far distad middle), one mcu-a crossvein present (*vs.*, absent) (Rasnitsyn 1993: 84). It differs from *Parabakharius* by its comparatively larger size (forewing about 2.5 mm long in *Parabakharius* vs. about 21.7 mm long in the new specimen), its forewing with Sc developed (vs. not developed in *Parabakharius*), its 1-Rs subvertical (*vs.*, oblique), its 1-M long (*vs.*, short), its crossveins r-rs and rs-m are well-defined (*vs.*, faint or absent), and its M+Cu that is not extremely sharply bent basally (*vs.*, sharply bent) (Rasnitsyn 1993: 82). The new specimen differs from *Parapamphilius* at least because of its 2r-rs much longer than 1r-rs (*vs.*, shorter or of similar width in *Parapamphilius*), and longer than pterostigma width (*vs.*, shorter than pterostigma width) (Rasnitsyn 1993: fig 5). Lastly, it differs from *Shurabisca* at least because its 1-M does not deviate sharply from M+Cu (*vs.*, the opposite in *Shurabisca*), and its Sc is developed (*vs.*, not developed) (Rasnitsyn 1968).

Etymology. The genus name is a combination of the name of Yanan Formation and of the genus name *Pamphilius* Latreille, 1802.

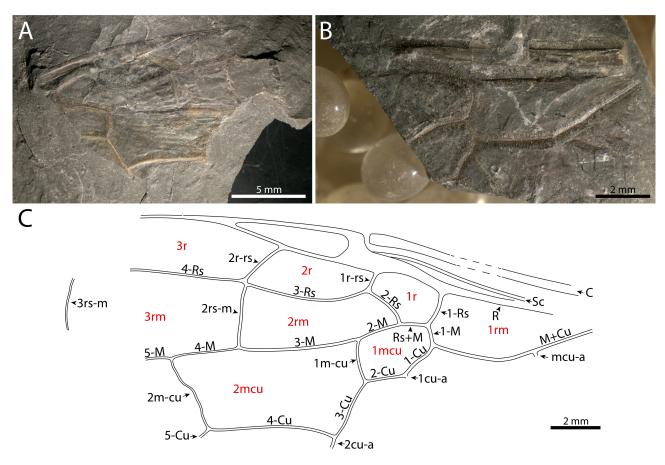


Figure 1. *Yananphilius peizhuangensis* gen. et sp. nov. holotype NIGP206614. A, Distal part of the forewing; B, Basal part of the forewing; C, Interpretative wing drawing with names of veins and cell labeled.

Yananphilius peizhaungensis sp. nov.

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Material. Holotype, NIGP206614, forewing (Fig. 1), divided into two pieces, part and counterpart which partly overlapped, with apex and posterior parts of the wing missing.

Etymology. The specific epithet is after the fossil locality "Peizhuang".

Diagnosis. As for the genus (vide supra).

Type locality and horizon. A locality near the Peizhuang Village, Yan'an City, Shaanxi Province, China; Middle Jurassic Yan'an Formation.

Description. Forewing, as preserved, about 21.7 mm long and 8.7 mm wide. Costal space wider than subcostal space; Sc long, thinner than C or R; pterostigma much longer (about 5.95 mm) than wide (about 1.35 mm), triangular, partially sclerotized; M+Cu straight basally, sharply bent distad mcu-a (angle about 150°); 1-M slightly about 0.67× as long as 1-Rs, both veins arched; cell 1r pentagonal, about 1.75× longer than wide; Rs+M short, shorter than 1-Rs; 2-Rs located slightly anteriad 1mcu cell midlength, strongly curved; 1r-rs much shorter than 2r-rs, subvertical to R; cell 2r quadrilateral, about 2.35× longer than wide; 2r-rs about twice as long as 1-Rs, bightly oblique, originating slightly distad pterostigma midlength, reaching Rs slightly distad 2rs-m; 3-Rs about as long as 3-M slightly gently curved; 2-M longer than Rs+M; cell 2rm thinnest along 2-Rs, about 3.3× longer than wide; M abscissae from 2 to 5 nearly aligned; 2rs-m and 3rs-m present; cell 3rm rectangular, about twice as long as wide; 1-Cu slightly longer than 1-Rs, forming an obtuse angle with M+Cu (about 118°), and 2-Cu (about 141°); cell 1mcu hexagonal, about 1.55× longer than wide; 2-Cu about as long as 1-Cu; 1m-cu well-developed, slightly curved, longer than 1-Rs, shorter than 3-Cu; cell 2mcu pentagonal, about 2.33× longer than wide; 3-Cu about half 4-Cu length; 2m-cu zigzagged (likely due to deformation), reaching M distad 2rs-m, about 1.84× as long as 1m-cu; 1cu-a and 2cu-a present as stems; free M and Cu present; anal vein not preserved.

Discussion

The wing venation of the new specimen superficially resembles that of certain pamphilioid wasps but lacks several key features of the latter superfamily. Notably, the forewing does not have a Sc1 and Sc2 (*vs.*, both of which are present in most pamphilioid wasps). Additionally, 1-Rs is about as long as 1-M (*vs.*, shorter in most pamphilioids) (e.g., Zhuang *et al.* 2023). Jurassic-period families with similar forewing venation, the Sepulcidae stand out. Sepulcidae, considered the stem group of Cephidae (Rasnitsyn 1968, 1988), include five subfamilies: Ghilarellinae, Parapamphiliinae, Sepulcinae, Trematothoracinae, and Xyelulinae.

The new specimen cannot be assigned to Ghilarellinae due to the presence of Sc (absent in Ghilarellinae), a long 1-Rs (vs., short), a distinctly curved M+Cu (vs., straight), and a small 1mcu cell (vs., large) (Li *et al.* 2024). Similarly, it does not belong to Trematothoracinae because of its unique forewing venation: 1-Rs is subvertical to R (vs., oblique in Trematothoracinae), M+Cu is strongly curved (vs., slightly curved basally and then straight), and cell 1r is much smaller. Moreover, the specimen features a long Sc running parallel to R and merging distally (vs., a short Sc, often subvertical to R near 1-Rs in Trematothoracinae) (e.g., Kopylov & Rasnitsyn 2017a; Jouault & Nel 2021).

The specimen also cannot be attributed to Sepulcinae, as it has a well-developed Sc vein (vs., absent in Sepulcinae), a 1-Rs that is not oblique (vs., oblique), and an M+Cu with a mcu-a stem (vs., absent). Additionally, the cu-a vein is located in the middle of the 1mcu cell (vs. far behind the middle in Sepulcinae) (Rasnitsyn 1993). Similarly, it cannot be assigned to Xyelulinae, which lack an Sc vein in the forewing (vs., present), have a long and oblique 1-Rs (vs., short and perpendicular to R), and an M+Cu that is not strongly arcuate (vs., strongly arcuate). However, the specimen shares one feature with Xyelulinae: a cu-a crossvein near the middle of cell 1mcu (Rasnitsyn 1993).

The wing venation of the new specimen strongly resembles that of Parapamphiliinae. Rasnitsyn (1993) described diagnostic features of this subfamily's forewing venation, which include (terminology adapted): in forewing C normally developed; Sc short, free, pressed to R, without anterior branch or, more often, absent; first segment of Rs (=1-Rs) usually subvertical, less often oblique; M+Cu more or less S-shaped, sometimes distal bend weakly expressed, then dimensions are very small, transverse mcu-a very weak or absent; additional cu-a often developed basal to fork M+Cu; cell 1mcu small, not sharply expanded towards apex, always with distinct bend of Cu where cu-a enters, the latter near the middle, less often far behind the middle of the cell, in which case Cu is also curved basal to transverse. The wing venation of the new specimen aligns with these characteristics, except for the unusually long Sc vein, which suggests it represents a new taxon within Parapamphiliinae.

Using Rasnitsyn's (1993) key to Parapamphiliinae genera, the new specimen keys out to *Parapamphilius* Rasnitsyn, 1968 or *Pamparaphilius* Rasnitsyn, 1993 because of its forewing with 1-M almost continues the direction of M+Cu and Sc is developed; the forewing is longer than 5 mm, with Sc developed, lr-rs is distinct, the base of Rs is subvertical, 2m-cu is connected to Cu at an angle, and Cu is slightly curved at cu-a. Among these, the specimen more closely resembles *Parapamphilius* Rasnitsyn, 1968 because of its pterostigma thicker at the base, the presence of a cu-a near the middle of the cell 1mcu, and the presence of a crossvein mcu-a (Rasnitsyn, 1993: fig 5). However, it would differ from the latter because its 2r-rs is much longer than 1r-rs (vs. shorter or of similar width in *Parapamphilius*), and longer than pterostigma width (vs. shorter than pterostigma width) (Rasnitsyn 1993: fig 5). Similarly, it shares with *Pamparaphilius* a crossvein 2r-rs longer than 1r-rs, and longer than the cross-section of the pterostigma, but differs from the latter because of its pterostigma thickened at the base (*vs.*, not thickened in *Pamparaphilius*), the presence of a cu-a at the level of the middle of cell 1mcu (*vs.*, behind the middle of the cell 1mcu), and the presence of a cu-a at the level of the middle of cell 1mcu (*vs.*, behind the middle of the cell 1mcu), and the presence of a madditional mcu-a stem (*vs.*, absent) (Rasnitsyn 1993: fig 6–7).

Recently, *Pamparaphilius khasurtensis* Kopylov & Rasnitsyn, 2017, described from the Aptian Khasurty locality, displayed aberrant venation, illustrating the potential for abnormal wing patterns in these wasps (Kopylov & Rasnitsyn 2017b). In the case of the new specimen, the distinct and long Sc vein is unlikely to be an aberration and justifies the creation of a new genus. This decision preserves the diagnostic value of previously established characters for distinguishing Parapamphiliinae genera while accommodating the unique wing venation of the new taxon.

Yananphilius peizhuangensis gen. et sp. nov. is the first Sepulcidae species reported from the Middle Jurassic Yan'an Formation in the Ordos Basin. This discovery increases our understanding of the diversity of the Parapamphiliinae during the Jurassic period.

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References

- Barth G., Ansorge J. & Brauckmann C. 2011. First record of the genus *Ipsvicia* (Hemiptera: Ipsviciidae) outside Gondwana—an Australian genus from the Upper Triassic of Germany. *Polish Journal of Entomology* 80: 645–657
- Blaimer B. B., Santos B. F., Cruaud A., Gates M. W., Kula R. R., Mikó I., Rasplus J.-Y., Smith D. R., Talams E. J., Brady S. G. & Buffington M. L. 2023. Key innovations and the diversification of Hymenoptera. *Nature Communications* 14: 1212. https://doi.org/10.1038/s41467-023-36868-4
- Darling D. C. & Sharkey M. J. 1990. Chapter 7. Order Hymenoptera. In: Grimaldi, D.A. (Ed.), Insects from the Santana Formation, Lower Cretaceous, of Brazil, vol. 195. Bulletinof the American Museum of Natural History pp.123–153.
- Jattiot R., Krogmann L. & Nel A. 2011. Revision of *Prosyntexis* from the Lower Cretaceous Crato Formation of Brazil (Hymenoptera: Sepulcidae: Trematothoracinae). *Zootaxa* 3058(1): 55–62. https://doi.org/10.11646/ zootaxa.3058.1.4
- Jouault C. & Nel A. 2021. A new species of *Prosyntexis* Sharkey, 1990 (Hymenoptera: Sepulcidae) from the Lower Cretaceous Crato Formation of Brazil confirmed by geometric morphometric analysis. *Palaeoentomology* 4(2): 171–177. https://doi.org/10.11646/palaeoentomology.4.2.6
- Kopylov D. S. & Rasnitsyn A. P. 2014. New Trematothoracinae (Hymenoptera: Sepulcidae) from the Lower Cretaceous of Transbaikalia. Proceedings of the Russian Entomological Society, St Petersburg 85: 199–206.
- Kopylov D. S. & Rasnitsyn A. P. 2017a. New sepulcids (Hymenoptera: Sepulcidae) from the Lower Cretaceous of Asia: II. Ghilarellinae and Trematothoracinae. *Paleontological Journal* 51: 291–303.
- Kopylov D. S. & Rasnitsyn A. P. 2017b. New sepulcids (Hymenoptera: Sepulcidae) from the Lower Cretaceous of Asia. I. Parapamphiliinae and Xyelulinae. *Paleontological Journal* 51: 69–76.
- Li X. Q., Rasnitsyn A. P., Gao J., Zhang Y. J., Shih C. K., Ren D., Zhao Y. Y. & Gao T. P. 2023. New taxa of Sepulcidae (Hymenoptera) from mid-Cretaceous Kachin amber. *Palaeoentomology* 6(2): 133–145. https://doi.org/10.11646/ palaeoentomology.6.2.5
- Li Y., Wang M., Rasnitsyn A. P., Shih C. K., Zhuang J. & Ren D. 2024. Two new species of Ghilarellinae (Hymenoptera, Cephoidea, Sepulcidae) from the Lower Cretaceous. *Cretaceous Research* 159: 105875. https://doi.org/10.1016/j.cretres.2024.105875
- Malm T. & Nyman T. 2015. Phylogeny of the symphytan grade of hymenoptera: new pieces into the old jigsaw (fly) puzzle. *Cladistics* 31(1): 1–17.

https://doi.org/10.1111/ cla.12069

- Peters R., Krogmann L., Mayer C., Donath A., Gunkel S., Meusemann K., Kozlov A., Podsiadlowski L., Petersen M., Lanfear R., Diez P., Heraty J., Kjer K., Klopfstein S., Meier R., Polidori C., Schmitt T., Liu S., Zhou X. & Niehuis O. 2017. Evolutionary history of the Hymenoptera. *Current Biology* 27: 1013–1018. https://doi.org/10.1016/j.cub.2017.01.027
- Rasnitsyn A. P. 1988. Sepulcidae and origin of Cephidae (Hymenoptera: Cephoidea), in Sistematika nasekomykh i kleshchei (Taxonomy of Insects and Mites), Tobias, V.I. (Ed.), *Tr. Vses. Entomol. Ob-va*, vol. 70, Leningrad: Nauka, 1988, pp. 68–73.
- Rasnitsyn, A.P. 1993. New taxa of Sepulcidae (Vespida), in Mezozoiskie nasekomye i ostrakody Azii (Mesozoic Insects and Ostracods from Asia), Ponomarenko, A.G. (Ed.), *Tr. Paleontol. Inst. Ross. Akad. Nauk*, vol. 252, Moscow: Nauka, 1993, pp. 80–99.
- Rasnitsyn A. P. 1968. Noviye Mezozoyskiye Pilil'shchiki (Hymenoptera, Symphata) [New Mesozoic Sawflies (Hymenoptera, Symphata)]. Yurskoy Nasekomiye Karatau [Jurassic Insects of Karatau] 190–236.
- Rasnitsyn A. P. & Ansorge J. 2000. New Early Cretaceous hymenopterous insects (Insecta: Hymenoptera) from Sierra del Montsec (Spain). PalZ 74 (3): 335–341.

https://doi.org/10.1007/BF02988105

- Rasnitsyn A. P. & Martínez-Delclos X. 2000. Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain. *Acta Geologica Hispanica* 35(1–2): 65–96.
- Sharkey M. J., Carpenter J. M., Vilhelmsen L., Heraty J., Liljeblad J., Dowling A. P. G., Schulmeister S., Murray D., Deans A. R.,

Ronquist F., Krogmann L. & Wheeler W. C. 2012. Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* 28(1): 80–112.

https://doi.org/10.1111/j.1096-0031.2011.00366.x

- Wutke S., Blank S. M., Boevé J.-L., Faircloth B. C., Koch F., Linnen C. R., Malm T., Niu G., Prous M., Schiff N. M., Schmidt S., Taeger A., Vilhelmsen L., Wahlberg N., Wei M. & Nyman T. 2024. Phylogenomics and biogeography of sawflies and woodwasps (Hymenoptera, Symphyta). *Molecular Phylogenetics and Evolution* 199: 108144. https://doi.org/10.1016/j.ympev.2024.108144
- Xu M. M., Hakim M. & Huang D. Y. 2023. New Jurassic protopsyllidiids from the Yan'an Formation, North China (Insecta: Hemiptera). Palaeoentomology 6(5): 542–548.

https://doi.org/10.11646/palaeoentomology.6.5.13

Zhuang J., Shih C., Wang M. & Ren D. 2022. Two new fossil sawflies of Pamphiliidae (Hymenoptera: Symphyta) from the Mesozoic of northeastern China. *Insects* 13: 402.

https://doi.org/10.3390/ insects13050402