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Research Article

New insights on the morphology and phylogeny of the Chinese dolichopterid eurypterid *Malongia* (Eurypterida, Dolichopteridae)

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Abstract

A recently recovered slab of siltstone preserving two individuals of *Malongia mirabilis* Wang et al., 2022 is described from the Early Devonian Xitun Formation in Yunnan Province, south-western China. This material reveals a suite of morphological features that were not documented in the original description of the species. Using these newly-recognised morphological characters, we revise the morphological character matrix and re-assess the phylogenetic affinity of *M. mirabilis*. Our phylogenetic analyses reveal that *Malongia* occurs in a polytomy with *Dolichopterus* and the clade comprising *Ruedemannipterus* and *Clarkeipterus*. The new material, therefore, improves our knowledge of the morphology of this poorly known Chinese dolichopterid and provides new evidence for evaluating the evolutionary history of Dolichopteridae on the South China Block.

Keywords

early Devonian, *Malongia mirabilis*, morphology, phylogenetic analyses, South China

Introduction

Eurypterids, commonly referred to as sea scorpions, are aquatic carnivorous chelicerates with a fossil record extending from the Early Ordovician to the Late Permian extinction event (Tetlie 2007; Lamsdell et al. 2013, 2015; Lamsdell 2013, 2025; Van Roy et al. 2025). This group is classified into two suborders: Eurypterina, characterised by paddle-like distal podomeres on the sixth prosomal appendage and Stylonurina, defined by the presence of transverse sutures on the ventral plates and with the absence of a modified podomere 7a on appendage VI (Tetlie 2007; Lamsdell 2025). Dolichopteridae Kjellesvig-Waering & Størmer, 1952, as defined by Lamsdell (2025), is a family within the suborder Eurypterina including six genera. Together with Strobilopteridae Lamsdell, 2025 and Erieopteridae Tollerton, 1989, Dolichopteridae constitutes the

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superfamily Dolichopteroidea Kjellesvig-Waering & Størmer, 1952 (Lamsdell 2025). Historically, *Dolichopterus* was originally established as a subgenus of *Eurypterus*, with *D. macrocheirus* Hall, 1859 as its type species. It was subsequently recognised as a distinct genus, based on differences in the morphology and organisation of the swimming appendages and genital appendages, although its higher-level systematic placement remained uncertain (Clarke and Ruedemann 1912). The family Dolichopteridae was erected by Kjellesvig-Waering and Størmer (1952) to accommodate the assemblage comprising *Dolichopterus* and *Strobilopterus*. Its taxonomic composition was later expanded to include *Ruedemannipterus* (Tollerton, 1989) and *Buffalopterus* (Tetlie & Cuggy, 2007). Although *Ruedemannipterus* and *Buffalopterus* were long regarded as only close relatives of dolichopterids (Lamsdell and Selden 2013; Lamsdell et al. 2015), the phylogenetic analyses conducted by Lamsdell et al. (2013) resolved *Clarkeipterus*, *Ruedemannipterus* and *Buffalopterus* within the family Dolichopteridae. Furthermore, *Pentlandopterus* and *Paraeurypterus* have since been transferred to this family (Lamsdell 2025).

The geographic distribution of dolichopterids was long believed to be restricted to Euramerican regions (Tetlie 2007). The only recognised exceptions were *Paraeurypterus anatoliensis* Lamsdell et al., 2013 and *Malongia mirabilis* Wang et al., 2022, both of which occur outside this palaeocontinent (Lamsdell et al. 2013; Wang et al. 2022; Lamsdell 2025). Wang et al. (2022) erected the genus *Malongia*, based on an incomplete specimen (holotype 2011xxs01a&b) preserved in ventral aspect from the Xiaxishancun Formation (Lochkovian, Early Devonian) of Yunnan, China. As diagnosed, the genus is currently characterised by subquadrate prosoma and multiple enlarged spines on appendages III–IV and was interpreted as a durophagous predator (Wang et al. 2022; Lamsdell 2025).

Here, we describe a new specimen with two individuals of *M. mirabilis* collected from the Xitun Formation. These individuals display morphological features consistent with the diagnosis of *M. mirabilis* and, crucially, both individuals preserve the carapace and dorsal exoskeletal structures, features that are incompletely preserved or absent in the original description. In addition, the newly-discovered dorsal morphological features enable us to supplement the existing morphological character matrix originally compiled by Lamsdell (2025).

Geological setting

The studied material was collected from the same locality as the *Qujingopterus* specimens reported by Ma et al. (2025), in the middle part of the Xitun Formation approximately 5 km south of Qujing City, Yunnan Province, China (geographic coordinates: 25.51124°N, 103.6739°E; see Ma et al. (2025), Fig. 1). The Xitun Formation is some 364 m thick and conformably overlies the green silty sandstone of the Xiaxishancun Formation, which is conformably overlain by the red calcareous shale of the Guijiatun Formation. The Xitun Formation consists mainly of greyish-blue and purple calciferous mudstones, which yield abundant bivalves, fish and rare fragmentary early land plants. Based on palynological data and carbon isotope analyses (Zhao et al. 2011, 2015, 2021; Xue 2012), the eurypterid beds, which are near the lower and middle part of the Xitun Formation, were deposited in the late Lochkovian to early Pragian.

Material and methods

A slab preserving two *Malongia mirabilis* individuals was studied in this research (KGS0200001). These specimens are deposited in the Kunming General Survey of Natural Resources Center (KGS), China Geological Survey, Kunming, Yunnan, China. Being preserved in siltstones, the material is flattened and shows some tectonic distortion. All photographs were taken with a Sony A7R3 digital camera, with an LAOWA 100 mm f/2.8 lens. The cross-polarisation technique was employed to mitigate reflection and to enhance contrast. Photographs were processed and arranged into figures using image editing software (CorelDRAW 2018 and Adobe Photoshop CS). Morphological terminology follows Tollerton Jr (1989) and Lamsdell (2025). The holotype of *Malongia mirabilis* (2011xxs01a&b) is housed at the Geological Museum, the School of Earth and Space Sciences, Peking University.

To assess the phylogenetic position of *Malongia mirabilis* relative to other dolichopterids, we re-coded morphological characters following the standardised trait definitions and scoring criteria established by Lamsdell (2025) and performed phylogenetic inference using the updated, taxon-rich character matrix in the same study. The matrix and associated character list are provided in the supplementary information as a NEXUS file. Analyses were conducted in TNT v.1.5 (Goloboff et al. 2008) using 100,000 replicates of random addition sequence (RAS) followed by tree bisection-reconnection (TBR) branch swapping; all characters were treated as unordered and equally weighted.

Abbreviations

KGS, Kunming General Survey of Natural Resources Center, China Geological Survey, Kunming, Yunnan, China; **C**: carapace; **MR**: marginal rim; I–VI: Prosomal Appendages I–VI; **CO**: coxa; **T**: tergite; **LE**: lateral eye; **MD**: median ridge; **TS**: transverse suture; **M**: metastoma; **G**: genital appendage; ventral plates.

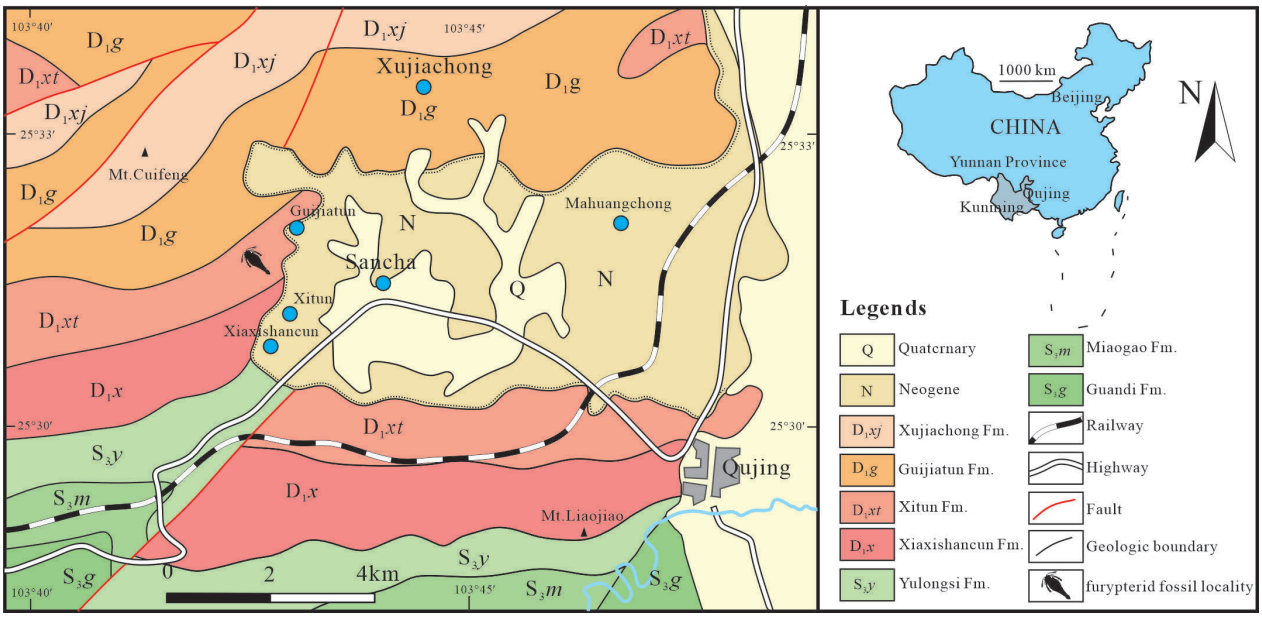

Figure 1. Generalised map showing geologic features of the Qujing area and the eurypterid fossil locality (modified from Hao et al. (2007): fig. 1).

Systematic Palaeontology

Order Eurypterida Huxley, 1857
Suborder Eurypterina Novojilov, 1962
Superfamily Dolichopteroidea Kjellesvig-Waering & Størmer, 1952
Family Dolichopteridae Kjellesvig-Waering & Størmer, 1952

Genus *Malongia* Wang et al., 2022

Type and only species. *Malongia mirabilis* Wang et al., 2022.

Emended diagnosis. Dolichopteridae with horseshoe-shaped prosomal carapace; carapace genal facets continuously inclined towards carapace centre; prosomal ventral plates of *Eurypterus* type; lateral eyes arcuate, positioned anteromesial on carapace; prosomal appendages I–IV spiniferous *Dolichopterus* type, appendage V non-spiniferous *Dolichopterus* type, appendage VI appears to be moderately expanded paddle of regular *Dolichopterus* type; metastoma lyrate (modified from Wang et al. (2022) and Lamsdell (2025)).

Malongia mirabilis Wang et al., 2022

Diagnosis. As for the genus.

Type material. 2011xxs01a&b (holotype).

Additional material. KGS0200001.

Description. Slab KGS0200001 and its counterpart comprise two individuals: one preserved in dorsal view and the other in ventral view. The dorsal-view individual consists of an incomplete carapace, partial appendages VI and an articulated prosoma with eight tergites. The preserved length of the individual > 55.5 mm, maximum width > 22.3 mm at third tergite. The carapace is incompletely preserved, measuring more than 14.3 mm in length and 15.7 mm in width, with its greatest width located at the mid-point and a lateral angle of 124°. A narrow marginal rim, 3 mm in width, fringes the carapace, bearing coarse surface ornamentation. The right lateral compound eye is intact; relatively large, measuring up to 4.6 mm in length and 2.3 mm in width. Arcuate with rounded extremities, the eye is covered dorsally by a well-developed rounded palpebral lobe and occupies an anteromesial position; a median ridge is present along the centriaxial region of the carapace. Only appendages VI are partially preserved, comprising four podomeres. The second podomere (VI–2) is rectangular, 1.1 mm long, at least 2.8 mm wide; third podomeres (VI–3) 3.1 mm long, approximately 6 mm wide. The fourth podomere (VI–4) is completely preserved, with a length of 4.2 mm and a width of approximately 3.9 mm; its surface and margins bear small knobs. The opisthosomal tergites attain a maximum length of 5.5 mm on the third tergite and a minimum length of 2.7 mm on the first. Each tergite is anteriorly curved along the mid-line and approximately 2.7–5.5 mm long. A row of tubercles is present along the posterior margin of each tergite.

The ventral-view individual reveals a carapace bearing six pairs of proximal podomeres and associated appendages, as well as an articulated opisthosoma composed of two ventral plates. The total length of the individual > 46.4 mm. Based on the impressed carapace trace, the carapace outline is distinctly horseshoe-shaped. Only the

ventral anterior region of the carapace is exposed; the frontal margin is gently convex and the marginal rim is narrow and approximately 2 mm wide. The ventral plates are splayed open and the resulting aperture comprises two symmetrical, unconnected elements, indicating that the configuration of prosomal ventral plates is comparable to the *Megalograptus* morphotype (Tollerton Jr 1989; Lamsdell 2025). The coxae of all appendages exhibit slight torsion, yet their relative spatial arrangement is preserved, thereby enabling unambiguous identification of each appendage. Podomeres are preserved exclusively on the left side. Appendages I and II are preserved only by their proximal podomeres, which are small and subrectangular, with lengths of 3.0 mm (coxa-equivalent in appendage I) and 1.2 mm (coxa-equivalent in appendage II), respectively. Appendage III preserves a pair of coxae; the right coxa is elongate rectangular and exhibits slight distortion, whereas the left coxa is subrectangular, measuring 2.8 mm in width and 4.3 mm in length. The three preserved podomeres are rectangular and exhibit nearly uniform width; however, the second (III–2) podomere is markedly shorter than the third (III–3) and fourth (III–4). Appendage IV preserves a pair of coxae and three podomeres. The right coxa is subtriangular in shape, whereas the left coxa is subrectangular, measuring 2.2 mm in width and 3.7 mm in length. Three podomeres are preserved: the second (IV–2) and third (IV–3) are subrectangular in shape, whereas the fifth podomere (IV–5) is incomplete. Appendage V preserves a pair of coxae, the right coxa being distorted, whereas the left coxa is triangular in shape and inserted between coxa IV and coxa VI, measuring 1.8 mm in width and 2.9 mm in length. Two podomeres are preserved, rectangular in shape. Appendage VI preserves a pair of subrhomboidal coxae and two podomeres (VI–2 and 3). The appendage gradually expands in width from the proximal to the distal end. The coxal gnathobase bears a row of triangular teeth, but the principal tooth is absent; nevertheless, the preserved morphology indicates that the principal tooth would have been larger than the other teeth. The opisthosoma is represented only by the incomplete second and third tergites. On the ventral plates, a transverse suture occurs at the anterior margin of the second tergite and curves anteriorly at the mid-line. An incomplete genital appendage is partially preserved on the median portion of the second ventral plates. The slender, type-A genital appendage extends to the posterior margin of the second ventral plates, with a total length of 6.2 mm.

Remarks. These two individuals share the same overall body proportions and nearly identical morphological features with the holotype of *Malongia mirabilis* and are, therefore, assigned to this species. However, their carapaces are horseshoe-shaped, a feature differing from that of the holotype. This discrepancy is interpreted as the result of taphonomic distortion affecting the holotype (Wang et al. 2022; Lamsdell 2025). Consequently, our specimens likely represent the natural carapace morphology of *M. mirabilis*. Additionally, the ventral plates are comparable to those of the holotype and exhibit comparable characteristic of the *Megalograptus* type. However, eurypterid carapaces are susceptible to cracking during moulting and the ventral plates on both sides show evidence of folding (Brandt 2022). Therefore, assignment to the *Megalograptus*-type may not be accurate. We follow the taxonomic treatment of Lamsdell (2025) and assign these ventral plates to the *Eurypterus*-type (Fig. 2).

Phylogeny

Phylogenetic reconstruction was performed using the revised morphological character matrix, originally compiled by Lamsdell (2025). For tree rooting and character polarisation across the Dolichopteridae, *Strobilopterus laticeps* was designated as the outgroup taxon to establish ancestral character state distributions for comparative evolutionary analysis. Within the recovered topology, *Paraeurypterus anatoliensis* Lamsdell et al., 2013 and *Pentlandopterus minor* Laurie, 1899 form successive early-diverging lineages, branching sequentially before the origin of a clade containing all remaining sampled dolichopterid species. This core clade yields a polytomy affecting the position of *Malongia*: relationships amongst *Malongia*, *Dolichopterus* and the *Ruedemannipterus*/*Clarkeipterus* clade remain unresolved. The topology allows three equally plausible phylogenetic hypotheses: *Malongia* could be the sister taxon to *Dolichopterus*, sister to the *Ruedemannipterus*/*Clarkeipterus* clade or sister to both lineages combined. It is, therefore, not possible to confirm whether *Malongia* constitutes a distinct monophyletic subgroup. By contrast, the *Dolichopterus* assemblage (including *D. jewetti* Caster & Kjellesvig-Waering, 1956 and *D. macrocheirus* Hall, 1859) and the *Ruedemannipterus* + *Clarkeipterus* grouping (comprising *R. stylonuroides* Clarke & Ruedemann, 1912, *C. otisius* Clarke, 1907 and *C. testudineus* Clarke & Ruedemann, 1912) each emerge as coherent subclades within the polytomy (Fig. 3).

Discussion

Previous work recovered *Malongia* as sister taxon to *Dolichopterus* (Lamsdell 2025). Our revised phylogenetic analyses, incorporating newly-described dorsal and ventral morphological characters of *Malongia mirabilis*, instead support an alternative systematic placement. Rather than being nested in a clade with *Dolichopterus*, our maximum-parsimony tree resolves *Malongia* in a polytomy with *Dolichopterus* and the clade comprising *Clarkeipterus* and *Ruedemannipterus*. The uncertainty surrounding its phylogenetic position, together with morphological apomorphies, is consistent with the

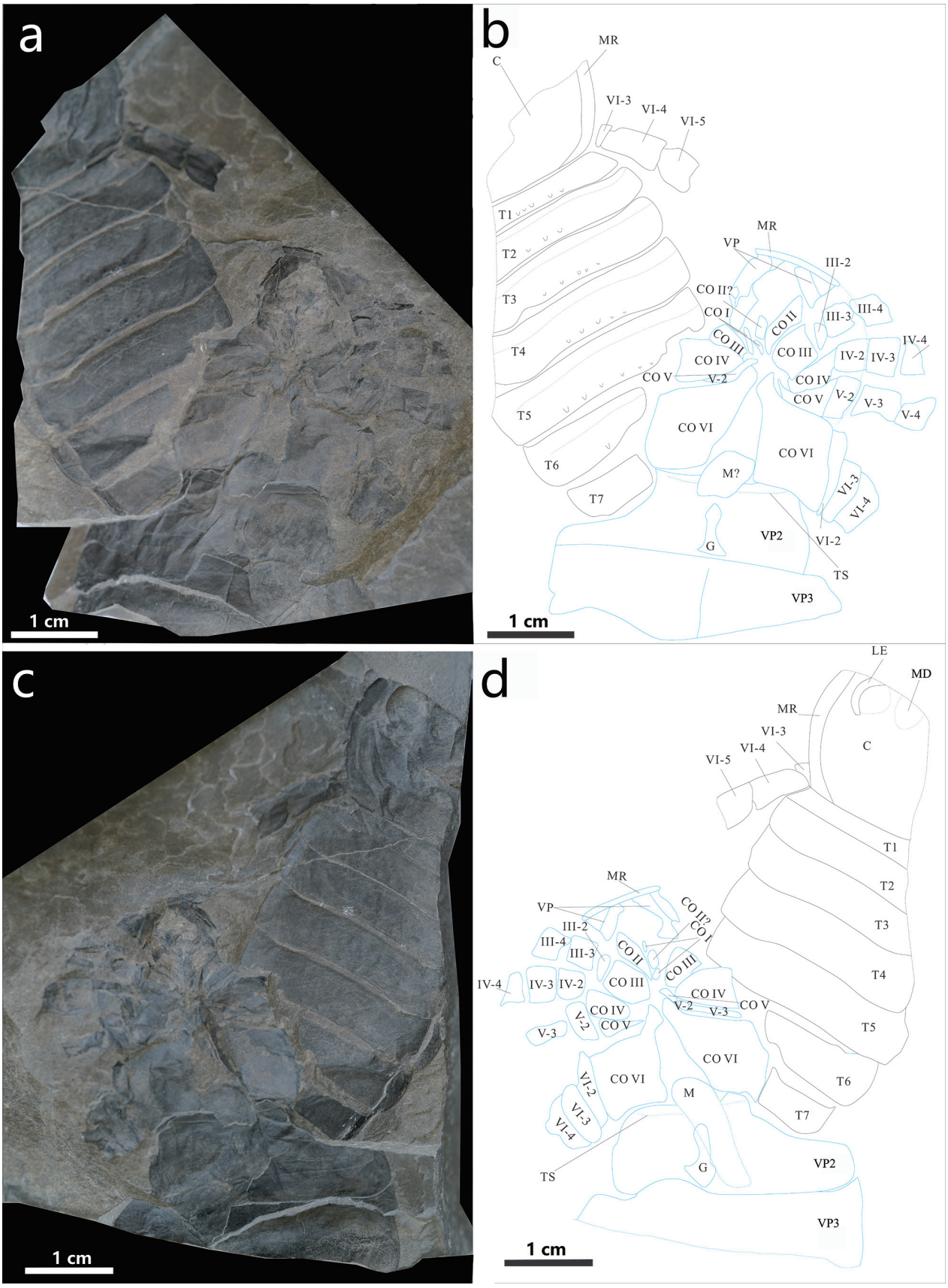

Figure 2. *Malongia mirabilis.* **a.** the specimen KGS0200001 (part); **b.** interpretive drawing of KGS0200001 (part); **c.** the specimen KGS0200001 (counterpart); **d.** interpretive drawing of KGS0200001 (counterpart).

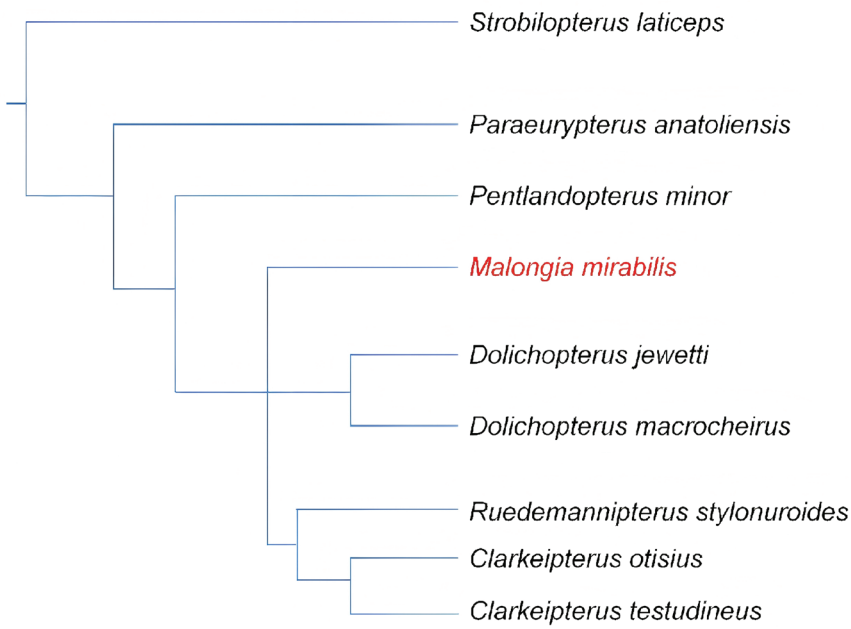

Figure 3. Phylogeny of Dolichopteridae, showing the relationships of *Malongia mirabilis*.

hypothesis that the ancestral lineage of *Malongia* underwent geographically isolated evolution on the South China Block following its divergence from the common ancestor shared with the *Dolichopterus* lineage. The South China Block rifted away from Gondwana during the Late Silurian-Early Devonian (Huang et al. 2018). Such biogeographic isolation may have restricted gene flow between South Chinese dolichopterids and their closely-related lineages distributed across Laurussia, facilitating the evolution of exclusive derived features and the origin of this independent evolutionary lineage.

In addition, both *Malongia mirabilis* and *Pterygotus wanggaii* Ma et al. 2023 recovered from the Xitun Formation and Xiaxishancun Formation provide direct fossil evidence for a close faunal linkage between these two units in the Qujing area, eastern Yunnan (Wang and Gai 2014; Wang et al. 2022; Ma et al. 2023; Wang et al. 2025). Beyond eurypterids, co-occurring fossil groups further reinforce tight biotic connectivity between the two formations: identical ostracod assemblages (Wang and Liu 1994), early vertebrate fish taxa (Zhao et al. 2021) and fragmentary primitive land plant remains (Xue 2012) are recovered from both the Xiaxishancun and Xitun successions, reflecting stable, homogeneous palaeoecological conditions without major faunal turnover across the formation boundary. The continuous depositional sequence and shared endemic eurypterid species demonstrate that both Xiaxishancun and Xitun Formations represent a single, long-lived palaeobiogeographic province on the South China block, with unimpeded biotic exchange and sustained faunal continuity during the Early Devonian.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
Regarding the use of AI in the preparation of this manuscript, the authors declare the following: DeepSeek
Used for: Language, style and writing
Before review by co-authors, AI was used to polish the draft.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Matrix and associated character list of eurypterids

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