



Short Communication

First mixopterid eurypterids (Arthropoda: Chelicerata) from the Lower Silurian of South China

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Eurypterids, or sea scorpions, are an important group of mid-Paleozoic chelicerate arthropods whose evolution and palaeoecological significance have attracted much attention in recent years [1–3]. One of the most remarkable eurypterid families is Mixopteridae, whose members are quite large and superficially scorpion-like eurypterids bearing highly specialized anterior appendages. Their second, and especially the third, pair of prosomal limbs are enlarged and very spiny. These limbs were presumably used for prey-capture, and analogies can be drawn with the “catching basket” [4] formed by the spiny pedipalps of whip spiders (Amblypygi) among the arachnids. Our knowledge of these bizarre animals is limited to only four species in two genera described 80 years ago: *Mixopterus kiaeri* from Norway [5], *M. multispinosus* from New York [6], *M. simonsoni* from Estonia [7], and *Lanarkopterus dolichoschelus* from Scotland [8]; all are Silurian in age and come exclusively from the palaeocontinent of Laurussia, which constrains our knowledge of the morphological diversity, geographical distribution and evolutionary history of the group. Here, we describe a new mixopterid, *Terropterus xiushanensis* gen. et sp. nov., from the Lower Silurian (Llandovery) Xiushan Formation of Xiushan (Fig. S1 online), characterized by a unique arrangement of spines on prosomal limb III; and two incomplete, but larger fossils (*Terropterus* sp.) from the Lower Silurian (Llandovery) Fentou Formation of Wuhan in Hubei Province (Fig. S1 online). These discoveries represent the first mixopterids from Gondwana

and the oldest known mixopterids, and thus add to our knowledge of mixopterid morphological diversity and geographical distribution.

Terropterus xiushanensis gen. et sp. nov. is known from several specimens of prosomal appendages, coxae, a single telson, a genital operculum and the genital appendage (Figs. 1 and S2d–i online). An extremely large, specialized second leg (III) occurs in both the families Mixopteridae and Megalograptidae among the eurypterids. The *Hughmilleria*-type appendages IV–V and styliform telson observed in *T. xiushanensis* distinguish it from megalograptids and support its assignment to the mixopterids. *T. xiushanensis* differs from other mixopterids mainly in the morphology of the appendages, including spination patterns, the relative length of each podomere and the shape of the coxae. They are characterized by retaining two spines on the fourth podomere of prosomal appendage III (Fig. 1a); the longest spines (normally three in number) on each of the following podomeres (III–5, III–6) (Fig. 1d–e) are evenly arranged, nearly the same length, and interlaced with other moderately long and short spines; appendage II (Fig. 1a) is short, with several pairs of spines at the distal end; appendages IV and V (Fig. 1a, c) bear slim and long spines at the end of each podomere, almost parallel to the direction in which the end of the limb is pointing.

Two larger specimens from the Fentou Formation (nearly coeval in age with the Xiushan Formation) include an appendage III, a carapace and part of the preabdomen (Fig. S2a–c online). We tentatively refer them to *Terropterus* sp. because their appendage III shows similar relative proportions of the limb joints and basic spine patterns with the corresponding appendage in *T. xiushanensis*. However, the former has a much larger size with more sparsely

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arranged and relatively longer spines than *T. xiushanensis*. Since there is no additional specimen, it is difficult to resolve whether this arrangement reflects a different species, or is simply due to ontogeny.

We present a phylogenetic analysis (Files S1 and S2 online) based on an updated version of the matrix of Lamsdell et al. [9]; adding *T. xiushanensis* to this matrix to evaluate the phylogenetic position of this new taxon within Eurypterida. We obtained a single most parsimonious tree resolving *T. xiushanensis* as the sister-group of *Lanarkopterus dolichoschelus*, and thus nested within Mixopteridae (Fig. S3 online). The topology recovered here is largely congruent

with that of Lamsdell et al. [9], and is consistent with the morphological comparisons of the mixopterid genera outlined above.

Mixopterids share a common pattern of highly specialized spinose appendages, albeit with marked differences between the various genera. *T. xiushanensis* reveals a higher diversity of mixopterid appendage morphology than previously thought. This is reflected mainly in the pattern of spines present on the podomeres and the relative length of each podomere of appendage III, the type of appendage II, the relative length of the distal spines on each podomere of appendages IV and V, and the morphology of the coxae.

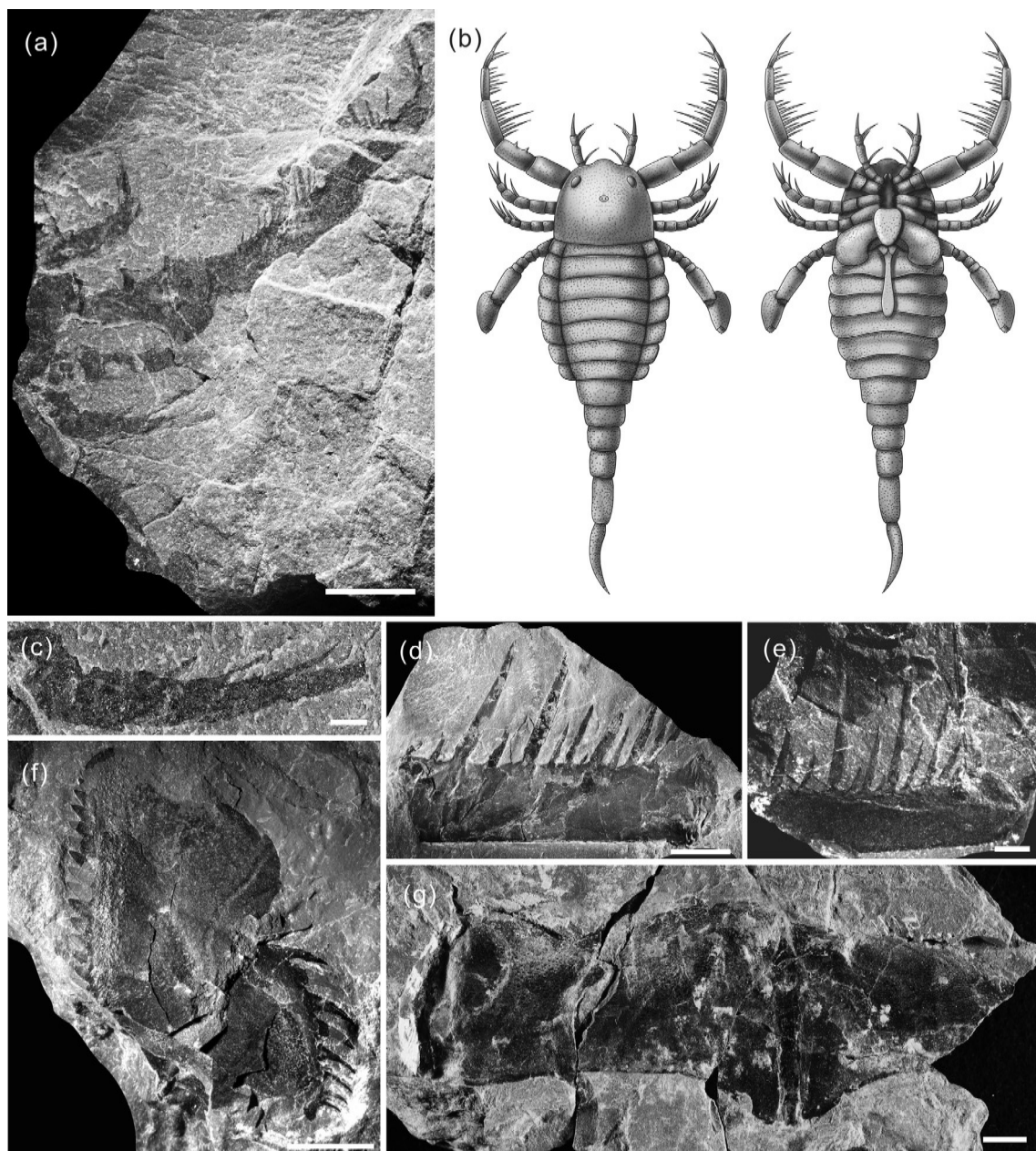


Fig. 1. Specimens and reconstruction drawing of *Terropterus xiushanensis* gen. et sp. nov. (a) Appendages II–VI, holotype, NIGP 174785. (b) Reconstruction drawing of *Terropterus xiushanensis*, dorsal and ventral views. (c) Close-up of appendage V. (d) Joint 5 or 6 of appendage III, paratype, NIGP 174786. (e) Joint 5 or 6 of appendage III, paratype, NIGP 174787. (f) Coxae, paratype, NIGP 174788. (g) Genital operculum and the genital appendage, paratype, NIGP 174789. Scale bars = 5 mm for (a), (d), (f), (g); 2 mm for (e); 1 mm for (c).

As the most enlarged and diverse limb, the mixopterid appendage III has always attracted much attention. *T. xiushanensis* offers new information on the spine pattern of appendage III (Fig. S4 online), and provides important evidence for a more detailed understanding of the homology and evolution of this specialized appendage. Previous researchers offered different explanations for the homology of the joints of appendage III. Caster and Kjellesvig-Waering [10] suggested that the very short joint in the older *Megalograptus* is missing or much reduced in *M. kiaria*. Subsequently, Ritchie [11] considered that the relative proportions of joints 1–5 and the pattern of spines present on these joints in *Lanarkopterus* show a remarkable similarity to the leg of *Megalograptus*, drawing the conclusion that this similarity of basic pattern is a derivation from a common ancestral pattern. However, our morphological comparison and phylogenetic analysis show that *Terropterus* bears a mixture of morphology of both *Lanarkopterus* and *Mixopterus*. It is most likely that some special appendage features, such as the presence of the extremely short joint, may not come from the ancestral type, but have evolved independently several times. Therefore, the evolutionary relationships of this group may be more complex than previously thought. The diversity of appendage structures in different mixopterid genera may have resulted from different modes of life, similar to that of the highly variable chelicerae of pterygotids. Specifically, the different patterns of spines and the arrangement of the podomeres could reflect different predation strategies and/or prey sizes. Furthermore, the total lengths of new specimens from Xiushan and Wuhan are estimated to have been about 40 and 100 cm, respectively. However, the adult may have been larger, if the specimens are juveniles. Bearing such large spiny legs and probably a poisonous telson to catch and strike the prey [1,5,12], *Terropterus* is likely to have played an important role of top predators in the marine ecosystem during the Early Silurian when there were no large vertebrate competitors in South China [13,14].

The palaeogeographical distribution of mixopterids (Fig. S4 online) was rather limited until now [5–8] and no examples of this group have been previously discovered in Gondwana. Our first Gondwanan mixopterid—along with other eurypterids from China and some undescribed specimens—suggests an under-collecting bias in this group [15]. Future work, especially in Asia, may reveal a more cosmopolitan distribution of mixopterids and perhaps other groups of eurypterids.

Conflict of interest

The authors declare that they have no conflict of interest.

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Author contributions

Bo Wang designed the project. Han Wang, Bo Wang, and Zhikun Gai wrote the manuscript. Jason Dunlop and Edmund A. Jarzembowski revised the draft and contributed to analytical work. Zhikun Gai, Han Wang, and Xiaojie Lei contributed to field work and provided specimens. Han Wang ran the phylogenetic analyses and prepared the figures. Xiaojie Lei contributed to the data-collecting work and discussion.

Appendix A. Supplementary materials

Supplementary materials to this article can be found online at <https://doi.org/10.1016/j.scib.2021.07.019>.

References

- [1] Selden PA. Autecology of Silurian eurypterids. *Spec Pap Palaeontol* 1984;32:39–54.
- [2] Lamsdell JC, Selden PA. From success to persistence: identifying an evolutionary regime shift in the diverse Paleozoic aquatic arthropod group Eurypterida, driven by the Devonian biotic crisis. *Evolution* 2017;71:95–110.
- [3] Lamsdell JC, McCoy VE, Perron-Feller OA, et al. Air breathing in an exceptionally preserved 340-million-year-old sea scorpion. *Curr Biol* 2020;30:4316–21.e2.
- [4] McLean CJ, Garwood RJ, Brassey CA. Sexual dimorphism in the size and shape of the raptorial pedipalps of giant whip spiders (Arachnida: Amblypygi). *J Zool* 2020;310:45–54.
- [5] Størmer L. Merostomata from the Downtonian sandstones of Ringerike, Norway. *Skr Norske Vidensk-Akad Oslo Mat-Naturvidensk Kl* 1934;10:1–125.
- [6] Clarke JM, Ruedemann R. The Eurypterida of New York. *N Y State Mus Mem* 1912;14:1–439.
- [7] Schmidt F. Nachtrag zur Monographie der Russischen Leperditen ii. Die Crustaceenfauna der Euryptereenschichten von Rootziküll auf Oesel. *Miscellanea silurica* iii. *Mem Acad Sci de St Petersburg* 1883;31:28–85.
- [8] Størmer L. *Mixopterus dolichoschelus* (Laurie ms), a Downtonian eurypterid from Scotland. In: Geological Survey Board, editor. Summary of progress of the Geological Survey of Great Britain and the Museum of Practical Geology for the year 1934, part 2. London: His Majesty's Stationery Office; 1936, p. 41–46.
- [9] Lamsdell JC, Briggs DEG, Liu HP, et al. The oldest described eurypterid: a giant Middle Ordovician (Darrivillian) megalograptid from the Winneshiek lagerstätte of Iowa. *BMC Evol Biol* 2015;15:169.
- [10] Caster KE, Kjellesvig-Waering EN. Upper Ordovician eurypterids of Ohio. *Palaeontogr Am* 1964;4:301–58.
- [11] Ritchie A. *Lanarkopterus dolichoschelus* (Størmer) gen. nov., a mixopterid eurypterid from the upper Silurian of the Lesmahagow and Hagshaw hills inliers, Scotland. *Scott J Geol* 1968;4:317–38.
- [12] Hanken NM, Størmer L. The trail of a large Silurian eurypterid. *Fossils Strata* 1975;4:255–70.
- [13] Janvier P. Early vertebrates. Oxford: Clarendon Press; 1996.
- [14] Wen-Jin Z, Min Z. Diversification and faunal shift of Siluro-Devonian vertebrates of China. *Geol J* 2007;42:351–69.
- [15] Tetlie OE. Distribution and dispersal history of Eurypterida (Chelicerata). *Paleogeogr Paleoclimatol Paleocool* 2007;252:557–74.



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