

## Rapid Communication

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# Early Devonian (Lochkovian) eurypterids from the Yunnan province of southwest China

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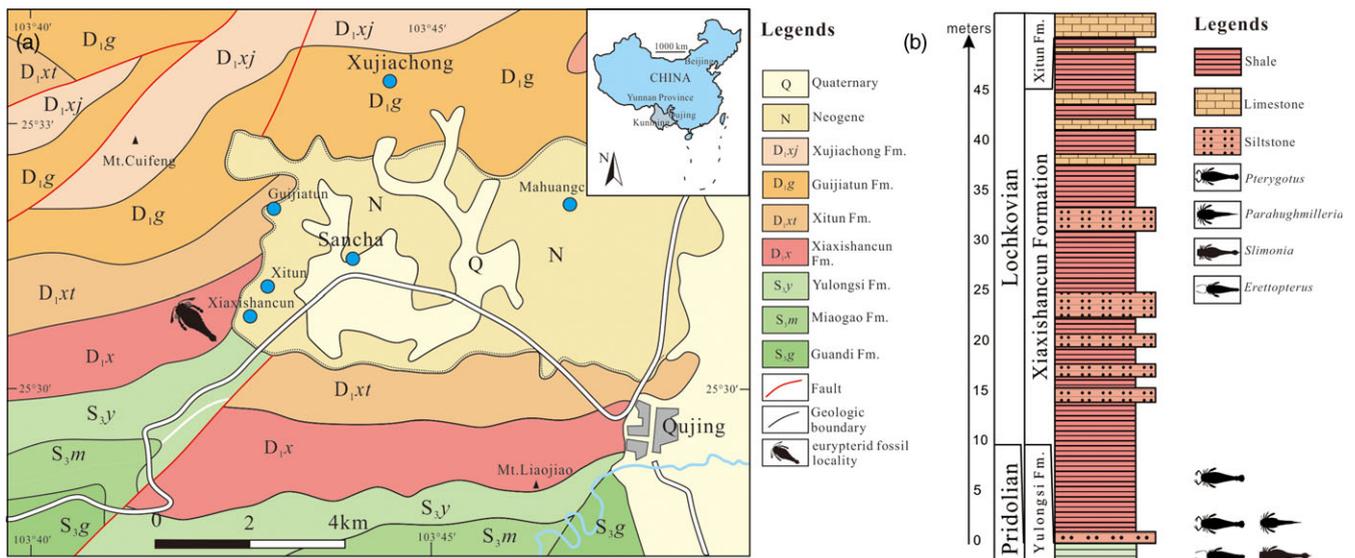
**Abstract**

Two new eurypterids, a pterygotid *Pterygotus wanggaii* n. sp. and an adelophtalmid *Parahughmilleria fuea* n. sp., are described from the Early Devonian (Lochkovian) Xiaxisancun Formation of Yunnan province, southwest China. This discovery represents the first record of *Parahughmilleria* from Gondwana and the first *Pterygotus* from China. *Pterygotus wanggaii* n. sp. is characterized by the first primary denticles (d1, d1') being located on the middle part of the cheliceral ramus and third primary denticles (d3, d3') elongate, even longer than the first primary denticles. *Parahughmilleria fuea* n. sp. is differentiated by being a large *Parahughmilleria* with strongly developed lateral epimera from tergites T4 to T12. These discoveries not only extend the geographical extent of the genera *Pterygotus* and *Parahughmilleria* from Euramerica to SW China, but also give insight into the similarity of ecosystem structures across the Early Devonian world. In addition, based on previous studies, the new discoveries further support the hypothesis that eurypterids underwent a crisis during the Silurian–Devonian boundary interval.

**1. Introduction**

Eurypterids, also known as sea scorpions, are aquatic carnivorous chelicerates. Their fossil record dates back to the early Middle Ordovician, with the clade going extinct in the Late Permian (Tetlie, 2007; Lamsdell *et al.* 2015; Lamsdell & Selden, 2017; Hughes & Lamsdell, 2020; Poschmann & Rozefelds, 2021). They include some of the largest arthropods known to have existed, growing to 2 m or more in length (Kjellesvig-Waering, 1964; Chlupac, 1994; Braddy *et al.* 2008; Lamsdell & Braddy, 2010). The family Pterygotidae is the most diverse clade of the order Euryptera, with about 56 species in five genera (Lamsdell, 2022; Lamsdell & Selden, 2017). Pterygotidae originated in the Llandovery (early Silurian), went extinct in the Middle Devonian (Tetlie, 2007; McCoy *et al.* 2015) and were characterized by the possession of a laterally expanded pretelson, with most species having enlarged chelicerae with elongated proximal podomeres (Tetlie & Briggs, 2009). Pterygotids attained a nearly global distribution (Poschmann & Tetlie, 2006; Miller, 2007; Tetlie & Briggs, 2009; Lamsdell & Legg, 2010; Wang & Gai, 2014) and were ecologically diverse predators with a range of visual acuity and a variety of cheliceral morphologies indicating adaptations towards a variety of benthic and actively swimming prey (Anderson *et al.* 2014; McCoy *et al.* 2015). The superfamily Adelophtalmoidea represents the most common eurypterids in the Late Palaeozoic, with about 46 species in seven genera (Tetlie, 2007; Shpinev, 2012; Lamsdell *et al.* 2014; Poschmann, 2015, 2020; Shpinev & Filimonov, 2018). Taxonomically they are the second most diverse of all eurypterid clades, after the Pterygotoidea, their putative sister group (Tetlie & Poschmann, 2008).

Eurypterids were first reported from Yunnan province by the Yunnan Geological Survey (1973). The specimens were collected near the Siying coal mine at the base of the Devonian Xiaxisancun Formation. No additional study of the material was undertaken and the samples have been lost, with no additional eurypterid material reported from Yunnan province until the 21st century. Besides the eurypterids from Yunnan province, a number of eurypterid groups have been reported from the South China Block (Tetlie, 2007; Zong *et al.* 2017; Wang *et al.* 2021), including pterygotoids, adelophtalmoids and mixopteroids. Wang & Gai (2014) recently reported the presence of Pterygotidae in the Lower Devonian Xitun Formation, based on an isolated chelicera with its two rami preserved. However, these authors left this specimen under open nomenclature, due to the poor preservation of the material and the fact that cheliceral morphology may be influenced by ontogeny and mode of life. Ma *et al.* (2022) erected the new species *Erettopterus qujingensis* based on a chelicera, metastoma and several tergites from the Late Silurian Yulongsi Formation, as well as describing an incomplete carapace of *Slimonia*



**Fig. 1.** (Colour online) (a) Generalized map showing geological features of the Qujing area and the eurypterid fossil locality (modified from figure 1 of Hao et al. 2007). (b) Schematic stratigraphic column for Xiaxishancun Formation showing distribution of eurypterids at localities in the Qujing area.

(Ma et al. 2022). Here, we report two new eurypterids from the Lower Devonian (Lochkovian) Xiaxishancun Formation of Yunnan, China, belonging to the pterygotid *Pterygotus* (Agassiz, 1839) and adelophthalmoid *Parahughmilleria* (Kjellesvig-Waering, 1961).

## 2. Geological setting and stratigraphy

Silurian – Lower Devonian deposits are well developed in the Qujing area. The Silurian layers are assigned to the Miaogao and Yulongsi formations while the Xiaxishancun, Xitun, Guijiatun and Xujiachong formations belong to the Devonian. The strata in Qujing are well exposed and show a successive transition from the shallow marine facies of the Upper Silurian Miaogao Formation to the non-marine facies of the Xujiachong Formation. Our study outcrop of the Xiaxishancun Formation is c. 5 km west of Qujing city near Xiaxishan reservoir (coordinates 103.698351° N, 103.698351° E; Fig. 1a). The Xiaxishancun Formation is c. 51 m thick and the bottom conformably overlies the black fissile shale of the Yulongsi Formation; its top is also conformable with a purple sandstone of the Xitun Formation. The Xiaxishancun Formation consists mainly of continental deposits characterized by yellow sandstone and green shale, which yield abundant fish remains (Lu et al. 2017), some primary plant fossils (Xue, 2012) and euchelicerates (Lamsdell et al. 2013b; Selden et al. 2015).

Based on palynological data and carbon isotope ( $\delta^{13}\text{C}_{\text{org}}$ ) analyses, the Xiaxishancun Formation is considered to be of Lochkovian age (Hao et al. 2007; Zhao et al. 2011, 2015, 2021). The miospore assemblage identified is the *Streelispora newportensis* – *Chelinospora cassicula* Assemblage Zone (Fang et al. 1994; Hao et al. 2007) which approximately corresponds to the *Emphanisporites micornatus* – *Streelispora newportensis* Assemblage Zone of the Lochkovian age (Richardson & McGregor, 1986; Fang et al. 1994; Hao et al. 2007). Furthermore, carbon isotope ( $\delta^{13}\text{C}_{\text{org}}$ ) analyses reveal positive  $\delta^{13}\text{C}_{\text{org}}$  shifts happening and reaching peak values as heavy as  $-25.2\%$  at the base of Xiaxishancun Formation (Zhao et al.

2011, 2015, 2021). These results replicate a globally known positive shift in  $\delta^{13}\text{C}_{\text{org}}$  from the uppermost Silurian to the lowermost Devonian. Hence, the eurypterid beds, which are near the base of the Xiaxishancun Formation, were deposited in the early Lochkovian (Fig. 1b).

## 3. Materials

The specimens (GMG20211001001–10) described in this paper were collected from the lower part of the Xiaxishancun Formation. Being preserved in siltstones, the material is flattened and shows some tectonic distortion. The fossils were prepared using pneumatic chisels. All photographs were taken with a Sony ILCE-7M3 digital camera with a FE 24–105 mm f/4 G OSS lens. Photographs were processed and arranged into figures using image editing software (CorelDRAW 2018 and Adobe Photoshop CS). Morphological terminology follows Tollerton (1989), with denticle terminology following Miller (2007). All specimens examined in this study are deposited in the Geological Museum of Guizhou (GMG), Guiyang, Guizhou province, China. The IVPP (Institute of Vertebrate Palaeontology and Palaeoanthropology)-I4593 measurement data were collected from Wang & Gai (2014).

## 4. Systematic palaeontology

Order Eurypterida Burmeister, 1843

Suborder Eurypterina Burmeister, 1843

Infraorder Diploperculata Lamsdell et al. 2013

Superfamily Pterygoidae Clarke & Ruedemann, 1912

Family Pterygotidae Clarke & Ruedemann, 1912

Genus *Pterygotus* Agassiz, 1839

Type species *Pterygotus anglicus* Agassiz, 1844

### 4.a. Diagnosis

Pterygotidae of larger size, with a subtrapezoid prosoma; free ramus of chelicera terminating in a curved denticle; denticles



**Fig. 2.** *Pterygotus wanggaii* n. sp. (a) Holotype GMG20211001003 ramus of chelicera; (b) interpretive drawing of ramus of chelicera GMG20211001003. Scale bar = 10 mm.

curved posteriorly, without marginal serrations (emended from Miller, 2007).

*Pterygotus wanggaii* new species (Figs 2–3)

2014 Pterygotidae gen. et sp. indet. Wang & Gai, p. 297.

#### 4.b. Type material

Holotype GMG20211001003; paratypes GMG20211001004–8; additional material IVPP-I4593.

#### 4.c. Diagnosis

*Pterygotus* with chelicera bearing three principal denticles and about six intermediate denticles; cheliceral denticles exhibiting size differentiation and with longitudinal striations on the surface; all denticles upright with slightly posterior curvature; first primary denticles (d1,d1') located on the middle part of ramus; third

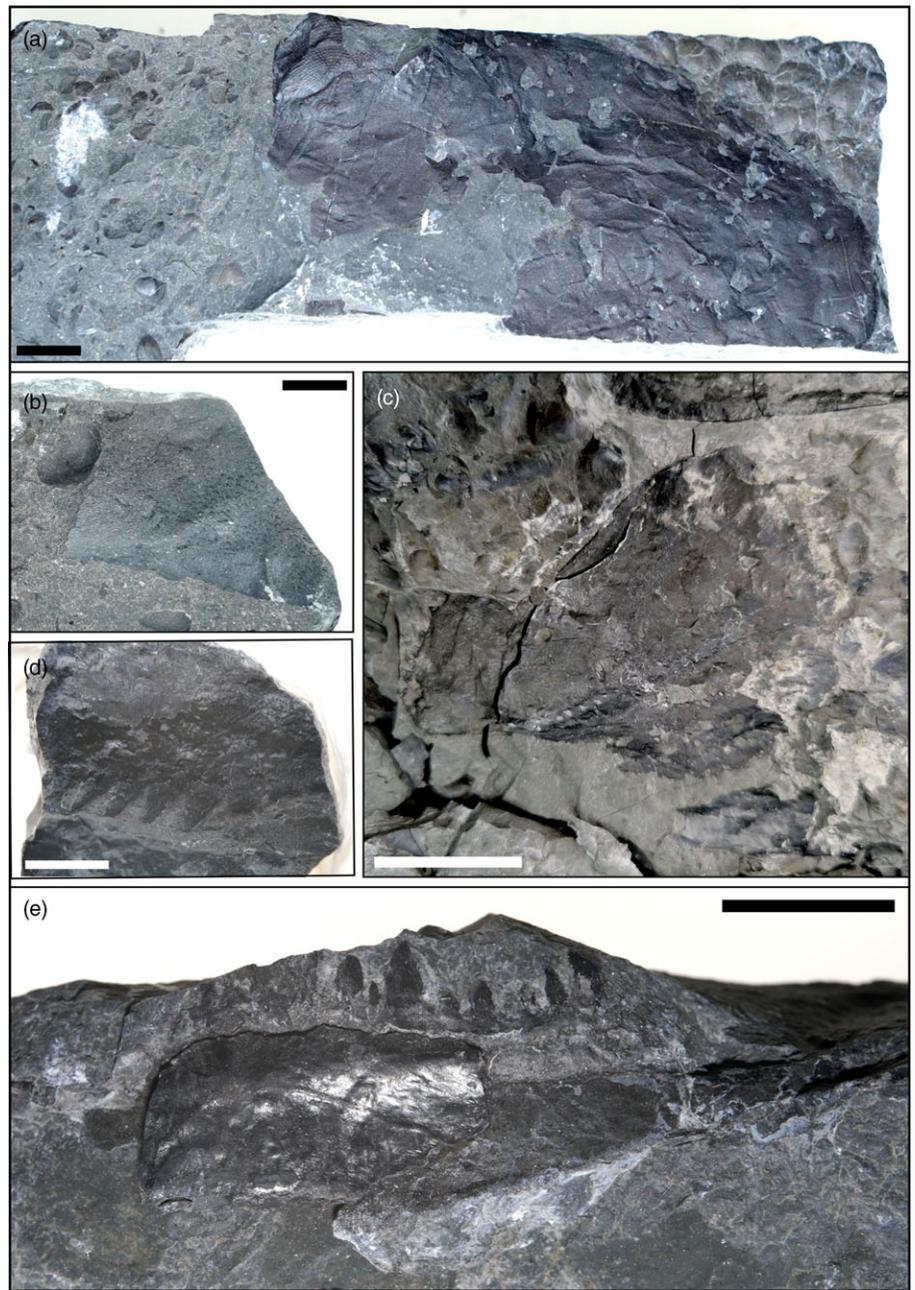
primary denticles (d3,d3') elongate, even longer than first primary denticles.

#### 4.d. Occurrence

Lower part of the Xiaishancun Formation and Xitun Formation (Wang & Gai, 2014; Lochkovian) Xiaishan Reservoir near Qujing city, Yunnan, SW China.

#### 4.e. Description

Specimen GMG20211001003 (Fig. 2) is an isolated chelicera comprising the fixed and free ramus and elongate basal podomere, total preserved length 96.4 mm. The fixed ramus is slightly longer than the free ramus. The rami of both appendages preserve fine detail of denticles. Denticles with fine longitudinal striations, without marginal serrations.



**Fig. 3.** (Colour online) *Pterygotus wanggaii* n. sp. (a) Partial carapace GMG20211001004; (b) partial isolated tergite GMG20211001008; (c) isolated coxa of prosomal appendage VI, GMG20211001007; (d) a portion of the coxa (gnathobase) of the walking leg, GM006; (e) partial isolated ramus specimen, GMG20211001005. All scale bars = 10 mm.

Fixed ramus preserved length 71.4 mm, maximum preserved width 16.4 mm. Terminal denticle (td) incomplete; however, the gentle curvature of the preserved ramus margin suggests the denticle may have been curved rather than angular in morphology. Primary denticle (d1) is more robust than others, length 9.0 mm, width at base 4.7 mm, upright with posterior curvature. Anterior principal denticle (d2) length 5.2 mm, width at base 1.8 mm, upright with posterior curvature. Third principal denticle (d3) length 8.2 mm, width at base 4.2 mm, upright with weak posterior curvature. Six intermediate denticles are interspersed between the primary denticles and a multitude of smaller denticles; the first (*i1*) occurs just posterior to the terminal denticle, only denticle base preserved, width at base 1.9 mm. Second intermediate denticle (*i2*) occurs 11.2 mm anterior of the primary denticle, length 1.3 mm, width at base 1.7 mm, upright. Third intermediate denticle (*i3*) located posterior to primary denticle, length 2.5 mm,

width at base 1.3 mm, upright. Fourth intermediate denticle (*i4*) located 4.3 mm posterior to primary denticle, height 2.1 mm, width at base 1.2 mm, upright with posterior curvature. Fifth intermediate denticle (*i5*) with base obscured by brachiopods, located 4.4 mm anterior to third primary denticle, preserved height 3.6 mm, denticle slightly angled towards ramus distal termination. Sixth intermediate denticle (*i6*) located 9.3 mm posterior to third primary denticle, height 2.6 mm, width at base 2.0 mm, upright with posterior curvature.

Free ramus preserved length 66.8 mm, maximum preserved width 23.4 mm. Terminal denticle (td') robust, angled slightly away from the ramus, height 9.2 mm, width at base 2.7 mm. The third principal denticle (d3') is the most robust denticle, length 12.1 mm, width at base 4.8 mm, upright with slight posterior curvature. Denticle morphology and arrangement on free ramus is similar to that of fixed ramus.

GMG20211001005 (Fig. 3e) Partial isolated ramus, preserving partial appendage with third principal denticle and several intermediate denticles. Ramus total length 46.3 mm, width 13.8 mm. The third principal denticle only preserves the basal 5 mm. All denticles with fine longitudinal striations.

GMG20211001004 (Fig. 3a) Partial carapace, preserving left margin, lateral compound eye and portions of anterior margin. Carapace preserved length 47.9 mm, width 104.4 mm. The weak crumples on the surface suggest that the specimen represents an exuvium. The lateral eye is flattened and positioned anterolaterally, abutting the carapace margin, and is oval in shape with a length of 12.0 mm.

GM20211001006 (Fig. 3d) A portion of the coxa (gnathobase) of a walking leg. The length of the coxa is 29.4 mm, 33.9 mm across the eight denticles on the gnathobase. The full gnathobasic surface is not preserved but at least eight teeth are present, generally uniform in shape and decreasing regularly in size from anterior to posterior.

GMG20211001007 (Fig. 3c) An almost completely preserved isolated coxa of appendage VI. The coxa is broad, expanding distally with a marked constriction between the gnathobase and the distal expansion. The length of the coxa is 80.7 mm from the distal portion of the expanded posterior to the gnathobasic edge. The maximum width of the coxa, located towards the posterior of the expanded region, is 57.2 mm; the gnathobasic surface is incomplete, with a preserved width of 22.5 mm, and the subsequent constriction is 18.5 mm wide at its narrowest point. The full gnathobasic surface is not preserved but at least nine teeth are present, generally uniform in shape and decreasing regularly in size from anterior to posterior. The coxa surface is ornamented with broad lunule scales grading to small tubercles at the coxa midline.

GMG20211001008 (Fig. 3b) Partial tergite, length 26.3 mm, preserved width 42.7 mm, ornamentation of dense lunule scales across the tergite anteriorly to posteriorly.

#### 4.f. Etymology

Named after the family names of Professors Wang Bo (王博) and Gai Zhikun (盖志琨), who reported the first specimen.

#### 4.g. Remarks

The holotype (GMG20211001003) of *Pterygotus wanggaili* n. sp. shares an almost identical denticle morphology and arrangement with specimen IVPP-I4593, which was described by Wang & Gai in 2014. Hence, IVPP-I4593 and our new material can be attributed to the same species. However, due to the poor preservation and without any other specimens, Wang & Gai (2014) did not assign IVPP-I4593 to any genus or species (Wang & Gai, 2014). Based on our new specimens it is clear that several characteristics of the species, such as the free ramus of chelicera terminating in a curved denticle, denticles curved posteriorly without marginal serrations, and an ornament of dense lunule scales across the tergite anteriorly to posteriorly, indicate an assignment to *Pterygotus*. We erect *Pterygotus wanggaili* n. sp. based on the robust ramus with first primary denticles (d1, d1') located on the middle part of ramus and elongate third primary denticles (d3, d3') which are even longer than first primary denticles and all primary denticles with slight posterior curvature.

The new species closely resembles other well-known *Pterygotus* species, particularly *Pterygotus cobbi* Hall, 1859 and *Pterygotus barrandei* Semper, 1898 with the elongated and broad primary denticles of the chelicera. However, the free ramus of *P. cobbi*

exhibits thinner, fewer and more widely spaced primary denticles and intermediate denticles are very rare (see (Hall, 1859; Leutze & Heubusch, 1963). In *P. barrandei*, the primary denticles are further apart and located more proximally on the ramus (Semper, 1898; Chlupac, 1994). The cheliceral morphology of *P. wanggaili* is distinct from that of *E. qujingensis*, from the Upper Silurian Yulongsi Formation of Yunnan Province, which exhibits a thinner ramus and less differentiation between the cheliceral denticles.

Superfamily Adelophthalmoidea Tollerton, 1989

Family Adelophthalmidae Tollerton, 1989

Genus *Parahughmilleria* Kjellesvig-Waering, 1961

#### 4.h. Diagnosis

Adelophthalmidae of small size; carapace semicircular; lateral eyes small, reniform and in centrilateral position of carapace; metastoma with deep triangular notch anteriorly; telson wide, lanceolate shape (Kjellesvig-Waering, 1961; Tollerton, 1989).

Type species *Parahughmilleria salteri* Kjellesvig-Waering, 1961

#### 4.i. Remark

Størmer (1973) reported two *Parahughmilleria* species from the uppermost Lower Emsian of Alken: *P. hefteri* and *P. major*. The latter species was separated from the former mainly because of its larger size coupled with a more slender body and slight differences in the morphology of the genital appendage. However, based on recent studies indicating that the differences between both supposed species are due to ontogeny and preservational variation, some authors consider *P. hefteri* and *P. major* to be synonymous (Poschmann & Tetlie, 2006; Lamsdell & Selden, 2013; Poschmann, 2015). Here, we are inclined to regard *P. major* as a synonym of *P. hefteri*.

*Parahughmilleria fuea* new species (Fig. 4)

#### 4.j. Type material

Holotype GMG20211001001a and GMG20211001001b (counterpart of GMG20211001001a); paratype GMG20211001002.

#### 4.k. Diagnosis

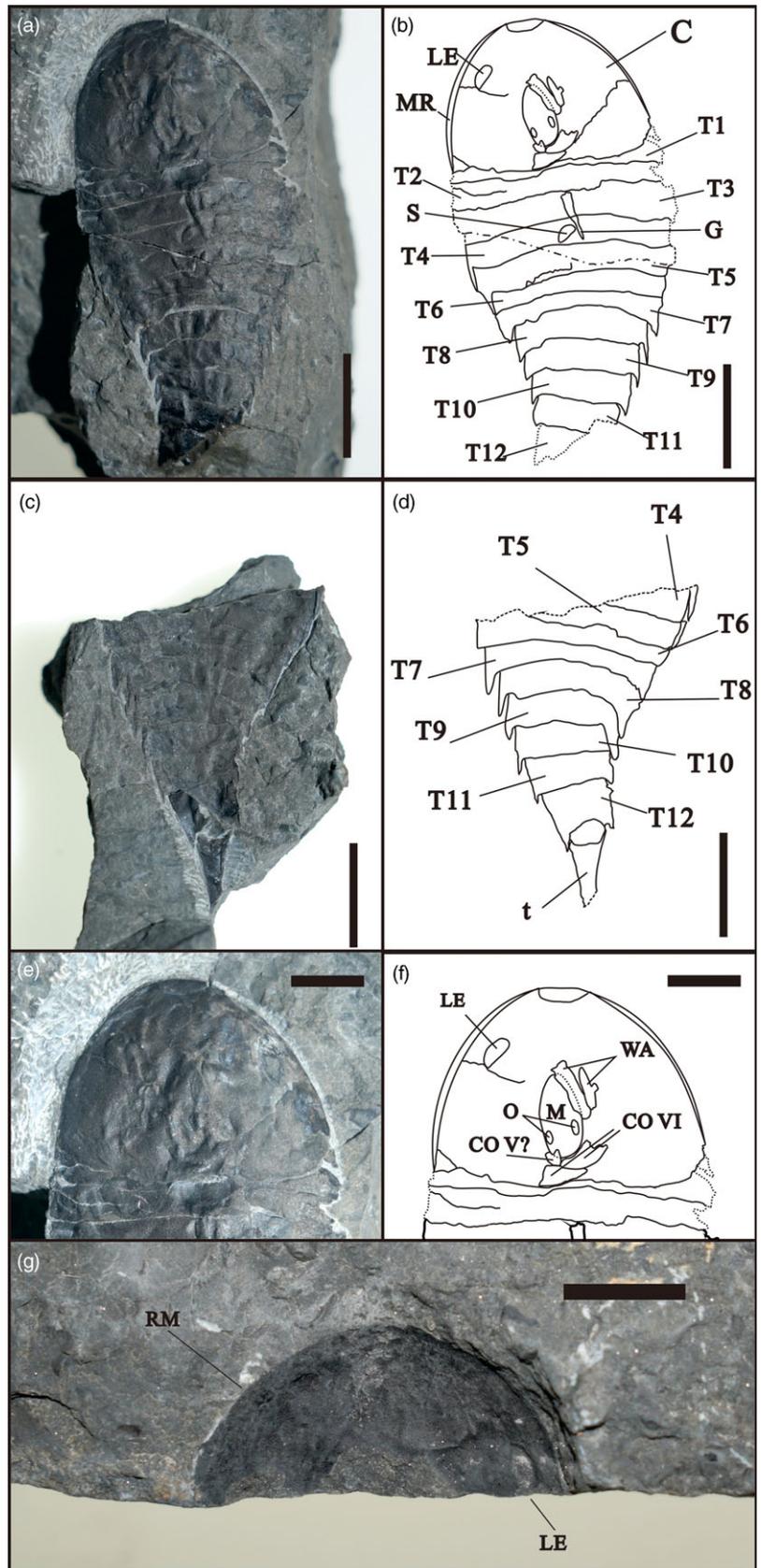
Large *Parahughmilleria* with strongly developed lateral epimera from tergites T4 to T12.

#### 4.l. Occurrence

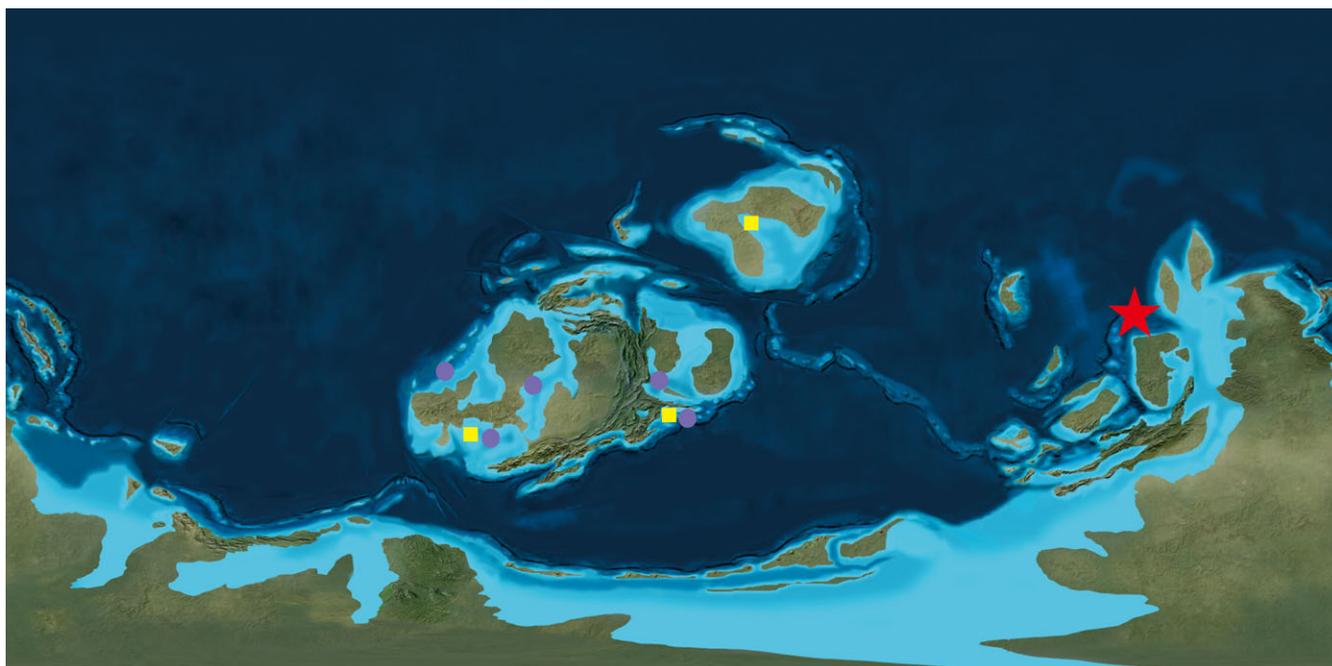
Lower part of the Xiaxisancun Formation; Xiaxisan Reservoir near Qujing city, Yunnan, SW China.

#### 4.m. Description

Two specimens are attributable to this species. GMG20211001001 (preserved as part and counterpart; Fig. 4a–f) consists of an articulated prosoma and opisthosoma but lacks the distal part of the telson; the prosomal appendages are partially preserved. The total length of the specimen is more than 110 mm and the maximum width is 39.4 mm. Carapace semicircular, length 28.2 mm, width at base 37.4 mm (L/W 0.75, lateral angle 107°). The carapace is arched and surrounded by a narrow marginal rim. The posterior margin of the carapace is crumpled weakly, but the available undistorted margins suggest it may be slightly convex. The lateral eyes are relatively small, 4.4 mm long, 2.2 mm wide, reniform and positioned centrilaterally. The median ocelli are small and rounded,



**Fig. 4.** (Colour online) *Parahughmilleria fuea* n. sp. (a) Holotype GMG20211001001a, nearly complete specimen, scale bar = 20 mm; (b) interpretive drawing of Holotype GMG20211001001a, T = tergite, LE = lateral eye, C = carapace, MR = marginal rim, G = genital appendage, S = spatulae, scale bar = 20 mm; (c) holotype GMG20211001001b, counterpart of GMG20211001001a, scale bar = 20 mm; (d) interpretive drawing of holotype GMG20211001001b, T = tergite, t = telson, scale bar = 20 mm; (e) details of carapace of holotype GMG20211001001a, scale bar = 10 mm; (f) interpretive drawing of carapace of holotype GMG20211001001b, M = metastoma, O = ocelli, LE = lateral eye, CO V = coxa V, CO VI = coxa VI, WA = walking appendage, scale bar = 10 mm; (g) incomplete carapace GMG20211001002, LE = lateral eye, MR = marginal rim, scale bar = 10 mm.



**Fig. 5.** (Colour online) Palaeogeographic distribution of Pridolian to Lochkovian *Pterygotus* and *Parahughmilleria*. Global palaeogeographic reconstruction for the Pridolian to Lochkovian (420 Ma) is after Blakey (2020). Circles represent localities of previously described *Pterygotus*; squares represent localities of previously described examples of *Parahughmilleria* (Tetlie, 2007); star shows location of the Chinese eurypterids.

positioned on the central part of carapace, with a diameter of 2.1 mm.

Metastoma 10.9 mm long, 5.4 mm wide (L/W 2.0), lateral part partially covered by podomeres from a walking leg, lateral angle *c.* 80°. Based on the wrinkle line and the uncovered left part, we suspect the metastoma is paraelliptical in shape (Tollerton, 1989). A pair of coxa VI are located at the posterior of the metastoma. The coxa are roughly triangular in shape, expanding distally with a marked constriction at the gnathobase. The length of coxa VI is 5.6 mm, the maximum width is 3 mm. Walking leg podomeres appear non-spiniferous. On the part (GMG20211001001a), the slender type-A genital appendage extends to the posterior margin of the fourth tergite, total length 8.9 mm. One smaller structure with a length of 3.3 mm and situated on the left side of the appendage is interpreted as a spatula.

The opisthosoma is widest at the third tergite. Each of the tergites curves anteriorly along the mid-line. The first tergite is slightly reduced, 3.8 mm long, with the succeeding preabdominal tergites 4.7–5.5 mm long. Only the first and second tergites lack posterolateral epimera, possibly weakly developed on the third tergite with small posterolateral corners. Fourth tergite with strongly developed triangular epimera, about 3.5 mm long. Seventh tergite *c.* 30.2 mm wide, tergite eight (first postabdominal tergite) 24.1 mm wide. Eighth to eleventh tergites with an almost constant length of *c.* 6.0 mm, becoming narrower posteriorly, with well-developed posterolateral epimera. The twelfth tergite (pretelson) and proximal part of the telson are preserved on the counterpart (GMG20211001001b), pretelson with a length of 9.5 mm and width of 13.6 mm. The telson is lanceolate, preserved length 15.0 mm, width at base 6.3 mm. The distal part of the telson is not preserved.

GMG20211001002 (Fig. 4g) preserves an incomplete carapace, damaged on the posterior side, preserved length of 14.7 mm and width of 30.3 mm. The carapace is arched and surrounded by a

narrow marginal rim. Centrimesially positioned lateral eye preserved on the right side. The lateral eye is relatively small, 4.3 mm long, 2.2 mm wide, reniform in shape.

#### 4.n. Etymology

Named after the family name of Ms Fu Lihong (付丽红) in recognition for her support of our research.

#### 4.o. Remarks

*Parahughmilleria fuea* n. sp. is relatively large compared with the other well-known species of *Parahughmilleria*, exhibiting a size much more typical of the largest adelophthalmoid *Adelophthalmus*. However, the L/W ratio of the metastoma, and the position of the compound eyes strongly indicate the Chinese adelophthalmoid can be assigned to *Parahughmilleria*. (Kjellesvig-Waering, 1961; Tollerton, 1989). *Parahughmilleria fuea* n. sp. shares many similarities with the *P. hefteri*, such as the elongate type-A genital appendage, the L/W ratio of metastoma, and the position of compound eyes (Størmer, 1973; Braddy, 2000; Poschmann & Tetlie, 2006; Poschmann, 2015). However, there are some differences between *Parahughmilleria fuea* n. sp. and Euramerican *Parahughmilleria*, with *P. fuea* n. sp. possessing strongly developed lateral epimera on the fourth to twelfth tergites whereas epimera are only observed on the seventh to twelfth tergites in the Euramerican species, even in larger specimens (Kjellesvig-Waering, 1961; Kjellesvig-Waering & Leutze, 1966; Størmer, 1973; Poschmann & Tetlie, 2006; Tetlie & Poschmann, 2008; Poschmann, 2015, 2017, 2020). The developed lateral epimera are unlikely to be an ontogenetic difference because epimera can also be observed in the different ontogenetic stages of the closely related *Adelophthalmus* (Shpinev & Filimonov, 2018).

## 5. Discussion

The eurypterid community from the Xiaxisancun Formation shares many similarities with that of the famous Willwerath Lagerstätte of Rhineland-Palatinate, Germany (Poschmann & Tetlie, 2006; Poschmann, 2017, 2020). The Willwerath Lagerstätte includes six eurypterid species referable to the genera *Jaekelopterus*, *Rhenopterus*, *Erieopterus*, *Adelophthalmus*, *Pruemopterus* and *Parahughmilleria* (Kjellesvig-Waering, 1961; Poschmann, 2020), some plant fossils (Alling & Briggs, 1961) and the putative euchelicerate *Willwerathia* (Anderson et al. 1998; but see Lamsdell, 2020). Like the Willwerath Lagerstätte, beside the eurypterids *Pterygotus wangi* n.sp. and *Parahughmilleria fuea* n. sp., the euchelicerate *Houia yueya* (Lamsdell et al. 2013; Selden et al. 2015) and plant *Zosterophyllum xishanense* (Hao et al. 2007; Xue, 2012) are also present in the Xiaxisancun Formation. The Willwerath Lagerstätte is characterized by grey silty mudstones and muddy siltstones interbedded with fine sandstones, and the palaeoenvironment is considered as marginal marine; the lithological combination and marine tidal flat habitat of the Xiaxisancun Formation concurs with this. The discoveries from the Xiaxisancun Formation provide strong evidence that eurypterids formed comparable communities globally and give insight into the similarity of ecosystem structure across the Early Devonian world.

In addition, all of the 20 previously known species of *Pterygotus* are described from Europe, North America and Australia (Tetlie, 2007), and four of five *Parahughmilleria* species are from Europe and North America, with the exception of *Parahughmilleria matarakensis* from Khakassia, Russia. The specimens described here broaden the distribution of *Parahughmilleria* and *Pterygotus* and represent the first Gondwanan record of *Parahughmilleria*. Moreover, the discoveries further support the notion that pterygotoids and adelophthalmoids had superior dispersal abilities leading to a more cosmopolitan distribution because of streamlined body form and substantial swimming abilities (Tetlie, 2007). These new discoveries from China not only provide a broader picture of the biogeography of the group but also demonstrate that species in Gondwana occupied similar environments to their Laurentian relatives Fig. 5.

Furthermore, it is very exciting to find new eurypterids in Gondwana, especially during the Silurian–Devonian boundary interval. As one of the most important geological–biotic events, the Silurian–Devonian boundary event was marked by a major positive excursion of  $\delta^{13}\text{C}$  (Małkowski & Racki, 2009; Zhao et al. 2011, 2015, 2021), global sea-level regression (Małkowski & Racki, 2009), graptolite extinction (Urbanek et al. 2010) and a decrease in cephalopod species diversity (Laptikhovskiy et al. 2013). Lamsdell & Selden (2017) suggested that eurypterids ended the Silurian on a bust, experiencing marked extinction during the Silurian–Devonian boundary interval. This phenomenon can also be confirmed in the Silurian–Devonian strata of the South China Block. The upper part of the Yulongsi Formation, which is considered as latest Pridolian in age (Qie et al. 2019; Rong et al. 2019; Zhao et al. 2021), is dominated by the *Erettopterus–Slimonia* association (Ma et al. 2022), whereas in the Xiaxisancun Formation the *Erettopterus* and *Slimonia* community suddenly disappeared and was replaced by *Parahughmilleria* and *Pterygotus*. Beside the turnover of eurypterids, other organisms also undergo major shifts, such as the increased diversity of fishes (Zhao & Min, 2010; Lu et al. 2017) and abundance of plants (Xue, 2012). In terms of environment, the Yulongsi Formation is considered lagoonal

based on the dark, organic, intensely laminated silt–mudstone (Wang, 2000). With the global sea-level regression during the Silurian–Devonian boundary interval, the Xiaxisancun Formation appears to consist of more siltstone layers and is considered a shallow tidal flat environment (Wang, 2000). These shifts in sea level and depositional environment are synchronous with the positive excursion of  $\delta^{13}\text{C}$  (Zhao et al. 2021). This discovery not only strongly supports the previously observed turnover of eurypterids at the end of the Silurian, experiencing marked extinction during the Silurian–Devonian boundary interval, but also indicates the environment experienced great change during the interval.

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