

Two new eurypterids (Arthropoda, Chelicerata) from the upper Silurian Yulongsi Formation of south-west China

Zhiheng Ma,¹ Paul A. Selden,^{2,3} James C. Lamshed,⁴ Tingshan Zhang,^{1*} Jingwen Chen,⁵ and Xi Zhang¹

¹School of Geoscience and Technology, Southwest Petroleum University, Chengdu, Sichuan, China <1625194814@qq.com> <zhangtingshan@swpu.edu.cn>

²Department of Geology, University of Kansas, Lawrence, Kansas, USA <selden@ku.edu>

³Natural History Museum, London, UK

⁴Department of Geology and Geography, West Virginia University, Morgantown, West Virginia, USA <james.lamshed@mail.wvu.edu>

⁵Fujian Key Laboratory of Mineral Resources, Fuzhou University, Fuzhou, China <cjw070715@foxmail.com>

Abstract.—Two new eurypterids, a pterygotid *Erettopterus qujingensis* n. sp., and a slimoniid, *Slimonia* sp., are described from the upper Silurian (Pridolian) Yulongsi Formation of Yunnan Province, China. *Erettopterus qujingensis* n. sp. is characterized by several inversely curved ramus denticles and a metastoma with a deep notch in the center. The discovery not only extends the geographic extent of the genus *Erettopterus* and *Slimonia* from Euramerica to southwest China, but also gives insight into the similarity of ecosystem structures across the Silurian world.

UUID: <http://zoobank.org/939e82cd-58fc-415b-9209-514aecef2267>

Introduction

Eurypterids, informally known as sea scorpions, are aquatic carnivorous or sweep-feeding chelicerates that originated in the early Middle Ordovician and went extinct in the late Permian (Tetlie, 2007; Lamshed et al., 2015; Lamshed and Selden, 2017; Hughes and Lamshed, 2020). They include some of the largest arthropods known to exist, growing to two meters or more in length (Kjellesvig-Waering, 1964; Chlupáč, 1994; Braddy et al., 2008; Lamshed and Braddy, 2010). The family Pterygotidae is the most diverse clade of the order Eurypterida, with ~46 species in five genera (Lamshed and Selden, 2017). Slimoniidae, comprising four species in the genera *Slimonia* and *Salteropterus*, resolving as a sister group to the pterygotids (Lamshed et al., 2015; McCoy et al., 2015; Lamshed and 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 peduncular podomeres (Tetlie and Briggs, 2009). Pterygotids attained a nearly global distribution (Poschmann and Tetlie, 2006; Miller, 2007; Tetlie and Briggs, 2009; Lamshed and Legg, 2010; Wang and Gai, 2014) and were ecologically diverse predators with a range of visual acuity and a variety of cheliceral morphologies indicating adaptations for capturing a variety of benthic and actively swimming prey (Anderson et al., 2014; McCoy et al., 2015).

Despite their longevity and wide geographic dispersal, eurypterids are generally rare in the fossil record, especially in China (Tetlie, 2007). This state has changed in recent years as research intensity increases, with the Chinese record of eurypterids expanding beyond the lower Permian *Adelophthalmus chinensis* from Hebei Province (Grabau, 1920) to include *Hughmilleria wangi* Tetlie, Selden, and Ren, 2007, described based on an almost complete specimen from the Silurian (late Llandovery) Xiaoxiyu Formation (Tetlie et al., 2007; Zong et al., 2017), and an isolated pterygotid chelicera with its two rami preserved from the Xitun Formation of the Lower Devonian in Yunnan Province (Wang and Gai, 2014). Several putative eurypterid specimens were also described by Chang (1957) from the Silurian of Hubei; however, the eurypterid affinity of this material is dubious, and the three described species are considered invalid (Tetlie et al., 2007). Recently a new eurypterid, *Terropterus xiushanensis* Wang et al., 2021, has been reported in the Chongqing area and is the first Mixopteridae to be found in China (Wang et al., 2021; Table 1). Here, we report eurypterid specimens representing a new species of the pterygotid *Erettopterus* (Salter in Huxley and Salter, 1859) and an occurrence of *Slimonia* (Page, 1856) from the upper Silurian (Pridolian) Yulongsi Formation of Yunnan, China.

Geological setting and stratigraphy

Pridoli–Lower Devonian deposits are well developed in the Qujing area. The Silurian layers are assigned to the Miaogao and Yulongsi formations while the Xiaxisancun, Xitun, Guijiatun, and Xujiachong formations belong to the Devonian. Our study outcrop of the Yulongsi Formation is ~11 km west of Qujing

*Corresponding author.

Table 1. Eurypterids recorded from China. Asterisks indicate taxa that might be based on dubious material.

Permian		
<i>Adelophthalmus chinensis</i>	Grabau, 1920	Hebei Province
Devonian		
Pterygotidae gen. et sp. indet.	Wang and Gai, 2014	Yunnan Province
Silurian		
<i>Erettopterus qujingensis</i> n. sp.	This paper	Yunnan Province
<i>Slimonia</i> sp.	This paper	Yunnan Province
<i>Hughmilleria wangi</i>	Tetlie et al., 2007	Hunan Province
<i>Terropterus xiushanensis</i>	Wang et al., 2021	Chongqing City
<i>Eurypterus loi</i> *	Chang, 1957	Hubei Province
<i>Eurypterus styliformis</i> *	Chang, 1957	Hubei Province
<i>Eurypterus yangi</i> *	Chang, 1957	Hubei Province
<i>Mioxopterus</i> sp.*	Chang, 1957	Hubei Province

City (coordinates 25.474544°N, 103.696914°E; Fig. 1). The Yulongsi Formation is ~250 m thick and conformable with the underlying Miaogao Formation; its top is also conformable with a yellow-green sandstone of the Xiashancun Formation. The Yulongsi Formation can be divided into three parts: the lower part begins with a large amount of black shale known as the “lower weathering shale,” with few fossils, but contains brachiopods, corals, bivalves, ostracodes, and gastropods. The middle part is gray and light gray calcareous shale with a thin gray layer of nodular limestone and limestone lenses containing brachiopods, bivalves, trilobites, and ostracodes. The upper part is black, gray-green and gray-blue shale, also known as the “upper weathering shale,” that contains brachiopods, bivalves, and jawless fishes (Wang, 2000, Fig. 2).

There were many debates about the age of the Yulongsi Formation. In the twentieth century, some scholars insisted that the whole formation was Devonian in age (Wu, 1977; Lin et al., 1982) or the boundary between Devonian and Silurian should be below the upper black shale of the formation (P’an et al., 1978; Yang and Li, 1978). However, with further research in the Qujing area—especially recent research in palynology and

other microfossils such as conodonts and chitinozoas (Wang, 1980; Fang et al., 1994; Tian et al., 2011; Peng et al., 2016)—all evidence indicates that the age of the Yulongsi Formation is Pridolian (Tian et al., 2011; Rong et al., 2019). All the specimens described in this paper were collected in the upper part of the Yulongsi Formation.

Materials

The specimens (YN-415001–11) described in this paper were collected from the upper part of the Yulongsi Formation. Being preserved in fine shales, the material is flattened and shows some tectonic distortion. The holotype (YN-415005) preserves the free ramus of the chelicera while the prosomal carapace, prosomal appendage VI, metastoma, and several tergites are represented among paratype material.

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 (Adobe Illustrator CS5 and Adobe Photoshop CS). Morphological terminology follows Tollerton (1989) with denticle terminology following Miller (2007).

Repository and institutional abbreviation.—All specimens and pictures examined in this study are deposited in the fossil specimen room of Southwest Petroleum University (SWPU), Chengdu, Sichuan Province, China.

Systematic paleontology

- Order Eurypterida Burmeister, 1843
- Suborder Eurypterina Burmeister, 1843
- Superfamily Pterygotoidea Clarke and Ruedemann, 1912
- Family Pterygotidae Clarke and Ruedemann, 1912

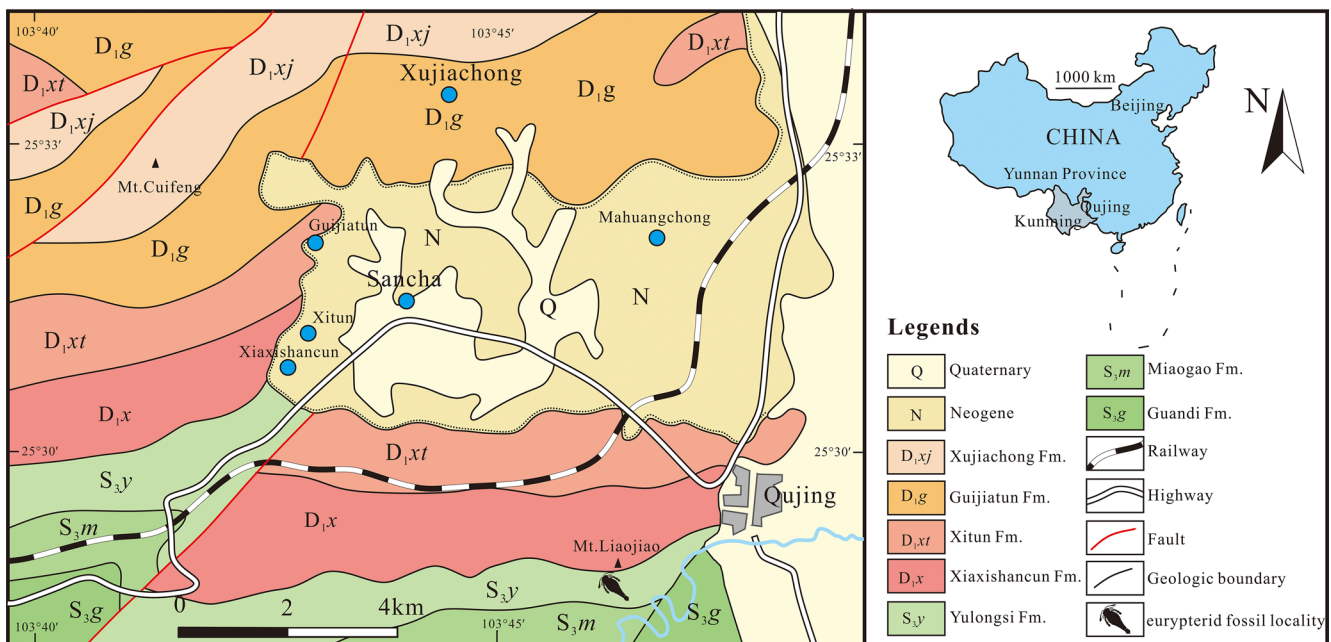


Figure 1. Generalized map showing geologic features of the Qujing area and the eurypterid fossil locality (modified from Hao et al., 2007, fig. 1).

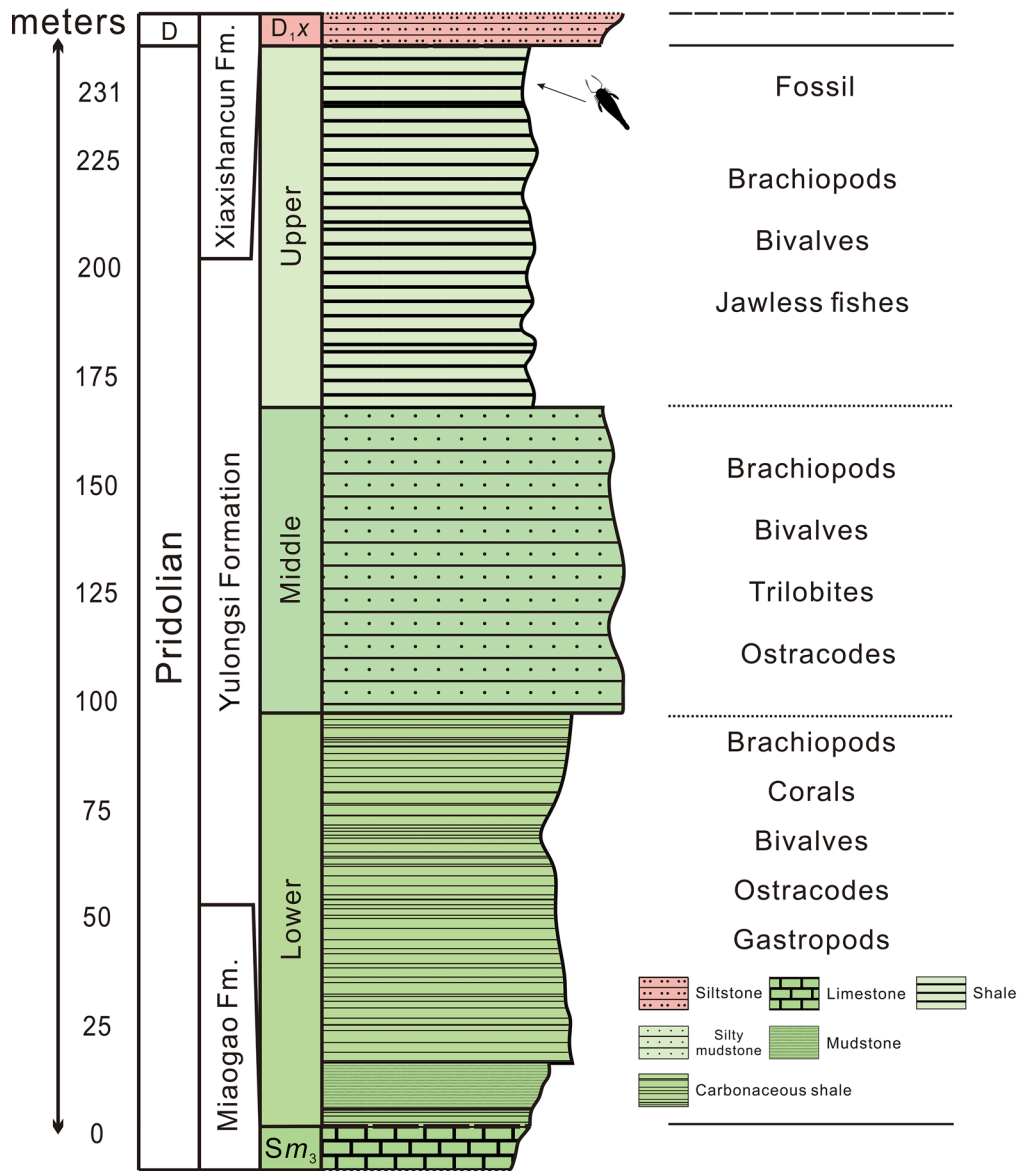


Figure 2. Schematic stratigraphic column for the Yulongsi Formation showing distribution of eurypterids at localities in the Qujing area.

Genus *Erettopterus* Salter in Huxley and Salter, 1859
 [= *Truncatiramus* Kjellesvig-Waering, 1961]

Type species.—*Pterygotus bilobus* Salter, 1856.

Remarks.—*Erettopterus* was diagnosed by Cieurca and Tetlie (2007) through the possession of a bilobed telson, although previous authors have also considered a deep anterior notch in the metastoma and a lack of enlarged, differentiated denticles in the chelicera to be diagnostic of the genus (Kjellesvig-Waering, 1964; Waterston, 1964). Although the available material does not preserve the telson, several other characteristics, including the relatively undifferentiated cheliceral denticles and the distribution of cuticular ornamentation of the tergites—with an ornament of dense lunule scales across the tergite anteriorly giving way to a

smooth unornamented surface posteriorly (also observed by Cieurca and Tetlie, 2007)—indicate that the species can be assigned to the genus with some confidence.

Erettopterus qujingensis new species
 Figures 3–5, Table 2

Type material.—Holotype YN-415005; paratypes YN-415001–4, 6–10.

Diagnosis.—*Erettopterus* with chelicera bearing three principal denticles and distal (terminal) denticle; cheliceral denticles exhibiting size differentiation, central principal denticle longer and broader than others; proximal denticles of free ramus angled inversely; metastoma broad oval in shape with rounded shoulders and a deep median notch.

Occurrence.—Upper part of the Yulongsi Formation (Pridolian); south of Liaojiang Mountain near Qujing City, Yunnan, southwestern China.

Description.—SWPU: YN-415005 (Fig. 4.1). An isolated free ramus, total preserved length 33 mm, maximum preserved width of ramus 4.1 mm. Terminal denticle 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 3.1 mm, width at base 1.8 mm, upright with posterior curvature. Anterior principal denticle ($d2'$) length 2.1 mm, width at base 1.1 mm, upright with posterior curvature. Third principal denticle ($d3'$) length 2.1 mm, width at base 1.2 mm, entire denticle angled towards ramus distal termination. Five intermediate denticles are interspersed between the primary denticles and a multitude of smaller denticles; the first ($i1'$) occurs just posterior of the terminal denticle and is at least 1.0 mm in height, width at base at least 0.3 mm, upright with little apparent curvature. Second intermediate denticle ($i2'$) occurs 2 mm anterior of the primary denticle, length 1.5 mm, width at base 0.8 mm, upright with

posterior curvature. Third intermediate denticle ($i3'$) located immediately posterior of primary denticle, length 1.7 mm, width at base 0.9 mm, upright. Fourth intermediate denticle ($i4'$) located 1.5 mm anterior of third principal denticle, height 1.5 mm, width at base 1.2 mm, entire denticle angled towards ramus distal termination. Fifth intermediate denticle ($i5'$) located 1.7 mm posterior of third primary denticle, height 1.3 mm, width at base 0.7 mm, denticle slightly angled towards ramus distal termination (Table 2).

SWPU: YN-415001 and YN-415002 (Fig. 3, part and counterpart). Material comprising at least two individuals. The large individual is represented by a series of three tergites and an isolated metastoma of either the same individual or one of a similar size. The smaller individual, preserved alongside the large metastoma, comprises a crumpled carapace, partial prosomal appendage VI, and seven articulated tergites.

The tergites of the large specimen are laterally incomplete, with the first tergite having a length of 44 mm and a preserved width of 107 mm, the second tergite a length of 50 mm and a preserved width of 108 mm, and the third a length of 72 mm and a preserved width of 72 mm. The last tergite is clearly folded in on itself part-way along its length, likely the result of

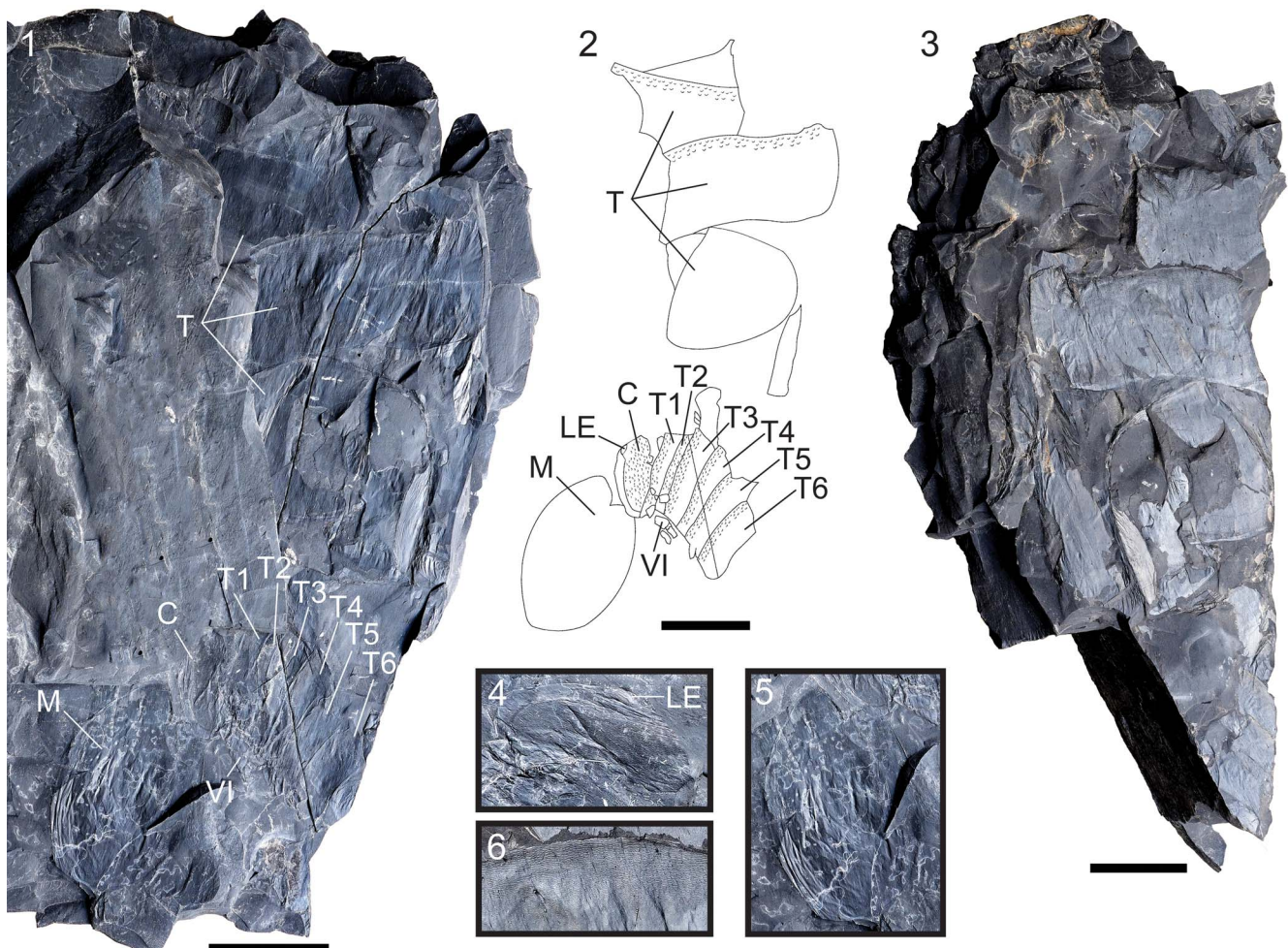


Figure 3. *Erettopterus qujingensis* n. sp. (1) Part YN-415001; (2) interpretive drawing of YN-415001; (3) counterpart YN-415002; (4) prosomal carapace of small specimen on YN-415001; (5) metastoma on YN-415001; (6) detail of anterior tergite ornamentation on YN-415002. C = carapace, LE = lateral compound eye, M = metastoma, T = tergites, VI = prosomal appendage VI. Scale bars = 50 mm.

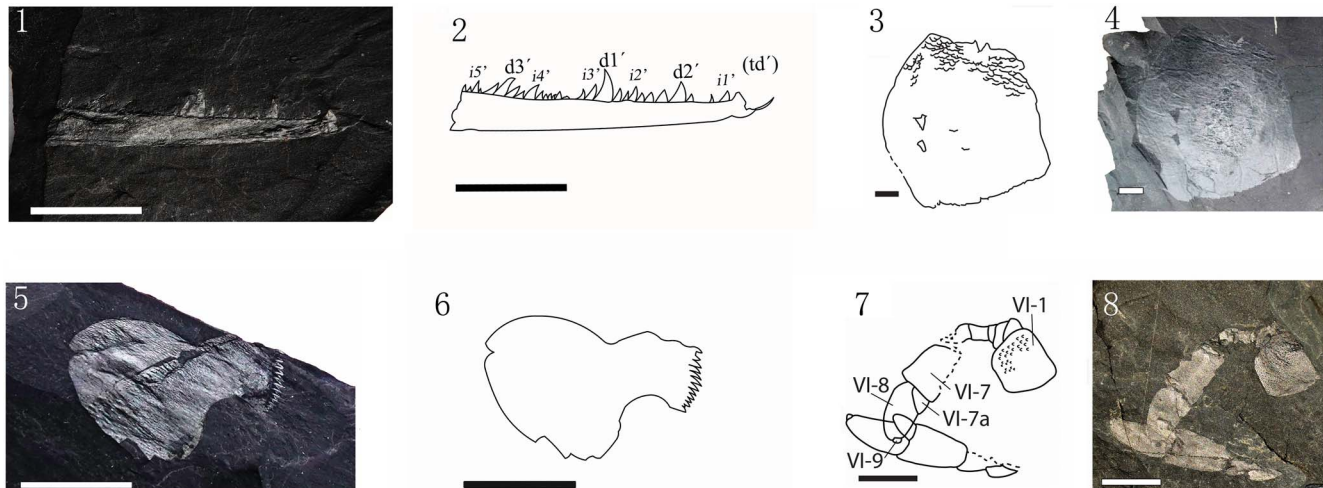


Figure 4. *Erettopterus qujingensis* n. sp. (1, 2) Holotype YN-415005, (1) free ramus of chelicera, (2) interpretive drawing of free ramus of chelicera; (3, 4) YN-415004, (3) interpretive drawing of partial metastoma, (4) partial metastoma; (5, 6) YN-415003, (5) isolated coxa of prosomal appendage VI, (6) interpretive drawing of partial metastoma; (7, 8) YN-415006, (7) interpretive drawing of prosomal appendage VI, (8) isolated pair of prosomal appendage VI. td' = terminal denticle on free ramus; d1'–d3' = principal denticles on free ramus; i1'–i5' = intermediate denticles on free ramus; VI-1, VI-7–VI-9 = prosomal appendage VI podomeres 1, 7–9; VI-7a = modified part of VI-7. Scale bars = 10 mm.

taphonomic deformation. The anterior 12 mm of each tergite is covered in small scales, getting progressively deeper and more angular posteriorly (Fig. 3.5). The metastoma is rhombiovent (sensu Tollerton, 1989), 84.3 mm long, with a maximum width at its midline of 55.1 mm giving an L:W ratio of 1.53, a lateral angle of 54° , and an angle of cordation 73° . The anterior shoulders are rounded with an angular anterior 13 mm deep notch.

The prosomal carapace of the smaller specimen is crumpled, with a preserved length of 32 mm and preserved width of 41 mm.

The overall shape of the prosomal shield is difficult to determine, but the available undistorted margins suggest it may have been subquadrate. An anterolaterally positioned lateral compound eye is preserved, overlapping the carapace margin and oval in outline (Fig. 3.3), 8 mm long by 2 mm wide. Podomeres of prosomal appendage VI are preserved alongside the first few tergites; although generally fragmentary, it is possible to identify the elongated podomere 7 of a swimming paddle with a length of 18 mm and a distal width of 10 mm. Six tergites are preserved in their entirety; the first is 8 mm long, 43 mm wide; the second

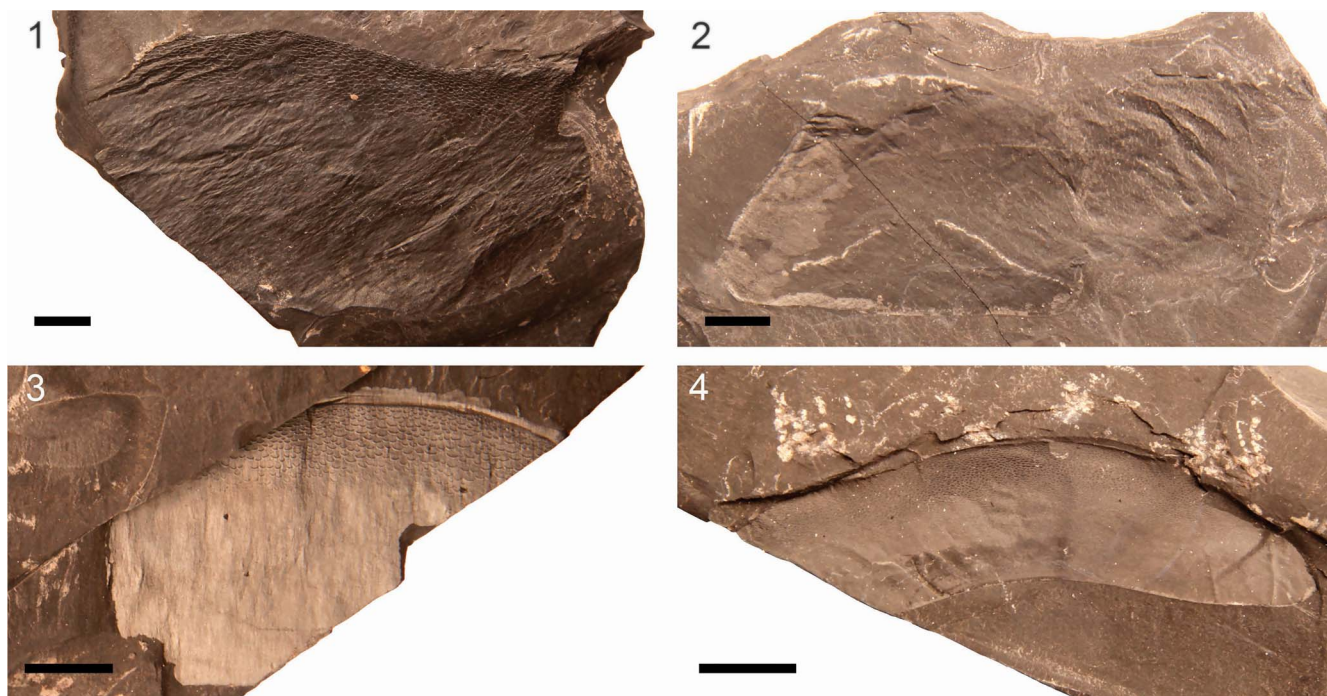


Figure 5. *Erettopterus qujingensis* n. sp. (1) Isolated tergite YN-415009; (2) isolated tergite YN-415007; (3) isolated tergite YN-415010; (4) isolated tergite YN-415008. Scale bars = 10 mm.

Table 2. Denticle dimensions for holotype YN-415005, free ramus of *Erettopterus qujingensis* n. sp. All measurements are in millimeters.

	d1'	d2'	d3'	i1'	i2'	i3'	i4'	i5'
Length	3.1	2.1	2.1	1.0	1.5	1.7	1.5	1.3
Width	1.8	1.1	1.2	0.3	0.8	0.9	1.2	0.7
angled towards	posterior	Posterior	inverse	posterior	posterior	upright	inverse	inverse

11 mm long, 47 mm wide; the third 12 mm long, 48 mm wide; the fourth 12 mm long, 48 mm wide; the fifth 14 mm long, 47 mm wide; and the sixth is 15 mm long, 45 mm wide. The seventh tergite is also partially preserved, with an observed length of 12 mm and an observed width of 34 mm. The anterior 5 mm of each tergite is covered in dense scales.

SWPU: YN-415004 (Fig. 4.2, 4.3). A partial metastoma was preserved in black shale. The only complete external margins preserved are those of the left side, a small portion of the margin of the lower right, and the center of the anterior notch. The overall shape appears to be rhombiovate; preserved length 81 mm, preserved width 80 mm. The anterior third of the metastoma is ornamented with lunate scales.

SWPU: YN-415003 (Fig. 4.4). 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 18.1 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 14.7 mm; the gnathobasic surface is incomplete with a preserved width of 6.1 mm, and the subsequent constriction is 5.3 mm wide at its narrowest point. The full gnathobasic surface is not preserved, but at least 11 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.

SWPU: YN-415006 (Fig. 4.5, 4.6). A pair of prosomal appendage VI paddles, one comprising nine podomeres (including the coxa) with the other preserving only the five distal podomeres. Paddle of *Hughmilleria* type (sensu Tollerton, 1989). The coxa, which preserved only the expanded distal portion, has a preserved length of 10.6 mm, a preserved width of 8.8 mm, and is ornamented with lunule scales. The second podomere is 2.9 mm long, at least 2.9 mm wide, and is broadly triangular in shape; the third podomere is rectangular, being 2.4 mm long and 3.6 mm wide; fourth podomere is incomplete, preserved dimensions 1.5 mm long, 2.1 mm wide; fifth podomere incomplete, preserved dimensions 2.8 mm long, 2.5 mm wide; sixth podomere incomplete, preserved dimensions 4.3 mm long, 2.2 mm wide, expanding to 4.0 mm wide distally, complex articulation visible at proximal podomere joint; seventh podomere 9.8 mm long, 4.5 mm wide proximally, widening evenly to 7.0 mm distally; modified 'podomere' 7a located along the inner paddle margin, triangular in shape, 3.1 mm long, 3.2 mm wide at its base; eighth podomere oval, 9.4 mm in length, 5.7 mm in width; ninth podomere small, 0.7 mm long, 1.1 mm wide, slightly recessed into eighth podomere.

SWPU: YN-415007 (Fig. 5.1). Partial tergite, length 48 mm, preserved width 92.5 mm. Anterior 11 mm ornamented with dense scales.

SWPU: YN-415008 (Fig. 5.2). Partial tergite, length 45.5 mm, preserved width 90 mm.

SWPU: YN-415009 (Fig. 5.3). Partial tergite, length 39 mm, preserved width 53 mm. Smooth articulating facet present across tergite anterior, 2 mm long. Anterior 9 mm of tergite ornamented with dense scales.

SWPU: YN-415010 (Fig. 5.4). Partial tergite, length 15 mm, preserved width 75 mm. Anterior 5 mm of tergite ornamented with dense scales.

Etymology.—The specific epithet is named after the type locality, near Qujing City.

Remarks.—*Erettopterus qujingensis* n. sp. shares a number of characteristics with other well-known *Erettopterus* species, particularly *E. osiliensis* Schmidt, 1883, with the anterior slant to the posterior denticles in the chelicera (Kjellesvig-Waering, 1964). *Erettopterus qujingensis* n. sp. can be distinguished from all other *Erettopterus* species by the shape of the metastoma, which is broader and more rounded than in either *E. osiliensis* or *E. bilobus*, and through the morphology of the ninth podomere of appendage VI, which is larger than in any other known *Erettopterus* species (see Woodward, 1866–1878; Ciarca and Tetlie, 2007; Lomax et al., 2011). The cheliceral morphology of *E. qujingensis* n. sp. is distinct from the pterygotid chelicera described by Wang and Gai (2014) from the Lower Devonian Xitun Formation of Yunnan Province, which exhibits a more robust and highly curved ramus and more differentiation between the cheliceral denticles.

A number of ontogenetic stages of *E. qujingensis* n. sp. are represented within the described material, with the large tergites and metastoma of SWPU: YN-415001 and YN-415002 and metastoma SWPU: YN-415004 representing the largest individuals. These specimens indicate that *E. qujingensis* n. sp. could attain lengths >90 cm.

Family Slimoniidae Novojilov, 1962

Genus *Slimonia* Page, 1856

Type species.—*Slimonia acuminata* Salter, 1856

Slimonia sp.

Figure 6

Diagnosis.—Carapace is long rectangular shape. Oval-shaped lateral eyes are preserved in the anterolateral corners and are elongate. Anterior margin of the carapace is ornamented by two rows of small pustules.

Occurrence.—Upper part of the Yulongsi Formation (Pridolian); south of Liaojiao Mountain, near Qujing City, Yunnan, southwestern China.

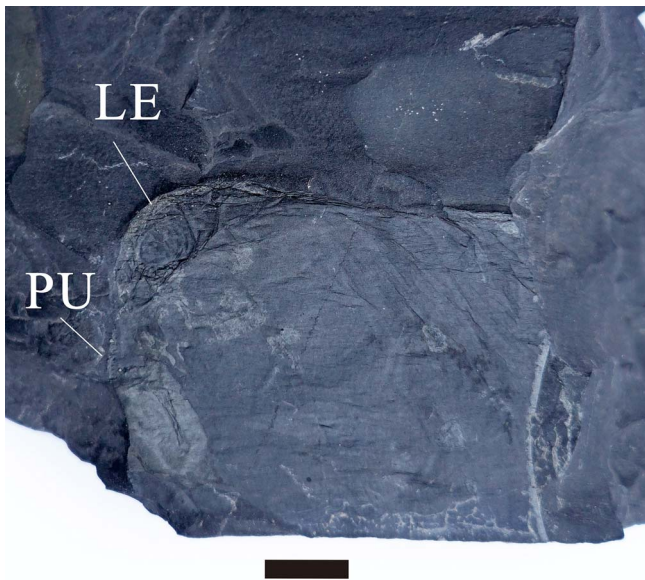


Figure 6. *Slimonia* sp.; partial carapace YN-415011. LE = lateral eye, PU = pustules. Scale bar = 10 mm.

Description.—Partial carapace specimen, preserving right margin, lateral compound eye, and portions of anterior and posterior margins. Carapace 43.7 mm long, preserved width 34.4 mm. Based on curvature of the anterior and posterior margins, the midline of the carapace is preserved, resulting in an estimated carapace width of 44 mm and suggesting a quadrate shape (Tollerton, 1989). The anterior margin of the carapace is ornamented by two rows of small pustules. The lateral eye is positioned anterolaterally,

abutting the carapace margin, and is oval in shape, with a length of 8 mm.

Material.—YN-415011 (Fig. 6).

Remarks.—The occurrence of pustules across the anterior carapace margin is diagnostic of *Slimonia* (Lomax et al., 2011), an assignment further supported by the shape and position of the lateral eyes. The prosomal carapace is markedly shorter than in *Slimonia acuminata*; however, because *Slimonia boliviana* Kjellesvig-Waering, 1973, is only known from its telson (Kjellesvig-Waering, 1973) and the prosomal carapace of *Slimonia dubia* Laurie, 1899, is also quadrate in shape (Laurie, 1899), it is not currently possible to determine whether the specimen described here represents a new species.

Discussion

The co-occurrence of *Erettopterus* and *Slimonia* in the Yulongsi Formation is especially interesting given the two genera also co-occur at the famous Wenlock localities of Lesmahagow, Scotland (Lomax et al., 2011). Finding similar eurypterid faunal compositions across different paleocontinents might suggest that eurypterids formed comparable communities globally. Broadly equivalent Silurian eurypterid faunas already have been documented between the Vernon Formation of New York and the Saaremaa Formation of Estonia (Ciurca and Tetlie, 2007). Comparison of associated faunas also would give insight into the similarities of ecosystem structures across the Silurian world. Like the Lesmahagow fauna, a few jawless fishes are also present in the Yulongsi Formation. The *Erettopterus* and *Slimonia* fossils of Lesmahagow occur in the

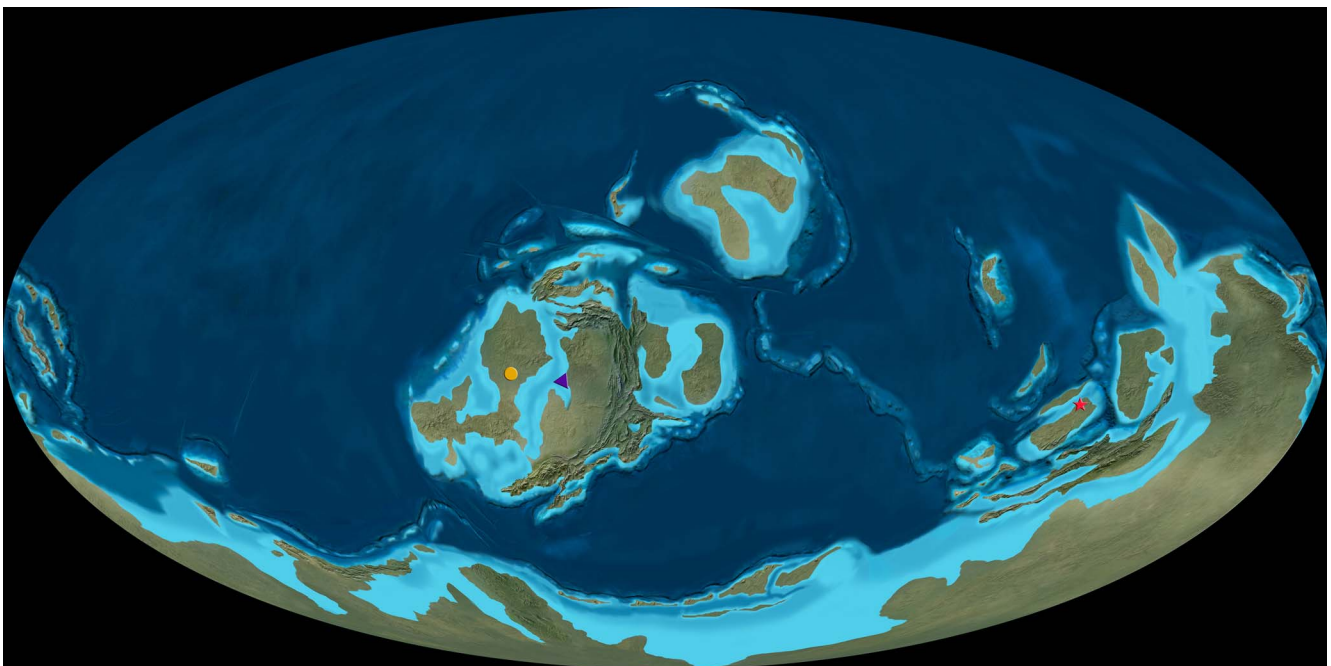


Figure 7. Paleogeographic distribution of Pridolian *Erettopterus* and *Slimonia*. Global paleogeographic reconstruction for the Pridolian (420 Ma) is after Blakey (2020). Circles represent localities of previously described Pridolian *Erettopterus*. Triangle represent localities of previously described Pridolian examples of both *Erettopterus* and *Slimonia* (Tetlie, 2007). Star shows location of the Chinese eurypterids.

Patrick Burn and Kip Burn formations of the Priesthill Group in the *Jamoytius* Horizon and *Ceratiocaris* and *Pterygotus* beds, respectively. The *Jamoytius* Horizon consists predominantly of dark, organic, intensely laminated silt-mudstone (Žigaitė and Goujet, 2012), indicative of an anoxic environment (Earnest, 1998) as part of a shallow, restricted marginal marine setting or possibly a lake (Žigaitė and Goujet, 2012; Clarkson and Harper, 2016). The Yulongsi Formation shows more similarities to the Kip Burn Formation. For example, in the Qujing region, the dominant lithology of the Yulongsi Formation is a dark gray, laminated mudstone comparable to the dark olive-gray mudstone with laminated siltstone of the Kip Burn Formation. Based on sedimentary and tectonic evidence, the Yulongsi Formation also appears to represent a period of gradual transition from a shallow marine to lagoonal environment (Wang, 2000).

All of the 17 previously known species of *Erettopterus* are known from Europe and North America (Tetlie, 2007), as are two of the three *Slimonia* species—*Slimonia boliviana* was described from a single telson from Pojo, Bolivia (Kjellesvig-Waering, 1973). The specimens described here broaden the distribution of *Erettopterus* and *Slimonia* and is the first Gondwanan record of *Erettopterus*. Moreover, the discoveries further support the notion that pterygotoids had superior dispersal abilities, leading to a more cosmopolitan distribution because of 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. 7).

Acknowledgments

Thanks J.A. Dunlop and two anonymous reviewers for helpful comments on manuscript. ZHM thanks L. Fu for help with figures and D. Wang (NIGPAS) for useful suggestions in the early stages of the manuscript. This work was supported by the National Natural Science Foundation of China (No. 41972120; 42172129), by the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (No. 173131), and China Postdoctoral Science Foundation (No. 2021M702720).

References

- Anderson, R.P., McCoy, V.E., McNamara, M.E., and Briggs, D.E.G., 2014, What big eyes you have: the ecological role of giant pterygotid eurypterids: *Biology Letters*, v. 10, p. 387–393.
- Blakey, R.C., 2020, 600 Ma to present: <https://deeptimemaps.com/>.
- Braddy, S.J., Poschmann, M., and Tetlie, O.E., 2008, Giant claw reveals the largest ever arthropod: *Biology Letters*, v. 4, p. 106–109.
- Burmeister, H., 1843, Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst systematische Uebersicht aller Seitherbeschriebenen Arten. Berlin, Georg Reimer, 147 p.
- Chang, A.-C., 1957, On the discovery of the Wenlockian *Eurypterus* fauna from South China: *Acta Palaeontologica Sinica*, v. 5, p. 446–450. [in Chinese with English summary]
- Chlupáč, I., 1994, Pterygotid eurypterids (Arthropoda, Chelicerata) in the Silurian and Devonian of Bohemia: *Journal of the Czech Geological Society*, v. 39, 147–162.
- Ciurca, S.J., and Tetlie, O.E., 2007, Pterygotids (Chelicerata; Eurypterida) from the Silurian Vernon Formation of New York: *Journal of Paleontology*, v. 81, p. 725–736.
- Clarke, J.M., and Ruedemann, R., 1912, The Eurypterida of New York: *New York State Museum Memoir*, v. 14, p. 1–439.
- Clarkson, E., and Harper, D., 2016, Silurian of the Midland Valley of Scotland and Ireland: *Geology Today*, v. 32, 195–200.
- Earnest, L. C., 1998, Sedimentary Environments and Biofacies of the Silurian Inlier at Lesmahagow Midland Valley of Scotland: Edinburgh, University of Edinburgh Press, 374 p.
- Fang, Z.-J., Cai, C.-Y., and Wang, Y., 1994, New progress in the study of the Silurian Devonian boundary in Qujing, eastern Yunnan: *Journal of Stratigraphy*, v. 18, p. 81–90. [in Chinese with English summary]
- Grabau, A.W., 1920, A new species of *Eurypterus* from the Permian of China: *Bulletin of the Geological Survey of China*, v. 2, p. 61–67.
- Hao S.-G., Xue J.-Z., Liu Z.-F., and Wang D.-M., 2007, *Zosterophyllum* Penhallow around the Silurian-Devonian boundary of northeastern Yunnan, China: *International Journal of Plant Sciences*, v. 168, p. 477–89.
- Hughes, E.S., and Lamsdell, J.C., 2020, Discerning the diets of sweep-feeding eurypterids: assessing the importance of prey size to survivorship across the Late Devonian mass extinction in a phylogenetic context: *Paleobiology*, v. 47, p. 271–283.
- Kjellesvig-Waering, E.N., 1961, The Silurian Eurypterida of the Welsh Borderland: *Journal of Paleontology*, v. 35, p. 789–835.
- Kjellesvig-Waering, E.N., 1964, A synopsis of the family Pterygotidae Clarke and Ruedemann, 1912 (Eurypterida): *Journal of Paleontology*, v. 38, p. 331–361.
- Kjellesvig-Waering, E.N., 1973, A new Silurian *Slimonia* (Eurypterida) from Bolivia: *Journal of Paleontology*, v. 47, p. 549–550.
- Lamsdell, J.C., and Braddy, S.J., 2010, Cope's Rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates: *Biology Letters*, v. 6, p. 265–269.
- Lamsdell, J.C., and Legg, D.A., 2010, An isolated pterygotid ramus (Chelicerata: Eurypterida) from the Devonian Beartooth Butte Formation, Wyoming: *Journal of Paleontology*, v. 84, p. 1206–1208.
- Lamsdell, J.C., and Selden, P.A., 2017, From success to persistence: identifying an evolutionary regime shift in the diverse Paleozoic aquatic arthropod group Eurypterida, driven by the Devonian biotic crisis: *Evolution*, v. 71, p. 95–110.
- Lamsdell, J.C., Briggs, D.E.G., Liu, H.P., Witzke, B.J., and McKay, R.M., 2015, The oldest described eurypterid: a giant Middle Ordovician (Darrwilian) megalograptid from the Winneshiek Lagerstätte of Iowa: *BMC Evolutionary Biology*, v. 15, 169. <https://doi.org/10.1186/s12862-015-0443-9>.
- Laurie, M., 1899, On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills: *Transactions of the Royal Society of Edinburgh*, v. 39, p. 575–589.
- Lin, B.-Y., Guo, D.-H., and Wang, X.-F., 1982, The Silurian system of China, in *Academy of Geological Sciences, ed., An Outline of the Stratigraphy in China*: Beijing, Geological Publishing House, p. 139–164. [in Chinese with English summary]
- Lomax, D.R., Lamsdell, J.C., and Ciurca, S.J., Jr., 2011, A collection of eurypterids from the Silurian of Lesmahagow collected pre 1900: *The Geological Curator*, v. 9, p. 331–348.
- McCoy, V.E., Lamsdell, J.C., Poschmann, M., Anderson, R.P., and Briggs, D.E.G., 2015, All the better to see you with: eyes and claws reveal the evolution of divergent ecological roles in giant pterygotid eurypterids: *Biology Letters*, v. 11, 20150564. <https://doi.org/10.1098/rsbl.2015.0564>.
- Miller, R.F., 2007, *Pterygotus anglicus* Agassiz (Chelicerata: Eurypterida) from Atholville, Lower Devonian Campbellton Formation, New Brunswick, Canada: *Palaeontology*, v. 50, p. 981–999.
- Novojilov, N.I., 1962, Order Eurypterida: Arthropoda, Tracheata, Chelicerata: *Fundamentals of Paleontology*, v. 9 p. 617–644.
- Page, D., 1856, *Advanced Text-book of Geology*, 1st edition. Edinburgh and London, Blackwood, 326 p.
- P'an, J., Wang, S.-T., Gao, L.-D., and Hou, J.-P., 1978, Continental Devonian of South China, in *Institute of Geology and Mineral Resources of the Chinese Academy of Geological Sciences, ed., Proceedings of the Devonian Conference in South China*: Beijing, Geological Publishing House, p. 240–269. [in Chinese]
- Peng, H.-P., Liu, F., and Zhu, H.-C., 2016, Revision of the Lower and Middle Devonian lithostratigraphy in Qujing and Zhanyi, eastern Yunnan Province, China: *Journal of Stratigraphy*, v. 40, p. 319–334.
- Poschmann, M., and Tetlie, O.E., 2006, On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 5. Rare and poorly known eurypterids from Willwerath, Germany: *Paläontologische Zeitschrift*, v. 80, p. 325–343.
- Rong, J.-Y., Wang, Y., Zhan, R.-B., Fan, J.-X., Huang, B., Tang, P., Li, Y., Zhang, X.-L., Wu, R.-C., Wang, G.-X., and Wei, X., 2019, Silurian integrative stratigraphy and timescale of China: *Science China Earth Sciences*, v. 62, p. 89–111. [in Chinese with English summary]
- Salter, J.W., 1856, On some new Crustacea from the uppermost Silurian rocks: *Quarterly Journal of the Geological Society of London*, v. 12, p. 26–34.

- Salter, J.W., 1859, Description of the species of *Pterygotus*, in Huxley, T.H., and Salter, J.W., On the anatomy and affinities of the genus *Pterygotus* and description of new species of *Pterygotus*: Memoirs of the Geological Survey of the United Kingdom, Monograph 1, p. 37–105
- Schmidt F., 1883, Die Crustaceenfauna der Eurypterenschichten von Rootzikull auf Oesel: Memoires l'Academie Imperiale des Sciences de St.-Petersbourg, ser. VII, v. 31, p. 28–88.
- Tetlie, O.E., 2007, Distribution and dispersal history of Eurypterida (Chelicerata): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 252, p. 557–574.
- Tetlie, O.E., and Briggs, D.E.G., 2009, The origin of the pterygotid eurypterids (Chelicerata: Eurypterida): Palaeontology, v. 52, p. 1141–1148.
- Tetlie, O.E., Selden, P.A., and Ren, D., 2007, A new Silurian eurypterid (Arthropoda: Chelicerata) from China: Palaeontology, v. 50, p. 619–625.
- Tian, J.J., Zhu, H.C., Huang, M., and Liu, F., 2011, Late Silurian to Early Devonian palynomorphs from Qujing, Yunnan, southwest China: Acta Geologica Sinica, v. 85, p. 559–568. [English edition]
- Tollerton, V.P., 1989, Morphology, taxonomy, and classification of the order Eurypterida Burmeister, 1843: Journal of Paleontology, v. 63, p. 642–657.
- Wang, B., and Gai, Z.K., 2014, A sea scorpion claw from the Lower Devonian of China (Chelicerata: Eurypterida): Alcheringa, v. 38, p. 296–300.
- Wang, C.-Y., 1980, Upper Silurian conodonts from Qujing, Yunnan: Acta Palaeontologica Sinica, v. 19, p. 369–378. [in Chinese with English summary]
- Wang, H., Dunlop J., Gai Z.-K., Lei X., Jarzembowski E.A., and Wang B., 2021, First mixopterid eurypterids (Arthropoda: Chelicerata) from the lower Silurian of south China: Science Bulletin, v. 66, p. 2277–2280.
- Wang J.-Q., 2000, Age of the Yulongsi Formation and the Silurian-Devonian Boundary in East Yunan: Journal of Stratigraphy, v. 2, p. 145–150. [in Chinese with English summary]
- Waterston, C.D., 1964, Observations on pterygotid eurypterids: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 64, p. 9–33.
- Woodward, H. 1866–1878, Monograph of the British fossil Crustacea belonging to the order Merostomata. Parts I–V: Palaeontographical Society Monographs, v. 19, 22, 25, 26, 32, p. 1–263.
- Wu, H.-J., 1977, Comments on new genera and species of Silurian–Devonian trilobites in southwest China and their significance: Acta Palaeontologica Sinica, v. 1, p. 95–117. [in Chinese with English summary]
- Yang, W.-X., and Li G.-X., 1978, Some questions on the Devonian system in eastern Yunnan, in Institute of Geology and Mineral Resources of the Chinese Academy of Geological Sciences, ed., Proceedings of the South China Devonian Conference: Beijing, Geological Publishing House, p. 167–171. [in Chinese with English summary]
- Žigaitė, Ž., and Goujet, D., 2012, New observations on the squamation patterns of articulated specimens of *Loganellia scotica* (Traquair, 1898) (Vertebrata: Thelodonti) from the Lower Silurian of Scotland: Geodiversitas, v. 34, p. 253–270.
- Zong, R.-W., Liu, Q., Wei, F., and Gong, Y.-M., 2017, Fentou Biota: a Llandoverian (Silurian) shallow-water exceptionally preserved biota from Wuhan, central China: Journal of Geology, v. 125, p. 469–478.

Accepted: 20 March 2022