

The first documentation of an Ordovician eurypterid (Chelicerata) from China

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Abstract.—An early form of eurypterids (Chelicerata), *Archopterus anjiensis* n. gen. n. sp., is described from the uppermost Ordovician Wenchang Formation of Anji County, Zhejiang Province, South China. It is the earliest record of eurypterids in China and likely the oldest representative of the Adelophthalmidae. The species, represented by a single specimen, is diagnosed by a ventrally preserved prosoma with a parabolic carapace, *Hughmilleria*-type prosomal appendages, a short vase-shaped metastoma, and a three-segmented type A (female) genital appendage. The specimen is preserved, together with diverse sponges, graptolites and occasional nautiloids, in a 10 m thick shale of marine deep-water setting. This finding extends the stratigraphic range of adelophthalmids from the previously recorded early Silurian into the Late Ordovician (some 10 million years older) and supports an earlier cryptic phase of eurypterid evolution in Gondwana.

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Introduction

The eurypterids are an extinct group of Paleozoic (specifically from Middle Ordovician to late Permian) aquatic predatory chelicerates. Some forms attained giant size (2.5 m long; Lamsdell and Braddy, 2010), but most were less than 50 cm long. Some 250 eurypterid species have been recovered from marine (often inshore) to freshwater settings. They are rarely preserved as fossils due to their unmineralized cuticle, but they do occur in large numbers in some Siluro-Devonian Konservat-Lagerstätten. Eurypterids attained their maximum diversity during the late Silurian and Early Devonian (Plotnick, 1999).

Ordovician eurypterids are extremely rare, so any reported occurrence is of great significance to understanding their early evolutionary history. Many reported species from the Ordovician of New York State are particularly dubious (see Braddy et al., 2004; Tollerton, 2004), being either misidentified fossils or pseudofossils. Three equivocal specimens from the Upper Ordovician of Shanxi Province (S. Yanbin, personal communication, 2002) were referred to ?Eurypterida indet. (cf. *Onychopterella*) or possibly nautiloids (Braddy et al., 2004). Unfortunately, these dubious fossils seem to have been lost, while the original report was not accompanied by figures and descriptions, so no restudy and further assignments are possible.

To date, only 12 species of Ordovician eurypterids are known in the world. Most of them are the large predatory

forms of the Megalograptidae, including *Pentecopecterus decorahensis* Lamsdell et al., 2015, *Echinognathus clevelandi* Walcott, 1882, *Eocarcinosoma batrachophthalmus* Caster and Kjellesvig-Waering, 1964, *Megalograptus alveolatus* Shuler, 1915, *M. welchi* Miller, 1874, *M. ohioensis* Caster and Kjellesvig-Waering, 1955, *M. shideleri* Caster and Kjellesvig-Waering, 1964, and *M. williamsae* Caster and Kjellesvig-Waering, 1964. The others are smaller forms, including *Orcanopterus manitoulinensis* Stott et al., 2005, *Brachyopterus stubblefieldi* Størmer, 1951, *Onychopterella augusti* Braddy, Aldridge, and Theron, 1995, and *Paraeurypterus anatoliensis* Lamsdell, Hoşgör, and Selden, 2013.

The earliest known eurypterid, *Pentecopecterus decorahensis* Lamsdell et al., 2015 from the Darrivilian of Iowa, was described as a megalograptid, but it lacks cercal blades, so it is more likely to be an intermediate between the megalograptids and the other Eurypterina. Lamsdell et al. (2015) resolved megalograptids in a more derived position than most workers (e.g., Tetlie, 2007), dragging down the ghost range of all eurypterid lineages into the Early Ordovician. Lamsdell et al. (2013) described *Paraeurypterus anatoliensis* from the Upper Ordovician (Katian) of southeast Turkey and regarded it as an intermediate between the Dolichopteridae and Eurypteridae. They also inferred long ghost ranges, and a “missing” Ordovician fossil record for eurypterids, proposing that they actually originated in Gondwana and radiated to Laurentia and Baltica in the Late Ordovician and early Silurian, a hypothesis adopted to explain their sudden diverse appearance in Europe and North America.

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Chinese eurypterids are known primarily from Silurian strata, with the mixopterid *Terropterus xiushanensis* from the Llandovery of Xiushan County, Chongqing Municipality, and Wuhan, Hubei Province (Wang et al., 2021). *Hughmilleria wangi* was recorded by Tetlie et al. (2007) from the late Llandovery of Hunan Province, to which the specimens figured by Wang et al. (1988) from the same horizon in western Hunan Province may also be related. From the Wenlock of Xintan, Hubei Province, *Eurypterus loi*, *E. styliformis*, and *E. yangi* were described by Chang (1957) on the basis of four specimens. It seems likely that these species are at least partly synonymous, but this material seems to have been lost, and they must be considered dubious (Tetlie, 2007). A pterygotid, *Erettopterus qujingensis*, and a slimoniid, *Slimonia* sp., were recently described by Ma et al. (2022) from the upper Silurian Yulongsi Formation of Yunnan Province. *Malongia mirabilis* (Wang et al., 2022), *Pterygotus wanggaii* (Ma et al., 2023), *Parahughmilleria fuea* (Ma et al., 2023), and an indeterminate pterygotid (Wang and Gai, 2014) were also reported from the Lower Devonian Xiaishancun Formation of Yunnan Province. *Adelophthalmus chinensis* was reported by Grabau (1920) from the Early Permian of Hebei Province.

In this paper, we describe a new eurypterid from the latest Ordovician (Hirnantian) Anji Biota of Zhejiang Province, South China (Fig. 1). Although some details are lacking in the single specimen available, there is sufficient information to support an assignment to the Adelophthalmidae, which extends their stratigraphic range back by some 10 million years.

Geological setting and preservation

The eurypterid was recovered from a 10 m thick sponge-bearing sequence of dark mudstone at locality Tianfucun in Anji County, Zhejiang Province, South China (Botting et al., 2017). This interval yielding the Anji Biota is dated by abundant graptolites to an age of the latest Ordovician *Metabolograptus persculptus* Biozone (Muir et al., 2020, 2021), i.e., right after the Hirnantian mass extinction (444 Ma). In the dark mudstone, sponges are exceptionally abundant and diverse, including remarkable early representatives of modern deep-sea lineages such as rossellids (Botting et al., 2020) and euplectellid hexactinellids (Botting et al., 2022), associated with abundant graptolites, occasional nautiloids, and rare arthropods. Judging from evidence from previous paleogeographic reconstructions and the tectonic setting, the Anji area represented a localized deep-water basin with an estimated depth of several hundred meters (Botting et al., 2018).

The preservation of sponges (and, potentially, the eurypterid) in the Anji Biota has been proposed to be through partial silicification of carbonaceous soft tissues, with early pyritization and subsequent pyrite dissolution (Wu et al., 2022). This was due to burial of the fossils by collapsing anoxic nepheloid layers (Botting et al., 2018; Wu et al., 2022) followed by rapid reoxygenation of the surface sediment as the temporary benthic anoxia dispersed. The absence of any burrowing, or of typical benthic fossils such as brachiopods and trilobites, is consistent with a low-oxygen but survivable (for sponges) environment on the

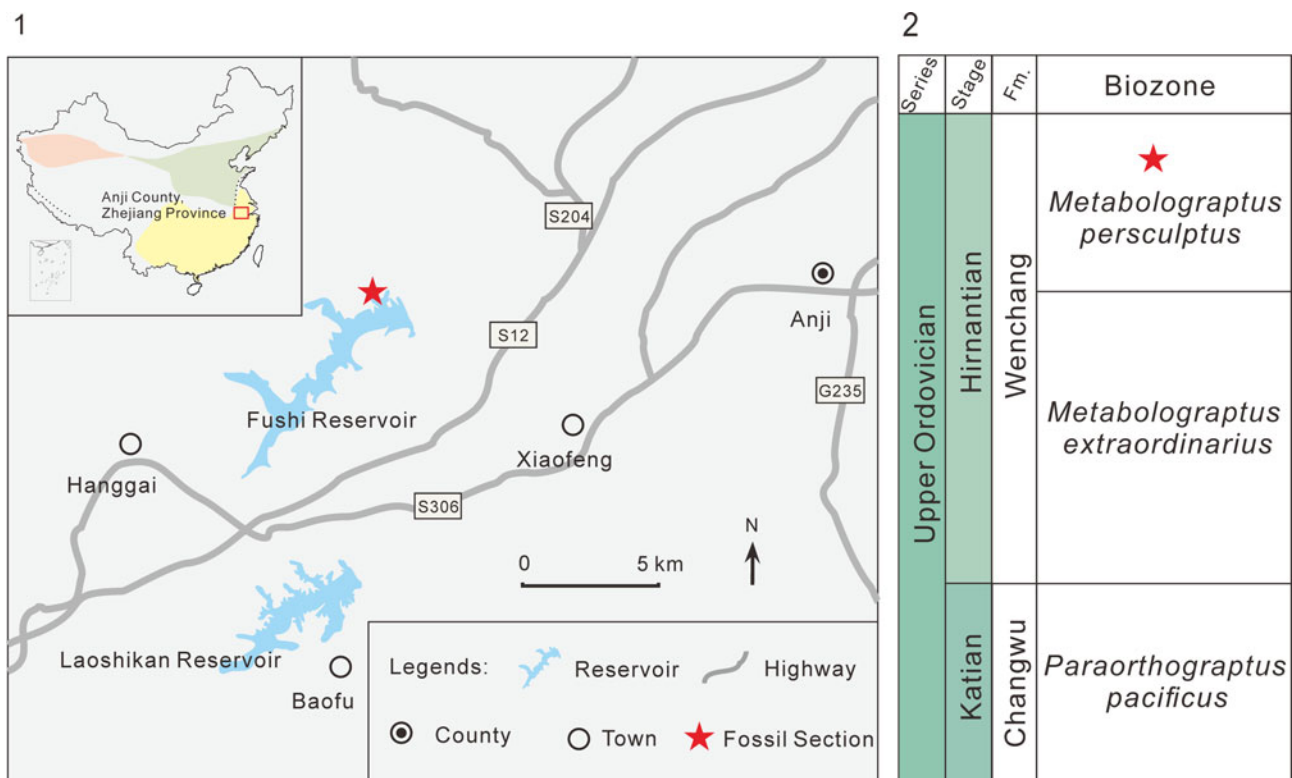


Figure 1. Regional map and stratigraphy. (1) Map of the Fushi Reservoir area (Anji County, Zhejiang Province, South China) showing location of the Tianfucun section where *Archopteris anjiensis* n. gen. n. sp. was recovered. (2) Lithostratigraphy and biozone showing the approximate position of *Archopteris anjiensis* n. gen. n. sp. in black mudstones of the Wenchang Formation.

seafloor, where oxygenation was too low for animals with higher metabolic requirements. The eurypterid was therefore probably living within the water column and entrained within a collapsing nepheloid layer. This is the only eurypterid specimen recovered among thousands of complete sponges, implying that it was either a very rare member of the community or an accidental immigrant into this environment.

Materials and methods

The eurypterid specimen is preserved in weathered (orange color) carbon in a dark gray, well-laminated mudstone matrix (Fig. 2). Eurypterid cuticle is preserved as orange films, but in places it has a shadowy appearance, and details are comparatively poor. Photographs were taken using a Nikon D810 camera under normal and polarized light, which helped resolve the appendages. Image processing was carried out with Adobe Photoshop CC2019 to adjust contrast and color, and plates and interpretive drawing (Figs. 2, 3) were prepared with CorelDRAW X7. Morphological terminology follows Wills (1964), for the genitalia, and Tollerton (1989), with modifications

(i.e., carapace and metastoma shapes; see the following), illustrating the problem of “forcing” terminology into “boxes” on the basis of a limited number of geometric measurements.

Repository and institutional abbreviation.—The specimen used in this study is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Nanjing, China, under the repository number NIGP 164906.

Systematic paleontology

- Subphylum Chelicerata Heymons, 1901
- Order Eurypterida Burmeister, 1843
- Suborder Eurypterina Burmeister, 1843
- Family Adelophthalmidae Tollerton, 1989
- Genus *Archopterus* new genus

Type and only species.—*Archopterus anjiensis* n. gen. n. sp.

Diagnosis.—As for the type species by monotype.

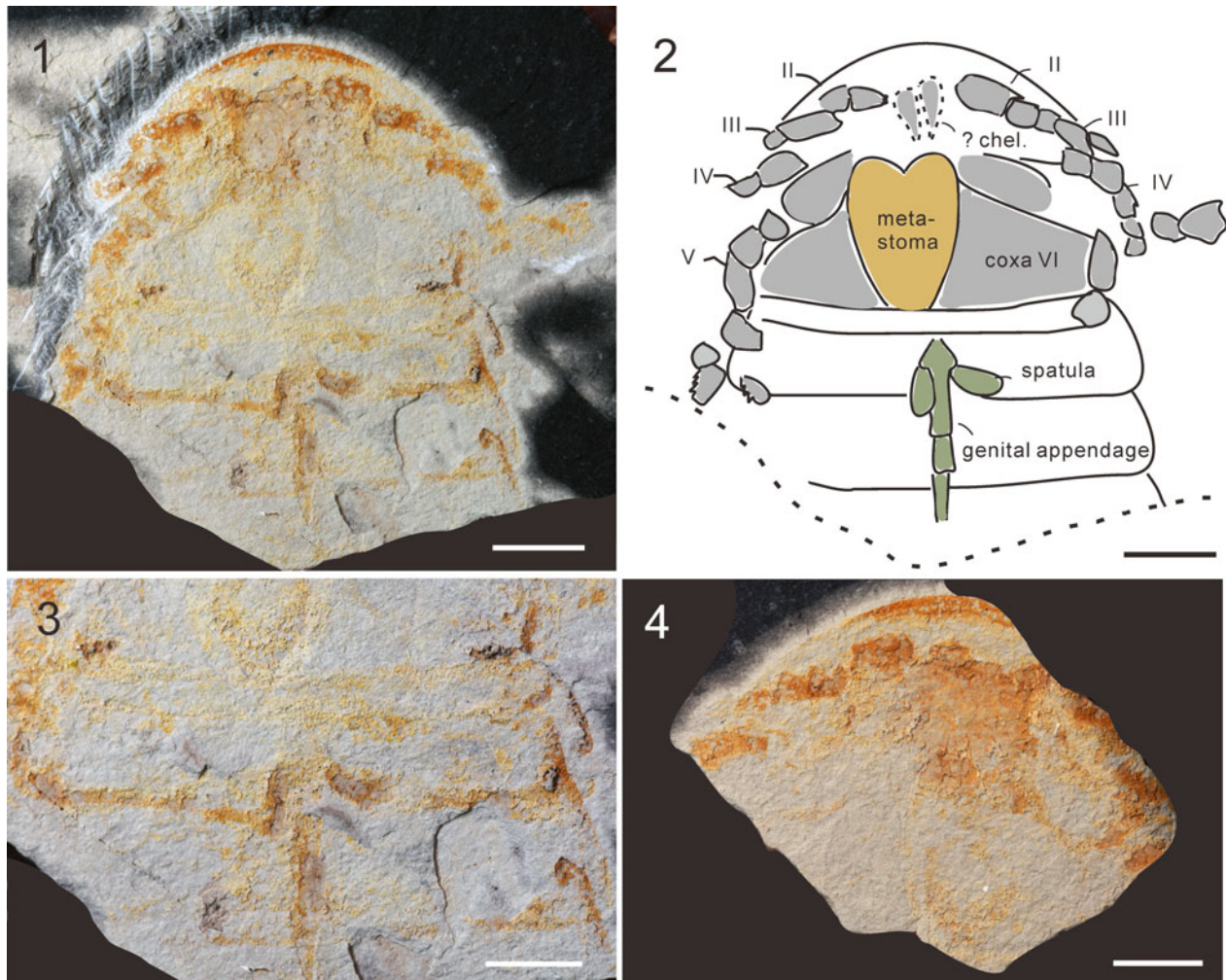


Figure 2. *Archopterus anjiensis* n. gen. n. sp. (1) Entire specimen, holotype (NIGP 164906). (2) Line drawing of the entire specimen. (3) Close-up of type A genital appendage. (4) Counterpart. Scale bars = 10 mm.

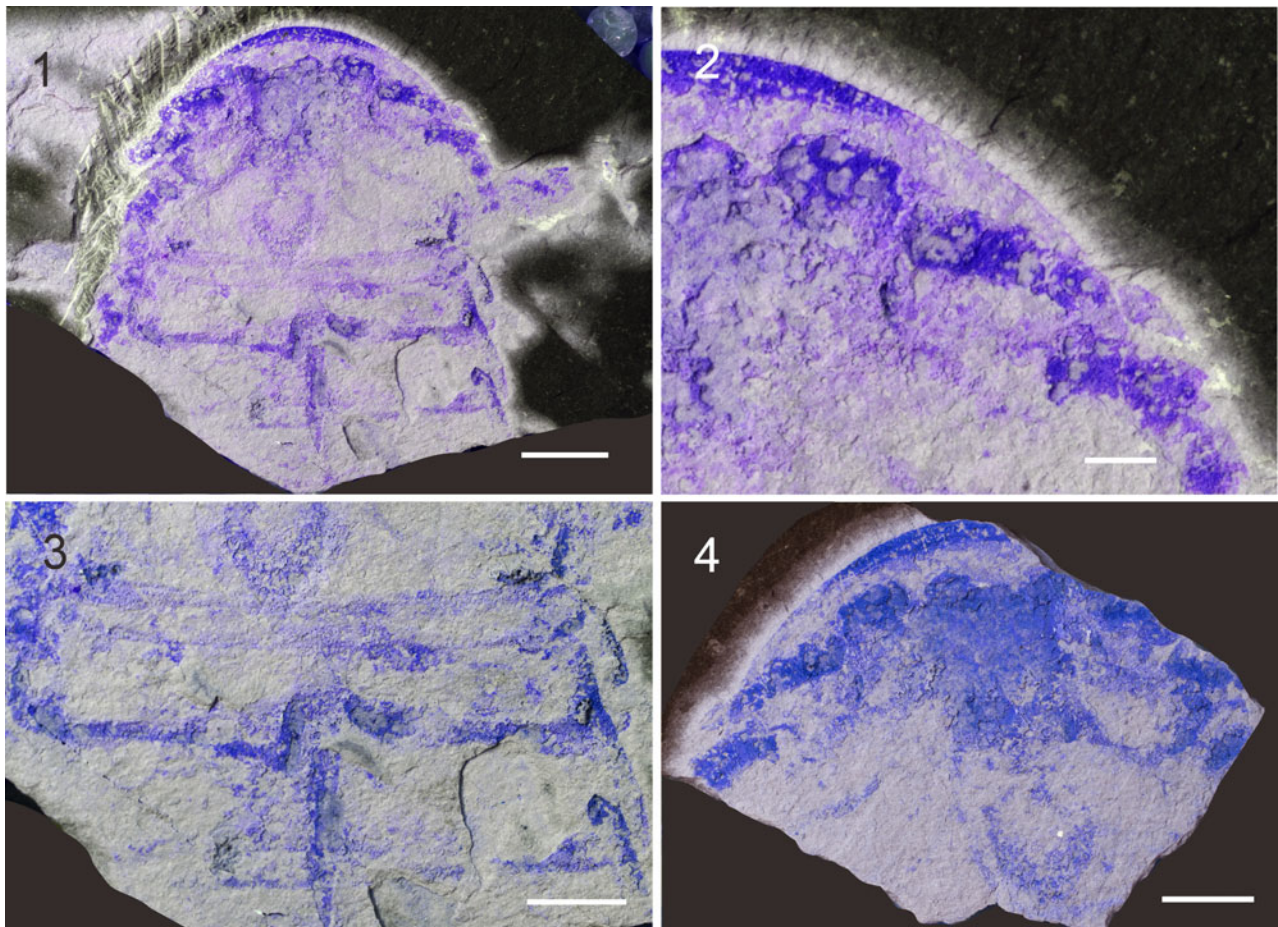


Figure 3. Enhanced image of *Archopterus anjiensis* n. gen. n. sp., the original color of the fossil adjusted to blue to improve contrast. (1) Entire specimen, holotype (NIGP 164906). (2) Close-up of appendage. (3) Close-up of type A genital appendage. (4) Close-up of metastoma (counterpart). (1, 3, 4) Scale bars = 10 mm; (2) scale bar = 2 mm.

Etymology.—Genus name from the Latin prefix *arch-*, meaning “ancient,” and *-opterus*, a common suffix for eurypterids, meaning “wing.”

Remarks.—With a parabolic-shaped carapace and *Hughmilleria*-type prosomal appendages, *Archopterus* has an intermediate Adelophthalmid–hughmilleriid affinity. Most characters are consistent with the Adelophthalmidae Kjellesvig-Waering, 1951, such as the carapace shape, spinosity of the appendages, and metastoma shape. Adelophthalmids were considered to have appeared in Baltica in the Silurian, with basal forms evolving in the Early Devonian of Euramerica (Tetlie, 2007). The family includes *Adelophthalmus* Jordan and von Mayer, 1854, and the basal forms *Bassipterus* Kjellesvig-Waering and Leutze, 1966, *Esyslopterus* Tetlie and Poschmann, 2008, *Nanahughmilleria* Kjellesvig-Waering, 1961, *Parahughmilleria* Kjellesvig-Waering, 1961, *Pittsfordipterus* Kjellesvig-Waering and Leutze, 1966, and *Unionopterus* Chernyshev, 1948 (see Braddy et al., 2021 for review). Recently, *Pruemopterus* has also been added to the family (Poschmann, 2020). With no spurs present on its abdominal segments, *Archopterus* is easily distinguished from *Adelophthalmus* (Størmer, 1955). Among basal forms, *Archopterus* is similar to *Parahughmilleria* in bearing a

complex three-segmented type A genital appendage, large spatula, and vase-shaped metastoma with an anterior notch, but *Parahughmilleria* has reduced appendage spinosity, with isolated spines in places and crenulated distal podomeres, larger epimera and genital spatulae, and coarser ornament. *Archopterus* is distinguished from *Nanahughmilleria* by the fact that the former has larger spatula, less spinosity on its appendages, and relatively larger size. *Bassipterus* is a rare basal form, with appendages II–V of *Hughmilleria* type with paired ventral spines on each podomere and the paddle bearing a serrated outer edge; these features are also similar to *Archopterus*, but *Bassipterus* has a more-complex genital appendage, especially in the second and third joints. Bearing a parabolic carapace, *Archopterus* can also be easily distinguished from other basal forms, such as *Esyslopterus*, *Unionopterus*, and *Pruemopterus*.

Archopterus anjiensis new species
Figures 2, 3

2017 unnamed hughmilleriid; Botting et al., fig. 2a.

Holotype.—NIGP 164906, Nanjing Institute of Geology and Palaeontology, CAS, China.

Diagnosis.—Adelophthalmid with a parabolic carapace, *Hughmilleria*-type prosomal appendages, vase-shaped metastoma, and three-segmented type A (female) genital appendage.

Occurrence.—Hirnantian (*Metabolograptus persculptus* Biozone) of the Wenchang Formation of Tianfucun, Anji County, Zhejiang Province, South China.

Description.—The carapace is 20 mm long and 28.8 mm wide (length/width ratio 0.69), with a lateral angle of 90° (i.e., “subquadrate” cf. Tollerton, 1989). The anterior margin is more curved than a typical subquadrate carapace, showing more of a parabolic shape. A narrow (ventral) marginal rim, 1.4 mm wide anteriorly, narrowing to 0.6 mm laterally, surrounds the anterior carapace. The doublure is unknown, although large scales are apparent bordering the marginal rim. A possible robust chelicera, basis square, 1.3 mm wide, fingers 1.3 mm long, occurs near the anterior midline. Partial remains of prosomal appendages II–VI are preserved, mainly on the left side of the specimen. Appendages II and III, of *Hughmilleria* type, are folded inward on the left side, overlying the posterior appendages, obscuring details. Appendage II is 1.5 mm wide, with the following (*preserved) lengths: II-1 (coxa), 1.9 mm; II-2, 2.4 mm; II-3, 1.1* mm. Appendage III is best preserved (unfolded) on the right side: III-1 (coxa) and III-2 are obscured, III-3 length 2.9 mm, width 1.9 mm, paired distal spines, 1.3–1.6 mm long; III-4 length 2.6 mm, width 1.9 mm, with a tiny anterior spine 0.9 mm long preserved; III-5 length 1.2 mm, width 1.7 mm, with paired tiny spines 0.7 mm long; III-6 length 1.5 mm, width 1.3 mm. Appendage IV is obscured on the left side, but podomeres 3–6 are best preserved on the right side: IV-3 is 1.5 mm long and wide; IV-4 is 2.5 mm long and 1.4 mm wide; IV-5 is 2.5 mm long and 1.3 mm wide; IV-6 is 2.5 mm long and 1.8 mm wide, with a short spur or spine distally. Appendage V is long, projecting posteriorly on the left side: V-1 (coxa) is large, length 7 mm, distal width 4 mm, the anterior gnathobase curved anteriorly; V-2 is 2.7 mm long, 2.8 mm wide; V-3 is 2.8 mm long, width uncertain; V-4 is 2.5 mm long, 2.1 mm wide; V-5 to V-9 uncertain, as disarticulated. Appendage VI may curl over the genital operculum on the left side and projects laterally on the right side, with only disarticulated podomeres.

A slightly displaced metastoma is faintly preserved, its anterior margin with a notch. The shape is classed as “vase shaped” on the basis of Tollerton (1989, fig. 5), with a possible flatter posterior margin.

The genital operculum is 8 mm long, each opercular lobe 15 mm wide, preserving large anterior (3 mm long), median, and posterior (4.8 mm long) plates. The genital appendage is interpreted as being a type A (female; Braddy and Dunlop, 1997, but see Kamenz et al., 2011); incompletely preserved part is 10 mm long, composed of three segments; deltoid plates are apparent anterior to the genital appendage; large spatulae can be seen. Two paired Blattfüsse are preserved, at least the second unfused, probably also the first (obscured by appendage). Large V-shaped scales are evident in places.

The first opisthosomal segment is reduced, approximately half the length of the others. The metasoma and telson are unknown. The eurypterid is estimated to have had a total body length of 15 cm.

Etymology.—The species is named after Anji County, where the type specimen was discovered.

Remarks.—Some obvious characters, such as the specific spatula size, can distinguish *A. anjiensis* from its most similar relatives, such as *Parahughmilleria hefteri* (Størmer, 1973) and *Nanahughmilleria norvegica* (Kiær, 1911).

Discussion

A. anjiensis represents the oldest adelophthalmid and extends the stratigraphic range of this family to Late Ordovician (by about ten million years), making Adelophthalmidae the longest-living eurypterid family (Ordovician to Permian). The new fossil also represents the first unequivocal Ordovician and the oldest eurypterid recorded in China, adding new knowledge to early evolution of eurypterids in Gondwana.

Associated with diverse sponges, *Archopterus anjiensis* was found in a deep-water environment of several hundred meters deep. This occurrence, along with some Ordovician eurypterids—e.g., *Megalograptus* from a normal marine environment (Caster and Kjellesvig-Waering, 1964)—may indicate that some early eurypterids favored a relatively deeper-water environment than their post-Ordovician relatives, although it is possible that this was a single vagrant individual washed out from more typical shallow-water environments. In addition, this occurrence indicates that adelophthalmids have been found in the widest range of habitats of all eurypterid groups.

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Declaration of competing interests

The authors declare that they have no competing interests.

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