A Taxonomic Revision of *Dongfangaspis qujingensis* from the Lower Devonian of Qujing, Yunnan Province

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Abstract

The affinity of 'Dongfangaspis qujingensis' , initially assigned to Dongfangaspis but later to Laxaspis, has long been controversial. However, the taxonomical revision raises a new problem of junior homonym since the type species of Laxaspis is L. qujingensis. Here, we describe some new materials of 'Dongfangaspis qujingensis' and Damaspis vartus from the Xishancun Formation (early Lochkovian, Early Devonian) in Qujing, Yunnan Province. 'Dongfangaspis qujingensis' strikingly resembles Damaspis vartus in the slightly longer headshield, bifurcated ends of the lateral transverse canals, unconnected V-shaped posterior supraorbital canals, and at least seven pairs of lateral transverse canals issuing from the lateral dorsal canal. These similarities indicate that 'D. qujingensis' is more suggestive of Damaspis than Dongfangaspis and Laxaspis. Therefore, we propose to remove 'Dongfangaspis qujingensis' from Laxaspis to Damaspis. The new specimens of Damaspis vartus reveal five long lateral transverse canals on the right side, corroborating that the asymmetric sensory canal system in the holotype is the intraspecific variation.

Full Text

Preamble

A Taxonomical Revision of 'Dongfangaspis qujingensis'from the Lower Devonian of Qujing, Yunnan Province

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Abstract

The taxonomic affinity of 'Dongfangaspis qujingensis' , initially assigned to *Dongfangaspis* but later transferred to *Laxaspis*, has long been controversial. However, this revision created a new problem of junior homonymy, as the type species of *Laxaspis* is *L. qujingensis*. Here we describe new materials of '*Dongfangaspis qujingensis*' and *Damaspis vartus* from the Xishancun Formation (early Lochkovian, Early Devonian) in Qujing, Yunnan Province. '*Dongfangaspis qujingensis*' strikingly resembles *Damaspis vartus* in possessing a slightly longer headshield, bifurcated ends of the lateral transverse canals, unconnected V-shaped posterior supraorbital canals, and at least seven pairs of lateral transverse canals issuing from the lateral dorsal canal. These similarities indicate that '*D. qujingensis*' shows greater affinity to *Damaspis* than to either *Dongfangaspis* or *Laxaspis*. Therefore, we propose removing '*Dongfangaspis qujingensis*' from *Laxaspis* and reassigning it to *Damaspis*. New specimens of *Damaspis vartus* reveal five long lateral transverse canals on the right side, corroborating that the asymmetric sensory canal system in the holotype represents intraspecific variation.

Key words: Qujing, Yunnan; Lower Devonian; Xishancun Formation; *Damaspis*, Polybranchiaspidae, Galeaspids

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1 Introduction

The Polybranchiaspidae represents the most diversified galeaspid family, comprising nine genera: *Bannhuanaspis*, *Dongfangaspis*, *Polybranchiaspis*, *Laxaspis*, *Damaspis*, *Siyingia*, *Cyclodiscaspis*, *Diandongaspis*, and *Altigibbaspis* (Liu, 1965, 1975; Wang and Wang, 1982a; Janvier et al., 1993; Si et al., 2015; Liu et al., 2018). This family documents the second radiation of galeaspids during the early Lochkovian of the Early Devonian (Zhao and Zhu, 2007). As an important component of the Xitun Vertebrate Fauna—which includes a diversity of galeaspids (Liu, 1965, 1975; P' an and Wang, 1978; Zhu, 1992; Gai and Zhu, 2007; Sun et al., 2022), thelodonts (Wang and Dong, 1989; Wang, 1995a, b), placoderms (Zhu, 1996), acanthodians (Wang and Dong, 1989), and sarcopterygians (Zhu and Schultze, 1997; Zhu et al., 1999)—the Polybranchiaspidae holds great significance for studies of Early Devonian biodiversity and evolution (Zhao and Zhu, 2015; Zhao et al., 2021). Except for *Bannhuanaspis* and *Dongfangaspis*, most polybranchiaspids are reported from the Xishancun Formation in Qujing, Yunnan Province.

However, species diagnoses within this family are often not distinctive, resulting in controversial taxonomic assignments. For example, *Dongfangaspis paradoxus* and *D. yunnanensis* (Fang et al., 1985) from the Xishancun Formation in Qujing, Yunnan, were subsequently recognized as junior synonyms of *Polybranchiaspis liaojiaoshanensis* (Zhu et al., 2015). Another taxonomically contentious species is '*Dongfangaspis qujingensis*'. This species was erected based on specimen GMC V1753, which preserves only an incomplete headshield (Pan and Wang, 1981). Zhu and Gai (2006) proposed that *D. qujingensis* shows greater similarity to *Laxaspis* than to *Dongfangaspis* in overall headshield shape, ornamentation, and number of branchial fossae, and consequently transferred '*Dongfangaspis qujingensis*' to the genus *Laxaspis*.

This taxonomic revision, however, created a new problem of junior homonymy, as the type species of *Laxaspis* is *L. qujingensis* (Liu, 1975). Therefore, a new species name should be proposed to replace '*D. qujingensis*'. One significant difference between '*Dongfangaspis qujingensis*' and *Laxaspis qujingensis* lies in the termination of the lateral transverse canals: the former exhibits bifurcated ends, whereas the latter shows stellate terminations. Zhu and Gai (2006) questioned whether the stellate ends of sensory canals in *L. qujingensis* might merely reflect ornamental features. Considering the possibility that '*D. qujingensis*' could be a junior synonym of *L. qujingensis*, they suggested retaining the original name '*Dongfangaspis qujingensis*' with quotation marks pending recovery of additional material and further observation (Zhu and Gai, 2006). Additionally, Pan (1992) described a new specimen of '*D. qujingensis*' (GMC V2072), which was later considered a junior homonym of '*D. qujingensis*' and representative of a new species of *Laxaspis* designated as *Laxaspis* cf. *L. qujingensis* (Zhu et al., 2015).

Since 2012, we have conducted several field expeditions to the lower part of the Xishancun Formation in Qujing and collected abundant new polybranchiaspid material, including *Polybranchiaspis*, '*D. qujingensis*', *Laxaspis*, and *Damaspis*. Based on these new materials, we present a detailed redescription of '*D. qujingensis*' to reveal its morphological nature and clarify its taxonomic assignment. Additionally, we describe new specimens of *Damaspis vartus* to verify uncertain morphological features of this species.

Our new materials and observations indicate that '*D. qujingensis*' shows greater affinity to *Damaspis* than to either *Dongfangaspis* or *Laxaspis*. Consequently, we propose removing '*Dongfangaspis qujingensis*' from *Laxaspis* and reassigning it to *Damaspis*.

2 Materials and Methods

The new material from the Xishancun Formation includes three nearly complete (IVPP V5017.2–4) and three fragmentary headshields (IVPP V5017.5–7) of '*Dongfangaspis qujingensis*', plus three incomplete headshields (IVPP V6259.4–6) of *Damaspis vartus*. All specimens were prepared mechanically

using a vibro tool with a tungsten-carbide bit or a needle, measured with a digital vernier caliper and ImageJ software, and examined under an Olympus SZ61 zoom stereo microscope. General morphology was photographed using a Canon EOS 5D Mark III camera with a Canon macro photo lens EF 100 mm 1:2.8 L. All fossils are permanently housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences for reference.

3 Systematic Paleontology

Subclass Galeaspida Tarlo, 1967
Order Polybranchiaspiformes Liu, 1965
Family Polybranchiaspidae Liu, 1965
Genus *Damaspis* Wang & Wang, 1982a

Type species: *Damaspis vartus* (Wang and Wang, 1982a)

Diagnosis (emended): Medium-sized polybranchiaspid fish with oval-shaped headshield longer than wide (length/width > 1); widest point situated between the third and fourth lateral transverse canals; median dorsal ridge low and posteriorly ascending; inner cornual process broad and leaf-shaped; paired V-shaped posterior supraorbital canals unconnected with each other; lateral dorsal canal extending along the mesial margin of the inner cornual process; at least seven pairs of lateral transverse canals issuing from the lateral dorsal canal; ends of lateral transverse canals bifurcated; 15–18 pairs of branchial fenestrae.

***Damaspis qujingensis* sp. nov.** (Figs. 1-3)
Dongfangaspis qujingensis Pan and Wang, 1981; Pan, 1992
'*Dongfangaspis qujingensis*' Zhu and Gai, 2006

Holotype: An incomplete headshield, GMC V1735.

Referred specimens: Three nearly complete headshields, IVPP V5017.2—4, and three fragmentary headshields, V5017.5—7.

Locality and horizon: Xishan Reservoir, Xicheng Street, Qilin District, Qujing City, Yunnan Province, China; Xishancun Formation, lower Lochkovian, Lower Devonian.

Measurements: See Table 1 .

Diagnosis: Oval headshield with maximum length of 112.4–117.7 mm and maximum width of 99.0–110.5 mm; transversely oval median dorsal opening with width/length ratio of approximately 1.7; two lateral transverse canals issuing from the infraorbital canals; four long and three short lateral transverse canals issuing from the lateral dorsal canal; ornamentation composed of large, stellate tubercles with individual diameters ranging from 1.0 to 2.0 mm.

Description: *Damaspis qujingensis* is a medium-sized polybranchiaspid jawless fish with an oval headshield [Figure 1: see original paper]A—D. The rostral

margin of the headshield is arcuate without a rostral process, while the posterior margin is deeply embayed (Figs. 1A−D, 2A). Maximum headshield length varies from 115.2 to 117.7 mm, maximum width from 98.4 to 110.5 mm, and midline length from 92.5 to 99.5 mm (Table 1). Maximum headshield width shows approximately 10% variation. On the dorsal surface, behind the dorsal commissure (dcm), a low, flat median dorsal ridge (md.r, Fig. 1A−C) rises and extends along the midline to the posterior margin, forming a median dorsal spine (md.s, Fig. 1A, C). Caudally, the headshield projects into a pair of inner cornual processes (ic, Figs. 1A, D, 2A) that are broad and leaf-shaped, with interprocess distance ranging from 41.6 to 46.1 mm. Ornamentation in all specimens consists of large stellate tubercles with individual diameters of 1.0–2.0 mm.

The median dorsal opening (md.o, Figs. 1A−C, 2A) is oval with its short axis aligned to the rostro-caudal axis. The long axis measures 19.6–23.2 mm and the short axis 12.2–13.6 mm (Table 1), yielding a long/short axis ratio of approximately 1.7.

The orbital opening (orb, Figs. 1A−C, 2A) occupies a dorsal position on the headshield and is oval with a long axis of 7.7–8.4 mm. Interorbital distance ranges from 45.6 to 48.7 mm (Table 1). The pineal opening (pi), well-preserved in specimen V5017.4 (Fig. 1C), lies on the midline posterior to the orbital openings. It is tiny and round with a diameter of approximately 2.0 mm (Table 1).

The sensory canal system, exposed as grooves in internal molds, displays a typical polybranchiaspid pattern. The infraorbital canal connects with the lateral dorsal canal to form the main longitudinal canal from which nine pairs of lateral transverse canals arise. Two pairs (ltca-b, Figs. 1A−C, 2A, 3A) issue from the infraorbital canal and seven pairs (ltc1-7, Figs. 2A−D, 3A) from the lateral dorsal canal. The fourth lateral transverse canal (ltc4) is the longest, nearly reaching the lateral margin in specimen V5017.4 (Fig. 1C). Notably, posterior to ltc4 there are 2–3 additional pairs of short lateral transverse canals (ltc5-7) arising from the lateral dorsal canal, observable in specimen V5017.6 (Fig. 2C). The lateral transverse canal ends are bifurcated, as seen in the holotype (Fig. 2A) and specimen V5017.4 (Fig. 1C). The dorsal commissure (dcm, Figs. 1A−C, 2A, C), level with the second lateral transverse canal, connects the bilateral lateral dorsal canals.

The supraorbital system comprises anterior and posterior supraorbital canals. The paired posterior supraorbital canals (soc2, Figs. 1A−C, 2A, 3A) are V-shaped, converging posteriorly toward the pineal opening but remaining unconnected. The anterior supraorbital canal (soc1, Figs. 1C, 2A) extends anteriorly nearly to the headshield margin and converges posteriorly with the posterior supraorbital and infraorbital canals anterior to the orbital openings.

The ventral surface bears a large, oval oralobranchial chamber (obr.c, Figs. 1D, 3B) bounded by paired ventral rims. The ventral rim (vr, Figs. 1D, 3B) is thin

but broadens gradually from the anterior margin, reaching maximum width at the inner cornual process base. The branchial region length in IVPP V5017.4 (Fig. 1D) is approximately 60.0 mm, constituting about one-half of total headshield length—a ratio identical to that in *Damaspis vartus*. Consequently, the number of branchial fossae (br.f, Fig. 3B) in *Damaspis qujingensis* is estimated at 18 pairs, as in *D. vartus* (Fig. 3B).

***Damaspis vartus* Wang & Wang, 1982a** (Figs. 4–6)

Holotype: A complete headshield and its external mold, IVPP V6259.1.

Paratype: Two incomplete headshields, IVPP V6259.2, 3.

Referred specimens: Three incomplete headshields, IVPP V6259.4—6.

Locality and horizon: Miandian Reservoir in the Triathlon Sports Park, Qilin District, Qujing City, Yunnan Province, China; Xishancun Formation, lower Lochkovian, Lower Devonian.

Measurements: See Table 1.

Diagnosis (emended): Oval headshield with maximum length of 93.4–103.4 mm and maximum width of 85.5–106.2 mm; transversely oval median dorsal opening with distinctly protruding anterior margin; four lateral transverse canals (ltca-d) issuing from the infraorbital canals; five long and three short lateral transverse canals issuing from the lateral dorsal canal; ornamentation composed of small granular tubercles at a density of 6–8 tubercles per square millimeter.

Remarks: The sensory canal system on the dorsal headshield of galeaspids is generally bilaterally symmetric. However, the holotype of *Damaspis vartus* exhibits an asymmetric system with five long lateral transverse canals on the left side but only four on the right, interpreted as intraspecific variation (Wang and Wang, 1982a). Two new specimens display five long lateral transverse canals on the right side, indicating that the fifth long lateral transverse canal is a natural feature of *Damaspis vartus*, while the four canals on the right side of the holotype represent intraspecific variation.

Description: The new specimens of *Damaspis vartus* comprise three incomplete headshields (IVPP V6259.4—6, Figs. 4, 5). Like the holotype, all bear oval headshields with maximum width situated between the third and fourth lateral transverse canals (ltc3 and ltc4, Figs. 4B, 5A, B, C). Maximum headshield length ranges from 93.4 to 103.4 mm and maximum width from 85.5 to 106.2 mm (Table 1). Specimen V6259.5a (Fig. 4A) preserves a complete, broad leaf-shaped inner cornual process (ic). The lateral headshield margin is smooth.

The median dorsal opening (md.o, Figs. 4A, B, 5C) is nearly oval with a roughly straight posterior margin and distinctly protruding anterior margin. The long axis measures 17.0–18.8 mm and the short axis 8.4–9.8 mm (Table 1), yielding a long/short axis ratio of approximately 2.0.

The shape and position of the orbital openings (orb, Figs. 4A, B, 5C) and pineal opening (pi, Fig. 5A [Figure 5: see original paper], C) in the new specimens resemble those of the holotype. Orbital openings are oval with long axes of 5.4–6.0 mm and interorbital distances of 31.2–37.4 mm (Table 1). The pineal opening is tiny and round with diameters of 0.9–1.3 mm (Table 1).

The sensory canal distribution pattern in the new specimens closely matches that of the holotype, characterized by bifurcated canal ends, paired V-shaped posterior supraorbital canals that remain unconnected, lateral dorsal canals extending along the mesial margin of the inner cornual process, and three short longitudinal canals issuing from the median transverse canal. Contrary to previous observations, four lateral transverse canals (ltca-d), rather than three, arise from the infraorbital canals (Fig. 4A). In specimens IVPP V6259.4b and V6259.5a (Figs. 4B, 5A), both internal molds, five long lateral transverse canals (ltc1-5) issue from the lateral dorsal canal on the right side, followed by three short canals (ltc6-8) in V6259.5a. The holotype also shows five lateral dorsal canals on the left but only four (ltc1-4) on the right, previously interpreted as intraspecific variation (Wang and Wang, 1982a).

Like the holotype, the new specimens are ornamented with small, dense, evenly distributed granular tubercles at approximately 6–8 tubercles per square millimeter. In specimen V6259.6, ten branchial fossae are observed, with an estimated total of approximately 18 pairs (Fig. 6B [Figure 6: see original paper]).

5 Discussion and Conclusion

'*Dongfangaspis qujingensis*' can be confidently assigned to Polybranchiaspidae (Liu, 1965) as it exhibits a suite of diagnostic familial features: an oval headshield, well-developed median dorsal ridge and spine, leaf-shaped inner cornual process, V-shaped posterior supraorbital canal, and more than four pairs of lateral transverse canals issuing from the lateral dorsal canal. '*D. qujingensis*' clearly differs from *Polybranchiaspis* (Liu, 1965; P' an and Wang, 1978; Tông-Dzuy et al., 1995) in possessing broad leaf-shaped inner cornual processes that extend substantially posterior to the median dorsal spine terminus; from *Siyingia* (Wang and Wang, 1982b) in lacking a tall, upright, compressed median dorsal spine; from *Cyclodiscaspis* (Liu, 1975) in lacking laterally positioned orbital openings; and from *Altigibbaspis* (Liu et al., 2018) in lacking a blade-like median dorsal ridge. Although initially assigned to *Dongfangaspis* and later referred to *Laxaspis* (Zhu and Gai, 2006; Zhu et al., 2015), our analysis suggests otherwise.

Dongfangaspis was erected by Liu (1975) based on *Dongfangaspis major* from the Guanshanpo Formation (Pragian, Early Devonian) in Jiangyou, Sichuan Province. Meng et al. (2022) described a new *Dongfangaspis* sp. specimen from the Haikou Formation (Eifelian, Middle Devonian) in Wuding, Yunnan Province. These specimens indicate that a large number of branchial fossae (approximately 45 pairs) constitutes an important diagnostic character for *Dong-*

fangaspis, clearly exceeding counts in all other polybranchiaspid genera (e.g., 12 pairs in *Polybranchiaspis*, 18 pairs in both *Laxaspis* and *Damaspis*). The branchial fossa count in '*Dongfangaspis qujingensis*' is established as 18 pairs, matching *Laxaspis* and *Damaspis* (Fig. 7 [Figure 7: see original paper]). Furthermore, *Dongfangaspis* is the only polybranchiaspid genus ranging from the Pragian of the Early Devonian to the Eifelian of the Middle Devonian (Meng et al., 2022), whereas '*D. qujingensis*' derives from the lower Lochkovian Xishancun Formation in Qujing, Yunnan Province. Therefore, assignment to *Dongfangaspis* is untenable.

Our new materials demonstrate that '*Dongfangaspis qujingensis*' shows greater affinity to *Damaspis* than to either *Dongfangaspis* or *Laxaspis*. Reexamination of all *Laxaspis* material, including *L. qujingensis*, *L. yulongssus* (Liu, 1975; Janvier and Phuong, 1999), and new specimens of *Laxaspis* cf. *L. qujingensis* from the lower Xishancun Formation (to be described elsewhere), confirms that stellate canal terminations represent a diagnostic character for *Laxaspis*. Thus, the bifurcated lateral transverse canal ends in '*Dongfangaspis qujingensis*' more closely resemble *Damaspis* than *Laxaspis* (Fig. 7).

'*D. qujingensis*' also exhibits other differences from *L. qujingensis*. Its median dorsal spine is much shorter than that of *L. qujingensis* (Fig. 7B, D) but more similar to *D. vartus*. Moreover, the posterior ends of the V-shaped posterior supraorbital canals are unconnected in '*D. qujingensis*' , whereas they connect behind the pineal opening in *L. qujingensis*. In contrast, '*D. qujingensis*' more closely resembles *Damaspis vartus* in headshield width/length ratio (less than 1), bifurcated sensory canal ends, unconnected posterior supraorbital canals, and possession of at least seven lateral transverse canal pairs issuing from the lateral dorsal canal (Fig. 7A, B). We therefore propose removing '*D. qujingensis*' from *Laxaspis* and reassigning it to *Damaspis*.

Compared with *Damaspis vartus*, '*D. qujingensis*' possesses a larger headshield with larger, stellate tubercles. Most significantly, our new data indicate that *Damaspis vartus* bears four lateral transverse canals (ltca-d) issuing from the infraorbital canals (two more than in '*D. qujingensis*') and five long lateral transverse canals issuing from the lateral dorsal canal, distinguishing it not only from '*D. qujingensis*' but from all other polybranchiaspid fish.

Given these differences, we recognize '*D. qujingensis*' as a new species of *Damaspis*, *Damaspis qujingensis*.

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Note: Figure translations are in progress. See original paper for figures.