A taxonomical revision of 'Dongfangaspis qujingensis' from the Lower Devonian of Qujing, Yunnan Province (Postprint)

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Abstract

The taxonomic assignment of "Dongfangaspis qujingensis" has long been controversial. Initially assigned to the genus Dongfangaspis, it was subsequently transferred to Laxaspis. However, because the type species of Laxaspis is Laxaspis qujingensis, this taxonomic revision has resulted in a junior homonym issue. Here we describe new material of "Dongfangaspis qujingensis" and Damaspis vartus from the Lochkovian (Early Devonian) Xishancun Formation in Qujing, Yunnan. "Dongfangaspis qujingensis" exhibits high similarity to Damaspis vartus in several features, including a head shield slightly longer than wide, bifurcated terminations of the lateral transverse canals, non-converging V-shaped postorbital canals, and at least seven lateral transverse canals issuing from the lateral dorsal canal. These similarities demonstrate that, compared with Laxaspis and Dongfangaspis, "Dongfangaspis qujingensis" is more closely allied to Damaspis. We therefore propose removing "Dongfangaspis qujingensis" from Laxaspis and reassigning it to Damaspis. The new specimens reveal that the additional fifth pair of elongated lateral transverse canals in Damaspis vartus represents a diagnostic feature of this species, while the asymmetric sensory canal system observed in the holotype should be interpreted as resulting from 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 affinity of 'Dongfangaspis qujingensis' , initially assigned to *Dongfangaspis* but later to *Laxaspis*, has long been controversial. However, this taxonomical revision raises a new problem of junior homonym since 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 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 represents intraspecific variation.

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

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1 Introduction

The Polybranchiaspidae is 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 represents 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)—this

family is of 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, the diagnoses of species are not distinctive, resulting in controversial assignments. For example, *Dongfangaspis paradoxus* and *D. yunnanensis* (Fang et al., 1985) from the Xishancun Formation in Qujing, Yunnan, were 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* is more suggestive of *Laxaspis* than *Dongfangaspis* in overall headshield shape, ornamentation, and number of branchial fossae, and consequently removed '*Dongfangaspis qujingensis*' to the genus *Laxaspis*.

This taxonomical revision, however, raises a new problem of junior homonym since 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 ends of the lateral transverse canals: the former has bifurcated ends, whereas the latter has stellated ends. Zhu and Gai (2006) doubted that the stellated ends of sensory canals in *L. qujingensis* merely reflect ornamentation patterns. Considering the possibility that '*D. qujingensis*' might be a junior synonym of *L. qujingensis*, they suggested retaining the original name with quotation marks pending collection of more 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* denominated as *Laxaspis* cf. *L. qujingensis* (Zhu et al., 2015).

Since 2012, the authors have organized several field excursions in the lower part of the Xishancun Formation in Qujing and collected abundant new polybranchiaspid materials, 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 assignment. Additionally, new specimens of *Damaspis vartus* are described here to verify uncertain morphological features of the species.

The new materials and observations indicate that '*D. qujingensis*' is more suggestive of *Damaspis* than *Dongfangaspis* and *Laxaspis*. Therefore, we propose to remove '*Dongfangaspis qujingensis*' from *Laxaspis* to *Damaspis*.

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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*' , and 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 studied under an Olympus SZ61 zoom stereo microscope. All specimens were photographed with a Canon EOS 5D Mark III camera coupled with a Canon macro photo lens EF 100 mm 1:2.8 L for general morphology. All fossils are permanently housed for reference in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences.

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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; 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 specimen: 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 to 117.7 mm and

maximum width of 99.0 to 110.5 mm; transversely oval median dorsal opening with width/length ratio of about 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, stellated tubercles with diameter of a single tubercle varying from 1.0 to 2.0 mm.

Description: *Damaspis qujingensis* is a medium-sized polybranchiaspid jawless fish with an oval-shaped headshield (Fig. 1A [Figure 1: see original paper]—D). The rostral margin of the headshield is arciform 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 headshield length along the midline from 92.5 to 99.5 mm (Table 1). Variation in maximum headshield width is about 10%. On the dorsal side of the headshield, behind the dorsal commissure (dcm), a low and 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 protrudes into a pair of inner cornual processes (ic, Figs. 1A, D, 2A) that are broad and leaf-shaped, with distance between them ranging from 41.6 to 46.1 mm. Ornamentation of the headshield in all specimens consists of large stellated tubercles with diameter of a single tubercle varying from 1.0 to 2.0 mm.

The median dorsal opening (md.o, Figs. 1A—C, 2A) is oval in outline with its short axis aligned with the rostro-caudal axis of the headshield. Length of the long axis varies from 19.6 to 23.2 mm, and length of the short axis from 12.2 to 13.6 mm (Table 1). The long axis of the median dorsal opening is about 1.7 times the length of the short axis.

The orbital opening (orb, Figs. 1A—C, 2A) occupies a dorsal position on the headshield. It is oval in outline with a long axis ranging from 7.7 to 8.4 mm. Distance between paired orbital openings 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 of the headshield posterior to the posterior margin of the orbital openings. The pineal opening is tiny and round with a diameter of about 2.0 mm (Table 1).

The sensory canal system, exposed as grooves in the internal moulds of specimens, displays a typical polybranchiaspid pattern. The infraorbital canal connects with the lateral dorsal canal to constitute the main longitudinal canal from which nine pairs of lateral transverse canals issue. Among them, 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, reaching nearly to the lateral margin of the headshield in specimen V5017.4 (Fig. 1C). Notably, posterior to the fourth lateral transverse canal, there are still 2–3 pairs of short lateral transverse canals (ltc5-7) issuing from the lateral dorsal canal, observable in specimen V5017.6 (Fig. 2C). The ends of the lateral transverse canals are bifurcated, as present in the holotype (Fig. 2A) and specimen V5017.4 (Fig. 1C). The dorsal commis-

sure (dcm, Figs. 1A−C, 2A, C), which is level with the second lateral transverse canal, connects the lateral dorsal canals on both sides.

The supraorbital system consists of posterior and anterior supraorbital canals. The paired posterior supraorbital canals (soc2, Figs. 1A−C, 2A, 3A) are V-shaped, converging posteriorly toward the pineal opening but not connected. The anterior supraorbital canal (soc1, Figs. 1C, 2A) extends anteriorly nearly to the margin of the headshield and converges posteriorly with the posterior supraorbital canal and the infraorbital canal anterior to the orbital openings.

The ventral side of the headshield shows a large oval-shaped oralobranchial chamber (obr.c, Figs. 1D, 3B), encompassed by a pair of ventral rims. The ventral rim (vr, Figs. 1D, 3B) is thin but broadens gradually from the anterior margin, reaching its broadest point at the base of the inner cornual process. Length of the branchial region (br. region) in IVPP V5017.4 (Fig. 1D) is approximately 60.0 mm, accounting for 1/2 of the whole headshield length—a ratio identical to that in *Damaspis vartus*. Therefore, the number of branchial fossae (br.f, Fig. 3B) in *Damaspis qujingensis* is estimated to be 18 pairs, as in *Damaspis vartus* (Fig. 3B).

***Damaspis vartus* Wang & Wang, 1982a** (Figs. 4–6)
Holotype: A complete headshield and its external mould, IVPP V6259.1.
Paratype: Two incomplete headshields, IVPP V6259.2, 3.
Referred specimen: 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 to 103.4 mm and maximum width of 85.5 to 106.2 mm; transversely oval median dorsal opening with anterior margin protruding obviously; 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 with 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, in the holotype of *Damaspis vartus*, the sensory canal system is asymmetric, 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 of *Damaspis vartus* display five long lateral transverse canals on the right side of the headshield, suggesting that the fifth long lateral transverse canal is a natural feature of *Damaspis vartus*, while the four long canals on the right side of the holotype represent intraspecific variation.

Description: The new specimens of *Damaspis vartus* include 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 inner cornual process (ic) that is broad and leaf-shaped. The lateral margin of the headshield is smooth.

The median dorsal opening (md.o, Figs. 4A, B, 5C) is nearly oval, with its posterior margin roughly straight and its anterior margin obviously protruding. Length of the long axis varies from 17.0 to 18.8 mm, and length of the short axis from 8.4 to 9.8 mm (Table 1). The long axis of the median dorsal opening is about 2.0 times the length of the short axis.

The shape and positions 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. The orbital openings are oval with long axis length varying from 5.4 to 6.0 mm. Distance between the two orbital openings ranges from 31.2 to 37.4 mm (Table 1). The pineal opening is round and tiny, with diameter varying from 0.9 to 1.3 mm (Table 1).

The distribution pattern of sensory canals in the new specimens is quite similar to that in the holotype, characterized by bifurcated ends of the sensory canals, paired V-shaped posterior supraorbital canals that are not connected, lateral dorsal canals extending along the mesial margin of the inner cornual process, and three short longitudinal canals issuing from the median transverse canal. Unlike previous observations, there are four lateral transverse canals (ltca-d), rather than three, issuing from the infraorbital canals (Fig. 4A). In specimens IVPP V6259.4b and V6259.5a (Figs. 4B, 5A), both internal moulds of the headshield, five long lateral transverse canals (ltc1-5) are observed issuing from the lateral dorsal canal on the right side, followed by three short lateral transverse canals in V6259.5a (ltc6-8). In the holotype, there are also five lateral dorsal canals on the left side but only four (ltc1-4) on the right—interpreted as a phenomenon of intraspecific variation (Wang and Wang, 1982a).

Like the holotype of *Damaspis vartus*, the new specimen is ornamented with small, dense, evenly distributed granular tubercles on the headshield, with about 6–8 tubercles per square millimeter. In specimen V6259.6, ten branchial fossae are observed, and the estimated number of branchial fossae is approximately 18 pairs (Fig. 6B [Figure 6: see original paper]).

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5 Discussion and Conclusion

'*Dongfangaspis qujingensis*' can be confidently classified within Polybranchiaspidae (Liu, 1965) because it displays a suite of diagnostic features of the family, including an oval-shaped headshield, 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*' obviously differs from *Polybranchiaspis* (Liu, 1965; P' an and Wang, 1978; Tông-Dzuy et al., 1995) by bearing broad leaf-shaped inner cornual processes that extend largely posterior to the end of the median dorsal spine; from *Siyingia* (Wang and Wang, 1982b) by lacking a high, upright, and compressed median dorsal spine; from *Cyclodiscaspis* (Liu, 1975) by lacking laterally positioned orbital openings; and from *Altigibbaspis* (Liu et al., 2018) by lacking a blade-like median dorsal ridge.

The species was initially assigned to *Dongfangaspis* but later referred to *Laxaspis* (Zhu and Gai, 2006; Zhu et al., 2015). *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 specimen of *Dongfangaspis* sp. from the Haikou Formation (Eifelian, Middle Devonian) in Wuding, Yunnan Province. These two specimens of *Dongfangaspis* indicate that a large number of branchial fossae (about 45 pairs) is an important diagnostic feature of *Dongfangaspis*—clearly larger than in all other polybranchiaspid genera such as 12 pairs in *Polybranchiaspis* and 18 pairs in *Laxaspis* and *Damaspis*. The number of branchial fossae in '*Dongfangaspis qujingensis*' is established as 18 pairs, as in *Laxaspis* and *Damaspis* (Fig. 7 [Figure 7: see original paper]). Additionally, *Dongfangaspis* is the only genus of Polybranchiaspidae that survived from the Pragian of the Early Devonian to the Eifelian of the Middle Devonian (Meng et al., 2022), whereas '*D. qujingensis*' is collected from the lower Lochkovian Xishancun Formation in Qujing, Yunnan Province. Therefore, assignment of '*D. qujingensis*' to *Dongfangaspis* is unreasonable.

Our new materials and observations reveal that '*Dongfangaspis qujingensis*' is more suggestive of *Damaspis* than *Dongfangaspis* or *Laxaspis*. We reexamined all materials of *Laxaspis*, including *L. qujingensis*, *L. yulongssus* (Liu, 1975; Janvier and Phuong, 1999), and new specimens of *Laxaspis* cf. *L. qujingensis* from the lower part of the Xishancun Formation in Qujing (to be described in another paper). The stellated ends of sensory canals can be corroborated in these three species of *Laxaspis* and can be regarded as a diagnostic character of *Laxaspis*. Therefore, the bifurcated ends of the lateral transverse canals in '*Dongfangaspis qujingensis*' are more similar to those of *Damaspis* than *Laxaspis* (Fig. 7).

'*D. qujingensis*' also displays other differences from *L. qujingensis*. For example, the median dorsal spine of '*D. qujingensis*' is much shorter than that of *L. qujingensis* (Fig. 7B, D) but more similar to that of *D. vartus*. Moreover, the posterior ends of the V-shaped posterior supraorbital canals are not connected in '*D. qujingensis*' , whereas they are connected behind the pineal opening in *L. qujingensis*. By contrast, '*D. qujingensis*' shows greater resemblance to *Damaspis vartus* than to *L. qujingensis* in headshield width/length ratio (less than 1), bifurcated ends of sensory canals, paired posterior supraorbital canals that are not connected, and at least seven pairs of lateral transverse canals

issuing from the lateral dorsal canal (Fig. 7A, B). Therefore, we propose to remove '*D. qujingensis*' from *Laxaspis* to *Damaspis*.

Compared with *Damaspis vartus*, '*D. qujingensis*' has a larger headshield and larger, stellated tubercles. Most prominently, 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, which not only distinguishes it from '*D. qujingensis*' but also from all other polybranchiaspid fish.

Considering these differences, we regard '*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.