The pelvic morphology of Parayunnanolepis (Placodermi, Antiarcha) revealed by tomographic data Postprint

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Abstract

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Full Text

The Pelvic Morphology of Parayunnanolepis (Placodermi, Antiarcha) Revealed by Tomographic Data

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Abstract

The pelvic morphology, and whether the pelvic fin is present or absent in the earliest jawed vertebrates, are key to interpreting the origin of vertebrate paired fins. *Parayunnanolepis xitunensis*, an antiarch placoderm from the Early Devonian of Yunnan, South China, was previously described to possess the earliest evidence of both dermal and endoskeletal pelvic girdles, presumably for the attachment of pelvic fins. Here, we redescribe the pelvic region of the holotype based on high-resolution computed tomographic data. Instead of having two large plates previously designated as dermal pelvic girdles, *Parayunnanolepis* possesses three pairs of lateral pelvic plates and one large oval median pelvic plate. The paired pelvic plates are flat ventral plates that differ from other dermal pelvic girdles in lacking a dorsal extension. There is no definitive evidence for the presence of an endoskeletal pelvic girdle in *Parayunnanolepis*, although this possibility cannot be ruled out. A comparison of dermal pelvic plates across various jawed stem-gnathostomes suggests that the presence of both paired and median pelvic plates is shared by different lineages and might be plesiomorphic. Jawed stem-gnathostomes may have recruited the ventral dermal skeleton of the post-thoracic body into different functional units.

Key words: Early Devonian, paired appendages, pelvic fin, placoderms, antiarchs, three-dimensional reconstruction

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1. Introduction

The pelvic fin and girdle are absent in jawless osteostracans that possess readily recognizable pectoral fins and girdles (Janvier, 1985; Janvier et al., 2004). The observation of pelvic morphology in taxa near the advent of jaws is thus critical for answering when and how the pelvic appendage arose somewhere along the gnathostome stem. Antiarcha is a group of armoured jawed fishes often placed at or near the base of the jawed vertebrate tree in recent phylogenetic analyses (Zhu et al., 2013, 2016, 2021, 2022; Brazeau and Friedman, 2015). Alternatively, the antiarchs are nested within a monophyletic Placodermi (Qiao et al., 2016; King et al., 2017). Conventionally, the nested antiarchs were thought to lack pelvic appendages, as evidenced by complete specimens (Hemmings, 1978; Ivanov et al., 1996; Johanson, 1997), although pelvic girdles were interpreted (Stensiö, 1948; Charest et al., 2018).

However, the lack of pelvic appendages in antiarchs was challenged by *Parayunnanolepis xitunensis*, a plesiomorphic antiarch placoderm from the Early Devonian of Yunnan, South China (Zhang et al., 2001; Wang and Zhu, 2021, 2022). *Parayunnanolepis* was reported to possess both a dermal and an endoskeletal pelvic girdle, implying that a full pelvic appendage is primitively present in antiarchs (Zhu et al., 2012b). Subsequent analysis of *Bothriolepis* further suggested that the endoskeletal pelvic girdle might be retained, although the pelvic appendage was reduced (Charest et al., 2018). It was thus implied that the pelvic appendage was already present in the first jawed vertebrates, with dermal and endoskeletal girdles as in the pectoral counterpart.

In this paper, we provide a revised description of the pelvic region in *Parayunnanolepis* based on high-resolution computed tomographic data and an updated comparison with pelvic morphology in other placoderms and jawed stem-gnathostomes. Our results suggest that the presence of both paired and median pelvic plates is shared by different placoderm lineages and might be plesiomorphic.

2. Material and Methods

The holotype of *Parayunnanolepis xitunensis* (IVPP V11679.1) is housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. The specimen was coated in ammonium chloride before photography (Fig. 1 [Figure 1: see original paper]) and further investigated using CT scanning at IVPP. Scanning was performed with a 225 kV micro-CT (developed by the Institute of High Energy Physics, CAS) at 150 kV and 100 µA, with an 11 µm voxel size. The scan employed a 720° rotation with a step size of 0.5° and an unfiltered aluminium reflection target. A total of 720 transmission images were reconstructed in a 2048 × 2048 matrix of 1536 slices. Three-dimensional segmentation was performed in Mimics (https://www.materialise.com/en/medical/software/mimics; Materialize). Surface meshes were then exported, surface-rendered, and imaged in Blender 2.79b (http://blender.org; Stitching Blender Foundation, Amsterdam, The Netherlands) and Vayu 1.0 (Lu, 2022, http://admorph.ivpp.ac.cn/download.html).

3. Results

The reconstructed tomographic data reveal a very different pattern of dermal pelvic plates compared to the previous description based on external microscopic observations. The originally described paired dermal girdles (Zhu et al., 2012b: supplementary fig. S1c) are in fact a single median dermal plate. The previously identified endoskeletal pelvic girdle, supposedly lining the interior of the dermal pelvic plate (Zhu et al., 2012b: fig. 2b [Figure 2: see original paper], en.pelv), is here redescribed as paired dermal pelvic plates (p.dplv) displaced beneath the median pelvic plate—all belonging to the dermal skeleton. These paired pelvic plates include three successively arranged pairs positioned at the anterior-most ventral side of the post-thoracic dermal skeleton and dorsal to the subanal lamina of the posterior ventrolateral (PVL) plates (Fig. 1G).

The first pair (p.dplv1, Fig. 1C–G) is significantly larger than the remaining two pairs and is mostly covered by the subanal lamina in ventral view (Fig. 1C). Each plate of the first pair is a flat element shaped roughly like a right-angled triangle, with one side facing laterally. The posterior angle overlaps a large area of the second pair of pelvic plates, while the anterior side is strongly curled ventrally. The ventral surface bears a depressed area (oa.mdp, Fig. 1E, F) that roughly matches the pointed anterior contour of the median pelvic plate.

Each plate of the second pair (p.dplv2, Fig. 1C–G) is an elongated element, while the third paired pelvic plates (p.dplv3, Fig. 1D–G) are smaller, plank-like structures overlapped by the posterior part of the second paired plate.

The large oval plate, previously designated as one of the paired dermal pelvic girdles (Zhu et al., 2012b: fig. S1c), is revealed by CT data to be a single median element (m.dplv, Fig. 1B, C, E–G). This plate is slightly dislocated to the left (Fig. 1B), but depressed areas on both the first paired pelvic plates and the ventral scutes indicate that the median plate extensively overlapped adjacent plates. The anterior end of the plate is slightly pointed, the center is domed, and the posterior margin is rounded. The straight anterolateral margins match the shape of the depressed area on the first lateral paired plates (oa.mdp, Fig. 1E, F), suggesting that the median plate completely covered the gap between the paired plates.

Given that the ventral side of the post-thoracic skeleton is covered by overlapping plates and scutes, the possible location of the anal opening is inferred to be anterior to the first paired plates and the median plate (an?, Fig. 1F), similar to the condition in *Sigaspis* (Fig. 2). In that case, the first paired plates could not have overlapped one another medially in life, although they are preserved this way.

Posterior to, and partly overlapped by, the median pelvic plates are serial ventral scutes in pairs (scu, Fig. 1C–F). Both the pelvic plates and scutes are externally covered with fine tubercles. The scutes differ from flanking body scales in being morphologically more similar to flat dermal plates than to dome-shaped scales. Nonetheless, the scutes can be easily distinguished from pelvic plates by their serial, rectangular shape. Interestingly, the scales immediately flanking the scutes (sc, Fig. 1B, D, F, G) show an intermediate condition: they are round and slightly domed like flank scales but significantly larger than those flank scales (scf, Fig. 1D, F, G). They possess fine tubercular ornamentation similar to that on the ventral scutes, whereas flank scales have one large central denticle surrounded by smaller tubercles.

4. Discussion

4.1 Comparison of the Dermal Pelvic Skeleton in Early Gnathostomes

The antiarch *Microbrachius* is the phylogenetically closest taxon to *Parayunnanolepis* with a relatively complete pelvic dermal skeleton preserved (Fig. 2). The paired dermal pelvic plates in *Microbrachius* are copulatory organs, evidenced by long denticles distinctive from the rest of the dermal ornamentation (Long et al., 2015). In male *Microbrachius*, the plates are fused at the midline and viscerally grooved to function as dermal claspers, while in females they are flat genital plates. Contrary to the condition in *Parayunnanolepis*, both male and female forms possess only one pair of dermal elements that are rigidly attached to the PVL plate, and there is no evidence of a median pelvic plate in *Microbrachius*.

In the iconic antiarch genus *Bothriolepis*, some specimens display one pair of pelvic plates presumably functioning as female genital plates. Charest et al. (2018) suggested these pelvic plates are of endoskeletal origin with both peri- and endochondral ossifications, by comparison with the endoskeletal girdle previously identified in *Parayunnanolepis*. In light of the new data provided here, these possible endoskeletal plates in *Bothriolepis* are not directly comparable to the pelvic plates in *Parayunnanolepis*, though they suggest that pelvic appendages might be present in antiarchs if the fin radials (Charest et al., 2018: fig. 2) are correctly identified.

The basal arthrodire *Sigaspis* exhibits extensive post-thoracic preservation displaying both paired and median pelvic plates very similar to those described here for *Parayunnanolepis* (Fig. 2) (Goujet, 1973). They differ in two respects: first, the initial paired plates in *Sigaspis* develop a dorsal or iliac lamina surrounding the fenestra for pelvic fin insertion, making it a functional dermal girdle; second, there are two median plates arranged along the midline rather than one. The dermal pelvic girdle was presumably lost in more deeply nested arthrodires such as *Coccosteus* (Trinajstic et al., 2015).

The Silurian "maxillate placoderm" *Qilinyu* possesses a median pelvic plate (shown but not labeled in Zhu et al., 2016: fig. S2) comparable to that in *Parayunnanolepis*, in addition to preserved squamation of the pelvic fins (Zhu et al., 2016). However, no paired pelvic plate has been identified in *Qilinyu*.

In the ptyctodontid *Rhamphodopsis*, the dermal pelvic girdle is a slender, curved plate attached externally to the endoskeletal pelvic girdle, which is a flat, oval ossification resembling the scapulacoracoid. The male clasper is capped with a dermal element and lined beneath by additional dermal plates, while the female genital plate is covered by specialized dermal scales (Fig. 2) (Miles, 1967; Trinajstic et al., 2015). Notably, all these copulatory dermal elements are positioned considerably posterior to the pelvic girdle and may not be strictly homologous to antiarch dermal claspers, which attach anteriorly to the posterior margin of the PVL plate.

The pelvic region of the early osteichthyan *Guiyu* also features a distinctive median element in addition to lateral dermal pelvic girdles (Zhu et al., 2012a). Evidently, arthrodires, antiarchs, and early osteichthyans all possess both median and paired pelvic elements. This pattern can be interpreted either as the primitive gnathostome condition or as the result of parallel evolution. Ptyctodonts lack median pelvic plates, and the presence of any median pelvic plate remains uncertain in acanthothoracids. Definitive conclusions regarding homology between lateral dermal pelvic elements across major early gnathostome groups cannot be drawn due to the absence of the PVL plate as a landmark in some taxa.

In general, caution is warranted when comparing post-thoracic plates across lineages, as they are much more variable and prone to parallel evolution than the head and trunk shields. As an analogy, in modern Loricariidae the dermal peri-anal plates are highly variable even among closely related taxa (Aquino and Schaefer, 2010: fig. 9 [Figure 9: see original paper]), making it impossible to establish primary homology between individual plates.

Notably, the paired dermal pelvic girdle in *Guiyu* shares with the dermal pelvic girdle in the acanthothoracid placoderm *Murrindalaspis* the presence of spine-like projections that brace the endoskeletal fin attachment (Long and Young, 1988). This pattern resembles the pectoral girdle, in which the dermal cleithrum or anterior lateral plate braces the endoskeletal scapulacoracoid and develops spiny lateral projections. This resemblance—characteristic of tetrapods but rarely present in aquatic basal gnathostomes—supports the argument that vertebrate anterior and posterior paired appendages are serially homologous structures from the early stage of their evolutionary history. However, in contrast to this condition, the putative dermal pelvic girdle in ptyctodonts and arthrodires, together with the dermal pelvic plates in antiarchs, are all simple, flat, and distinct from the curved, embracing morphology of a typical dermal pectoral girdle. As such, current data suggest that serial similarity between pectoral and pelvic appendages was not primitively present in gnathostomes. The dermal pelvic plates might originally have been a series of dermal elements lining the ventral side of the body that were later recruited by the development of other functional units, such as locomotive appendages (pelvic fins and girdles) or copulatory organs (claspers).

4.2 Functional Speculation on the Pelvic Plates in *Parayunnanolepis*

As previously described (Zhu et al., 2012b), both dermal and endoskeletal pelvic girdles were thought to be present in *Parayunnanolepis*. The endoskeletal pelvic girdle in early vertebrates has no other known function than fin insertion, so the presence of a pelvic fin is usually inferred. However, the endoskeletal pelvic girdle is now identified instead as paired dermal plates—flat dermal elements along the ventral surface of the post-thoracic body that lack any dorsal or iliac lamina to encircle the endoskeletal girdle, if present. The lateral and posterior margins of these pelvic plates are also all tightly connected to other dermal elements in situ, making fin insertion in these areas impossible. Thus, it is uncertain whether the paired pelvic dermal plates in *Parayunnanolepis* functioned as "girdles." They also differ from known female genital plates in *Microbrachius* in shape, position (anterior rather than trailing the posterior margin of the PVL), and in lacking distinctive auxiliary structures such as sharp, long denticles. With uncertain evidence from derived antiarchs (Upeniece and Upenieks, 1992; Charest et al., 2018), the presence of pelvic fins and girdles in antiarchs thus remains inconclusive.

If present, the only possible location for the endoskeletal pelvic girdle and fin insertion in *Parayunnanolepis* is the V-shaped space between the anterior boundary of the diagonally aligned squamation and the ventral pelvic plates (fin.inser?, Fig. 1G). Lastly, each large ventral scute extensively overlaps the posterior ones like tiles, indicating that the scale-covered post-thoracic tail must have been quite rigid. Thrust locomotion was thus likely achieved primarily by swinging this rigid tail around the significantly scaleless gap between the scale-covered post-thoracic tail and the thoracic armor (gap, Fig. 1F, G).

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