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

ZHU You-An^{1*} WANG Ya-Jing² QU Qing-Ming³
LU Jing^{1,4} ZHU Min^{1,4*}

(1 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044)

(2 School of Earth Sciences and Engineering, Nanjing University Nanjing 210023)

(3 State Key Laboratory of Cellular Stress Biology, School of Life Sciences, Xiamen University Xiamen 361005)

(4 University of Chinese Academy of Sciences Beijing 100049)

* Correspondence authors: Zhu You-An, zhuyouan@ivpp.ac.cn; Zhu Min, zhumin@ivpp.ac.cn

Abstract The pelvic morphology, and whether the pelvic fin is present or absent in the earliest jawed vertebrates are key in 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 the 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, and 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 the possibility cannot be ruled out. A comparison of the dermal pelvic plates in various jawed stem-gnathostomes suggests the presence of both paired and median pelvic plates is shared by different lineages and might be plesiomorphic. The 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 the jawless osteostracans that possesses 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 in answering when and

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how the pelvic appendage arose, somewhere along the gnathostome stem. Antiarcha is a group of armoured jawed fishes often placed at the base, 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 in a monophyletic Placodermi (Qiao et al., 2016; King et al., 2017). Conventionally, the nested antiarchs were thought to lack pelvic appendages, 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 a dermal and endoskeletal girdle 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 the pelvic morphology in other placoderms or jawed stem-gnathostomes. The result suggests that the presence of both paired and median pelvic plates is shared by different lineages of placoderms and might be plesiomorphic.

2 Material and methods

The holotype of *Parayunnanolepis xitunensis* was further investigated for anatomical details, and was coated in ammonium chloride before the photograph used in Fig. 1 was taken. The specimen (IVPP V11679.1) is housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China (IVPP).

The holotype of *Parayunnanolepis* was further investigated for anatomical details by CT scanning at IVPP, using 225 kV micro-CT (developed by the Institute of High Energy Physics, CAS) at 150 kV and 100 μ A, with a 11 μ m voxel size. The scan was conducted using 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 \times 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 into, 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 display 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) is in fact a single median dermal plate. The previously identified endoskeletal pelvic girdle, supposedly lining inside the dermal pelvic plate (Zhu et al., 2012b:fig. 2b, en.pelv), is here redescribed as the paired dermal pelvic plates (p.dplv) displaced under the median pelvic plate, all belong to the dermal skeleton. These paired pelvic plates include three successively arranged pairs, placed in the anterior most position of the 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) are significantly larger than the rest two pairs, and is mostly covered by the subanal lamina in ventral view (Fig. 1C). Each of the first pair is a flat plate shaped roughly

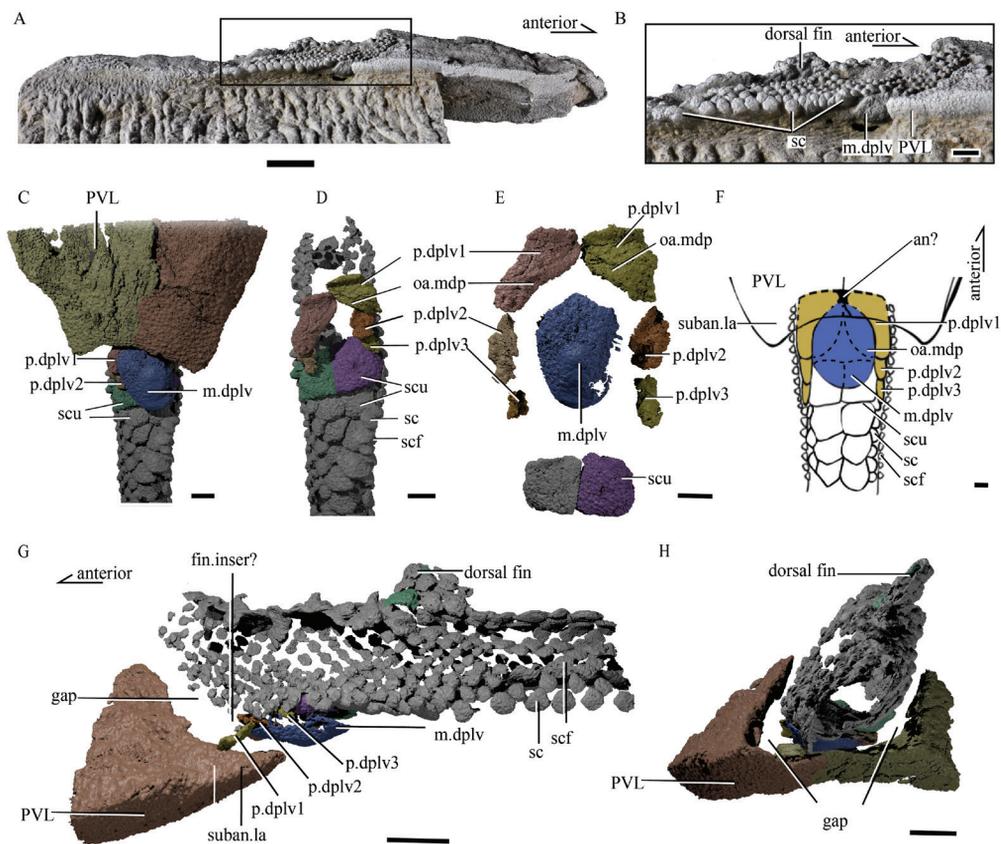


Fig. 1 The pelvic morphology of *Parayunnanolepis xitunensis*

A. the right ventrolateral view of the holotype IVPP V11679.1, coated in ammonium chloride sublimate; B. close-up of the pelvic region in right ventrolateral view; C–E, G, H. the reconstructed pelvic skeleton:

C. ventral view *in situ*, D. ventral view with trunk shield removed, E. exploded ventral view, G. left lateral view, H. posterior view; F. reconstructed pelvic morphology in line drawings. Scale bars = 5mm
 an?. possible position of the anus; fin.inser?. potential position of pelvic fin insertion, if present;
 m.dplv. median dermal pelvic plate; oa.mdp. overlapped area for the median dermal pelvic plate;
 p.dplv1–3. first, second and third paired dermal pelvic plates; PVL. posterior ventrolateral plate;
 sc. ventrolateral scales; scf. flanking scales; scu. ventral scutes;
 suban.la. subanal lamina of the posterior ventrolateral plate

like a right-angled triangle, with one side facing laterally. The posterior angle overlaps a large area of the second pair of the pelvic plates. The anterior side is strongly curled ventrally. The ventral surface has a depressed area (oa.mdp, Fig. 1E, F), roughly matching the pointed anterior contour of the median pelvic plate. Each of the second pair of pelvic plates (p.dplv2, Fig. 1C–G) is an elongated plate, and the third paired pelvic plates (p.dplv3, Fig. 1D–G) are smaller, and plank-like, in turn overlapped by the posterior part of the second paired plate.

Previously designated as one of the paired dermal pelvic girdles (Zhu et al. 2012b:fig. S1c), the large oval plate is shown by the 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 the depressed areas both on the first paired pelvic plates and on the ventral scutes suggest that the median plate overlaps the adjacent plates extensively. The anterior end of the plate is slightly pointed. The centre of the median plate is domed, and the posterior margin is round. The straight anterolateral margins matching the shape of the depressed area of the first lateral paired plates (oa.mdp, Fig. 1E, F). This suggests that the restored median plate covered the gap between the paired plates completely. Given the ventral side of the post-thoracic skeleton is covered by overlapping plates and scutes, the possible location of the anal opening is left to be anterior to the first paired plates, and the median plate (an?, Fig. 1F), similar to the anal opening in *Sigaspis* (Fig. 2). In that case, the first paired plates in life could not overlap one another medially, although they are preserved this way.

Posterior to, and partly overlapped by the median pelvic plates, are the serial ventral scutes in pairs (scu, Fig. 1C–F). The pelvic plates and the scutes are all covered externally with

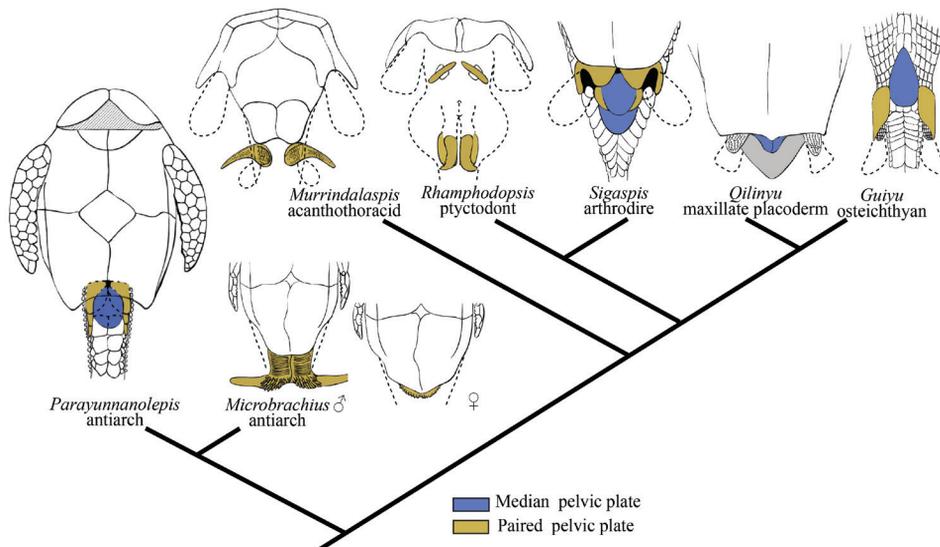


Fig. 2 Pelvic dermal skeleton in various early jawed vertebrates

The phylogeny is a summary from Zhu et al. (2019). The phylogenetic position of *Murrindalaspis*, an incompletely known acanthothoracid placoderm, is inferred by the position of *Romundina*, a better known acanthothoracid but lacking pelvic preservation

fine tubercles. The scutes differ from the flanking body scales in being morphologically more like the flat dermal plates rather than the dome-shaped scales. Nonetheless the scutes can be easily distinguished from the pelvic plates in being serial and rectangular-shaped. Interestingly, the scales immediately flanking the scutes (sc, Fig. 1B, D, F, G) show an intermediate condition, in being round and slightly domed like the flank scales, but they are significantly larger than the flank scales (scf, Fig. 1D, F, G). They have fine tubercular ornament as on the ventral scutes, whereas the 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 the former are copulatory organs, evidenced by the long denticles distinctive to the rest of dermal ornaments (Long et al., 2015). In male *Microbrachius*, the plates are fused in the midline, and are viscerally grooved to function as dermal claspers. In the female these are flat genital plates. Contrary to the *Parayunnanolepis* condition, in both male and female forms they only include one pair of dermal elements that are rigidly attached to the PVL plate. 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) suggest these pelvic plates are of endoskeletal origin with both peri- and endochondral ossifications, by comparison with the endoskeletal girdle previously identified in *Parayunnanolepis*. In the light of the new data provided here, these possible endoskeletal plates in *Bothriolepis* are not a direct comparison to the pelvic plates in *Parayunnanolepis*, but they suggest that the pelvic appendage might be present in antiarchs, if the fin radials (Charest et al., 2018:fig. 2) are correctly identified.

The basal arthrodire *Sigaspis* has 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 1) the first paired plates in *Sigaspis* develop a dorsal or iliac lamina surrounding the fenestra for the pelvic fin insertion, making it a functional dermal girdle; 2) there are two, instead of one, median plates arranged along the midline. The dermal pelvic girdle was presumably lost in higher nested arthrodires such as *Cocosteus* (Trinajstić et al., 2015).

The Silurian “maxillate placoderm” *Qilinyu* possesses a median pelvic plate (shown but not labelled in Zhu et al., 2016:fig. S2) comparable to that in *Parayunnanolepis*, in addition to the 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 and curved

plate attached externally to the endoskeletal pelvic girdle, which is a flat and oval ossification resembling the scapulacoracoid. The male clasper is capped with dermal element and lined beneath by additional dermal plates, and the female genital plate is covered by specialized dermal scales (Fig. 2) (Miles, 1967; Trinajstić et al., 2015). Notably, all these copulatory dermal elements are considerably posterior in relation to the pelvic girdle, and may not be strictly homologous to the antiarch dermal claspers, which are positioned anteriorly, attaching 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 the lateral dermal pelvic girdles (Zhu et al., 2012a). Evidently, the arthrodires, antiarchs and the early osteichthyans all possess both median and paired pelvic elements, either this can be interpreted as the primitive gnathostome condition, or else the result of parallel evolution. Ptyctodonts lack median pelvic plates, and the presence of any median pelvic plate is currently uncertain in acanthothoracids. Definitive conclusions cannot be drawn on the homology between the lateral dermal pelvic elements across the major early gnathostome groups, due to the absence of the PVL plate as a landmark in some of the taxa. In general, one should be cautious when comparing the 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 in closely related taxa (Aquino and Schaefer, 2010:fig. 9), and it is not possible 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* in having spine-like projections and bracing 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, characterizing the tetrapods but rarely present in aquatic basal gnathostomes, is a support for the argument that the vertebrate anterior and posterior paired appendages are serial homologous structures, from the early stage of their evolutionary history. However, in contrast to the condition above, 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, the 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 the locomotive appendages (pelvic fin and girdles) or copulatory organs (claspers).

4.2 Functional speculation of the pelvic plates in *Parayunnanolepis*

As previously described (Zhu et al., 2012b), both dermal and endoskeletal pelvic girdles were present in *Parayunnanolepis*. The endoskeletal pelvic girdle in early vertebrates has no other known function than for the fin insertion, so the presence of pelvic fin is usually inferred.

However, the endoskeletal pelvic girdle is now identified instead as paired dermal plates, which are flat dermal plates along the ventral surface of the post-thoracic body, lacking 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 the other dermal elements *in situ*, making the insertion of the pelvic fins to these parts impossible. Thus, it is not certain if the paired pelvic dermal plates in *Parayunnanolepis* are functional “girdles”. They also differ from the known female genital plates in *Microbrachius* in shape, in positioned anterior to, rather than trailing the posterior margin of the PVL, and in lacking the distinctive auxiliary structures such as the sharp, long denticles. With the 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 place 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 of the large ventral scutes extensively overlap the posterior ones like tiles, indicating that the scale-covered post-thoracic tail must be quite rigid. The thrust locomotion is thus largely achieved by the swinging of the rigid tail around the significantly scaleless gap (gap, Fig. 1F, G) between the two components, the scale-covered post-thoracic tail and the thoracic armour.

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基于CT数据的副云南鱼腰带部位形态再研究

朱幼安¹ 王雅婧² 瞿清明³ 卢静^{1,4} 朱敏^{1,4}

(1 中国科学院古脊椎动物与古人类研究所, 中国科学院脊椎动物演化与人类起源重点实验室 北京 100044)

(2 南京大学地球科学与工程学院 南京 210023)

(3 厦门大学生命科学院细胞应激生物学国家重点实验室 厦门 361005)

(4 中国科学院大学 北京 100049)

摘要: 腰带部位的形态, 以及腹鳍在最早的有颌脊椎动物中是否存在, 是解答脊椎动物附肢如何起源的关键。我国云南曲靖下泥盆统西屯组中的西屯副云南鱼(*Parayunnanolepis xitunensis*)过去被描述为具有外骨骼和内骨骼的腰带。基于高精度CT数据重新描述了西屯副云南鱼正型标本的腰带部位形态。结果显示副云南鱼并没有像之前描述的那样, 同时保存一对大的膜质腰带和对应内骨骼腰带, 而是在腰带部位拥有三对成对的膜质骨片, 以及

一块较大的中线膜质骨片。这些成对的膜质骨片是平坦的，位于躯体腹面，区别于其他早期有颌类拥有背侧叶的膜质腰带。目前仍没有决定性证据证明副云南鱼是否具有内骨骼腰带。比较早期有颌类各大类群中腰带部位膜质骨骼形态，可以看到腰带部位同时存在成对和中线膜质骨片这一型式在这些大类群中也有发现，可能是有颌类的祖征。有颌类在早期演化中可能将腰带部位的膜质骨片整合入不同的功能结构单元中。

关键词：早泥盆世，成对附肢，腹鳍，盾皮鱼，胴甲鱼类，三维重建

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