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An antiarch placoderm shows that pelvic girdles arose at the root of jawed vertebrates

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Almost all gnathostomes or jawed vertebrates (including osteichthyans, chondrichthyans, 'acanthodians' and most placoderms) possess paired pectoral and pelvic fins. To date, it has generally been believed that antiarch placoderms (extinct armoured jawed fishes from the Silurian–Devonian periods) lacked pelvic fins. The putative absence of pelvic fins is a key character bearing on the monophyly or paraphyly of placoderms. It also has far-reaching implications for studying the sequence of origin of pelvic girdles versus that of movable jaws in the course of vertebrate evolution. *Parayunnanolepis xitunensis* represents the only example of a primitive antiarch with extensive post-thoracic preservation, and its original description has been cited as confirming the primitive lack of pelvic fins in early antiarchs. Here, we present a revised description of *Parayunnanolepis* and offer the first unambiguous evidence for the presence of pelvic girdles in antiarchs. As antiarchs are placed at the base of the gnathostome radiation in several recent studies, our finding shows that all jawed vertebrates (including antiarch placoderms) primitively possess both pectoral and pelvic fins and that the pelvic fins did not arise within gnathostomes at a point subsequent to the origin of jaws.

Keywords: pelvic girdles; placoderms; antiarchs; jawed vertebrates; Devonian

1. INTRODUCTION

Vertebrates include agnathans (jawless fishes) and gnathostomes (jawed fishes and tetrapods). While some agnathans (i.e. osteostracans) possessed paired pectoral fins found in gnathostomes, no agnathans had paired pelvic fins. On the other hand, almost all gnathostomes (living osteichthyans and chondrichthyans, plus extinct forms known as 'acanthodians' and placoderms) have both paired pectoral and pelvic fins [1]. The putative absence of pelvic fins among the antiarch placoderms [2] has been a puzzling exception with far-reaching implications for studying the

sequence of origin of major evolutionary novelties (pectoral fins, pelvic fins and movable jaws) in the evolutionary history of vertebrates in general and gnathostomes in particular.

Traditionally grouped within the class Placodermi [1–5], the antiarchs from the Silurian and Devonian periods are characterized by a distinct bony form with box-like thoracic exoskeleton and with elongate pectoral fins encased in interlocking dermal plates [1,6–8]. Morphological features attributed to antiarchs and their interpretation play a pivotal role in recent analyses of early gnathostome interrelationships [2,9–12]. In particular, the putative absence of pelvic fins in antiarchs constitutes a key character bearing on placoderm monophyly [2,12,13] or paraphyly [9–11]. Sometimes coupled with the assumed osteostracan-like vascularization of the pectoral fin and branchial chamber ([9], contra [13]), the putative absence of pelvic fins has been considered (implicitly or explicitly) to be primitive (as in agnathans) [10] rather than due to secondary loss within placoderms. Consequently, antiarchs are often regarded as a highly primitive clade, placed either in an unresolved trichotomy with all other jawed vertebrates (non-antiarch placoderms, chondrichthyans, 'acanthodians' and osteichthyans) and the jawless osteostracans [11], or as the sister-group to all other jawed vertebrates though crownward to the jawless osteostracans [10]. These results imply that paired pelvic appendages (pelvic fins/hind limbs) appeared within the gnathostomes at a point subsequent to the development of movable jaws.

As the post-thoracic anatomy of antiarchs is rarely preserved, the presence or the absence of pelvic fins in most antiarchs has been difficult to ascertain. Pelvic fins are known to be absent in a number of well-preserved Middle–Late Devonian euantiarchs, including *Bothriolepis gippslandiensis* [14], *Asterolepis* [15], *Remigolepis* [16] and *Pterichthyodes* [17]. *Bothriolepis canadensis*, from the Late Devonian of Quebec, has traditionally been reconstructed with small pelvic fins [5], but this interpretation has been brought into question [18].

First described by Zhang *et al.* [19], *Parayunnanolepis xitunensis* from the Early Devonian (Xitun Formation, Lochkovian, *ca* 413 Ma) of Yunnan, China [20] represents the only example of a primitive non-euantiarchan antiarch with extensive post-thoracic preservation. The original description, based in large part on the almost complete holotype (Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V11679.1), showed no trace of pelvic appendages in the figured and photographed material or in the reconstruction. This specimen has been subsequently cited as confirming the lack of pelvic fins in early antiarchs and thus in all antiarchs in general [2,10,18]. A re-examination of this specimen with additional preparation of the ventral surface now reveals the unambiguous presence of pelvic fins as indicated by paired pelvic girdles (figure 1) to be described below.

2. MATERIAL AND METHODS

The studied specimen (IVPP V11679.1), housed in the IVPP, Beijing, is the holotype of *P. xitunensis* from the Xitun Formation (Lochkovian, Early Devonian) of Yunnan, China [19,20]. The specimen was prepared mechanically to reveal the ventral surface of the body
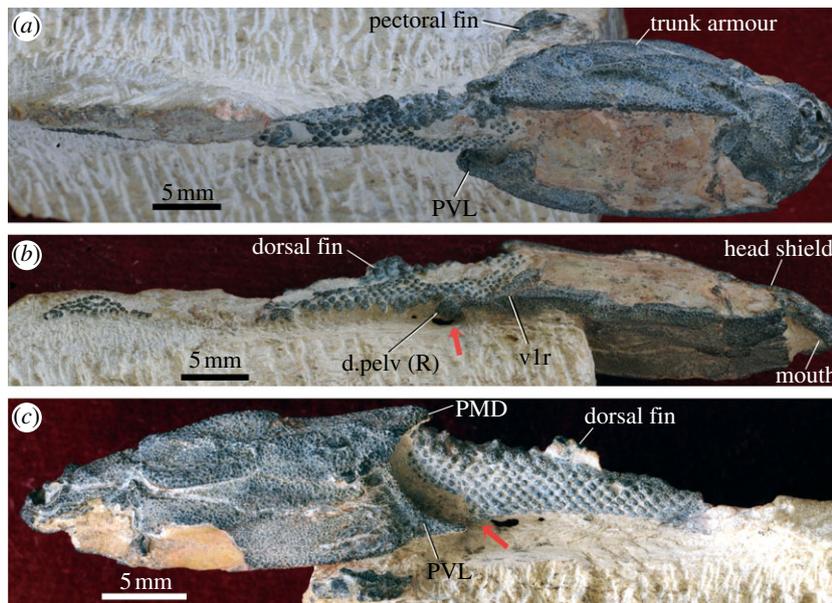
Figure 1. *Parayunnanolepis xitunensis*, a primitive antiarch with pelvic girdles from the Lower Devonian of China (IVPP V11679.1). (*a*) Dorsolateral view, (*b*) right ventrolateral view showing the dermal pelvic girdle immediately behind the trunk armour, and (*c*) left lateral view. The red arrow in (*b*) points to the close-up area in figure 2*c*, and the red arrow in (*c*) points to the close-up areas in figure 2*a,b*. d.pelv, dermal pelvic girdle; PMD, posterior median dorsal plate; PVL, posterior ventrolateral plate; R, right side; vlr, ventrolateral ridge of trunk armour.

immediately behind the trunk shield. The phylogenetic framework used here is based on Janvier [1], Young [2] and Brazeau [10].

3. MORPHOLOGICAL OBSERVATIONS

The holotype (V11679.1) consists of an articulated head and trunk armour (with most of the pectoral fins missing) along with the unarmoured post-thoracic anatomy all the way to the posterior tip of the tail (figures 1 and 2*a*−*c*; electronic supplementary material, figure S1*a*−*d*). As with *Phymolepis cuifengshanensis* [21], the orbital fenestra is marked posteriorly by a prominent postpineal thickening (pp.th; electronic supplementary material, figure S1*a*) that presents a raised crest on the postpineal and lateral plates.

The unarmoured post-thoracic portion accounts for about 58 per cent of the total length of the fish (35 mm out of 60 mm) and is covered by roundish non-overlapping scales. Much of the dorsal and lateral squamation is preserved. About 20 mm down the length of the post-thoracic portion, a small area of the tail (*ca* 10 mm long) is missing. Except for the area immediately behind the trunk shield, most of the ventral surface is currently obscured by matrix.

In lateral view, the scales on the post-thoracic body are arranged in posteroventrally oriented bands with abrupt variations in scale size down the length of the fish. The largest scales, some exceeding 1 mm in diameter, are present on the dorsal fin and adjacent dorsal areas. Scales halfway down the length of the tail are *ca* 0.6−0.8 mm in diameter, while the areas immediately posterior to the trunk armour and on the tip of the tail have the smallest scales (*ca* 0.4 mm in diameter). Anterior to the dorsal fin, the median dorsal scales are raised and form a row of tapering conical structures. No evidence of a spinose median dorsal fringe posterior to the dorsal fin is observed, contrary to the original outline restoration [19].

The dermal pelvic girdles (figure 2*c*) bear the same tuberculated ornamentation as the trunk armour and lie in a ventro-lateral position immediately behind the trunk armour, as in arthrodire placoderms [2]. The presence of external ornament on the pelvic girdles reminds of the condition in acanthothoracids like *Murrindalaspis* [22], rather than arthrodires [2] and ptyctodonts [23]. The ventral girdle surface is flat and rhombic (*ca* 4 mm in length), with the lateral margin curving dorsally and merging into the low, oblong lateral surface (figures 1*b* and 2*c*). The curvature thus formed between the two surfaces probably lies at about the same level as the ventro-lateral ridge of the trunk armour. Owing to the lateral compression of the unarmoured posterior trunk during preservation, the left girdle is medially displaced and is partially overlapped (in ventral aspect) by the right girdle. Attached to the medial surface of the left dermal girdle is the left endoskeletal girdle, a massive plate-like structure that is compressed but reveals a discernible length of *ca* 2.6 mm (figures 1*c* and 2*b*). However, no facet for pelvic fin radials can be detected due to the poor preservational condition of internal structures. The dermal and endoskeletal girdles are significantly larger than nearby scales (less than 1 mm in diameter).

As the curvature between the ventral and lateral surfaces of the right dermal girdle appears to be horizontally aligned with the ventro-lateral margin of the trunk armour, the pelvic fins must have occupied a lateral (rather than ventral) position in life. Immediately posterior to the right pelvic girdle, the only clearly visible area of the ventral surface reveals a single row of large ventrolateral scales. Partially exposed squamation suggests that smaller scales occupied the ventral surface medial to this row.

The dorsal fin was originally restored by Zhang *et al.* [19] as a broad-based triangular structure. Re-examination of the holotype suggests a more
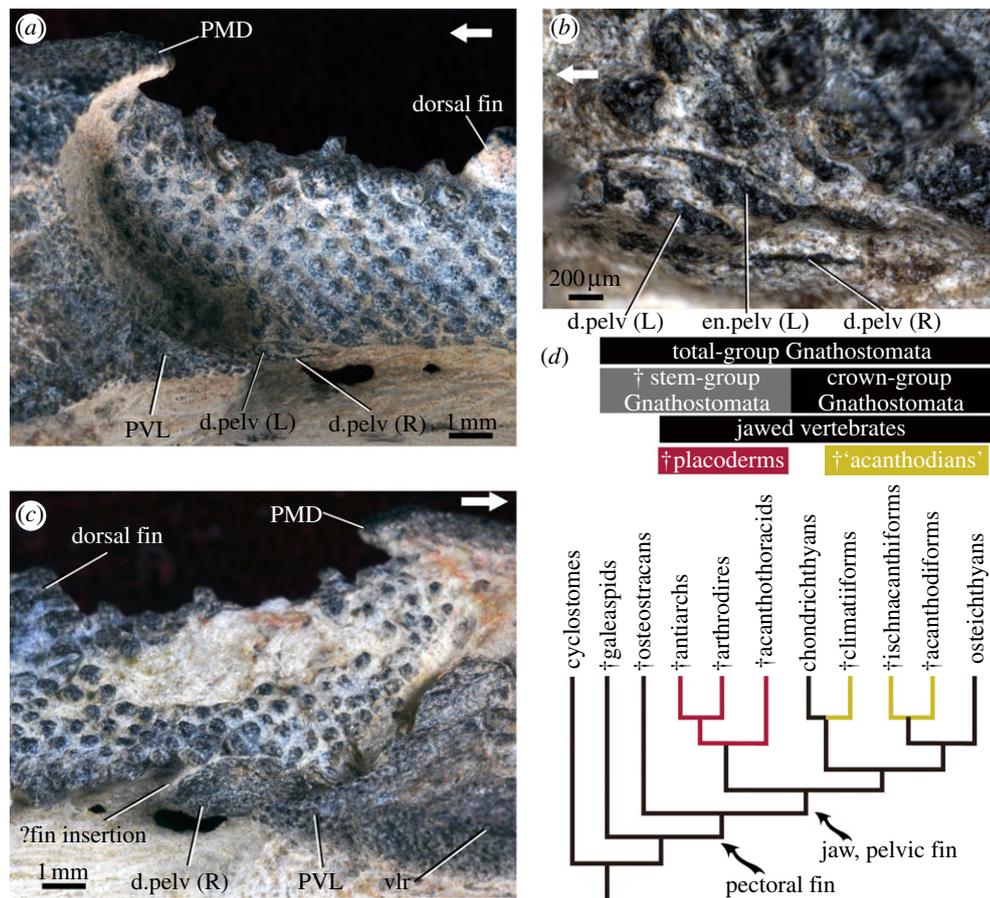
Figure 2. *Parayunnanolepis xitunensis* (IVPP V11679.1) and the phylogenetic framework of jawed vertebrates. (*a*) Close-up of dermal and endoskeletal pelvic girdles in left lateral view, (*b*) close-up of (*a*), (*c*) close-up of the right dermal pelvic girdle in right ventrolateral view, and (*d*) origin of girdle-supported pectoral and pelvic fins close to the root of jawed vertebrates. Composite cladogram based on Brazeau [10] for 'Acanthodii' and Young [2] for the relationships of other groups. White arrows point to the anterior end of the fish. en.pelv, endoskeletal pelvic girdle; L, left side; and other abbreviations see figure 1.

compact, short-based fin, judging by the near complete outline of the preserved fin-base. Median dorsal scales immediately posterior to the fin-base indicate an abrupt posterior termination of the dorsal fin rather than the gentle, sloping gradient depicted by Zhang *et al.* [19]. Distinct dorsal flexure in the terminal portion (*ca* 6 mm long) of the notochordal mass of the tail may indicate the presence of a membranous hypochordal lobe (electronic supplementary material, figure S1*a,c*), as distinct from the originally restored tail tapering to a finless tip [19].

4. DISCUSSION
The presence of pelvic girdles in the primitive antiarch *Parayunnanolepis* conclusively refutes the prevailing notion that all antiarchs lack pelvic appendages like jawless osteostracans [2,10]. Viewed in this light, the absence of pelvic fins in derived antiarchs (e.g. *Bothriolepis*) can be best interpreted as secondary loss (as in some non-antiarch placoderms such as the petalichthyid *Lunaspis*) [2], rather than as a retained primitive feature [10]. While other characters bearing on placoderm monophyly (e.g. pectoral fin vascularization) may still be debatable [2,9,13], absence of pelvic fins can no longer be deemed as an unambiguous character supporting placoderm paraphyly [10].

This pelvic girdle discovery shows that all jawed vertebrates (including antiarch placoderms) primitively possess both pectoral and pelvic appendages (figure 2*d*; electronic supplementary material, figure S1*e*). While girdle-supported pectoral fins must have arisen before the origin of movable jaws [24], girdle-supported pelvic fins should no longer be inferred as having originated at a point subsequent to the origin of jaws [10] (electronic supplementary material, figure S1*e*). Together with recent findings of paired appendages and girdles in other gnathostome groups [1,24,25], this discovery highlights the prevalence of parallel loss and/or reduction of pelvic fin and girdle components as a recurring phenomenon in the diversification of gnathostome groups, including placoderms.

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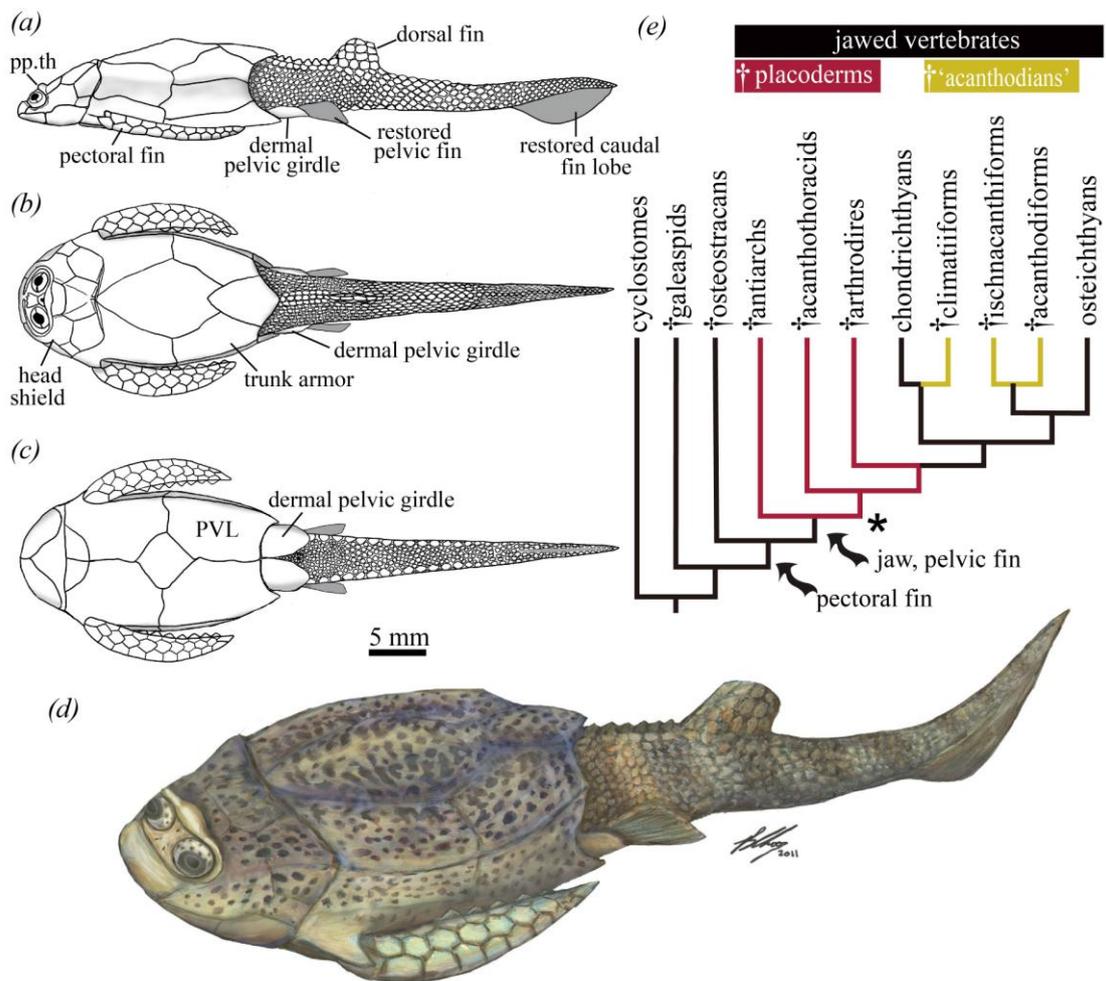
Supplementary Figure - S1 - (*a-c*) Revised restoration of *Parayunnanolepis xitunensis* Zhang *et al.*, 2001 (Lochkovian, Early Devonian) in lateral (*a*), dorsal (*b*) and ventral (*c*) views. (*d*) Life reconstruction of *P. xitunensis*. (*e*) Alternative phylogeny of basal gnathostomes favoring placoderm paraphyly, simplified from [10]. Asterisk indicates previously inferred node for the origin of girdle-supported pelvic fins [10]. pp.th, postpineal thickening.