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On the homology of the posteriormost gill arch in polypterids (Cladistia, Actinopterygii)

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Polypterids are unusual among ray-finned fishes in possessing only four rather than five gill arches. We review the two current hypotheses regarding the homology of the last gill arch in polypterids: that it represents (1) the fifth or (2) the fourth arch of other actinopterygians. Arguments for the alternative hypotheses drawn from different anatomical systems are compiled and evaluated. We conclude that in polypterids the last arch represents the fourth arch of other Actinopterygii and the fifth arch is absent. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, **138**, 495–503.

ADDITIONAL KEYWORDS: branchial circulation – branchial muscles – branchial nerves – *Erpetoichthys* – *Polypterus*.

INTRODUCTION

The African freshwater fish family Polypteridae comprises two genera, *Polypterus* (bichirs), with ten species, and the monotypic *Erpetoichthys* (reedfish) (Poll & Gosse, 1995). Since their discovery at the beginning of the nineteenth century, polypterids have attracted the interest of numerous comparative vertebrate anatomists and systematists. Although they have been assigned variously to different higher level groups of bony fishes, they are currently considered to be the most basal living actinopterygians (Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989). Polypterids retain several primitive characters that are unknown in other Recent Actinopterygii but occur variously among fossil ray-finned fishes and other osteichthyans, e.g. the presence of thick, palaeoniscoid-type, rhombic ganoid scales, paired gular plates, paired lungs opening to the ventral wall of the pharynx, and a holoblastic egg development (Kerr, 1907; Daget, 1950; Greenwood, 1984; Bartsch, Gemballa & Piotrowski, 1997). Polypterids also show a number of autapomorphies such as separate dorsal finlets, specialized anatomy of the pectoral fins, a particular type of sexually dimorphic anal fin associated with a unique mating behaviour, and a reduced number of gill arches (Müller, 1846; Greenwood, 1984; Gardiner & Schaeffer, 1989; Britz & Bartsch, 1998).

Polypterids are unusual among actinopterygian fishes in possessing one fewer gill arches, i.e. four rather than the usual five that characterize gnathostome vertebrates (Figs 1,2). Whereas the homology of the first three arches has never been questioned, two hypotheses concerning the homology of the posteriormost arch of polypterids exist: (1) the fourth gill arch is lacking and the posteriormost arch is the fifth (Wiley, 1979; Rosen *et al*., 1981); (2) the fifth gill arch is lacking, and the posteriormost arch is the fourth (Müller, 1846; Gegenbaur, 1898; Daget, 1950; Jollie, 1962; Nelson, 1969).

The presence of only four gill arches was noted and/or illustrated by many other authors (e.g. in addition to those noted above, Agassiz, 1833–1843; Hyrtl, 1869; van Wijhe, 1882; Goodrich, 1909, 1930; Allis, 1922; Jordan, 1925; Purser, 1926; Moy-Thomas, 1933; de Beer, 1937; Berg, 1947; Pehrson, 1947; Daget, 1958; Devillers, 1958; De Smet, 1965; Poll, 1965; Poll & Deswattines, 1967; Jarvik, 1980; Patterson, 1982; Jollie, 1984; Lauder & Wainwright, 1992). Surprisingly, however, this fact has rarely been mentioned in more recent con-

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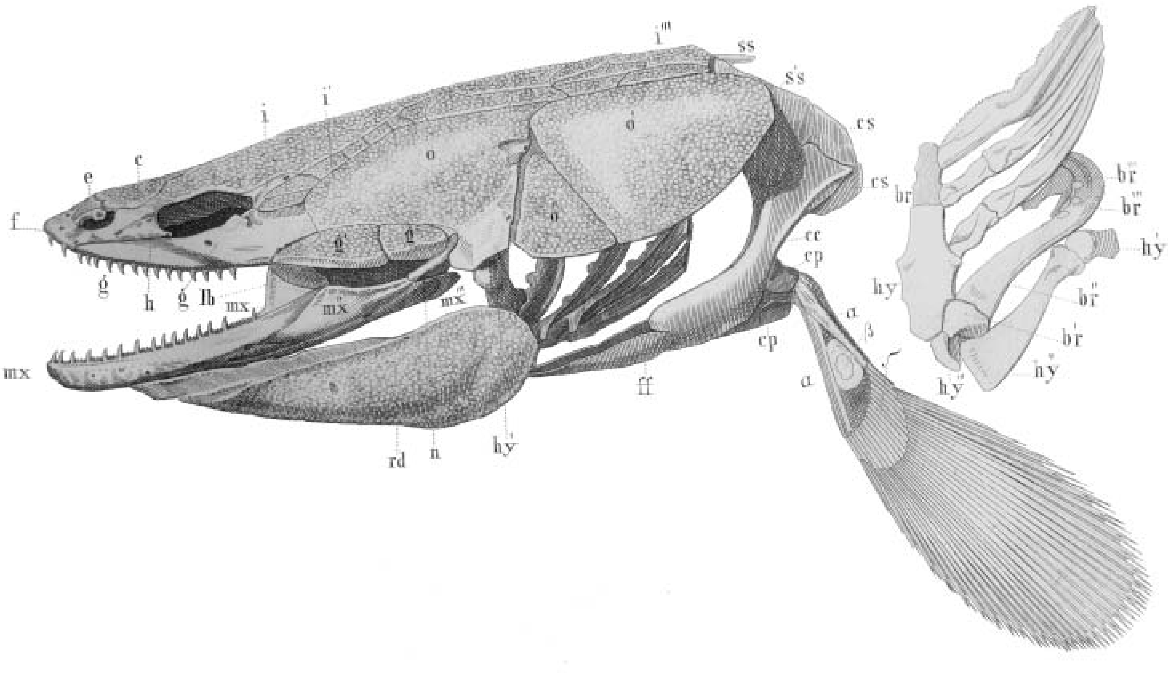

Figure 1. *Polypterus bichir*, skull in lateral view and copula and right ventral gill arches in ventral view, reproduced from Müller (1846). Note presence of only four gill arches.

tributions dealing with polypterids (e.g. Lauder & Liem, 1983; Gardiner, 1984; Greenwood, 1984), was not included in Gardiner & Schaeffer's (1989) list of cladistian synapomorphies, and is omitted from recent textbooks (Gosse, 1990; Nelson, 1994; Poll & Gosse, 1995; Bond, 1996; Moyle & Cech, 1996; Helfman, Collette & Facey, 1997; Liem *et al*., 2000; Berra, 2001).

The most recent paper we found in which *Polypterus* was described and illustrated to have only four gill arches is Wacker, Bartsch & Clemen (2001). Those authors accepted, without discussion, the last arch as the fourth, as did some of the earlier authors mentioned above. Accordingly, the question of the identity of the last arch in polypterids has not been addressed since Wiley (1979) and Rosen *et al*. (1981) argued that it represents the fifth rather than the fourth.

The current paper reviews the arguments for the alternative views and proposes the most plausible hypothesis of homology based on available evidence.

ARGUMENTS SUPPORTING THE HYPOTHESIS THAT THE LAST ARCH IN POLYPTERIDS IS THE HOMOLOGUE OF THE FIFTH ARCH IN OTHER ACTINOPTERYGIANS

I. MUSCLES USUALLY ASSOCIATED WITH THE FIFTH ARCH INSERT ON THE LAST ARCH IN POLYPTERIDS

Edgeworth (1935: 9) pointed out that the posteriormost of the four gill arches in *Polypterus* is associated with three muscles that typically are associated with the fifth arch of 'other Ganoids . . . the Cuccularis, the Coracobranchialis and the Sphincter oesophagi'. He did not, however, invoke this fact as support of the hypothesis that the last arch in *Polypterus* represents the fifth arch of other actinopterygians. Instead, he noted that 'This at first sight suggests that any one branchial segment has dropped out between the 1st and 4th of *Polypterus*, but there is no evidence of this in developmental stages in the shape of an atrophying gill-cleft and the breadths of the four segments are equal. It follows that the number of segments has been lessened by the second method mentioned above'. He explained this second method as 'separation of the branchial region into fewer segments without the loss of any particular segment'. Edgeworth (1935) thus did not believe that one specific segment was actually lost but that the whole developmental process that produced the differentiation of the arches was remodelled.

We believe that Edgeworth confused two processes, ontogeny and phylogeny. Clearly, if a species possesses four segments as a derived state compared to one that possesses five, the most parsimonious interpretation is that the first species has lost a segment. How this phylogenetic loss is expressed in ontogeny is incidental, and the question remains: which of the five segments present in most gnathostomes is lacking in *Polypterus*?

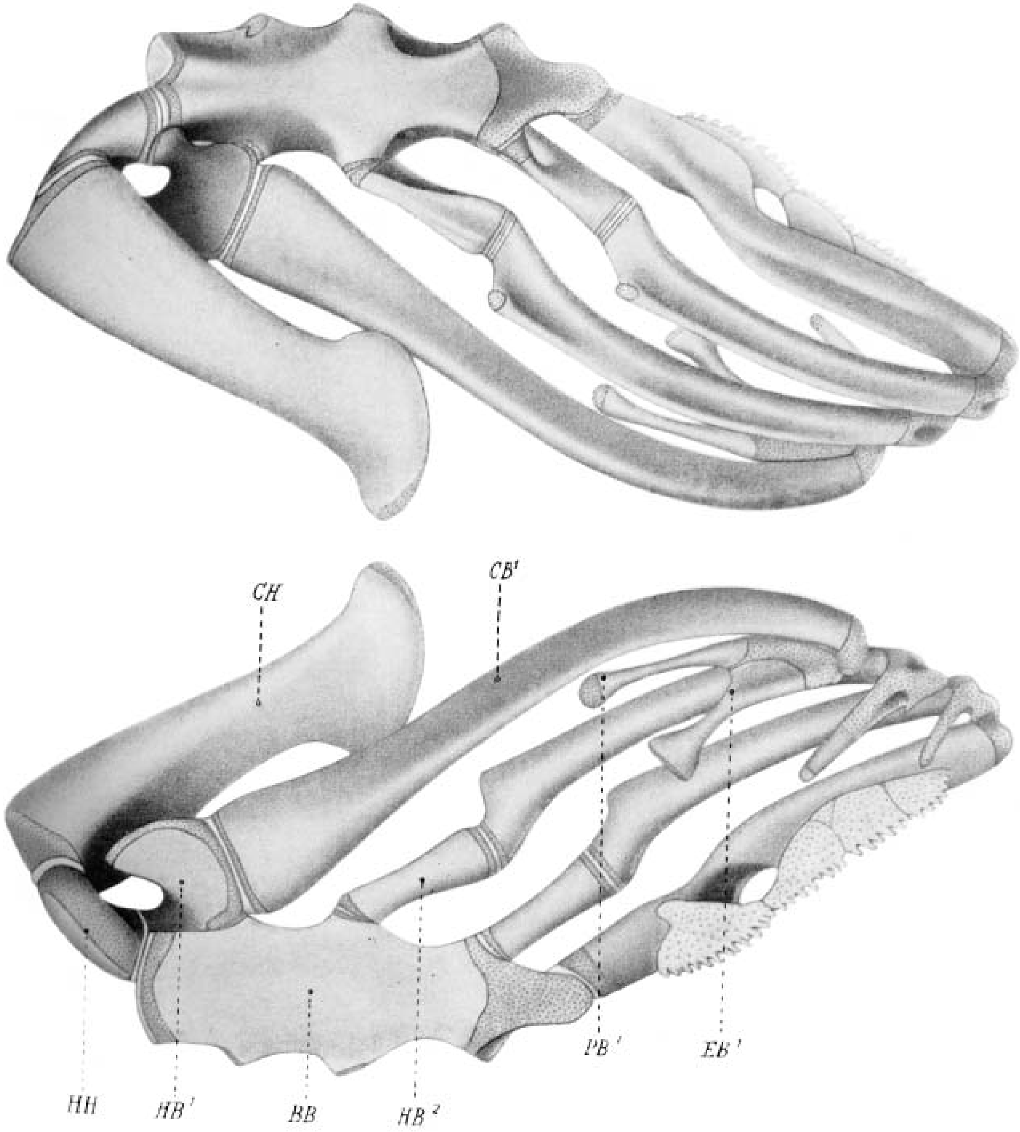

Figure 2. *Polypterus bichir*, copula and right gill arches in ventral (above) and dorsal (below) views, reproduced from Allis (1922). Note decreasing size of dorsal gill arch elements from first to third arch.

The association of specific muscles with a specific gill arch therefore potentially has bearing on the identity of that arch, and Edgeworth's (1935) observations in this regard must be addressed. Edgeworth's (1935) cuccularis, also called trapezius in earlier papers, is the protractor pectoralis of recent authors (Winterbottom, 1974; Greenwood & Lauder, 1981). Edgeworth was correct in reporting that polypterids have a protractor pectoralis but incorrect in claiming that it inserts on a gill arch. Instead, it originates with the levator muscles of the gill arches from the otic region of the skull and inserts on the cleithrum, a fact that Edgeworth (1911: 240) himself had noted earlier: 'In *Polypterus senegalus* there is a trapezius arising in common with the fourth levator and passing back to the shoulder girdle (Text-Fig. 37)'. Other authors have described an identical configuration of the protractor pectoralis in polypterids (Allis, 1922; Greenwood & Lauder, 1981), and it thus has no bearing on the identity of the last gill arch in polypterids.

Edgeworth was correct, however, that the other two muscles, the coracobranchialis (= pharyngoclavicularis of Allis, 1922 and Wiley, 1979; pharyngocleithralis of Winterbottom, 1974 and more recent authors) and sphincter oesophagi, insert on the last arch in polypterids, as they do in most other actinopterygians, where the last arch is known to be the fifth. Although not bearing directly on the homology of the last arch in *Polypterus* we know of at least two other actinopterygian families in which there is conclusive evidence that the fifth ceratobranchial (Cb5) has been lost, and these two muscles have shifted their usual association with that element to the fourth arch. Within the Anguilliformes, Nelson (1967) reported a graded series ranging from a reduction in size of Cb5 to its complete loss in two separate lineages, Congroidei (some ophichthids), and Anguilloidei (all muraenids). Furthermore, in his description of the branchial muscles of several eels, Nelson (1967) reported the presence of a single pharyngocleithralis in all taxa he examined (other teleosts have two; Winterbottom, 1974), including those that have lost Cb5, but he did not describe or illustrate the site of its attachment in the latter taxa.

Our dissections of the muraenid *Gymnothorax buroensis* (USNM 141538) and the ophichthid *Leiuranus semicinctus* (USNM 238885) show that the pharyngocleithralis arises from the cleithrum and attaches to ceratobranchial 4 (Cb4). The muscle in these species thus has the identical position as its homologue in polypterids. The same applies to the Sphincter oesophagi, which also attaches to Cb4 in the two taxa mentioned above. In conclusion we find in some eels an anatomical situation analogous to that of polypterids, demonstrating that a shift of muscle insertion from the fifth arch to the fourth can actually occur (see also further discussion below).

II. WILEY'S ARGUMENT

Wiley (1979: 160) assumed that the missing arch in *Polypterus* is the fourth arch. His argumentation for this view, however, was not founded directly in the homology of the arch itself. Instead, he invoked indirect evidence based on the homology of the M. rectus ventralis of *Polypterus*: 'If it is hypothesized that the fourth arch is the missing arch in *Polypterus*, then the rectus ventralis of *Polypterus* has the same innervation as the obliquus ventralis 4 of other actinopterygians and the transversus ventralis posterior and pharyngoclavicularis would also retain their normal innervation via the fifth arch post-trematic branch of the vagus . . . Polypterids, then, are unique among examined osteichthyans in having a rectus ventralis modified from an obliquus ventralis 4'. Homology of the rectus ventralis of *Polypterus*, however, has no immediate bearing on the homology of the posteriormost gill arch, because even if loss of the fourth arch is **not** assumed, homology of the rectus ventralis of *Polypterus* with the obliquus ventralis 4 of other actinopterygians may be a valid hypothesis.

Although Wiley (1979) cited Edgeworth (1935), he failed to mention Edgeworth's (1935) characters potentially supporting his hypothesis, i.e. that the three muscles that attach to the posterior arch in polypterids (but see our remarks above on the protractor pectoralis in polypterids) usually attach to the fifth arch in other actinopterygians.

As Wiley (1979: 151) pointed out, his main objective was to test the hypotheses if '. . . Brachiopterygians (polypterids) are either (a) sarcopterygians (Nelson, 1969; Bonde, 1975) (b) actinopterygians (Gardiner, 1973; Schaeffer, 1973), or (c) a collateral group with actinopterygians and sarcopterygians (Daget, 1950; Jessen, 1973)'. One of his points was to dismiss the homology of the rectus ventralis of *Polypterus* with the subarcualis rectus of *Neoceratodus* and larval amphibians, two muscles that according to his view are 'strikingly similar', and it was in this context that he homologized the last arch of polypterids with the fifth arch of other osteichthyans. Wiley (1979: 168) concluded that 'Brachiopterygians therefore can be classified within the Actinopterygii'.

III. THE LAST ARCH IN POLYPTERIDS HAS NO ASSOCIATED DORSAL AND VENTRAL ELEMENTS

Rosen *et al*. (1981: 237) were aware that polypterids have only four gill arches and erroneously claimed that 'Nelson, 1969, has argued that an intermediate arch has been lost and his proposal is supported by the similarity in structure and associated dorsal arch elements on the first arch and the absence of dorsal elements on the fourth and last arch with the first and fifth arches of other fishes'. We found no such argument in Nelson (1969) and note that, to the contrary, he accepted the alternative hypothesis on p. 489, footnote 1: 'The absence of a fifth infrapharyngobranchial as a supporting element by itself is no more remarkable than the secondary absence of endoskeletal supports from other fishes: (1) from some eels (Nelson, 1966) and probably also *Polypterus* (fig. 3C) the absence of fifth ceratobranchials supporting the lower pharyngeal tooth plates (in *Polypterus* it is likely but not certain that the lower pharyngeal plates, as are those of many eels, secondarily are supported by the fourth ceratobranchials); . . .' and on p. 521: 'Ceratobranchials likewise are seldom reduced; the only examples known to the writer are the fifth ceratobranchials in *Polypterus*, *Calamoichthys*, and some eels'. Finally, Nelson (1969: 505, fig. 15a) labelled the articulation of the last arch with the basibranchial plate in *Polypterus* as the articular facet of the fourth ceratobranchial. We are unable to explain the erroneous

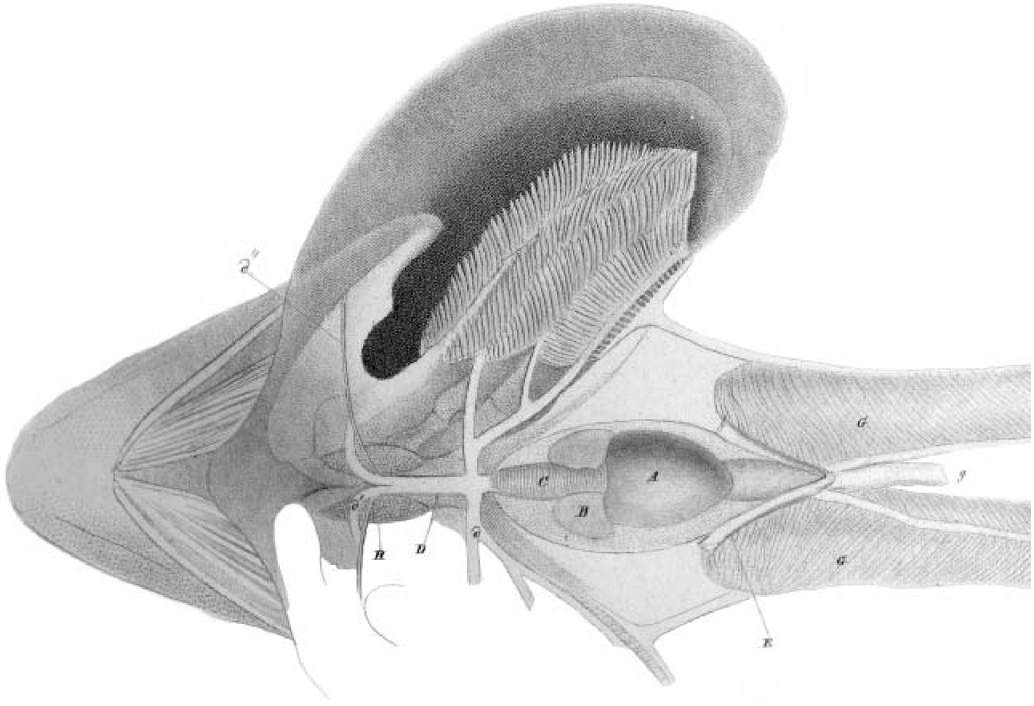

Figure 3. *Polypterus bichir*, ventral view of heart, afferent branchial arteries, pulmonary arteries, lungs, and left branchial arches with gill filaments, reproduced from Müller (1846). Note hemibranch on last arch and presence of four afferent branchial arteries.

interpretation of Nelson's (1969) homology proposal by Rosen *et al*. (1981). Their evidence that the last arch in polypterids is the fifth is then reduced to the fact that, like the fifth arch in other actinopterygians, it has no dorsal elements associated with it. However, a separate little cartilage is developed at the distal tip of the last ceratobranchial of *Polypterus* and was described and interpreted as a fourth epibranchial by Daget *et al.* (1964: fig. 29), as a fourth pharyngobranchial by Clemen, Bartsch & Wacker (1998: fig. 12), and as a fourth epipharyngobranchial by Wacker *et al*. (2001: fig. 17), although the latter authors inconsistently labelled the element as pharyngobranchial four in their figure. We confirmed the presence of this cartilaginous element also for *Erpetoichthys*. We do not comment here on the homology of this element as either an epibranchial, pharyngobranchial or epipharyngobranchial but just note that polypterids have a dorsal gill arch element at the tip of the last ceratobranchial. It is worth noting here that in *Polypterus*, and *Erpetoichthys*, the size of dorsal gill arch elements decreases sequentially from 1 to 3 (Rosen *et al*., 1981, fig. 48B; Clemen *et al.*, 1998, figs 12 and 13; pers. obs.), the third being a mere fraction of the size of the first (Fig. 2) – accordingly extreme reduction of the dorsal element of the fourth arch is not so surprising. The association of a dorsal element with the last ceratobranchial of polypterids thus rejects the only evidence presented by Rosen *et al*. (1981) that this arch is the fifth.

IV. HYPOBRANCHIAL FOUR ABSENT

There is an additional feature in which the posterior gill arch in polypterids resembles the fifth arch of other actinopterygians, although it has not been cited previously as evidence that the last element is the fifth arch. The last arch in polypterids lacks a hypobranchial (Figs 1,2), whereas a hypobranchial is commonly present on the fourth arch among basal osteichthyans (Nelson, 1969). However, hypobranchial four has been lost on at least two other occasions where Cb4 is still well developed, in chondrosteans (van Wijhe, 1882: fig. 2; Marinelli & Strenger, 1973: fig. 282; Grande & Bemis, 1991: figs 17 and 38; Findeis, 1997: fig. 13) and in teleosts (Nelson, 1969). Nelson (1969) did not note the absence of the fourth hypobranchial in chondrosteans.

ARGUMENTS SUPPORTING THE HYPOTHESIS THAT THE LAST ARCH IN POLYPTERIDS IS THE HOMOLOGUE OF THE FOURTH ARCH IN OTHER ACTINOPTERYGIANS

I. The last arch of polypterids bears a hemibranch and an afferent and efferent branchial artery (De Smet, 1965; Poll, 1965; Poll & Deswattines, 1967)

We know of no other actinopterygians in which the fifth arch supports gill filaments or possesses the respective arteries.

Müller (1845: 121, 1846: 149) apparently was the first author who pointed out that the fourth arch of *Polypterus* bears a hemibranch (Fig. 3), that there is no gill slit behind it, and that the lower pharyngeal jaws (his 'Ossa pharyngea inferiora', i.e. the fifth ceratobranchials) are lacking. Although he did not explicitly state it, this suggests that Müller equated the last arch of *Polypterus* with the fourth arch of other fishes based on the presence of gill filaments.

The presence of a hemibranch on the last gill arch of polypterids was noted subsequently by several authors (van Wijhe, 1882; curiously Allis, 1922 did not report it but figured it on pl. 17; Goodrich, 1930; Daget, 1950, 1958; Daget *et al.*, 1964; De Smet, 1965; Poll & Deswattines, 1967). The hemibranch is supplied by afferent and efferent branchial arteries (Müller, 1846; Purser, 1926; Goodrich, 1930; Daget *et al.*, 1964; De Smet, 1965; Poll, 1965; Poll & Deswattines, 1967) that from their position in relation to the other branchial arteries must be considered the fourth branchial arteries. Edgeworth (1935), Wiley (1979) and Rosen *et al*. (1981), on the other hand, did not mention the presence of filaments on the last arch or its supply with afferent and efferent branchial arteries, indicating that they were either unaware of them or did not consider them pertinent to the homology problem.

II. Innervation argument

Where it has been described for other actinopterygians, as in the chondrosteans *Polyodon* (Norris, 1925), *Acipenser* (Sewertzoff, 1911; Norris, 1925; Marinelli & Strenger, 1973), and *Scaphirhynchus* (Norris, 1925), the ginglymodan *Lepisosteus* (Norris, 1925), the halecomorph *Amia* (Allis, 1897), and the teleosts *Menidia* (Herrick, 1899), *Scomber* (Allis, 1903), and *Polycentrus* (Freihofer, 1978), the vagal nerve has four main branchial trunks (1–4) associated sequentially with gill arches 2 through 5. The fourth vagal trunk is thus associated with the fifth gill arch and, among other things, innervates its musculature, i.e. the pharyngocleithralis and the transversus. ventralis posterior. As described by Allis (1922), and described and illustrated by Piotrowski & Northcutt (1996), only branchial trunks 1–3 are present in *Polypterus*, the fourth, we conclude, having been lost. This conclusion is supported by the fact that the last branchial trunk of the vagus shows the same branching pattern and position relative to the gill arches as the third trunk in other actinopterygians, i.e, its pretrematic branch runs along the third gill arch and its post-trematic branch runs along the fourth arch.

Innervation of the pharyngocleithralis and transversus ventralis posterior musculature in *Polypterus* offers additional support that the fourth branchial trunk of the vagus is missing. Where known in other actinopterygians (Allis, 1897; Herrick, 1899; Allis, 1903; Norris, 1925; Freihofer, 1978), these muscles are innervated by fibres of the post-trematic branch of the fourth vagal trunk ('Rami pharyngei inferiores' of Stannius, 1849 and 'pharyngeal branch of the nervus vagus' of Allis, 1922). According to Allis (1922: 288), in *Polypterus* these muscles are instead innervated by small branches of the intestinal branch of the vagus. In contrast, on p. 259, Allis (1922) stated that innervation of the pharyngocleithralis and transversus posterior muscles are 'by the pharyngeal branch of the vagus nerve, as stated in one of my earlier works (Allis, 1917; p. 358)'. However, the only reference to that muscle in *Polypterus* we found on that page (Allis, 1917: 358) stated: 'In sections of a 75-mm specimen of *Polypterus senegalus* I also find these muscles innervated by a branch of the vagus and not by spino-occipital nerves'. Although we are unable to resolve Allis's (1922) conflicting statements, we note most importantly that Allis (1922) and Piotrowski & Northcutt (1996) did not report a separate fourth trunk of the vagus and thus no 'pharyngeal branch' of that nerve in *Polypterus*.

Wiley (1979: 160) remarked that: 'the pharyngoclavicularis and the transversus ventralis posterior are innervated by what Allis termed the "pharyngeal branch of the vagus" (i.e. X4)', and a few lines down: 'the transversus ventralis posterior and pharyngoclavicularis (in *Polypterus*, note by the authors) would also retain their normal innervation via the fifth arch post-trematic branch of the vagus (X4, the pharyngeal branch)'. He thus apparently was unaware of Allis's (1922) conflicting descriptions of the innervation of these muscles and of the fact that *Polypterus* has no such 'fifth arch post-trematic branch of the vagus'.

Surprisingly Piotrowski & Northcutt (1996) made no mention of the unusual reduced number of gill arches and vagal branchial trunks in *Polypterus*, nor did they provide any information on the innervation of the pharyngocleithralis and transversus ventralis posterior muscles. They noted a small 'pars posterior' of the third branchial trunk of the vagal nerve overlooked by Allis (1922), but they found this branch to innervate the posterior part of the fourth levator. It therefore cannot represent a vestigial fourth vagal branch.

We conclude that in polypterids the lack of a separate fourth branchial trunk of the nervus vagus and a modified innervation of the pharyngocleithralis and transversus ventralis muscles, i.e. a shift from the fourth branchial trunk to the intestinal branch of the vagus, represent additional evidence that the fifth gill arch was lost in polypterids.

III. The fifth arch is lost in some anguilliforms

We know of no other actinopterygians that have lost arches anterior to the fifth when that element is still present. We noted above that contrary to the claim of Rosen *et al*. (1981), Nelson (1969) believed that the missing arch in *Polypterus* is the fifth and, as proposed by Gegenbaur (1898), that the autogenous toothplates on the dorsal surface of Cb4 are shifted remnants of the fifth arch. He compared this case to the situation he encountered in congroid and anguilloid eels. In these taxa a reduction of ceratobranchials five occurs starting from a Cb5 of normal size bearing an autogenous lower pharyngeal toothplate on its dorsal surface, through those with a smaller Cb5 in which the lower pharyngeal toothplate has clearly shifted towards Cb4, to taxa that have completely lost Cb5 and have Cb4 alone supporting the toothplate. In the case of eels, this observable transformation series demonstrates convincingly that the arch that is lost is the fifth. We recognize that this argument presents no direct evidence that the missing arch in polypterids is the fifth, but merely that such a transformation can occur.

IV. Ontogenetic argument: sequence of chondrification in the gill arches

In actinopterygians, ceratobranchial elements probably chondrify sequentially from the first arch to the fifth, although we have found no documentation of this for arches 1–4. Nonetheless, we know of numerous examples demonstrating that Cb5 is the last of the five arches to appear in ontogeny, i.e. its chondrification begins only after the first four arches are chondrified (e.g. *Lepisosteus*, de Beer, 1937: plate 39, fig. 1; *Salmo*, de Beer, 1937: plate 43, fig. 4; *Centropomus*, Potthoff & Tellock, 1993: fig. 20; *Pantodon* and *Morone*: pers. obs.). Thus from a developmental (specifically heterochronic) perspective, it is the most likely to be reduced or lost competely through developmental truncation.

CONCLUDING REMARKS

The hypothesis of Wiley (1979) and Rosen *et al*. (1981) that the last of the four gill arches of polypterids represents the fifth of other actinopterygians would require, among other things, extensive modifications of the circulatory and nervous systems that we consider extremely unlikely. Furthermore, Wiley's (1979) argument does not stand up to closer scrutiny, and that of Rosen *et al*. (1981) originated with an erroneous interpretation of Nelson (1969), and was said to be supported by absence of a dorsal element associated with the last ceratobranchial, which, as we discussed above, is incorrect. Accordingly, we reject that hypothesis in favour of the more parsimonious alternative that the last arch represents the fourth of other actinopterygians. We believe that the latter hypothesis is most strongly supported by the presence of gill filaments on the last arch, the fact that the branchial circulation and nervous supply of that arch are unmodified when compared to those of the fourth arch of other actinopterygians, and the fact that the fourth branchial trunk of the vagus, always associated with the fifth arch, has been lost, resulting in a concomitant modified innervation of the pharyngocleithralis and transversus ventralis muscles. Other features of the last arch of polypterids that most commonly characterize the fifth arch of other actinopterygians, i.e. association with certain muscles, and absence of a separate hypobranchial, are known to characterize the fourth arch of some other actinopterygian taxa, and examples are given.

We conclude, based on arguments relating to evidence drawn from several aspects of the anatomy, that, as one would expect from a developmental perspective, the fifth gill arch of polypterids has been lost and the posteriormost arch is the homologue of the fourth of other actinopterygians.

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