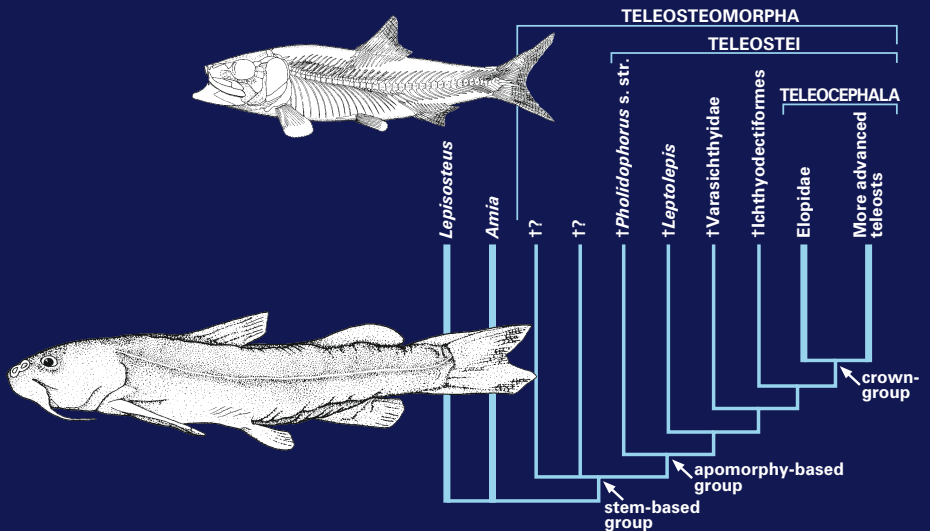


Origin and Phylogenetic Interrelationships of Teleosts

Honoring Gloria Arratia

Joseph S. Nelson, Hans-Peter Schultze & Mark V. H. Wilson (editors)



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Occipito-vertebral fusion in actinopterygians: conjecture, myth and reality. Part 1: Non-teleosts

Ralf Britz and G. David Johnson

The great tragedy of Science – the slaying of a beautiful hypothesis by an ugly fact.

T. H. Huxley [1894 ‘Collected Essays’ 8: p. 229]

Abstract

We revisit the century old hypothesis that the occipita of different actinopterygians are not comparable, because a varying number of vertebrae forms the occiput in the different actinopterygian groups. We applied an ontogenetic approach to this issue and also utilized the number of myosepta that attach to the back of the skull as indication for occipito-vertebral fusion. We found that there is no incorporation of vertebrae or parts thereof into the occiput in *Polypterus* and *Erpetoichthys* in development. Uniquely among actinopterygians, the first neural arch fails to develop a corresponding centrum in polypterids and shifts onto the occipital bone in later development, creating the false impression of an accessory neural arch or of a neural arch, the centrum of which has fused to the occiput. Three myosepta, the primitive number for actinopterygians, attach to the occiput in polypterids, providing another source of evidence for lack of incorporation of vertebrae into the occiput. The occiput of the chondrosteian *Acipenser* is comparable at an early developmental stage to that of polypterids in that three myosepta attach to it. Subsequently, in early development at least, the first neural arch is incorporated into the occiput. Additional arches continue to fuse to the expanded occiput in later development. In the ginglymodan *Lepisosteus*, three myosepta attach to the back of the skull in early development, demonstrating that its occiput is the same as in polypterids and *Acipenser*. The first two neural arches are incorporated into the occiput during further development, as evidenced by five myosepta attaching to the back of the skull. We found that *Atractosteus* differs from *Lepisosteus* in that only the first neural arch is incorporated into the occiput, evidenced by only four myosepta attaching to the back of the skull. The occiput of early developmental stages of *Amia* has four myosepta attaching and a free centrumless first neural arch, showing that at least part of a vertebra has been incorporated. This hypothesis gains support from the presence of haemal processes at the posterior base of the occiput, which are otherwise present only on vertebrae. We discuss Fürbringer’s work on the spino-occipital nerves of gnathostomes, point out its shortcomings and argue that his conclusions about the great variation in number of vertebrae fused to the back of the skull in gnathostomes is a myth. We conclude that a major confounding factor in the interpretation of the occiput in actinopterygians has been the failure to distinguish between evolutionary and developmental incorporation of vertebrae.

Introduction

This project originated when we discovered that the first vertebra in representatives of the family Molidae, the ocean sunfishes, fuses with the basioccipital during development (see Britz & Johnson 2005). When reviewing the relevant literature to determine how common occipito-vertebral fusion is among teleosts, this empirical observation ultimately led us into an investigation of the theory that gnathostome ver-

tebrates have incorporated a variable number of anterior vertebral segments into the back of the skull thus distinguishing them from their closest relatives, the hagfishes and lampreys (see Gegenbaur 1872, Fürbringer 1897, Gaupp 1906, de Beer 1937, Veit 1947, Bemis & Forey 2001 for reviews of this issue).

This newly formed part of the gnathostome skull is the occipital region or 'neocranium' of Fürbringer (1897). The vertebral incorporation theory is based on different lines of evidence, of which the most important two are: (1) close resemblance of the occipital skull to the anterior vertebral column first noted by Goethe in 1790 (according to Wohlbold 1924) and Oken (1807) in the era of idealistic morphology and 'Naturphilosophie', and pointed out most recently by Rosen (1985) and Bemis & Forey (2001) and (2) the fact that a varying number of nerves resembling spinal nerves exits the cranium posterior to the nervus vagus (Stannius 1849; Sagemehl 1884, 1885; Gegenbaur 1872, 1887; van Wijhe 1882; Fürbringer 1897; Herrick 1899; Norris 1925; Bemis & Forey 2001). The goal of our paper is not to review the hypothesis of the vertebral nature of the occiput (for recent reviews of this topic see Kuratani 2008, Kuratani & Schilling 2008), but to revisit the factual evidence for the idea that a varying number of vertebrae fuse to the occiput in actinopterygians during ontogeny. To accomplish this, we have selected representatives of those taxa that were cited as candidates for occipito-vertebral fusion by Bemis & Forey (2001).

Part 1 of our study deals with the nonteleostean actinopterygians, the Cladistia (bichirs and reedfish), the Chondrostei (sturgeons), the Ginglymodi (gars), and the Halecomorphi (bowfin). Teleosts are covered in Part 2 (Johnson & Britz, this volume).

Materials and methods

This study is based on the following cleared and stained (c&s) material (Taylor & van Dyke 1985), unless otherwise indicated. Institutional abbreviations: **BMNH**, The Natural History Museum, London; **FMNH**, Field Museum, Chicago; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington DC.

Polypteridae: *Polypterus ornatipinnis*: BMNH 2008.10.6.1-120, 120 specimens, 9 mm notochord length (NL), 57 mm standard length (SL); *P. endlicheri*: BMNH 2008.10.6.121, 305 mm SL, dry; *Erpetoichthys calabaricus*: BMNH 2008.10.6.122-153, 32 specimens, 9.6 mm NL, 125 mm SL.

Acipenseridae: *Acipenser ruthenus*: BMNH 2008.10.6.154-179, 26 specimens, 12.5 mm NL, 50 mm SL

Lepisosteidae: *Lepisosteus* sp.: BMNH 2008.10.6.180-181, 2 specimens, 22.5 mm NL, 34 mm SL; *Atractosteus* sp.: FMNH 109207, 24.7 mm NL; FMNH 109154, 25.8 mm NL; FMNH 110222, 25.5 mm NL.

Amiidae: *Amia calva*: USNM 304418, 44 mm NL; FMNH 102453, 30 mm NL.

Selected developmental stages of the different taxa were photographed with a ProgRes 12C digital camera attached to a Zeiss Tessovar, or a Zeiss Axiocam attached to a Zeiss Discovery V12; the latter are composite images prepared with the Zeiss Video Imaging Z-stack software to increase depth of field.

Our approach to identify fusion of vertebrae into the occiput utilizes, whenever available, evidence from two different sources: (A) developmental osteology and (B) number of myosepta attached to the skull. As we showed previously for the tetraodontiform molids and ostraciids (Britz & Johnson 2005) study of the developing occipital skeleton and first few vertebrae can reveal ontogenetic fusion of vertebrae into the back of the skull, where it occurs. This line of evidence can be corroborated by information on the number of cranial myosepta based on the following rationale first established by Allis (1899), reiterated by Patterson & Johnson (1995) and demonstrated for additional actinopterygians in this study and Johnson & Britz (this volume). Primitively three myosepta attach to the skull of actinopterygians, and the most anterior one of these is associated with the ventral limb of the posttemporal of the shoulder girdle. The second cranial myoseptum commonly attaches to the middle part of the exoccipital and the third to the base of the exoccipital. The fourth myoseptum is then the first vertebral myoseptum and attaches to the first vertebra. If fusion of the first vertebra to the occiput has occurred, this must be reflected by four instead of three myosepta attaching to the skull. For some taxa for which sufficient ontogenetic information was not available, our conclusions relied primarily on myoseptal evidence.

Results and Discussion

Cladistia. The occipito-vertebral region of the polypterid skeleton is unusual among actinopterygians, as was pointed out in the earliest detailed anatomical account of *Polypterus* by Agassiz (1833-1843). In adult specimens of *Polypterus* and *Erpetoichthys* the occiput is formed by a single endoskeletal bone, often referred to as the occipital (Fig. 1). The occipital surrounds the foramen magnum completely, occupying the space where the basioccipital and exoccipitals are developed in other bony fishes. Agassiz (1833-1843, p. 38) concluded that either these bones «manquent complètement, ou sont réunis aux os principaux, don't ils ne sont que démembrés» (lack completely or are fused into the compound bone, of which they are only parts). It is the unusual structure of the occipital bone in polypterids and its associated free neural arch (see further below) that has led to the view that one (Owen 1866; Traquair 1870; Bridge 1888; Fürbringer 1897; Lehn 1918; Jollie 1980, 1984a; Bartsch & Gemballa 1992; Claeson & Hagadorn 2008) or more vertebrae (Sewertzoff 1895, Allis 1922, Patterson & Johnson 1995, Bemis & Forey 2001) are fused into the back of their skull. In contrast, only Gegenbaur (1887) argued against the idea that the occiput of *Polypterus* had incorporated a vertebra. Daget (1950) and Daget et al. (1964) held even a third view, arguing that *Polypterus* had entirely lost the first postoccipital vertebra and the centrum of the second, so that the articulation between the skull and the vertebral column is with the third postoccipital vertebra.

Clearly, ontogenetic information is needed to clarify the composition of the occiput. Therefore, we investigated the development of the occiput and first vertebrae in polypterids, based on large developmental series of *Polypterus ornatipinnis* and *Erpetoichthys calabaricus*. As the two taxa are essentially identical in the development of this character complex, we focussed on *Polypterus*.

The precursor of the occipital bone at 9 mm is the paired pila occipitalis, an obliquely anterodorsally oriented cartilage rod completely removed from the otic capsule on the dorsolateral aspect of the notochord (Figs. 2A, 3A). During subsequent development, the pila contacts the tectum synoticum (11.5 mm, Figs. 2B, 3B) and eventually fuses with it (17.5 mm, Figs. 2C, 3C). The first signs of ossification of the pila, the exoccipital, appear at 11.5 mm (Figs. 2B, 3B) and the bone grows mainly by expanding its base. The next stage in the formation of the occipital is an almost complete ring of mineralized tissue developed in the sheath of the notochord at 23 mm (Figs. 2D, 3D: MCh). It extends from directly beneath the bases of the exoccipitals around the notochord ventrally to a pair of perichondral ossifications located at the posterior ends of the parachordal cartilages (marked by arrows in Fig. 3D). The ring is situated, as far as we can tell from c&s specimens, in a deeper layer of the tunica interna of the notochordal sheath and is separated from both the exoccipital ossifications and the pair of perichondral ossifications. During further development, the bases of the exoccipitals fuse in the midline above the notochord and with the mineralized notochordal ring and the paired perichondral ossifications at the posterior ends of the parachordals, thus establishing the occipital bone at 26 mm (Figs. 2E, 3E). The ossification of the exoccipital part of the occipital, however, does not extend to the dorsal midline and the two bones remain separated there by a wide area of cartilage even in our 57 mm specimen (Fig. 2F), but they are fused in adult *Polypterus* (Fig. 1).

The occipital bone in *Polypterus* thus develops from (1) ossification of the pilae occipitales, which represent the paired exoccipitals, (2) from a perichordal ossification around the occipital part of the notochord and (3) a paired endoskeletal ossification of the posterior ends of the parachordals; the latter two most likely are the homologue of the basioccipital of teleosts.

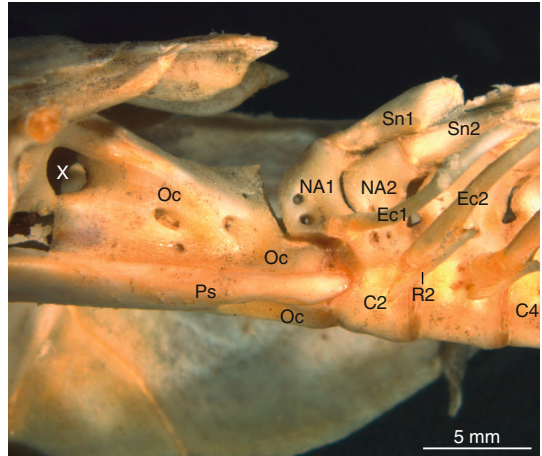


Fig. 1.

Polypterus endlicheri (BMNH 2008.10.6.121), occiput and anterior vertebrae in lateral view. Abbreviations: C, centrum; Ec, epicentral; NA, neural arch; Oc, occipital; Ps, parasphenoid; R, rib; Sn, supraneural; X, vagus foramen.

In the latest review, Bemis & Forey (2001) acknowledged that the occipital of *Polypterus* occupies the space of the exoccipitals and the basioccipital in other actinopterygians, and cited Patterson (1975) as having stated that this bone “arises from paired ossification centers” (p. 358). Patterson (1975) made two statements about the paired origin (p. 445): “The basi-exoccipital (Bexo) shows no sign of separate exoccipital (paired) and basioccipital (median) ossification centres, and its shape suggests that it may not ossify from three centers, as does the basi-exoccipital of *Polypterus* (Pehrson 1947), or from four centers” and (p. 463): “The basi-exoccipital arises from paired centers above the notochord.” However, in Pehrson (1947: p. 404), the only place with mention of the occipital is “The first ossifications in the neural cranium are the sphenoid and the occipital which are already developed in the 24 mm specimen (fig. 2).” The 24 mm specimen was the smallest available to Pehrson (1947) and the only source we could make out for Patterson’s remark that the occipital in *Polypterus* ossifies from two centers may have been the illustration of Pehrson’s 24 mm specimen (his fig. 2), which shows the neurocranium in lateral view with the occipital marked as a striped area. This, however, is not enough evidence to conclude that the occipital arises from two centers and Patterson (1975) may have been hasty in his conclusions, which were readily accepted by Bemis & Forey (2001).

The pilae occipitales of *Polypterus* resemble in their early developmental stage an anteriorly inclined neural arch (Figs. 2a, 3a). They do not arise as dorsal extensions from the posterior ends of the parachordals as in teleosts (de Beer 1937), but are autogenous, as in *Amia* and *Dipnoi* (de Beer 1937), as previously pointed out by Moy-Thomas (1933). This is most likely the plesiomorphic condition for at least osteognathostomes (osteichthyans of some authors; but see alternative interpretation below under Chondrostei). The autogenous origin and later fusion of the pilae occipitales with the tectum synoticum may have led some previous authors to conclude erroneously that a vertebra is incorporated into the back of the skull in polypterids.

A source that might have contributed to the confusion of previous authors in this context is Fürbringer’s (1897) idea of the neocranium of gnathostomes, which hypothesizes that gnathostomes acquired their occipital region (the neocranium) through fusion, in evolutionary terms, of vertebral material into the head of non-gnathostomes (the palaeocranium). This is a plausible assumption as the vagus issues from the skull just in front of the pilae occipitales in gnathostomes, but issues behind the skull in lampreys and hagfishes. However, acquisition of the occiput occurred in the lineage leading to the gnathostomes, so it is a synapomorphy of that group, and as such a plesiomorphy at the level of polypterids. The pilae occipitales of polypterids, which originate autogenously, and later fuse with the tectum synoticum therefore do not represent a vertebra that fuses to the skull at the level of the gnathostomes, as proposed previously by Fürbringer (1897), Budgett (1902), Lehn (1918), Allis (1922), Bartsch & Gemballa (1992), and Bemis & Forey (2001).

The occipital of polypterids supports on its posterior dorsal surface an autogenous neural arch with no corresponding centrum (Fig. 1), first mentioned by Traquair (1870). It is this free neural arch in addition to the unusual structure of the occipital bone in polypterids that has led authors from Owen (1866) to Bemis & Forey (2001) and Claeson & Hagadorn (2008) to believe that one or two vertebrae are fused into the back of their skull. Only Gegenbaur (1887: p. 107) concluded that “Hier wird nicht angenommen werden können, dass der occipitale Wirbelbogen seinen Körper dem Basilare abgegeben hat.” (“It cannot be assumed here that the centrum of the free neural arch has contributed to the basioccipital.”).

As with the occipital in *Polypterus*, ontogenetic studies are decisive to clarify this issue. The two anteriormost basidorsals are present already at 9 mm as tiny conical cartilages on the dorsolateral aspect of the notochord, with the first being smaller than the second (Figs. 2A, 3A). During further development additional basidorsals chondrify in anteroposterior direction (Figs. 2B, 3B). The first neural arch eventually ossifies, as all succeeding arches (Fig. 2C, 3C), and develops anterior and posterior flanges of membrane bone (Fig. 2D), which leads to the formation of a foramen for the first spinal nerve (Figs. 2E,F). In all our specimens the first basidorsal/neural arch is situated in the fourth myoseptum (Fig. 3A-C), that is the first vertebral myoseptum and is the largest element of the series, at least between 11.5 and 57 mm (Fig. 2B-F). Vertebral centra have started to form at 26 mm as small half-rings of mineralized tissue around the dorsal face of the notochord beneath the neural arch bases starting from neural arch 2 (Figs. 2E, 3F). They are located in the notochordal sheath and represent chordacentra. All centra are present in our 57 mm specimen, except the one that would be associated with the first neural arch. Even in later stages including the adult the first neural arch remains without a centrum and sits on top of the posterior end of the occipital bone (Fig. 1). The occipital of the adult thus articulates posteriorly with the centrum of

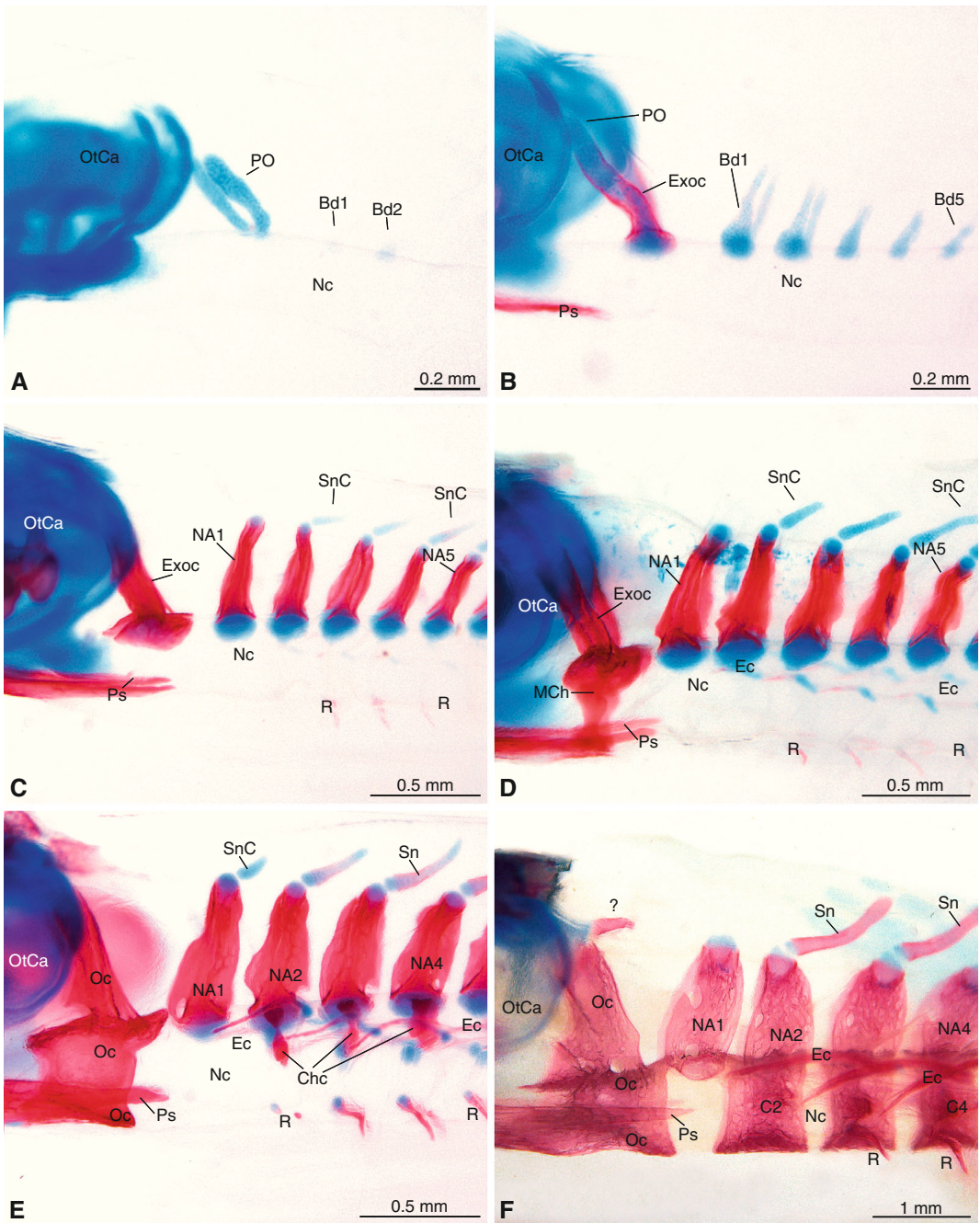


Fig. 2.

Polypterus ornatipinnis (BMNH 2008.10.6.1-120), development of occiput and anterior vertebrae in lateral view. **A**, 9 mm NL. **B**, 11.5 mm NL. **C**, 17.5 mm SL. **D**, 23 mm SL. **E**, 26 mm SL. **F**, 57 mm SL. Abbreviations: **Bd**, basidorsal; **C**, centrum; **ChC**, chordacentrum; **Ec**, epicentral; **Exoc**, exoccipital; **MCh**, mineralisation in notochordal sheath; **NA**, neural arch; **Nc**, notochord; **Oc**, occipital; **OtCa**, otic capsule; **PO**, pila occipitalis; **Ps**, parasphenoid; **R**, rib; **Sn**, supraneural; **SnC**, supraneural cartilage; **X**, vagus foramen. Note that epicentrals in **D** and **E** have a cartilaginous distal area, but are bony proximally.

the second vertebra, a condition that is unique among actinopterygians and another autapomorphy of polypterids.

Bemis & Forey (2001: p. 358) noted that in *Polypterus* during “development another arch seems to be incorporated (Fig. 20.5b,c) but whether centra are incorporated is moot.” Their fig. 20.5b,c, however, does not show any incorporation, and what they may have referred to is the closer association of the first neural arch with the occipital bone (see Fig. 1), which has no significance in this context. They (p. 358-359) further argued that “at least two vertebral segments (that is, at least two neural arch elements) are included in the occiput of *Polypterus* because the first rib occurs on the first free centrum (Figure 20.5c).” Their illustration “after Allis 1922”, however, shows two unlabeled, rod-like structures on both the first neural arch and the first vertebra with a centrum. Allis (1922) illustrated only the neurocranium with no associated neural arches or vertebrae, which means that the vertebral elements in their fig. 20.5C including the rod-like structures were added by Bemis & Forey (2001). The size and position of these structures suggest to us that they illustrated the elements that were historically called dorsal ribs, but are actually epicentral bones (see the argument by Britz & Bartsch 2003) and thus are irrelevant to the discussion. Nevertheless, *Polypterus* has true ribs on the first and consecutive centra. This landmark, however, has no bearing on the issue of incorporated neural arches in *Polypterus*, given our ontogenetic data and the arguments presented above and in the following paragraphs.

The first neural arch of polypterids, which is free and lacks a corresponding centrum was frequently used before Bemis & Forey (2001) as evidence for incorporation of at least one centrum into the back of the skull. As we detailed above this autogenous neural arch fails to develop a corresponding centrum in ontogeny. Its position in the fourth myoseptum clearly identifies it as the first neural arch and the homologue of that arch in other actinopterygians. This myoseptal relation of the free neural arch with the fourth myoseptum was also recognized and illustrated by de Smet (1975: p. 90). He referred to the free neural arch as a “semi-vertèbre post-occipital” and seems to have been confused about its identity, because he considered the second vertebra of *Polypterus* to be «la première vertèbre» (de Smet 1975: p. 90-91). The relative position of the first neural arch of polypterids to other structures of the occiput changes during development: it initially appears as the largest neural arch and is removed from the occiput in larvae and small juveniles, then lags behind in growth and eventually becomes situated on top of the posterior end of the occipital in larger juveniles and adults. This unusual position of the first neural arch in adult polypterids and the unique articulation between their occiput and the second vertebra has undoubtedly contributed to the confusion about its identity.

We also note that, contrary to the claim of Fink & Fink (1981), the free neural arch of *Polypterus* has nothing to do with the accessory neural arch of teleosts, which is always situated in the third myoseptum, i. e. the last occipital myoseptum (see Part 2 on teleosts).

In summary, there is no evidence that in polypterids a postoccipital segment, in the form of an entire vertebra, a centrum or a neural arch fuses with the back of the skull during ontogeny and we can thus reject previous claims to that effect by Owen (1866), Traquair (1870), Bridge (1888), Budgett (1902), Lehn (1918), Allis (1922), Jollie (1980, 1984a), Bartsch & Gemballa (1992), Patterson & Johnson (1995), Bemis & Forey (2001) and most recently Claeson & Hagadorn (2008).

Chondrostei. Numerous authors have agreed that several vertebrae have fused to the skull in chondrosteans (Bridge 1878; Gegenbaur 1887; Sewertzoff 1895, 1928; Holmgren & Stensiö 1936; de Beer 1937; Marinelli & Strenger 1973; Jollie 1980; Bemis & Forey 2001). However they either disagreed about or didn't mention how many vertebrae had been incorporated. For example, Gegenbaur (1887) stated that six vertebrae are connected to the cranium in adult *Acipenser* based on the number of foramina for what he regarded as spinal nerves; Bridge (1878), based on the same source of evidence, concluded that 8-9 vertebrae are incorporated in *Polyodon*, but Fürbringer (1897) disagreed assuming fusion of only 6 or 7 vertebrae.

As for *Polypterus*, we approached this issue with a developmental and myoseptal perspective using an ontogenetic series of *Acipenser ruthenus*, of which we describe and illustrate three stages.

At 13 mm, both ear capsules are well chondrified, and they are connected along the notochord by cartilage of the parachordals with the developing occipital region (Fig. 4A). The latter consists of a laterally directed lobe of cartilage with a foramen in the middle, and a second, less obvious foramen, in front of it. A third foramen is present posteriorly, where it is almost entirely enclosed by a dorsal process of the posterior end of the parachordal cartilage. Two myosepta attach to the lobe-like part and a third myoseptum to the posterior process. The fourth myoseptum attaches to the first true basidorsal.

At 14 mm, chondrification of the occipital region has progressed, so that the occiput is now also in cartilaginous contact with the otic region dorsally, leaving only the vagus foramen open (Fig. 4B,D,E). The lateral wall of the occiput bears three foramina for the spino-occipital nerves (Fig. 4D). The first basidorsal is now in cartilaginous contact along the notochord with the posterior end of the occiput (Fig. 4E). Three myosepta attach to the otico-occipital region and the fourth to the first neural arch as in the previous stage (Fig. 4B,D,E). However, in the area of attachment of the first myoseptum, a connective tissue condensation marks the beginning of the chondrification of the posterior process of the otic capsule (Fig. 4E).

At 23 mm, the posterior process has chondrified and the first myoseptum is no longer visible, the second is present close to the posterior edge of the posterior process, and the third attaches to the back of the occiput (Fig. 4F). The fourth, as in previous stages, attaches to the first neural arch, which is now broadly connected through cartilage to the occiput at its base along the notochord. Two long cartilaginous processes from the base of the occiput extend on both sides of the notochord posteriorly to the level of the second neural arch.

Patterson (1975: p. 464) claimed that “In *Acipenser* the occipital arch fuses with three neural arches while the metotic fissure is still open, and then fuses with the upper part of the otic capsule, leaving a large vagus foramen.” As with *Polypterus*, his source is unclear, and the only reference cited by Patterson (1975) that includes information on *Acipenser* development is de Beer (1937), whose account is based on Sewertzoff (1928). De Beer (1937: p. 90) described two of Sewertzoff’s stages, in which the metotic fissure is still open and said about the first: “In the hinder part of the parachordals, the rudiments are seen of four occipital arches ...” Regarding the second stage, de Beer (1937: p. 90) stated this: “The four occipital arches of the previous stage have joined dorsally, above the three thereby enclosed hypoglossal foramina, to form a broad occipital arch ... Behind the occipital arches some rudiments of neural (occipitospinal) arches may be seen, which will ultimately become attached to the skull.” Sewertzoff’s (1928: p. 205) original report of these specimens reads: “At the stage we describe we find three distinct occipital arches ..., the anterior one at this early stage is very rudimentary ... These arches are distinctly seen on the section of fig. 15. The dorsal ends of these three occipital arches are connected with each other by a band of mesenchyme, so that they really represent the occipital part of the skull.” So both de Beer (1937) and Sewertzoff (1928) interpreted these neural arch like structures as actually representing the occiput and not as vertebral arches fusing onto the occiput, as Patterson (1975) seems to have implied.

In summary, the occiput of *Acipenser* is much more elongated than in *Polypterus*, and the way it develops may reflect more an original vertebral segmentation than in any other actinopterygian studied by us. If this is true, it will have to be shown by close comparisons to the development of other lower gnathostomes, like sharks, about which we have very limited information dating back to de Beer’s monograph (1937). Nevertheless, the occiput of *Acipenser* has the same number of myosepta, i.e. three, attached to it in early development as most other actinopterygians. In later developmental stages, the occiput expands posteriorly and captures the territory of the anterior neural arches. It is connected at least with the first neural arch in the stages we studied, but in larger specimens additional vertebrae appear to be incorporated (Sewertzoff 1928, Marinelli & Strenger 1973). The same seems to be true for other species of sturgeons as e.g. *Scaphirhynchus* (Bemis & Forey 2001).

Ginglymodi. As far back as Gegenbaur (1887), it has been suggested that vertebrae have been incorporated into the occiput of *Lepisosteus* (Schreiner 1902; Veit 1907, 1911; Hammarberg 1937). As in chondrosteans there is disagreement about the number of incorporated segments. Gegenbaur (1887, 1898) concluded that one segment is included, while Schreiner (1902), Veit (1911), Hammarberg’s (1937) description and illustrations, and Jollie (1984b) suggest that two, and de Beer (1937) that three segments have fused with the occipital arch.

Bemis & Forey (2001) conjectured “that two and probably three segments, including centra, are integrated into the occiput of *Lepisosteus*, an inference that also may be supported by the observation that the first rib occurs on the first free centrum”. They stated (p. 360) that “Our 34 mm specimen shows that there is at least one free neural arch associated with the occiput (Figure 20.5g) and a specimen of the same length illustrated by Hammarberg (1937: fig. 22) shows two.” Bemis & Forey’s (2001) figure 20.5 shows three stages of occiput development for *Lepisosteus*, fig. 20.5F a 20 mm specimen after de Beer (1937), fig. 20.5G a 34 mm specimen mistakenly attributed to de Beer (1937: pl. 39), and fig. 20.5H an adult specimen of unknown length. A comparison with de Beer (1937) shows that that plate 39 illustrates only

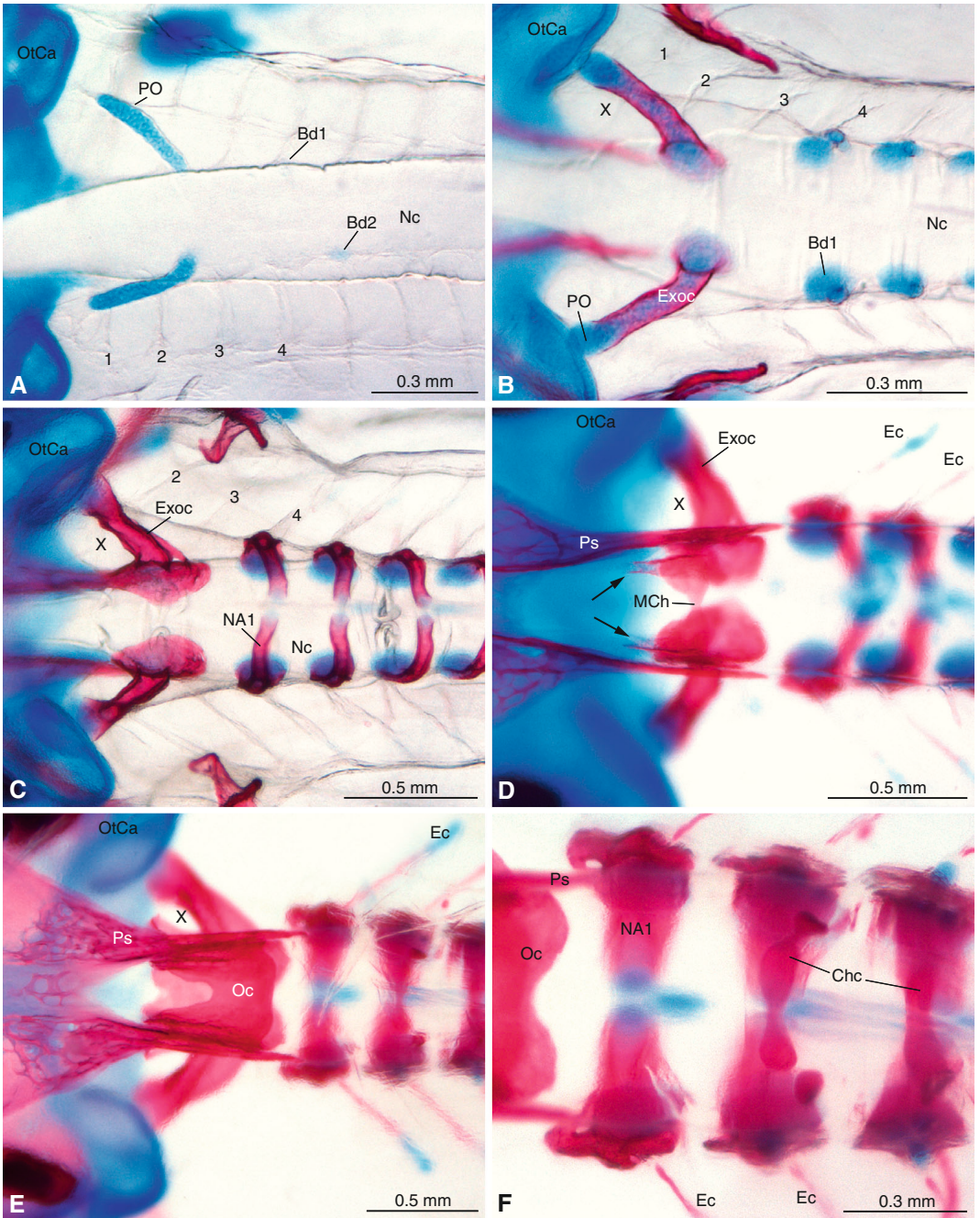


Fig. 3. *Polypterus ornatipinnis* (BMNH 2008.10.6.1-120), development of occiput and anterior vertebrae in dorsal (A-C) and ventral view (D-F). **A**, 9 mm NL. **B**, 11.5 mm NL. **C**, 17.5 mm SL. **D**, 23 mm SL, note arrows that mark paired perichondral ossification. **E**, 26 mm SL. **F**, 26 mm SL. Abbreviations: **Bd**, basidorsal; **C**, centrum; **ChC**, chordacentrum; **Ec**, epicentral; **Exoc**, exoccipital; **MCh**, mineralisation in notochordal sheath; **NA**, neural arch; **Nc**, notochord; **Oc**, occipital; **OtCa**, otic capsule; **PO**, pila occipitalis; **Ps**, parasphenoid; **X**, vagus foramen; **1,2,3,4**, first, second, third and fourth myoseptum.

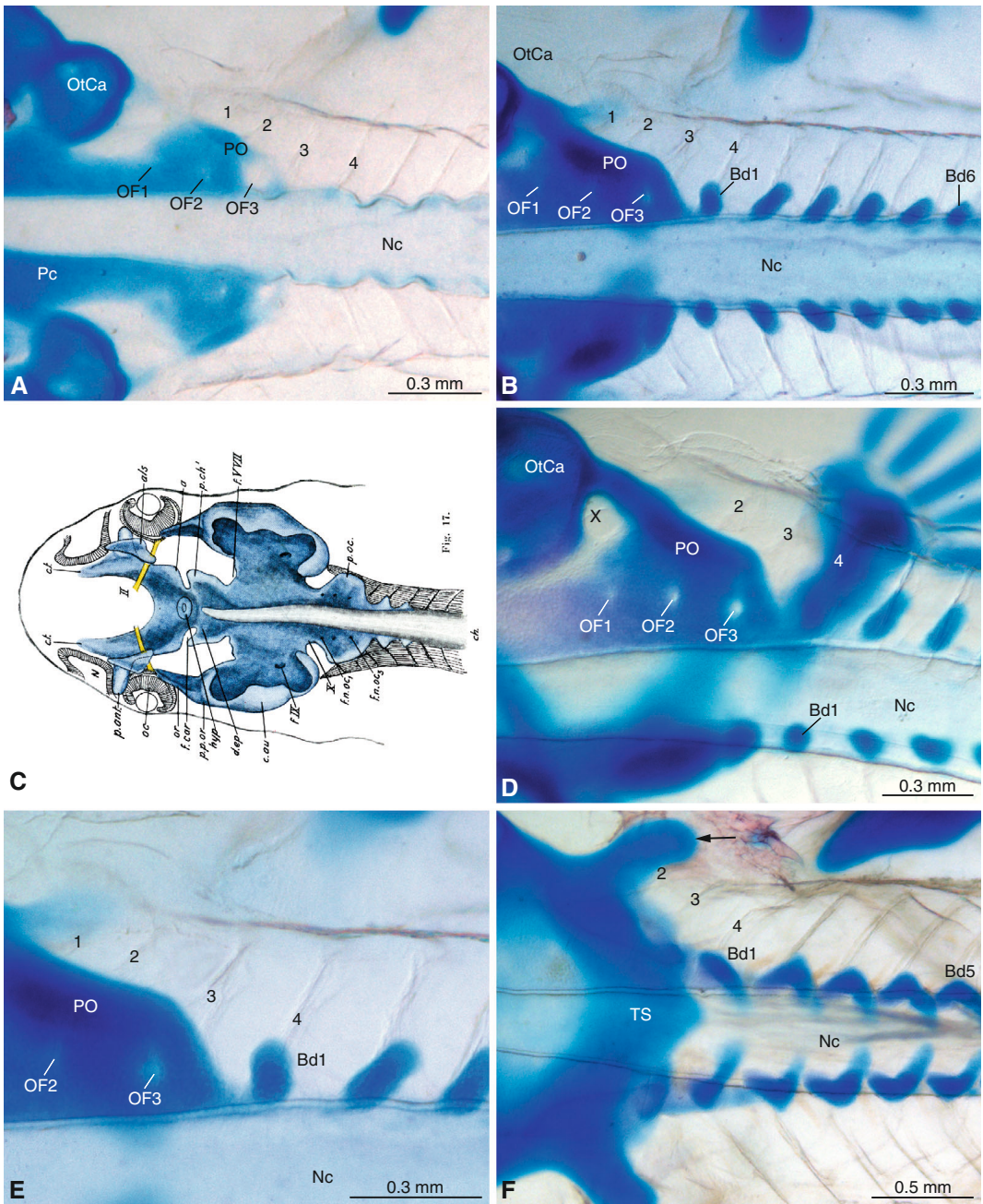


Fig. 4. *Acipenser ruthenus* (BMNH 2008.10.6.154-179), development of occiput and anterior vertebrae in dorsal view. **A**, 13 mm NL. **B**, 14 mm NL. **C**, reproduction of Sewertzoff's Fig. 14 of an *Acipenser* larva of unspecified length. **D**, 14 mm NL, same as in **B**, close-up, oblique dorsal view. **E**, 14 mm NL, same as in **D**, close-up of posterior occipital region and first three basidorsals of right side. **F**, 23 mm NL, arrow points to developing postoccipital process. Abbreviations: **Bd**, basidorsal; **Nc**, notochord; **OF**, occipital foramen; **OtCa**, otic capsule; **Pc**, parachordal; **PO**, pila occipitalis; **TS**, tectum synoticum; **X**, vagus foramen; **1,2,3,4**, first, second, third and fourth myoseptum.

a 20 mm specimen and that there is no illustration or mention in the text of a 34 mm specimen, and it can be derived from Bemis & Forey's (2001) quoted sentence above that this illustrated specimen is actually their 34 mm specimen. Their illustration shows the occiput separate from the first neural arch, which lacks a centrum followed by neural arches 2-4 with associated centra. We restained and restudied Bemis & Forey's (2001) specimen and found a very different situation, which we illustrate in Fig. 5C. The area of the pila occipitalis behind the vagus is ossified perichondrally as the exoccipital. The basioccipital is well ossified; it is separated from the exoccipital by a band of cartilage and is confluent with two neural arch like structures on its posterodorsal aspect. The anterior arch is rudimentary and represented by a short fully ossified process, while the posterior arch is much longer and resembles subsequent neural arches in that its distal tip is cartilaginous and the body and base are perichondrally ossified (Fig. 5C). We conclude that Bemis & Forey (2001) overlooked the anterior rudimentary arch and misinterpreted the larger posterior arch as being free from the occiput, which it is not. In a smaller specimen (22.5 mm) both neural arch elements are still mostly cartilaginous (Fig. 5A) and only their bases are confluent with the posterior extensions of the parachordals.

Veit (1911) and Hammarberg (1937) provided a similar picture about the development of the occiput in *Lepisosteus*, which is consistent with our findings and interpretations. In early development at around 11 mm the pila occipitalis arises as a dorsal extension of the posterior part of the parachordal without contact to the dorsal part of the otic capsule leaving a large metotic fissure. Contact is established by 12 mm, closing the metotic fissure forming the vagus foramen. At this stage the two neural arches have just appeared, and by 16mm they are well developed and continuous in cartilage. Hammarberg's 33.4 mm specimen corresponds well to the 34 mm specimen we studied, in contrast to what Bemis & Forey (2001) described and illustrated for that specimen. Accordingly, we agree with Schreiner (1902), Veit (1911), Hammarberg (1937), and Jollie (1984b) that two neural arches are incorporated into the occiput of *Lepisosteus* at an early developmental stage, and our evidence from the arrangement of the myosepta supports this view. Given that two segments are fused to the occiput, we would expect two more myosepta to attach to it, in addition to the three primitively present in actinopterygians. And this is exactly the case. In the 34 mm specimen five myosepta attach to the occiput, the fourth to the first neural arch rudiment and the fifth to the larger posterior neural arch (Fig. 5B). The same is true for the 22.5 mm specimen we studied (Fig. 5A). **We thus conclude that two vertebrae or at least parts thereof are fused to the occiput in *Lepisosteus*.** Based on the available data it is still unclear if an entire two vertebrae including their centra are incorporated into the occiput of *Lepisosteus* or if it is only their neural arches (see discussion in *Amia* below).

When we checked small specimens of the ginglymodan genus *Atractosteus*, we discovered an interesting difference from *Lepisosteus*. The 24.7 mm specimen we illustrate, and the other two specimens we studied, have only the first neural arch confluent with the occiput, and not the first two as in *Lepisosteus*. This suggests that only one vertebral segment and not two are incorporated in *Atractosteus*, as also evidenced by only four myosepta attaching. **We conclude that one vertebra or at least parts thereof is fused into the occiput of *Atractosteus*.** As in the case of *Lepisosteus*, it is not clear if it is an entire vertebra or just the neural arch that fuses in development.

Halecomorphi. Bridge (1877) pointed out that two vertebrae have been incorporated into the occiput of *Amia*, a view supported by Hay (1895), Allis (1897), Schreiner (1902), Patterson (1975), and Jollie (1984c), while Sagemehl (1884) and Gegenbaur (1898) and recently Bemis & Forey (2001) held that the number was more likely to be at least three. Grande & Bemis (1998) noted that adult *Amia* usually have 2 (p. 56), but that their largest dried specimen had 3 vertebrae fused to the occiput.

The only studies that included developmental stages are those of Schreiner (1902), Jollie (1984c) and Grande & Bemis (1998); illustrated specimens of the latter were subsequently used by Bemis & Forey (2001).

Grande & Bemis (1998) listed specimens from 12 mm to 735 mm in their material, but the smallest specimen illustrated for the composition of the occiput is 32 mm (figs. 25C, 37A,B; erroneously indicated as 30 mm in the latter). In this specimen, which resembles the 30 mm specimen illustrated in Fig. 6A, there is a free neural arch above the second centrum and the bone at the base of the occiput was interpreted as basioccipital plus the first centrum. On page 57 we find the statement that "The first centrum evidently fuses into the condyle before the fish reaches 30 mm SL (Figs. 25C, 37C,D)" but they admitted that they "did not have any stages clearly showing a mineralized, unfused, first centrum ..."

Support for Grande & Bemis's (1998) assumption that their 32 mm specimen already had one ver-

tebra fused to the basioccipital comes from the results of Schreiner (1902). His descriptive text with few illustrations is not easy to follow, but he described fusion of the initial 'anlage' of the first centrum with the cartilaginous occiput between 16 and 17 mm total length.

Further support for this early fusion is derived from the presence of a pair of cartilaginous nodules at the base of the basioccipital, first described by Sagemehl (1884) and used by him for the same argument. They are in the same position and have the same shape and arrangement as similar elements on the first (free) centrum (Fig. 6C). Homology of these elements has been a matter of disagreement and we use the neutral descriptive term haemal processes introduced by Grande & Bemis (1998) for them. The presence of these haemal processes at the posterior base of the basioccipital indicates that parts of a vertebra have been incorporated.

Additional supportive evidence is derived from our myoseptal approach, the foundation of which is that three myosepta are primitively attached to the normal occiput in at least actinopterygians (Allis 1899). The dorsal view of our 30 mm specimen clearly shows that one myoseptum attaches to the tectum area and another two to the exoccipital (Fig. 6B). The fourth myoseptum is then associated with the free neural arch and attaches at the base of the cranium at the posterior end of the basioccipital region (Fig. 6B). We take this as evidence that the segment associated with the free neural arch has been fused to the basioccipital. Grande & Bemis (1998) noted that at 75 mm a second centrum is fully fused establishing the normal adult condition.

Based on the results of previous studies and our own observations we conclude that small *Amia* have one vertebra or at least parts thereof incorporated into the occiput and adult individuals have a second vertebra fused to it.

In very large specimens of *Amia* one additional a third, vertebra, may be incorporated (Grande & Bemis 1998). While it seems clear that the centrum of the second vertebra and, subsequently that of the third fuse with the basioccipital, it is less clear if the first centrum develops early in ontogeny and subsequently fuses with the basioccipital. Based on the available evidence we are inclined to conclude that a centrum never forms in the first vertebral segment and only the cartilaginous haemal processes of that segment are incorporated.

The very early incorporation in development of a vertebra or parts thereof into the occiput is a character that *Amia* shares with *Lepisosteus* and *Atractosteus*, which we initially were inclined to interpret as a synapomorphy of the two taxa that would support a monophyletic Holostei. However, the details of the incorporation differ significantly between the taxa. In the two lepisosteids it is one or two neural arches that fuse to the occiput at the cartilaginous state, whereas it is haemal processes that are incorporated in *Amia*. This difference may indicate that the incorporation between the two taxa is not homologous. More developmental evidence on this character complex in the two taxa is clearly needed to better understand the anatomical situation.

General discussion and conclusions

Ontogenetic versus evolutionary fusion. We found that an important factor confounding the interpretation of the actual composition of the occiput in basal actinopterygians is that authors from Traquair (1870) to Bemis & Forey (2001) did not make it clear if they referred to either ontogenetic or evolutionary incorporation of vertebrae into the skull when they discussed occipito-vertebral fusion. We pointed out above that the pila occipitalis in *Polypterus* has frequently been interpreted as a neural arch that has fused to the cranium, but that such an interpretation is only valid if *Polypterus* is compared to non-gnathostome vertebrates. The same is true for the occiput of *Acipenser*, *Lepisosteus*, *Amia*, and the teleosts covered in part 2 of this contribution. In contrast to the majority of previous workers, we argue that the occiput of all actinopterygians we investigated is homologous and includes the same number of segments as indicated by the primitive number of three myosepta that attach to it. Any deviations from this primitive pattern are due to ontogenetic fusion of segments, which may include neural arches, centra, haemal processes, or a combination of these. We suspect that this is also true of other osteognathostomes or even gnathostomes, and recommend that representatives of chondrichthyans, dipnoans, and actinistians be studied in a similar way as we did for actinopterygians. We note, however, that the occiput anlage of *Acipenser* and *Lepisosteus* among basal actinopterygians is much more elongate and extensive than that of *Polypterus* and *Amia*, which comprises just a narrow occipital pila. The more elongate occipital anlage of *Acipenser* and *Lepisosteus* is more reminiscent of an original composition of several segments. It is, nevertheless, difficult

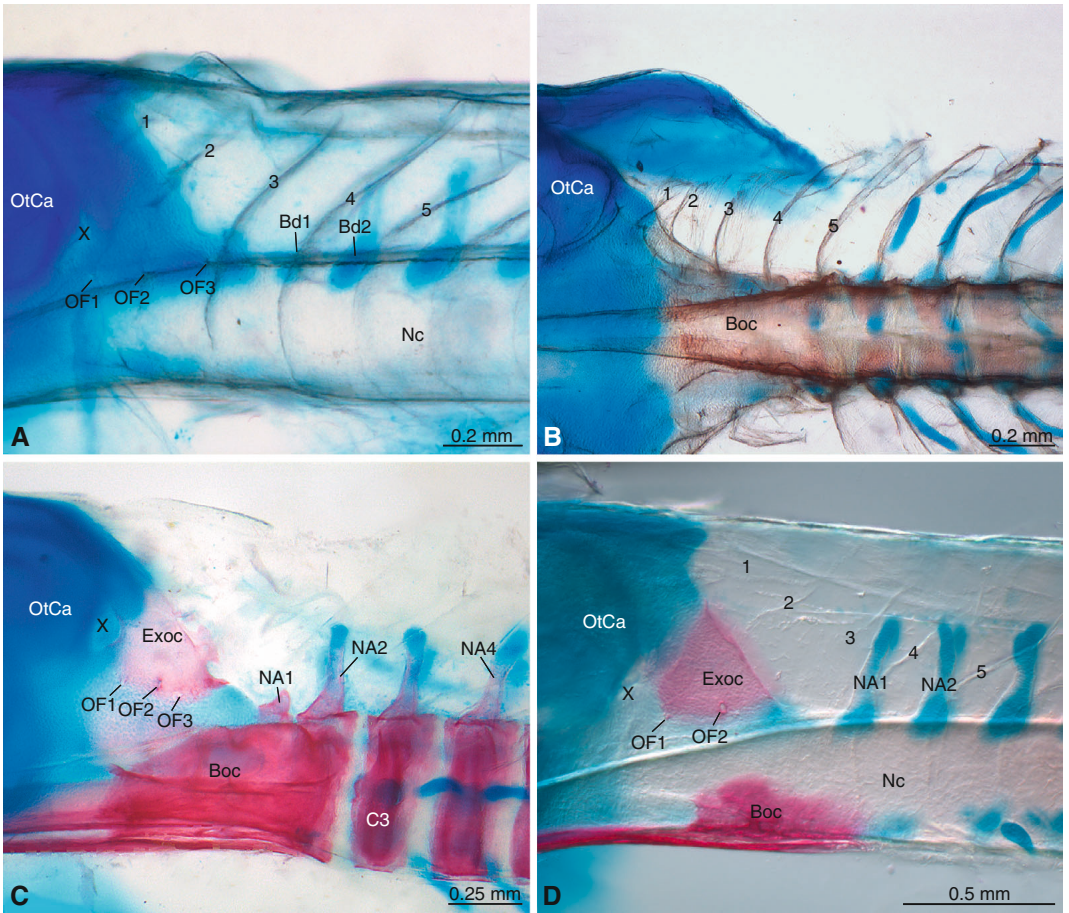


Fig. 5.

Lepisosteidae, development of occiput and anterior vertebrae in lateral (A, C, D) and ventral view (B). **A**, *Lepisosteus* sp. (BMNH 2008.10.6.180-181), 22.5 mm NL. **B**, *Lepisosteus* sp. (BMNH 2008.10.6.180-181), 34 mm SL. **C**, *Lepisosteus* sp. (BMNH 2008.10.6.180-181), 34 mm SL. **D**, *Atractosteus* sp. (FMNH 109207), 24.7 mm NL. Abbreviations: **Bd**, basiodorsal; **Boc**, basioccipital; **C**, centrum; **Exoc**, exoccipital; **NA**, neural arch; **Nc**, notochord; **OF**, occipital foramen; **OtCa**, otic capsule; **X**, vagus foramen; **1, 2, 3, 4**, first, second, third and fourth myoseptum.

to evaluate which one is the more primitive condition for osteognathostomes, the elongate or the narrow anlage. Judging from de Beer's (1937) figures of the dipnoans *Neoceratodus*, *Protopterus* and *Lepidosiren*, it seems that a simple, narrow pila occipitalis as in *Polypterus* and *Amia* could be the primitive state.

Much of the confusion of ontogenetic versus evolutionary fusion seems to have originated through a strict segmentationist view on the occipital cranium of vertebrates, with the main early proponents Gegenbaur (1872, 1887, 1898), Fürbringer (1897), Goodrich (1930) and de Beer (1937). This is best exemplified by de Beer's (1937: pl. 8) famous figure showing how many segments contribute to the skull in the different vertebrate groups (see Fig. 7). Each of his illustrations actually represents a compound of ontogenetic and evolutionary fusions. The occiput of *Acipenser* is considered by de Beer (1937) to be made up of six segments, in an evolutionary sense, to which another six fuse during ontogeny, so that the skull of *Acipenser*, according to him has incorporated 12 segments. While we did not study the later development of the occiput in *Acipenser*, we can say that at least in the very early stages when the occiput forms as an outgrowth from the posterior end of the parachordals, it has only three myosepta attached to it. We interpret this to mean that it forms from the same number of segments evolutionarily as the occiput

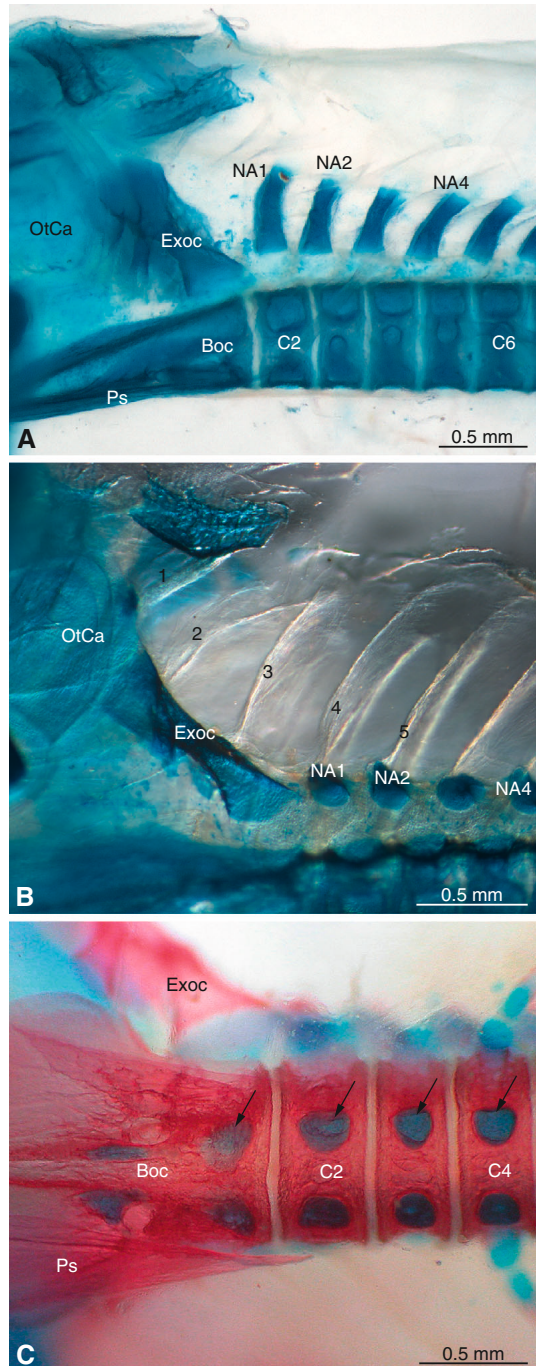
Fig. 6.

Amia calva, occiput and anterior vertebrae, in lateral (A), dorsal (B), and ventral (C) view. A, B, FMNH 102453, 30 mm NL. C, USNM 304418, 44 mm NL. Arrows point to haemal processes on occiput, and second to fourth centrum. Abbreviations: **Boc**, basi-occipital; **C**, centrum; **Exoc**, exoccipital; **NA**, neural arch; **OtCa**, otic capsule; **Ps**, parasphenoid; **1,2,3,4**, first, second, third and fourth myoseptum. ▷

in *Polypterus*, *Amia*, *Lepisosteus* and teleosts, before postoccipital segments fuse ontogenetically to it. This is in contrast to textbook knowledge about the actinopterygian occiput, which is still heavily influenced by a segmentationist view (see e.g. Liem et al. 2001).

Spino-occipital nerves. Early segmentationists' arguments were largely based on the fact that between the last cranial nerve (the vagus) and the first spinal nerve a varying number of nerves issue from the cranium and the postoccipital area in gnathostome vertebrates (Stannius 1849; Sagemehl 1884, 1885; Gegenbaur 1872, 1887; van Wijhe 1902; Fürbringer 1897; Herrick 1899; Norris 1925). Fürbringer (1897: p. 353) took this initial observation to another level of apparent greater accuracy, when he distinguished two groups of spino-occipital nerves and drew wide-ranging conclusions from the pattern of their occurrence: occipital nerves which "belong to the occipital region of the skull since a long time" ("gehören der Occipitalregion des Schädels schon seit langer Zeit an"), and occipito-spinal nerves which are "still in statu nascendi regarding their incorporation into the skull, they represent nerves that are in a transitional state between occipital nerves and spinal nerves" ("befinden sich hinsichtlich ihrer Aufnahme in das Cranium noch in statu nascendi, sie sind Uebergangsnerven zwischen den occipitalen und den freien spinalen Nerven"). He stressed that both terms, "occipito" and "occipito-spinal" were preliminary and that future studies would have to show if a distinction between these two categories would stand up to closer scrutiny. He developed a system to name the two different categories, the occipital nerves with the last letters of the alphabet (v, w, x, y, z) and the occipito-spinal nerves with the first few letters (a, b, c, etc.). He concluded (p. 358) that the number of occipital nerves may vary considerably

even in closely related taxa, for example ranging from 0-5 among chondrichthyans. He stressed (p. 362) that their number also varies by one within species and sometimes between left and right sides of the same specimen. In basal (non teleostean) actinopterygians, Fürbringer's ganoids, he noted (p. 448) that the cranium has "elongated posteriorly by assimilation of a number of vertebrae and thus captured the



Segments	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Metotic Somites				1	2	3	4	5	6	7	8	9	10	11	12
Acipenser	[Diagram: occipital region]			[Diagram: spinal region with 12 metotic somites]											
Amia	[Diagram: occipital region]			[Diagram: spinal region with 12 metotic somites]											
Lepisosteus	[Diagram: occipital region]			[Diagram: spinal region with 12 metotic somites]											
Salmo	[Diagram: occipital region]			[Diagram: spinal region with 12 metotic somites]											

Fig. 7.
de Beer's 1937 scheme of composition of occiput in selected actinopterygians.

front of the medulla and the first few spinal nerves. Thus to the original set of older occipital nerves (as in selachians) the younger set of occipito-spinal nerves has been added" ("durch Assimilation einer Anzahl von Wirbeln ... caudalwärts verlängert und damit den Anfang der Medulla und die ersten Spinalnerven in seinen Bereich aufgenommen ... Es ist somit zu dem ursprünglichen Kontingent der älteren occipitalen Nerven noch der jüngere Zuwachs occipito-spinaler Nerven hinzugekommen."). In his table on p. 450, Fürbringer listed the different states that he found in his ganoids. He concluded that the number of occipital and occipito-spinal nerves varies considerably within the genus *Acipenser* and also between *Chondrostei* and the other 'ganoids' *Polypterus*, *Lepisosteus* and *Amia* (occipital nerves are lacking in teleosts according to Fürbringer 1897: p. 465). Fürbringer (1897) noted that *Polypterus* has one occipital and one occipito-spinal nerve, *Acipenser* two occipital, five or six occipito-spinal and two to three associated nerves, *Lepisosteus* one occipital and 3 or 4 occipito-spinal nerves, and *Amia* one occipital and three occipito-spinal nerves. The first, and it seems the only substantial, critique with factual evidence of Fürbringer's (1897) far reaching ideas was put forward by Allis (1899). By comparing the pattern of nerve foramina, spino-occipital nerves and number of myomeres and myosepta that attach to the skull in *Amia* and *Scomber*, Allis (1899) demonstrated convincingly that Fürbringer's (1897) terminology is insufficient and leads to erroneous conclusions about the homology of the nerves and the anterior muscle segments.

Fürbringer's (1897) distinction of occipital and occipito-spinal nerves according to when they were incorporated into the occiput (older and younger) makes little sense, as he uses absolute time as the distinguishing factor, which is typical of prephylogenetic thinking. In the cladistic paradigm, one rather refers character changes to branches between nodes on a tree, which in the case of the two types of nerves would reveal quickly that their distinction cannot be upheld. We note that despite their considerable difference in number among gnathostomes (Fürbringer 1897), the nerves of the plexus cervicobrachialis, which includes spino-occipital (occipital + occipito-spinal) and anterior true spinal nerves in chondrichthyans (see Fürbringer 1897, Norris & Hughes 1920), actinopterygians (see Allis 1897, 1899, 1903, 1909, 1922; Fürbringer 1897; Herrick 1899, 1900; Norris 1925), and Dipnoi (Fürbringer 1897), innervate the same structures, the hypobranchial musculature associated with the gill arches (coracobranchiales and sternohyoideus) and the muscles of the pectoral fin. We believe that counting spino-occipital nerves to derive the number of segments that have been incorporated into the occiput is too simplified an approach. Counting only the number of foramina in the occiput is even less accurate, because more than one nerve may issue through a single opening, because some of these nerves may issue via foramina in

the membrane between the occiput and the first neural arch, and because of intraspecific variation. If we are correct that osteognathostomes have the same number of occipital myosepta in early developmental stages, then we would expect that differences in the number of spino-occipital nerves (defined as nerves exiting the skull or postoccipital membrane posterior to the vagus and anterior to the first spinal nerve associated with the neural arch that develops in the fourth myoseptum) are taxon specific autapomorphies.

Acknowledgments

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The origin and the phylogenetic interrelationships of teleosts have been controversial subjects ever since Greenwood, P. H., Rosen, D. E., Weitzman, S. H. and Myers, G. S. in 1966 presented a revision of teleost phylogeny. Different taxa (*Amia*, *Lepisosteus*, *Amia* + *Lepisosteus*, †Pycnodontiformes, †*Dapedium*, †Pachycormiformes, and others) have been proposed as the sister group of teleosts. Tremendous advances have occurred in our knowledge of Neopterygii, basal to teleosts, and in their major component the teleosts over the past 40 years. Many new key fossils have been studied, and many extant teleost clades have been traced back to the Jurassic in detailed studies by Gloria Arratia in 1987, 1996, and 2000. In addition to new fossils, a large number of new morphological and molecular characters have been incorporated in recent phylogenetic analyses, adding to our arsenal of approaches. This book gives a modern view of these approaches. It includes a compilation of synapomorphies of numerous teleostean taxa with a new proposal of their classification, a proposal that pycnodonts are the fossil sister group of teleosts, a phylogeny based on mitochondrial genome sequences, separate analyses of basal teleostean taxa (Osteoglossomorpha, Clupeiformes, Gonorynchiformes, Cypriniformes, Characiformes, Siluriformes, Salmoniformes, Esociformes) and the euteleostean Aulopiformes, karyological studies of Cyprinodontidae, and morphological analyses of the posterior part of the neurocranium. A biography of Gloria Arratia is also presented.

The book represents contributions to the symposium "Origin and phylogenetic interrelationships of teleosts" sponsored by the American Society of Ichthyologists and Herpetologists (ASIH) and organized by the three editors of this volume and held at the Society's annual meeting in St. Louis, Missouri, on 14 July 2007. At the same meeting, Gloria Arratia was honored with the Robert H. Gibbs, Jr. Memorial Award, 2007, for her outstanding contributions to systematic ichthyology. The volume presents the current state of phylogenetic knowledge of the origin of teleosts and the interrelationships of teleost groups, both key issues in fish systematics, based on both morphological (of extant and fossil taxa) and molecular evidence. The many contributors to the volume present and evaluate progress in studying both characters and taxa and in establishing databases (morphological and molecular) that will be of use in future.