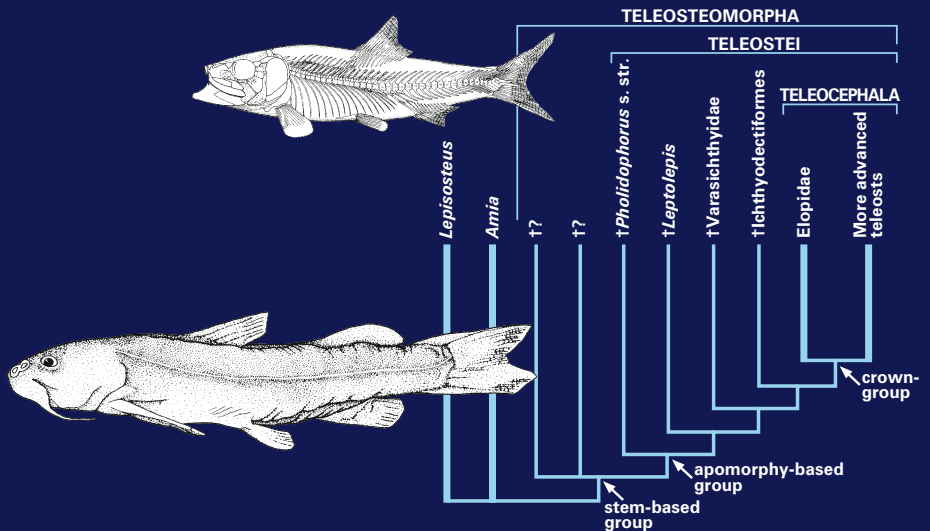# Origin and Phylogenetic Interrelationships of Teleosts

Honoring Gloria Arratia

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

TELEOSTEOMORPHA

TELEOSTEI

TELEOCEPHALA

Lepisosteus

Amia

†?

†?

†*Pholidophorus* s. str.

†*Leptolepis*

†Varasichthyidae

†Ichthyodectiformes

Elopidae

More advanced teleosts

crown-group

apomorphy-based group

stem-based group

Contents

Occipito-vertebral fusion in actinopterygians: conjecture, myth and reality.
Part 2: Teleosts

G. David Johnson and Ralf Britz

The apomorphy of today is the synapomorphy of tomorrow.

Tyson Royal Roberts [From Ichthyology to Philosophy – Roads less travelled, 2005: p. 16]

Clearly, the occipital condyle region of the teleost neurocranium warrants closer attention.

Peter Forey [A revision of the elopiform fishes, fossil and Recent, 1973: p. 14]

Abstract

The composition of the occiput of teleosts has been the subject of much conjecture for more than a century. We review various lines of putative evidence that have been presented in support of the hypothesis that one or more vertebrae (or parts thereof) have fused with the occiput in one or another teleost. As in Part 1 of this paper, which deals with nonteleosts, we maintain that ontogeny and attachment of anterior myosepta provide the only unequivocal landmarks for elucidating the composition of the occiput. With this fundamental approach, we show that *Heterotis* and *Megalops* are the only teleosts, aside from molids, ostraciids and male cetomimids, in which a vertebral centrum is fused ontogenetically to the occiput. We review and clarify the distribution of the so-called accessory neural arch, ANA, long touted as evidence for occipito-vertebral fusion in teleosts and demonstrate that it has nothing to do with incorporation of the first centrum of the vertebral column. The ANA develops in the posteriormost occipital myoseptum, the third, and is never associated with a centrum, whereas the first centrum and its respective neural arch develop in the fourth myoseptum. We find no reason to question the primary homology of the ANA of *Elops* with that of clupeocephalans and conclude that the level at which it may be synapomorphous can only be determined by parsimony argumentation.

Introduction

As we discussed in Part 1 of this paper, conjecture about the origin and composition of the vertebrate skull has moved the imagination and pen of vertebrate comparative anatomists for over two centuries. Here, as there, our focus is on the occipital region of actinopterygian fishes. In Part 1 we reviewed previous hypotheses proposing fusion of varying numbers of vertebrae to the occiput during ontogeny in *Polypterus*, *Acipenser*, *Lepisosteus*, and *Amia* and presented factual evidence that we believe unequivocally supports or rejects these hypotheses. We move now to teleosts, where the myth that "The occipital condyle of lower teleosts is primitively formed by the inclusion of a centrum into the neurocranium …" (Forey 1973), has persisted for over a century (Bemis & Forey 2001), despite the absence of ontogenetic or other unequivocal evidence to support it. Our purpose is to review the conjectures of previous authors about this phenomenon, discuss the various lines of evidence that have been touted to support its reality, most importantly the so-called accessory neural arch, and present our own lines of ontogenetic

and myoseptal evidence to dispel the myth. Additionally, we address the issue of the homology of the accessory neural arch.

Materials and methods

This study is based on the following cleared and stained (Taylor & van Dyke 1985) and dry skeletal specimens, only the latter so indicated. Institutional abbreviations: **AMNH**, American Museum of Natural History; **BMNH**, The Natural History Museum, London; **CU**, Cornell University Museum of Vertebrates, Ithaca, N.Y.; **ROM**, Royal Ontario Museum, Toronto; **HSU**, Humboldt State University, Arcata, CA.; **SIO**, Scripps Institute of Oceanographic Science, La Jolla, CA.; **UMA**, University of Massachusetts, Amherst, MA.; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C. In the text and the list below, all lengths are Standard (SL) unless otherwise stated.

Osteoglossidae: *Heterotis niloticus*, BMNH 1904.1.20.16, 55 mm; BMNH 2009.1.19.1**,** 230 mm, dry; T. Moritz pers. coll., 430 mm, dry. *Osteoglossum bicirrhosum*, BMNH 2009.1.19.3, 68 mm; USNM 198123, 3, 59-65 mm.

Elopidae: *Elops saurus*, USNM 397553, 5 specimens, 23.6-30.9 mm; USNM 186363, 2 specimens, 86-137 mm; USNM 111310, ca. 500 mm, dry; USNM 47307, ca. 500 mm, dry. *E. machnata*, BMNH 1962.8.28.21, 65 mm.

Megalopidae: *Megalops cyprinoides*, MCZ 54189, 18.4 mm; BMNH 1955.9.19.832, 59 mm; USNM 173578, 2 specimens, 79-114 mm; AMNH 214538, 435 mm; *M. atlanticus*, AMNH 22175, ca. 55 mm; USNM 132933, 74 mm; USNM 357435, 80 mm; AMNH 55321, 90 mm; USNM 260335, ca. 480 mm, dry; CU 94239 (formerly UMA 10353), 830 mm TL, dry; USNM 26252, ca. 960 mm, dry; USNM 111356, ca. 1300 mm, dry; CU 90720, 1640 mm.

Albulidae: *Albula vulpes* USNM 128393, 3 specimens, 24.2-37 mm.

Clupeidae: *Sprattus sprattus*, BMNH 2009.1.19.4, 23.8 mm.

Engraulidae: *Anchoa mitchilli*, BMNH 2009.1.19.5, 21.3 mm.

Platytroctidae: *Holtbyrnia latifrons*, SIO71-112, 61 mm.

Salangidae: *Neosalanx brevirostris*, HSU 85-38, 2 specimens, 35-48 mm.

Salmonidae: *Oncorhynchus*, BMNH 2005.7.5.1-11, 11 specimens, 22.5-28.0 mm.

Esocidae: *Esox americanus*, ROM 24422, 5 specimens, 9.9-16.9 mm NL; BMNH 1982.11.60.16, 61 mm; USNM 391633, 124 mm; *E. lucius*, ROM 598CS, 2 specimens, 62-77.5 mm; BMNH 2009.1.19.5, 27 specimens, 9.5 mm NL, 47 mm SL; *E. niger*, USNM 327690, 98 mm; USNM 284095, 536 mm, dry; USNM 11136, 613 mm, dry.

Synodontidae: *Synodus* sp., USNM 397554, 35.1 mm; *S. variegatus*, USNM 315318, 75 mm.

Myctophidae: *Myctophum obtusirostris*, AMNH 29140, 2 specimens, 55-73 mm.

Polymixiidae: *Polymixia lowei*, USNM 159300, 115 mm.

Percopsidae: *Percopsis omiscomaycus*, USNM 237017, 71 mm.

Moronidae: *Morone americana*, USNM 391632, 2 specimens, 14.7-16.3 mm.

Arripidae: *Arripis georgianus*, USNM 287442, 68 mm.

See Britz & Johnson (this volume) for methods.

Results and Discussion

Heterotis and other osteoglossomorphs

Our investigations indicate that *Heterotis* and *Megalops* (discussed below) are the only teleosts, other than molids and ostraciids (Britz & Johnson 2005) and male cetomimids (Johnson et al. 2009), in which a vertebral centrum is fused ontogenetically to the occiput. Ridewood (1905) noted for *Heterotis* that "The occipital half vertebra comes away readily from the exoccipitals and basioccipital, and leaves their posterior ends rough." We confirmed this in his 230 mm specimen, and microscopic examination of the exposed surfaces indicates that this first centrum is fused to the basioccipital, but remains free from the exoccipitals. Similarly, Taverne's (1977: p. 171, fig. 94) description and illustration of a 62 mm specimen of *Heterotis* indicate that the first vertebra is fused to the basioccipital, and shows a clear line of demarcation dorsally in the exoccipital region. The same configuration is evident in our 430 mm dry specimen (Fig. 1B). As both Ridewood and Taverne showed, this fused first centrum bears a fused neural arch
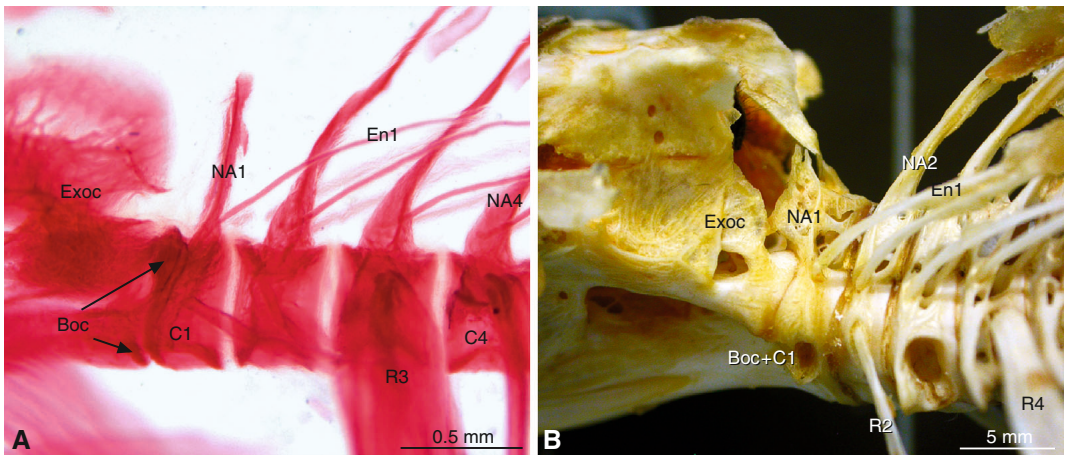
Fig. 1.
Occiput and anterior vertebrae, lateral view, in *Heterotis niloticus*: **A,** BMNH 1904.1.20.16, 55 mm; **B,** T. Moritz pers. coll., 430 mm. Abbreviations: **Boc**, basioccipital; **C**, centrum; **En**, epineural; **Exoc**, exoccipital; **NA**, neural arch; **R**, rib.

with associated epineural bone and a large bone labeled "rib" by Ridewood and "ossified ligament" by Taverne that articulates distally with the medial surface of the upper end of the pectoral girdle. The fused neural arch and associated epineural can also be seen in our dry specimen, from which the first "rib" has been removed. Patterson & Johnson (1995) believed this bone to be an ossified Baudelot's ligament and took its attachment on the "occiput" along with the origin of the first rib on the "second" vertebra, as corroborative evidence of the fusion of the first vertebra to the basioccipital. Bemis & Forey (2001: figs. 20.6 F, G) seemed to accept this evidence, but their figures of two smaller specimens (11.5 mm TL, 33 mm TL) are based on Daget & d'Aubenton (1957: figs. 9, 13), and show incorporation of a centrum into the basioccipital prior to the fusion of the first vertebra. However, Daget & d'Aubenton (1957) were wrong, as our figure of a larger, 55 mm cleared and stained specimen (Fig. 1A) clearly shows. They mistook the posterior, dorsally projecting, wedge-shaped portion of the basioccipital for the first centrum, which we believe is autogenous at this stage. In our larger 55 mm specimen, this dorsal portion of the basioccipital is readily visible, and the first centrum remains free from the basioccipital ventrally, with only superficial fusion to it along the lateral surface.

We conclude that Ridewood's (1905) and Taverne's (1977) interpretations of the occipital region in *Heterotis* are fundamentally correct – the first vertebra fuses ontogenetically to the basioccipital, but remains separate from the exoccipitals. However, this fusion occurs relatively late in ontogeny (it appears to be just beginning in our 55 mm specimen), and the hypothesis of a much earlier fusion suggested by Daget & d'Aubenton (1957) and Bemis & Forey (2001) is based on confusion of the basioccipital with the first centrum, an error that has often been made in interpreting the configuration of the posterior occiput of teleosts (e. g., see Rosen 1985), and, in part, led to the longstanding confusion about the occipito-vertebral situation in *Arapaima* (Ridewood 1905, Taverne 1977, Lundberg & Chernoff 1992, Bemis & Forey 2001), only recently clarified by Hilton et al. (2007).

Bemis & Forey (2001) noted that *Osteoglossum* also has Baudelot's ligament on the basioccipital and the first rib on the second vertebra (Patterson & Johnson 1995: table 3) and suggested that a vertebral element may be incorporated there as well. Our observations indicate that in *Osteoglossum* there is no evidence in ontogeny that a centrum has been incorporated into the occiput (also see Hilton et al. 2007).

Elopocephalans

Conjecture about occipito-vertebral fusion in elopocephalans has been confounded by the presence in numerous noncteosquamate taxa of the so-called 'accessory neural arch'. This and other putative evidence for incorporation of one or more vertebra into the occiput are discussed below.

Accessory neural arch as evidence of occipito-vertebral fusion. The first reports of an unattached neural arch behind the occiput without a corresponding centrum (accessory neural arch of Rosen 1985) in teleosts appear to be those of Brühl (1856) and Bruch (1861). Fink & Fink (1981) noted the presence of this arch in *Polypterus*, *Amia*, and many primitive teleosts, inferring that it is primitive for teleosts and interpreting its absence in ostariophysans as synapomorphous. A more extensive survey of the accessory neural arch (ANA) by Patterson & Johnson (1995) (see Johnson & Patterson 1996: p. 278 for additional taxa) included osteoglossomorphs, which lack it, and rejected Fink & Fink's (1981) report that it is present in *Polypterus* and *Amia* (see discussion in Part 1 of this paper). Accordingly, they concluded that the ANA was not present at the base of teleosts, and that if its mosaic distribution is the result of multiple losses of a homologous structure, it is a synapomorphy of Elopocephala, requiring its loss within that group "at least 10 times (at least once in elopomorphs, at least twice in clupeomorphs, and in at least seven different eutelostean lineages – ostariophysans, esocoids, argentinoids, osmeroids, stomiiforms, aulopiforms, ctenosquamates)."

We confirm that the ANA is distributed as described by Patterson & Johnson (1995) and Johnson & Patterson (1996), and note that reports of its presence in other taxa (see below) are erroneous.

In their review of occipital structure in actinopterygians, Bemis & Forey (2001: p. 360) mistook Rosen's label "ANA" in his fig. 35 to mean accessory neural arch and so stated: "This neural arch has become known amongst teleost workers as the 'accessory neural arch' and has some significance in derived teleosts such as anglerfishes and toadfishes where it has expanded to become an integral part of the neurocranium (Rosen 1985)." However, Rosen used the label "**ACCNA**" for accessory neural arch , and his "**ANA**" actually signified "**ankylosed** neural arch", about which he said this (p. 31): "In each of the batrachoid-lophiiform and ophidiiform-gadiform groups, the exoccipital condyles primitively receded from the posterior occipital margin and consist of widely separated, cartilage-filled tubes to which prezygapophyses from the first cervical articulate." Thus, Bemis & Forey (2001) were mistaken about the presence of an accessory neural arch in some "derived teleosts" (specifically paracanthopterygians) and, as reported by Patterson & Johnson (1995), an ANA is unknown in ctenosquamates. Their report of an ANA in *Arapaima* (Bemis & Forey 2001: p. 363) was also erroneous (see Hilton et al. 2007). Rosen (1985) mistakenly reported an ANA in the ctenosquamate *Neoscopelus*, based on a misinterpretation of figs. 61-62 in Rosen & Patterson (1969) and consequently suggested that the Ctenosquamata should perhaps be restricted to the Myctophidae and Acanthomorpha, (an hypothesis rejected by Johnson, 1992, on this and other grounds). Rosen's (1985: fig. 9) illustration showing an ANA in *Albula* is also in error, and here he apparently mistook the dissociated neural arch of the first vertebra for it.

Coburn & Futey (1996: p. 344) speculated that the accessory neural arch was present in cypriniform otophysans and that it "was incorporated into the exoccipital as a reinforcing strut". They admitted, however, that the "strut forms in situ in cypriniforms, providing no evidence for fusion of an arch with the occiput." We fully concur with their conclusion, which clearly contradicts their initial speculation. We also found not even a sliver of evidence for presence of an accessory neural arch in the numerous developmental stages of various species from all otophysan subgroups listed in Hoffmann & Britz (2006) and Britz & Hoffmann (2006). Ignoring the absence of evidence for an accessory neural arch in otophysans, Coburn & Chai (2003: p. 175), cited Coburn & Futey's (1996) speculation that the accessory neural arch "might have been incorporated into the occiput of cypriniform fishes" in their study of *Chanos* development. Coburn & Chai (2003) described "paired nodules of cartilage" in 12 specimens of *Chanos* ranging from 13.3-15.5 mm SL. In only five of those they reported them as separate from the tectum synoticum (incorrectly called supraoccipital cartilage by them), and in the other specimens they were either confluent with the tectum on one or both sides. They further cited two specimens between 14.5 and 16.5 mm SL as having a "membrane ossification suggestive of the incorporation of an archlike bony fragment into the expanding occiput (Fig. 4, ANA?)." As previously in Coburn & Futey (1996), Coburn & Chai (2003: p. 178) seem to have been highly skeptical of their own conclusions as they admitted that "in sum, the evidence that these paired cartilages and their associated ossifications are an ANA is mixed and will require examination of additional material."

We find their whole homology argument contorted and unconvincing, if not forced, and we will discuss it in detail. First, Coburn & Chai (2003) consider two structures, the membrane bone lamina and the cartilaginous nodules, in *Chanos* to represent the accessory neural arch. It is nowhere clearly stated if they think that the accessory neural arch is represented by both or by just one of them. If represented by both, Coburn & Chai (2003) would have to assume that part of the accessory neural arch develops in

cartilage and the other part in membrane bone and that both have no physical contact to each other. We find that neither the nodules, nor the membrane bone lamina on the exoccipital of *Chanos* have anything in common in terms of anatomical or positional similarity with the accessory neural arch of teleosts despite Coburn & Chai's (2003) claims. The membrane bone lamina on the exoccipital is part of the long posterior extensions of that bone that form a roof over the first neural arch in the adult (see fig. 6 in Fink & Fink 1981). We are also convinced that the cartilaginous nodules develop in connection with the posterior extension of the tectum synoticum that forms an initial cartilaginous roof over the articulation of the occiput and the first vertebra, which is later replaced by the exoccipitals. We thus conclude that *Chanos* has no accessory neural arch and the modifications Coburn & Chai (2003) described are autapomorphies of that taxon related to its modified occipital structure.

Finally, the hypothesis of de Pinna & Grande (2003) and Grande & de Pinna (2004) that the ANA is present and modified as the claustrum in otophysans was convincingly rejected by Britz & Hoffmann (2006).

There has been much conjecture about the ANA as evidence that an anterior centrum has been incorporated indistinguishably into the basioccipital in many lower teleosts (most recently reviewed by Bemis & Forey 2001). Taverne (1974: p. 57) described a large, more or less triangular plate on either side of the foramen magnum above the basioccipital in *Elops*, which he said represents "the neural arch of the first vertebra that is integrated into the basioccipital, in the embryonic stage." Rosen (1985: p. 22) had this to say: "As hypothesized, the presence of an accessory neural arch, in the absence of an underlying centrum, is inferred to represent a retention of the neural arch component of a vertebral segment that either is incomplete or had been incorporated indistinguishably into the braincase." One logical consequence of this hypothesis would be that 'indistinguishable' (i.e., lacking ontogenetic or topographical evidence) incorporation of an anterior centrum into the occiput is synapomorphous at the same level as the ANA. Patterson & Johnson (1995: p. 17) rejected the notion that there is any correlation between the presence of ANA and occipito-vertebral fusion, as do we, below.

Other putative evidence for occipito-vertebral fusion. In his review of "The Neurocranial Joint with the First Vertebra" Rosen (1985), appeared (not always clear) to accept or at least argue that the first vertebra has been incorporated into the occiput in the following teleost taxa: the elopomorphs *Elops*, *Megalops*, and *Albula* (based on his own observations, the interpretations of Ridewood (1904), and those of Forey 1973, who disagreed about *Albula*); the clupeomorphs *Denticeps* (based on Greenwood's, 1968 description), *Chirocentrus*, *Dorosoma*, *Clupea*, *Dussumieria*, *Engraulis*, *Coilia*, (based on Ridewood's (1904) interpretation of the clupeoid occipital region), and *Sierrathrissa* (as suggested but left unresolved by Whitehead & Teugels 1985); the salmonoids (sensu Johnson & Patterson 1996) *Coregonus*, *Prosopium*, *Thymallus*, *Salmo*, *Oncorhynchus*, *Spirinchus*, and *Osmerus* (based on his own observations and the interpretations of Cavender & Miller 1972) ; the alepocephaloid, *Alepocephalus* (as proposed by Gosline 1969); and, based on his own observations, the esociform, *Esox* (also mistakenly reported by Jollie 1975), the aulopiforms, *Aulopus* and *Chlorophthalmus*, and the ctenosquamate, *Neoscopelus*. His arguments for this included, but were not limited to, the presence of an accessory neural arch.

In their discussion of landmarks for investigating the boundary between the neurocranium and the vertebral column, Bemis & Forey (2001: p. 360) summarized Rosen's review as follows: "Rosen (1985) believed that vertebrae are included in the teleostean braincase. He had three lines of argument. First, the primitive teleost *Elops* has a centrum-like end to the basioccipital that is ornamented with striation on the lower part of the basioccipital just like the ornament on the succeeding free centra, implying incorporation of a centrum (sculp, Figure 20.6a). Second, his specimen of the salmonid *Prosopium* has a vertical cleft incising the basioccipital region (Rosen 1985: fig. 13b), and he interpreted this to mean that this cleft represents a separation between the posterior centrum-like element from the anterior basioccipital proper. Third, there is a neural arch above the posterior end of the basioccipital in *Elops* and a pair of pits on the dorsal surface of the basioccipital of the tarpon, *Megalops* (but no associated neural arches)."

We generally concur with Bemis & Forey's assessment of Rosen's arguments, but as we noted above, he also reported an ANA in numerous clupeocephalans and inferred occipito-vertebral fusion in those taxa based on its presence there. Furthermore, Rosen also seems to have relied heavily on Cavender & Miller's (1972) conclusion that there is evidence of the first vertebra having fused with the braincase in the Pliocene fossil, †*Smilidonichthys*, and that such a fusion is neither unusual nor restricted to only a few teleosts. We find Cavender & Miller's arguments (pp. 30-31) completely unconvincing and note that the
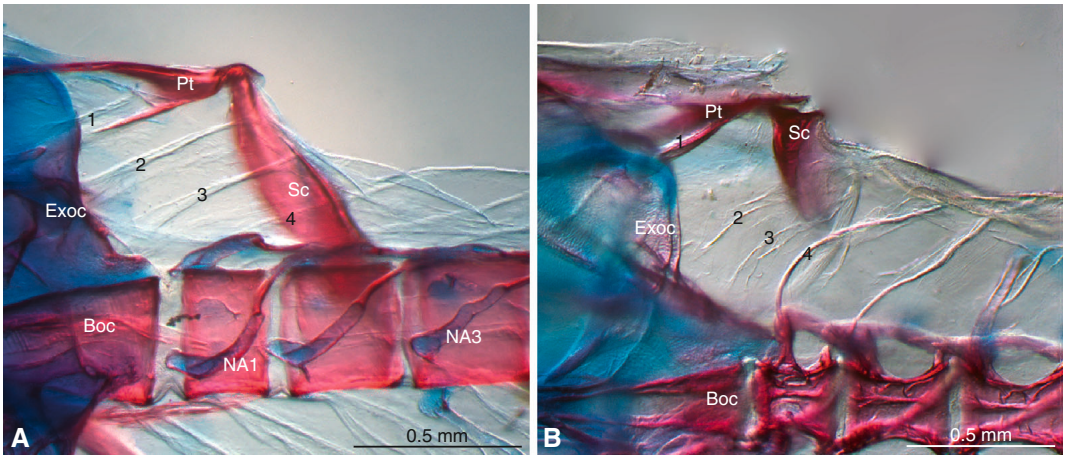
Fig. 2.
Occiput, anterior vertebrae and myosepta in: **A,** *Sprattus sprattus,* BMNH 2009.1.19.4, 23.8 mm, dorsal view; **B,** *Morone americana,* USNM 391632, 14.7 mm, ventral view. Abbreviations: **Boc,** basioccipital; **Exoc,** exoccipital; **NA,** neural arch; **Pt,** posttemporal; **Sc,** supracleithrum; **1,2,3,4,** first, second, third and fourth myoseptum.

only illustration showing the putative fusion is a reconstructed interpretation of the ventral aspect of the braincase (their fig. 4), which is wholly inadequate as evidence of occipito-vertebral fusion.

Throughout his discussion of various taxa, Rosen (1985) further amplified his first and second lines of evidence (topographical resemblance of the posterior end of the basioccipital to a centrum). He noted (Rosen 1985: p. 6) that in Ridewood's (1904, 1905) view (i.e., that the primitive tripartite occipital condlyle is primitive for teleosts, but masked in many nonneoteleostean taxa by fusion of the first centrum and the resultant exclusion of the exoccipital condyles from the joint surface), "what is identified as the basioccipital in most teleosts is actually a vertebra fused to the braincase", and that "Removal of this vertebra should, therefore, reveal the primitive tripartite arrangement." Although he did not seem to fully embrace it, Rosen summarized the alternative hypothesis of Patterson (1975: p. 318) as follows: "the basioccipital condyle, rather than being a vertebra, is made up of a plug of osteoid tissue representing the ossification of the small anterior part of the notochord that penetrates the basioccipital bone, and that it is the growth of this osteoid plug that excludes the exoccipitals from the posterior face of the occiput."

Bemis & Forey (2001) also referred to the osteoid plug hypothesis: "According to Patterson (1975) this plug sometimes resembles a centrum but in reality has nothing to do with a centrum, nor does it reflect incorporation of an additional vertebral segment into the braincase of teleosts." It seems, however, that they were confused about Patterson's argument, attributing to him (his p. 317) that the osteoid plug might be unique to some pholidophorids and leptolepids, when in fact he believed it to be present in numerous lower teleosts, including *Elops,* where it could give "the impression, especially in lateral view, that a centrum or part centrum is fused with the basioccipital …" (Patterson 1975: p. 318). Their interpretation of the occipital region in *Elops* indicates that Bemis & Forey (2001) either didn't understand or didn't accept Patterson's osteoid plug hypothesis. We agree with Patterson that bony exclusion of the exoccipitals from the posterior face of the occiput is not, per se, evidence that a vertebra has been incorporated into the basioccipital, although rather than attributing this to an "osteoid plug", we see it as a specific developmental pattern of the basioccipital that involves mineralization around the anterior tip of the sheath of the chorda, where it penetrates the chondrocranial base (see, for example, our Figs. 5A and 6A of *Megalops* and *Elops*).

Another set of occipito-vertebral landmarks addressed by Bemis & Forey (2001) is that used by Johnson & Patterson (1995) to argue that, with the exception of *Heterotis* (see above), Recent teleosts lack a vertebral component in the occiput, i.e., a survey of the positions of intermuscular bones, ribs, and ligaments based on the following premise: "Allis (1898, 1903) showed that in *Scomber* the configuration of the anteriormost myotomes and the attachment of their myosepta to the occiput are the same as in *Amia,* given that in *Amia* two vertebrae fuse with the occiput during ontogeny." "In *Scomber,* the second
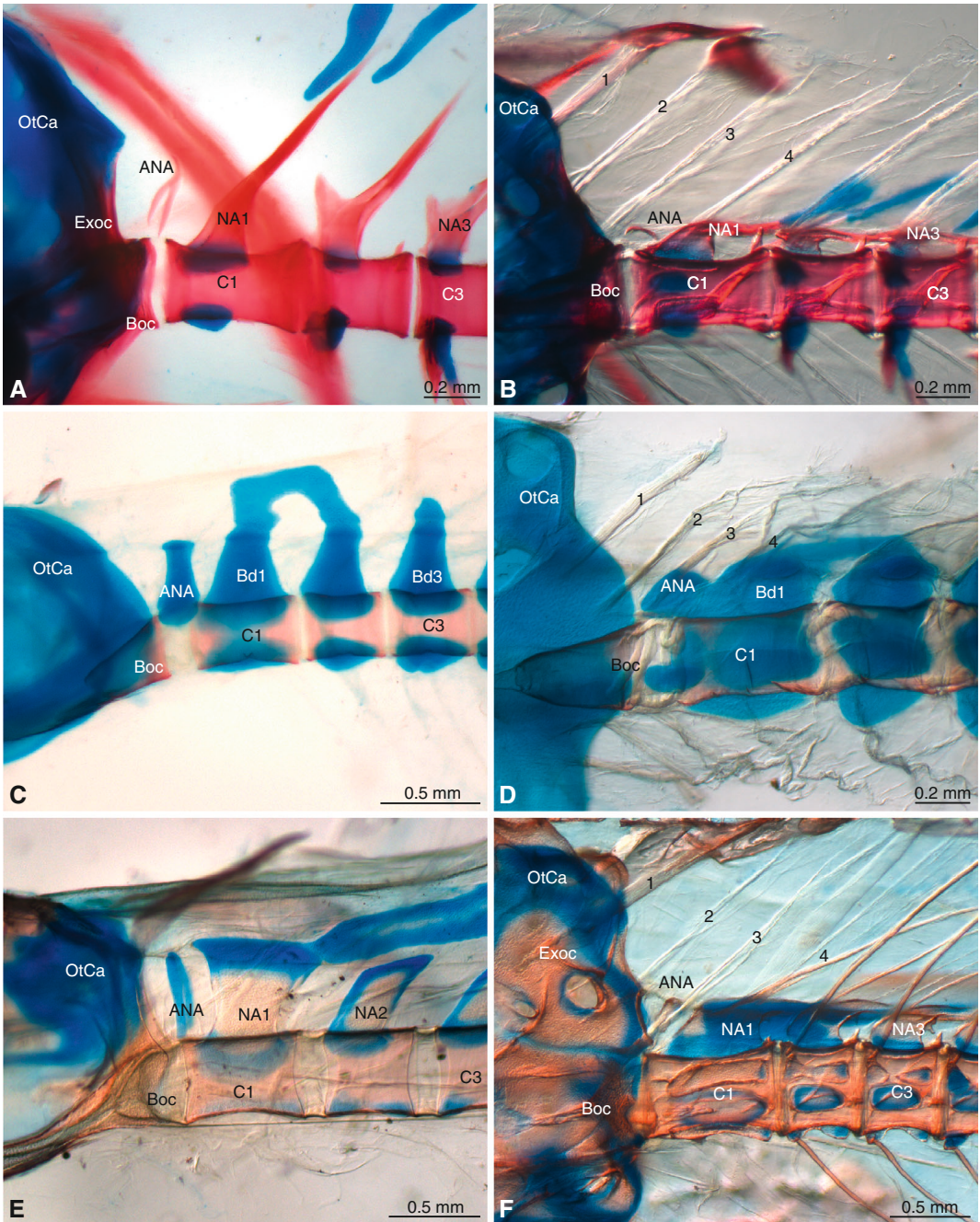
Fig. 3.
Occiput, accessory neural arch, anterior vertebrae and myosepta in the clupeocephalans: **A, B,** *Anchoa mitchilli*, BMNH 2009.1.19.5, 21.3 mm, lateral and dorsal views, respectively; **C, D,** *Neosalanx brevirostris*, HSU 85-38, 35 mm, lateral and ventral views, respectively; **E,** *Synodus* sp., USNM 397554, 31 mm, lateral view; **F,** *S. varie-gatus*, USNM 315318, 75 mm. Abbreviations: **ANA**, accessory neural arch; **Bd**, basidorsal; **Boc**, basioccipital; **C**, centrum; **Exoc**, exoccipital; **NA**, neural arch; **OF**, occipital foramen; **OtCa**, otic capsule; **1, 2, 3, 4**, first, second, third and fourth myoseptum.

and third myosepta attach to the occiput close behind (i.e., posteromedial to) the first myoseptum, and Baudelot's ligament lies in the third myoseptum; the fourth myoseptum attaches to the first vertebra and contains the first epineural. The match between anterior myosepta in *Amia* and *Scomber* implies that the pattern in *Scomber* is general for teleosts. If so, no teleost should have more than three serially homologous intermuscular on the braincase, unless one or more vertebrae are fused into the occiput, and none we know of has more than three." (Patterson & Johnson 1995). Because ribs and Baudelot's ligament also develop within the myosepta, Patterson & Johnson (1995) further argued that deviations from the generalized teleost pattern, wherein the first rib attaches to the third vertebra and Baudelot's ligament to the first, could imply incorporation of a vertebra into the occiput. In view of that, as we noted above, they accepted attachment of the first rib on the second vertebra and Baudelot's ligament on the occiput in *Heterotis* as evidence that the first centrum is fused with the basioccipital there.

Despite what Bemis & Forey (2001) called "remarkable constancy" in the pattern of association of ribs and Baudelot's ligament with the vertebrae, they pointed out that "there are some distinct variations (Patterson & Johnson 1995: table 3) that are scattered amongst lower teleosts in such a fashion that suggests that we cannot rely on these topographic landmarks to establish the composition of the occiput." We agree that there is some variability in terms of which myoseptum the first rib and first intermuscular ossify within, and note that the origin of Baudelot's ligament sometimes appears to extend across the occipito-vertebral boundary, although in this case there are actually two ligaments involved (see Patterson & Johnson 1995: p. 19, tables 3-5). Accordingly we believe that the only unequivocal landmarks for investigating occipito-vertebral structure are the myosepta themselves, and this, combined with ontogeny, is our approach here. Following Allis (1898, 1903) and Patterson & Johnson (1995), we identify the first myoseptum as that within which the lower limb of the posttemporal develops and accept that the primitive and generalized configuration for teleosts is one in which the first three myosepta attach to the occiput and the fourth attaches to the first vertebra. We illustrate this configuration in a lower teleost, the clupeid *Sprattus*, and a derived one, the acanthomorph *Morone* (Fig. 2A,B).

Clupeocephala and the accessory neural arch (ANA)

As discussed above and in Part 1 of this paper, the accessory neural arch does not occur in osteoglossomorphs or nonteleostean actinopterygians. Patterson & Johnson (1995: p. 17) concluded that whatever the origin of the ANA, "it does not represent the remains of a missing vertebra", and that its presence in *Elops* and widespread distribution among clupeocephalans could represent a synapomorphy of Elopocephala, wherein any interpretation requires that it has been lost numerous times. On the other hand, Bemis & Forey (2001) postulated that the ANA of *Elops* (which they labeled occipital neural arch, ocna) is not homologous with that of clupeocephalans, arguing that its "position is much more like the regular neural arches which are incorporated with centra into the skull of *Amia*", whereas that of clupeocephalans "is not part of the regular neural arch series". For that reason, they hypothesized that the ANA may be a clupeocephalan synapomorphy, an idea fist proposed by (though not credited to) Rosen (1985: p. 9) They based their hypothesis on rather limited data, comparison of Rosen's (1985: fig. 10) drawing of a 60 mm TL cleared and stained *Elops* and their 650 mm TL *Elops* skeleton with a developmental series of two clupeocephalans, the clupeid *Alosa sapidissima*, and *Esox lucius*. We discuss the situation in *Elops* below. As for clupeocephalans, Bemis & Forey (2001) offered three counts on which the ANA of *Alosa* differs from a regular neural arch, tissue origin, position in relation to the underlying centra, and timing of developmental sequence.

On the first count, tissue origin, they stated that in Alosa, the ANA "appears to be formed directly in membrane bone". However, they noted that for clupeocephalans this condition "may not prove to be general because cartilaginous precursors are present in *Esox lucius*, *Salmo salar*, and *Protosalanx chinensis* (Johnson & Patterson 1996: figs. 11b and 12f)." Furthermore, de Pinna & Grande (2003: figs. 1, 2) illustrated a cartilaginous precursor of ANA in the clupeids *Pellona harroweri*, *P. flavipinnis* and the osmerid *Osmerus mordax*, and reported that they also observed it in *Anchoa marini*, and, contra Bemis & Forey (2001), in *Alosa sapidissima*. Coburn & Chai (2003: fig. 2) illustrated it in *Dorosoma cepedianum*, and our Figures 3B,C and 4B show a cartilaginous component in the salangid *Protosalanx*, the aulopiform *Synodus*, and the alepocephaloid *Holtbyrnia*, respectively. It is clear then that the generalized condition for clupeocephalans is that ANA develops in cartilage (as it does in *Elops*), not in membrane bone as claimed by Bemis & Forey, and thus, on this count, is no different from a regular neural arch.

On the second count, position in relation to the underlying centra, Bemis & Forey (2001) reported that the ANA of *Alosa* and *Esox* arises in what they called an "intervertebral position" between the basioccipital and the first vertebra and "only later becomes located dorsal to the basioccipital." (The term "intervertebral" is incorrect, because they were referring to a position between the basioccipital and the first vertebra.) One might question the significance of the difference between the relative positions of the ANA in their figs. 20.7A (22 mm TL) and B (24 mm TL) of *Alosa*, there seems to be little difference between them in de Pinna & Grande's (2003) figures 1B (19.5 mm SL) and 1C (22 mm SL) of *Pellona*, and the early stage cartilaginous ANA in Coburn & Chai's (2003) figure 2 (17 mm SL) of *Dorosoma* lies directly over the basioccipital. Thus, although more data is needed, we can say that an early so called "intervertebral position" does not characterize all clupeocephalans, and we suspect that there may be substantial variability in position of ANA relative to the basioccipital at its initial appearance. In fact, it is an artificial construct, and has nothing to do with movement of the ANA but rather with the relative development of the basioccipital at the first appearance of the ANA. In any case we fail to see how this relative position criterion tests homology of the ANA and maintain that a critical criterion for this is the identity of the myoseptum in which it develops.

On the third count, timing of developmental sequence, Bemis & Forey (2001) described that in *Alosa*, the arches and ribs are present in cartilage prior to development of the ANA, which appears at a later stage, after the neural arches have begun to ossify in a rostrocaudal gradient and noted that they observed the same developmental sequence in *Esox*. Their illustrations of *Alosa* (fig. 20.7) show neural arches present before the ANA but do not demonstrate sequence of ossification, because they did not distinguish between bone and cartilage! However, de Pinna & Grande (2003: fig. 1) described and illustrated this distinct delay in chondrification and ossification of the ANA in another clupeid, *Pellona*, and reported that it also occurs in *Anchoa*. They noted (based on pers. comm. M. Coburn and D. Johnson) that the difference in deveopmental timing is less pronounced in *Dorosoma*, *Esox* (contra Bemis & Forey 2001) and the salmonid *Coregonus*. Our observations of developmental series of *Esox americanus* and *E. lucius* show that the ANA appears in cartilage together with the first few neural arches and ossifies in sequence with them, i.e., its chondrification and ossification are not delayed relative to that of the regular neural arches. (Jollie 1975: p. 78 was mistaken when he wrote that "around the time when *E. lucius* reaches 27 mm, the basioccipital is peculiar in that it includes the first vertebral body, the neural arch of which lies free"). Developmental timing of the ANA is known for relatively few clupeocephalan taxa, but once again we can say that a distinct delay relative to the regular neural arches is not universal for the group.

According to Bemis & Forey (2001), "many more developmental sequences on different taxa are needed to establish whether the accessory neural arch is, in fact, part of a developmental sequence different from usual neural arches". Above, we show that the three lines of evidence they presented to support such a difference do not withstand closer scrutiny. We also see no substantive basis for their speculation "that in clupeocephalans the development of the centrum becomes decoupled from that of neural and haemal arches allowing the possibility of the development of an accessory neural arch". De Pinna & Grande (2003) also disagreed with part of the Bemis & Forey (2001) hypothesis, concluding that "nonhomology between ANA and the neural arch series seems unlikely, in view of their numerous similarities of shape and position and the potential plasticity expected for such structures. However, Bemis & Forey's proposal that ANA is a clupeocephalan character may still be correct, in the sense that ANA in clupeocephalans may be a neural arch different (segmentally) from the one seen in the similar position in more primitive lineages". By more primitive lineages, de Pinna & Grande (2003) meant *Amia*, *Lepisosteus*, and *Elops*, accepting Bemis & Forey's premise that the condition in all three is the result of anterior centra having been incorporated into the occiput (as we show below, this is not the case for *Elops*). De Pinna & Grande (2003) speculated for clupeocephalans "that the peculiar traits of the ANA, when compared to regular neural arches, might be induced by simple alterations in the balance of certain proteins during development." These alterations (i.e., increase in the ratio of chondritin to bone morphogenetic protein) would supposedly suppress development of a neural arch (ANA) closest to the developing basicranium and perhaps even "an entire vertebral body (closest to the basicranium, anterior to the vertebra normally identified as v1)", by which they presumably meant centrum. In the absence of any empirical evidence, we reject this speculative explanation for delayed development of the ANA, and note that it is inapplicable to a putatively reduced centrum, because there was never one associated with the ANA.

To summarize, based on the preceding discussion we reject both the empirical and the speculative arguments presented by Bemis & Forey (2001) that the ANA is not part of the regular neural arch series
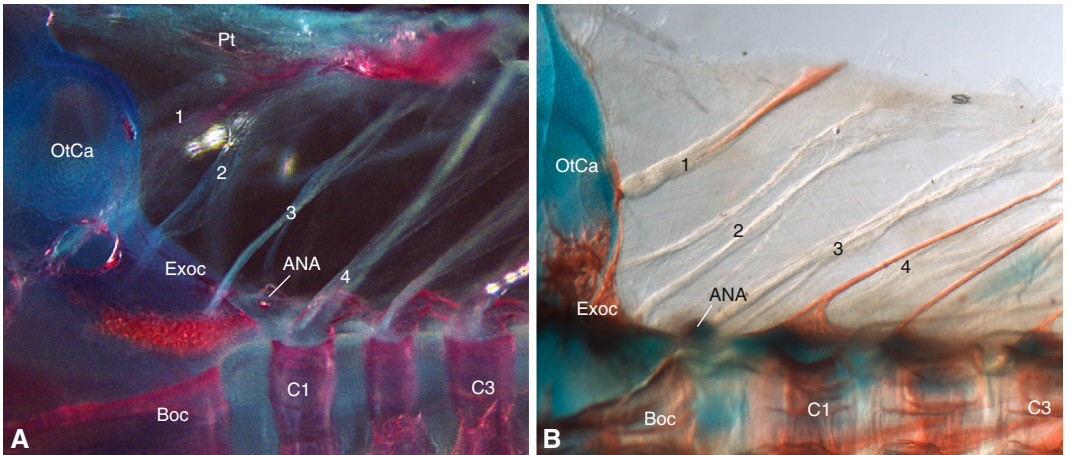
Fig. 4.
Occiput, accessory neural arch, anterior vertebrae and myosepta, ventral view, in the clupeocephalans: **A,** *Oncorhynchus*, BMNH 2005.7.5.1-11, 26.5 mm; **B,** *Holtbyrnia latifrons,* SIO71-112, 61 mm. Abbreviations: **ANA**, accessory neural arch; **Boc**, basioccipital; **C,** centrum; **Exoc**, exoccipital; **OtCa**, otic capsule; **Pt**, posttemporal; **1**, **2**, **3**, **4**, first, second, third and fourth myoseptum.

as well as the ones presented by those authors and de Pinna & Grande (2003) that the ANA may be a clupeocephalan synapomorphy. On the other hand, based on the unequivocal occipito-vertebral landmarks we described above, the myosepta, we agree with the former authors and disagree with the latter that the ANA is not part of the regular neural arch series. We illustrate in Figure 2 the generalized occipito-vertebral arrangement for teleosts lacking an ANA wherein the first three myosepta attach to the occiput and the fourth attaches to the first neural arch and centrum. If the ANA of clupeocephalans represents the first element in the neural arch series, then it is clear enough that it must lie in the **fourth** myoseptum, as it does in those taxa with no ANA. It does not – it lies instead in the **third**, as we show in the engraulid *Anchoa* (fig. 3B), the salangid *Protosalanx* (Fig. 3D), the aulopiform *Synodus* (Fig. 3F), the salmonid *Salmo* (Fig. 4A), and the alepocephaloid *Holtbyrnia* (Fig. 4B). We have observed the same condition in all other clupeocephalans examined with an ANA. We conclude then, that the ANA of clupeocephalans, is not part of the regular neural arch series and that it does not represent retention of a neural arch that has been lost or incorporated into the occiput.

Elopocephala and the accessory neural arch (ANA)

Having established that the ANA is not evidence for occipito-vertebral fusion in clupeocephalans and that such fusion does not occur there, (except in the acanthomorph molids, ostraciids and male ceto-mimids), we now review the putative evidence for identity of the ANA and occipito-vertebral fusion in the elopomorphs *Megalops* and *Elops*, the only nonclupeocephalan teleosts that have been reported to have an ANA.

*Megalops***:** A review of the literature indicates that of the several authors who have described and/or illustrated the occiput of *Megalops*, only the earliest (Brühl 1846) and most recent (Bemis & Forey 2001) were somewhat confused about its configuration. Shufeldt (1885: p. 816, figs. 33-34) referred to "the suspicious-looking basioccipital" of *Megalops*, but nonetheless correctly described "that it is so far anchylosed with the first vertebra of the column that it is impossible to remove the latter in the specimen without doing it injury". He also described the two circular pits on the dorsal surface of the fused vertebra and noted that "Dr. Gill states that these are intended to lodge the extremities of the neural arch." Ridewood (1904) accepted Shufeldt's interpretation.

Although he didn't describe it, Greenwood (1970: pls. 1, 3) labeled a "fused vertebral centrum" at the back of the basioccipital in *Megalops cyprinoides* and *Megalops atlanticus*, respectively. Forey (1973) described and illustrated the same for both taxa as well as *Elops* and listed the first vertebral centrum
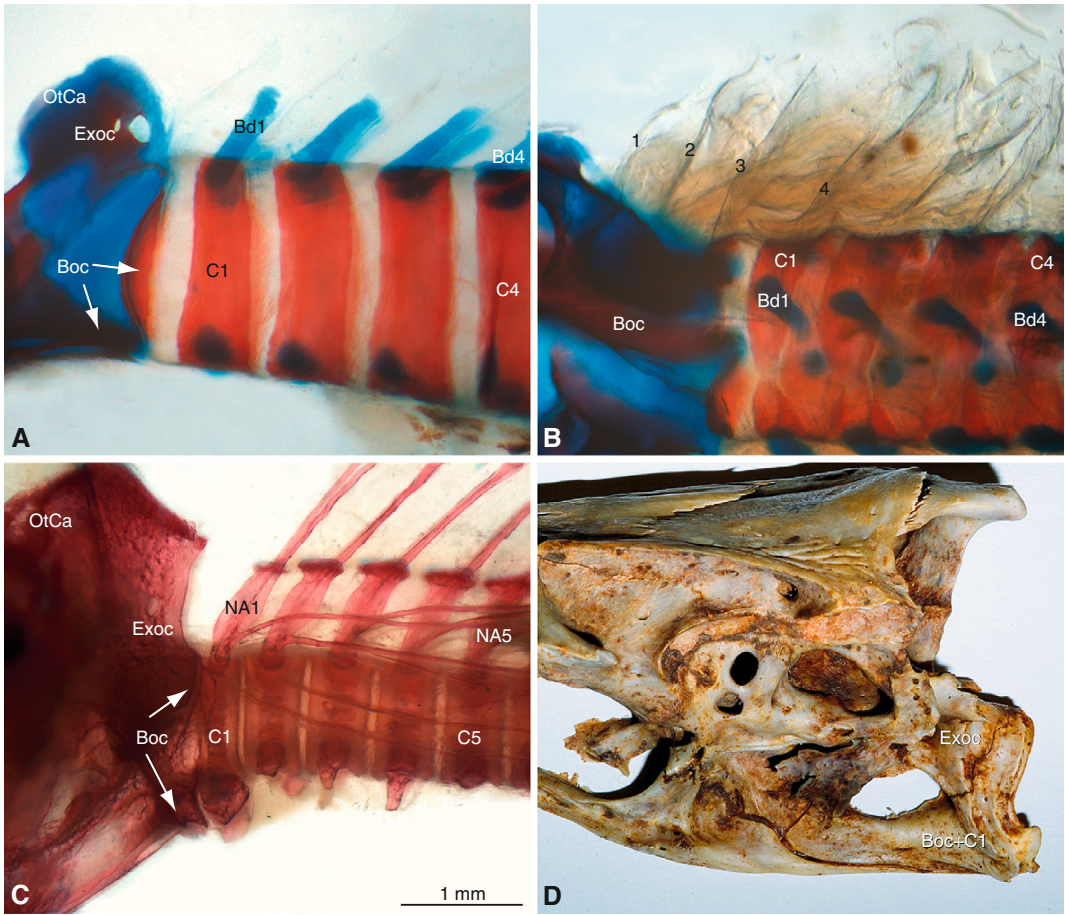
Fig. 5.
Occiput and anterior vertebrae, lateral (**A**, **C**, **D**) and ventral showing myosepta (**B**) views in the elopiforms: **A**, **B**, *Megalops cyprinoides*, MCZ 54189, 18.4 mm; **C**, *M. cyprinoides*, BMNH 55.9.19.832, 59 mm; **D**. *M. atlanticus*, USNM 111356, ca. 1300 mm. Abbreviations: **Bd**, basidorsal; **Boc**, basioccipital; **C**, centrum; **Exoc**, exoccipital; **NA**, neural arch; **OtCa**, otic capsule; **Pt**, posttemporal; **1**, **2**, **3**, **4**, first, second, third and fourth myoseptum.

"forming a functional part of the neurocranium" as a diagnostic feature of his Elopoidei. Taverne (1974), citing Ridewood (1904) and Greenwood (1970), noted that in *Megalops*, one can see the suture between the body of the basioccipital and what he called a half vertebra, with which an autogenous neural arch is associated.

Rosen (1985), referring to Cavender & Miller's (1972) claim about a fused centrum in the "basicranial-vertebral joint" in several salmonids and elopiforms, noted that "Their claim is problematical because ontogenetic data illustrating the course of vertebral fusion are lacking for most cited examples." His exception was *Megalops atlanticus*, for which he illustrated (figs. 9A,B) a "10 cm TL" specimen in which the first vertebra and neural arch are free, and an "80 cm subadult" in which he noted "the ankylosis of the first vertebra with the basioccipital and the presence of wells for the small neural arch shown in A". Although we agree with Rosen that the first vertebra of *Megalops atlanticus* is free in early ontogeny, we found it closely attached to the basioccipital in a 74 mm specimen (USNM 132933) and fused to it in an 83 mm (105 mm TL) specimen (USNM 357435) and were thus initially unable to explain Rosen's illustration of it as completely free and removed from the occiput in his uncatalogued "10 cm TL" specimen. We subsequently examined the now catalogued specimen (AMNH 22175) that exactly matches Rosen's (fig. 9A)

illustration and found it to be less than 55 mm SL (ca 75 mm TL), thus explaining the discrepancy. We also examined the specimen Rosen (fig. 9B) claimed to have illustrated as an "80 cm subadult" (AMNH 55321) and found it to be only 90 mm (110 mm TL) and to have the first centrum tightly attached, but not fully fused to the basioccipital. Furthermore, the neural arch of the first centrum is present, not absent as shown in Rosen's illustration. Perhaps Rosen cited the wrong catalog number, but if this is the specimen he illustrated, he did not accurately represent it. In any case, based, on our own observations, we conclude that the first vertebra of *Megalops atlanticus* remains free in early ontogeny until ca. 80-90 mm, when it begins to fuse to the basioccipital.

We add a much earlier stage in the development of the occiput of *Megalops* (*M. cyprinoides*, 18.4 mm, partly disarticulated, Figs. 4A,B), wherein the first vertebra and neural arch are fully removed from the occiput, and the posterior condylar surface of the basioccipital has just begun to ossify around the notochord. By 59 mm (*M. cyprinoides*, Fig. 4C), the wedge-shaped posterior portion of the basioccipital extends dorsally between the exoccipitals and the first vertebra and has begun to fuse with the latter. The next size available to us was a 435 mm dry skeleton, and there the first vertebra is fused along its entire anterior surface to the basioccipital, and the second and succeeding vertebrae are free. The same is true in five dry skeletons of *M. atlanticus* ranging in size from 480-1640 mm, and we illustrate this terminal condition in our ca. 1300 mm specimen (Fig. 4D, first neural arch removed). We concur, then, with the preceding authors that a single centrum is incorporated into the occiput of *Megalops* and that its neural arch remains autogenous.

In the earliest account of the occiput of *Megalops*, Brühl (1856) incorrectly assumed that the basioccipital is long and supports an accessory neural arch on its dorsal surface. In the most recent account, Bemis & Forey (2001) confounded the issue in several ways. They agreed with Rosen (1985) that *Megalops* incorporates "centra" into the occiput and stated that "Another aspect of this is revealed by our postlarval ontogenetic series of tarpon, which demonstrates progressive incorporation of centra into the occipital region (e.g., c2 in Fig. 20.6d)." In fact, Rosen's evidence was for the fusion of a single centrum (the first), as is ours, and we have found nothing to suggest that fusion of additional ones occurs. We believe that Bemis & Forey's (2001) surmise about incorporation of the second centrum is a result of their misunderstanding of the structure of the basioccipital. As discussed above, they incorrectly interpreted the wedge-shaped posterior portion of the basioccipital as representing a centrum in both *Heterotis* and *Arapaima* (Hilton et al. 2007). The illustrations of their "ontogenetic series of tarpon", *M. atlanticus* (830 mm and >1500 mm TL, figs. 20.6C,D) show the basioccipital with no wedge-shaped posterior portion (contra our Figs. 4A,C) and, although the illustrations are insufficiently detailed to say for certain, it appears then that they identified that portion of the basioccipital as the first vertebra, which would consequently lead to identification of the first centrum as the second and thus lead to their conclusion that the second is also fused to the occiput. As our Fig. 4C of *M. cyprinoides* shows, the first centrum has begun to fuse to the basioccipital by 59 mm, and in *M. atlanticus* we found it to be partly fused in an 80 mm specimen (USNM 357435) and the configuration of the occiput in that specimen to be no different from that in a ca. 480 mm specimen (USNM 260335), that illustrated in our ca. 1300 mm specimen (Fig. 4D), and that in a 1640 mm specimen (CU 90720). We have examined the 830 mm TL specimen illustrated by Bemis & Forey (2001: fig. 20.6C) and can now explain why it appears to have an occipital configuration so different from their >1500 TL specimen. The discrepancy is the result of their misidentification of dried bits of Baudelot's ligament as posterior extensions of the parasphenoid, giving the impression that the latter bone extends posteriorly by approximately the length of one centrum. In any case, they concluded about the anterior vertebrae of *Megalops* that "the reshaping of the occipital region to incorporate them suggests to us that tarpon retains the same pattern of occipital incorporation of centra that occurs in *Amia*. We, of course, disagree, because, as we showed in Part 1, the incorporation of the first segment in *Amia* (and *Lepisosteus*) occurs so early in ontogeny that we are unable to determine if a separate first centrum ever forms there, and the basioccipital has no wedge-shaped dorsal extension. The situation in *Megalops* is much more like that we showed for *Heterotis*, wherein the first segment develops a normal, fully ossified vertebra that then fuses with the wedge-shaped posterior portion of the basioccipital.

The issue was further clouded when Bemis & Forey (2001) stated that "The elopomorphs *Elops* and *Megalops* have at least one centrum and neural arch incorporated into the occiput", (although elsewhere, p. 360, they mistakenly reported that the pair of pits on the dorsal surface of the basioccipital of *Megalops* has "no associated neural arches") and that "This arch is usually homologized with the accessory neural arch which occurs, in sporadic fashion, throughout clupeocephalans." They went on to argue that the

accessory neural arch of *Elops* is not homologous with that of clupeocephalans, a hypothesis that we address below. They made no further mention of their inference that *Megalops* has an accessory neural arch, and we can state unequivocally that it does not. Our 18.4 mm specimen of *M. cyprinoides* (Fig. 4B) shows clearly that the first centrum (the one that eventually fuses to the occiput) and its associated neural arch develop within the fourth myoseptum. As we demonstrated above for clupeocephalans, the accessory neural arch has no centrum associated with it and develops within the posteriormost cranial myoseptum, i.e., the third.

Elops: Unlike *Megalops*, confusion about the nature of the occiput of *Elops* was widespread among previous authors, due in large part to the presence of an accessory neural arch. Forey (1973: p. 12) said about the first "thin vertebral centrum" of *Elops* that it "is firmly united with the cranium, so much so that in older individuals it is difficult to recognize as a discrete entity" and noted that ventrally "it bears parapophyses but no pleural ribs, while dorsally there is an autogenous neural arch and spine." He illustrated the fused vertebra (his fig. 3) but not the neural arch and spine (in fact, there is no spine associated with this arch), the presence of which he believed to "represent a primitive stage, directly comparable to *Tarpon*". Taverne (1974: p. 35) reported for *Elops* that "It appears that one vertebra has fused to the body of the basioccipital leaving no trace of a suture (though he did not label it as such, figs. 2-5). He further surmised (p. 57, fig. 30) that the "more or less triangular plate" lying between the neurocranium and the neural arch of the first vertebra represents the neural arch of the vertebra that was incorporated into the basioccipital in the "embryonic stage." Rosen (1985) noted that *Elops* "appears to have a vertebra that is ontogenetically a part of the basioccipital", citing illustrations in Forey (1973), where it is labeled as such and his own fig. 10, where it is not, though in the legend of the latter Rosen noted "sculpturing around the ventral half" of "the basioccipital to illustrate the latter's resemblance to a foreshortened cervical vertebra". Rosen's (1985: fig. 10) illustration accurately depicts the triangular accessory neural arch (his ACCNA), but his statement in the legend that it "corresponds with a pair of dorsal indentations or wells as in *Megalops*", is erroneous – there are no such indentations in *Elops*.

Bemis & Forey (2001) concluded, as they did for *Megalops*, that *Elops* has "at least one centrum and neural arch incorporated into the occiput", and noted that the latter is "sutured through synchondrosis entirely with the exoccipital (ocna, Figure 20.6b)." Their "occipito-vertebral confusion" is unfortunately again evident in the following statement, "In *Elops* as in the osteoglossomorph *Arapaima* (Taverne, 1977: fig. 125) the so-called accessory neural arch is definitely attached to the basioccipital and exoccipital through cartilage." First, Taverne's figure of *Arapaima* clearly and correctly shows the first neural arch and spine (there is no accessory neural arch, see Hilton et al. 2007) to be entirely free from the exoccipitals. Second, although the accessory neural arch of adult *Elops* is in close contact with the exoccipitals along much of its anterior border (Fig. 6D), it is neither sutured nor attached to it through cartilage – the fact that perichondral ossification of both of these elements has occurred by 27 mm (Fig. 6C,D) establishes that they cannot be cartilaginously connected later in ontogeny. Nonetheless, Bemis & Forey (2001) were impressed by the close contact of the arch with the exoccipitals and by the fact that it "develops directly above the centrum-like expansion of the basioccipital", and they noted "that the relationships are not quite as described" by Rosen (1985), who applied the term accessory neural arch to it. They termed it instead "the occipital neural arch (ocna)", concluding that its position "is much more like the neural arches which are incorporated with the centra into the skull of *Amia*, so we would suggest that *Elops* retains the primitive actinopterygian condition". Further contributing to the latter conclusion was their conviction that the striations on the lower part of the "centrum-like end to the basioccipital just like the ornament on the succeeding free centra" (their fig. 20.6a, labeled sculp) implied incorporation of a centrum, as suggested by Rosen (1985). As we show in Figure 6A-C, there is no mystery about the occiput of *Elops* – it is fundamentally like that we described and illustrated in clupeocephalans with an accessory neural arch (Figs. 3-4). The ANA develops in cartilage in the third myoseptum and has no centrum associated with it. The first vertebra develops in the fourth myoseptum well removed from the basioccipital and remains autogenous. Although the ANA of many clupeocephalans differs from the ANA of *Elops* in that it develops later than the succeeding neural arches and remains relatively small and well-separated from the exoccipitals, that of *Esox* chondrifies and ossifies in sequence with the succeeding neural arches and, in adults, further resembles that of *Elops* (Fig. 6D) in being broad and attached to the exoccipitals anteriorly (see Patterson & Johnson 1995: fig. 8). Accordingly, we find no morphological evidence to suggest that the ANA of *Elops* and that of various clupeocephalan taxa are not homologous structures.
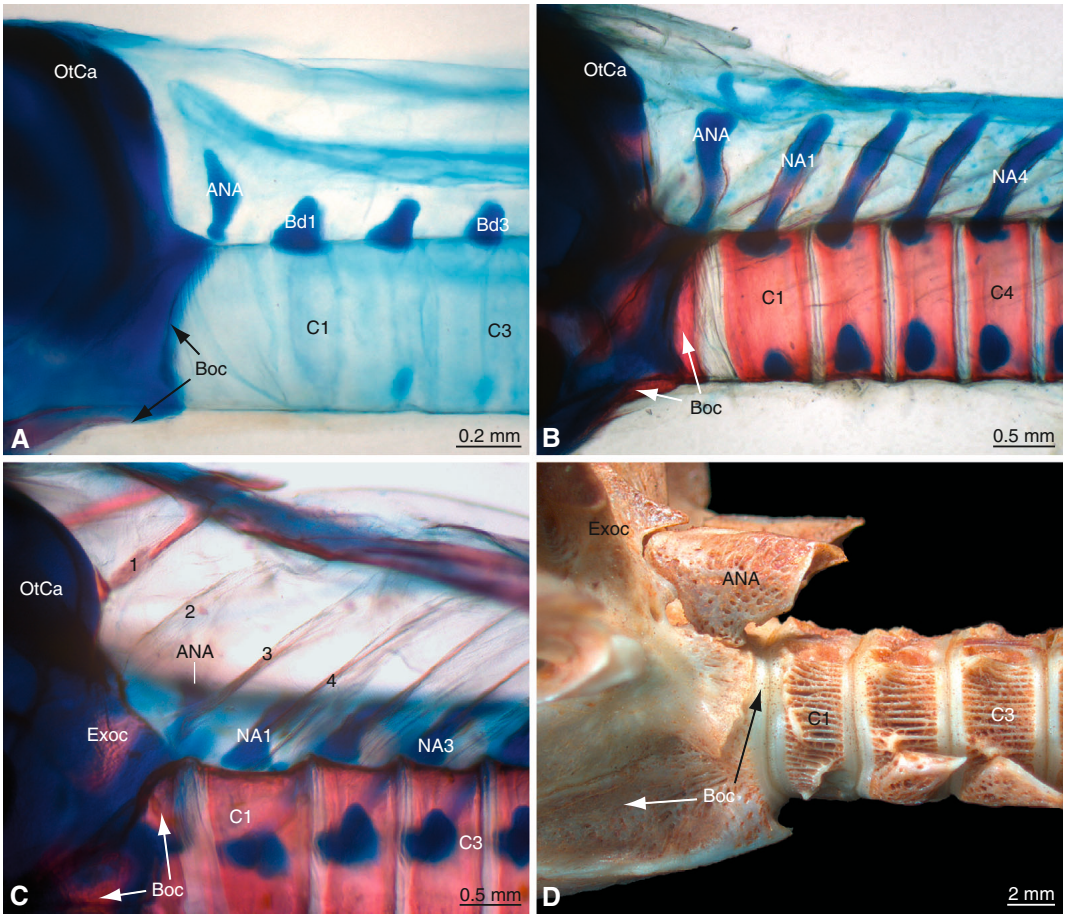
Fig. 6.
Occiput, accessory neural arch, anterior vertebrae and myosepta, lateral (**A**, **B**, **D**) and ventrolateral (**C**) views, in the elopiform *Elops saurus*: **A**, USNM 397553, 26.7 mm; **B**, **C**, 26.3 mm; **D**, USNM 111310, ca. 500 mm. Abbreviations: **ANA**, accessory neural arch; **Bd**, basidorsal; **Boc**, basioccipital; **C**, centrum; **Exoc**, exoccipital; **NA**, neural arch; **OtCa**, otic capsule; **Pt**, posttemporal; **1**, **2**, **3**, **4**, first, second, third and fourth myoseptum.

Conclusions

The composition of the occiput of teleosts has been the subject of much conjecture for more than a century. Various lines of evidence have been presented in support of the hypothesis that one or more vertebrae ("or a half centrum") have fused with the occiput in one or another teleost. Although seemingly resolved by Patterson & Johnson (1995), a more recent review by Bemis & Forey (2001) perpetuated the teleost "occipito-vertebral confusion". Our purpose here has been to put the issue to rest once and for all by reviewing previous hypotheses and bringing to bear our own ontogenetic and myoseptal evidence, the latter, we maintain, providing the only unequivocal landmarks for investigating occipito-vertebral structure. With this straightforward approach, we have shown that *Heterotis* and *Megalops* are the only teleosts, other than molids, ostraciids and male whalefishes, in which a vertebral centrum is fused ontogenetically to the occiput. The so-called accessory neural arch, ANA, long touted as evidence for occipito-vertebral fusion in teleosts, develops in the posteriormost occipital myoseptum, the third, and thus has nothing to do with incorporation of the first centrum of the vertebral column, which develops in the fourth myoseptum. Furthermore, contra Bemis & Forey (2001), we find no reason to question the

primary homology of the ANA of *Elops* with that of clupeocephalans and thus concur with Patterson & Johnson (1995) that the level(s) at which it may be synapomorphous can only be determined on the grounds of parsimony.

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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.