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The caudal skeleton of basal teleosts, its conventions, and some of its major evolutionary novelties in a temporal dimension

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Abstract

The present study represents an evaluation of the current knowledge of the caudal endoskeleton of basal fossil and extant teleosts and gives new information on the origin, development and homology of the elements of the caudal skeleton. One of the major problems is the lack of metamerization in the posterior region of the body that makes identification of elements and homology statements difficult. The definitions of preural region, ural region, and preural centrum 1 are analyzed. Other landmarks that facilitate the identification and homologization of certain caudal elements are also reviewed. New studies on the early development of the caudal skeleton of basal extant teleosts demonstrate that the ural region develops from an early polyural skeleton into a diural skeleton or into a compound terminal centrum in different ways in different teleosts. The two ural centra present in adult teleosts develop ontogenetically and phylogenetically from a polyural stage independently in different teleostean lineages origin. Thus, the two ural centra of the diural skeleton are not homologous across teleosts. Consequently, we propose to study the origin and composition of the ural region of different teleosts using the polyural terminology. This assumes a one-to-one relationship between ural centra and their respective hypaxial (e. g., ural 1/hypural 1; ural 2/hypural 2; ural 3/hypural 3) and epaxial elements. Polyural terminology facilitates interpretation of the composition of the two ural centra and their relationships to epaxial and hypaxial elements of the caudal fin. The compound terminal centrum (synonym: urostyle) present in most ostarioclupeomorphs (or otocephalans) and many euteleosts is currently assumed to be the result of a fusion involving preural centrum 1 and the first ural centrum. According to our studies based on day-to-day ontogenetic series, the compound terminal centrum is the result of an early fusion of preural centrum 1 with different ural centra in different teleosts. From the highest number of 13 hypurals found in the Early Jurassic †*Pholidophorus bechei*, a decreased number of 8 or 7 hypurals is observed in Late Jurassic elopiforms and 6 or fewer hypurals in extant teleosts. In most cases the reduction in number of hypurals has been interpreted as a fusion of elements, but this has not been shown ontogenetically. A complete series of true uroneurals occurs first in "true" teleosts (†*Leptolepis coryphaenoides* plus more advanced teleosts) at the base of the teleostean radiation. The homology of uroneurals is still not understood for most fossil and extant teleosts, with a reduction in number ranging from 7 to 3 to none in different extant teleostean lineages. In fossil basal "true" teleosts, the anterior-most uroneural seems to be a modification of ural neural arch 2 or 3, whereas the anterior-most uroneural is a modification of ural neural arch 4 in elopiforms, some osteoglossomorphs and salmonids. The origin and development of the pleurostyle (currently interpreted as a modified uroneural) in ostarioclupeomorphs remain unclear. The pleurostyle differs between groups, being chondral in some, but a membrane bone in others. "Uroneurals of a peculiar sort" develop as modified epaxial elements of preural as opposed to ural centra in fossil †pachycormiforms, some †aspidorhynchiforms and †'pholidophoriforms'. The homology of epurals is not fully understood for most basal teleosts. Epurals of basal teleosts are neural spines separated from neural arches. Basal teleosteomorphs and a few basal teleosts (and salmonids) possess simultaneously epurals derived from neural spines of both preural and ural centra. However, aspidorhynchiforms lack epurals. In †*Leptolepis coryphaenoides* plus more advanced teleosts the anterior-most epural corresponds to the neural spine of ural centrum 1, the second epural to ural centrum 2, and so on. In fossil and extant elopiforms, the three epurals correspond to ural centra 1–3 (polyural terminology), whereas in basal osteoglossomorphs the only epural present seems to belong to ural centrum 2 (polyural terminology). According to the present evidence, the origin of the one or two epurals present in ostarioclupeomorphs, as well as their homology, remains unknown.

Introduction

In the mid-1980's we began a series of studies on the caudal skeleton, and consequently the formation and development of the caudal vertebrae, in some selected advanced actinopterygians, including holosteans and basal teleosts. In 1986, we published our first paper on the formation of the caudal skeleton with the description of the polyural skeleton (numerous ural centra, each bearing a hypural) in *Lepisosteus* and *Amia* (SCHULTZE & ARRATIA 1986). This paper was followed by publications on the formation of the diural (two ural centra, each bearing more than one hypural) skeleton in *Hiodon*, *Elops* and *Albula* (SCHULTZE & ARRRATIA 1988) and in different species of Salmonidae (ARRATIA & SCHULTZE 1992) in the Journal of Morphology. Additionally, we published in 1989 a paper in the Zoological Journal of the Linnean Society, where we addressed the problem of homology of different structures of the caudal skeleton (SCHULTZE & ARRATIA 1989) including new landmarks for the identification of some of the endoskeletal caudal elements. These publications were accompanied by other series of papers addressing aspects such as (1) intraspecific variation of the caudal skeleton in Recent teleosts (e. g., epural and fusion of structures in catfishes; ARRATIA 1993); (2) descriptions and analyses of problematic caudal skeletons of some fossils that have been previously interpreted as possible teleosts, e. g., †pachycormiforms (ARRATIA & LAMBERS 1996) and †*Prohalecites* (ARRATIA & TINTORI 1999); and (3) studies of the caudal skeletons of fossil and extant basal teleosts, trying to interpret the evolutionary transformations involved and their phylogenetic significance (ARRATIA 1991, 1996, 1997, 1999, 2010). In all these papers we addressed the crucial necessity to study the ontogeny and the fossils – when available – to understand the homologies of the skeletal elements in the caudal skeleton, especially of serial elements. Despite this, ontogenetic studies of the caudal endoskeleton have rarely been made until recently. These newer studies have been focused on development of the caudal skeleton in euteleosts, especially the advanced ones (e. g., BRITZ & JOHNSON 2002, 2012; HILTON & JOHNSON 2007; GRÜNBAUM & CLOUTIER 2010; HILTON & BRITZ 2010; HILTON et al. 2010; KONSTANTINIDIS & JOHNSON 2012). Although there is an extensive array of publications on development of teleosts, in which the appearance of cartilaginous hypurals, epurals and other caudal elements are shown in association with pre- and post-flexion stages of the notochord, detailed information on the origin and development of the elements forming the centra (e. g., chordacentra, autocentra, and arcocentra) as well as of the uroneurals, compound centra, and other elements is often lacking.

In this paper we will present a summary of our findings and interpretations and demonstrate again the crucial importance of the information provided by (1) fossils and (2) early ontogeny for homologization of elements in the caudal skeleton of teleosts and during the major shift from a hemiheterocercal to a homocercal tail in the early evolution of the group. We will start by introducing the convention by NYBELIN (1963) and its terminology of the caudal skeleton. Then, we will introduce other landmarks for the identification of elements of the caudal skeleton. We will also present and analyze our convention. Here we will describe briefly the metamerization in the caudal region and the formation of vertebrae in general, before we can go into details of the polyural and the diural caudal skeletons. We will introduce the reader to the loss of metamerization in the most caudal region and the difficulties of establishing homologies resulting from this fact. We will offer new information on the so-called compound terminal centrum of some ostarioclupeomorphs and discuss the problem of homologies involved. We will document evolutionary transformations of the hypurals and epurals as characters of teleosts at particular phylogenetic levels, and we will document the evolutionary transformations of the uroneurals as teleostean characters supporting different phylogenetic levels. We will also analyze the hypothetical relationship between urals and uroneurals proposed by PATTERSON (1973). We will end by presenting some of the major evolutionary changes in the caudal skeleton of basal teleosts.

Methods and materials

Methods

Some of the fossil (†) specimens were mechanically prepared, whereas others were acid prepared according to the technique described in TOOMBS & RIXON (1959). Some of the fossil specimens were photographed and studied under ultraviolet light (for details on the methodology see TISCHLINGER & ARRATIA this volume). Most of the extant fishes included in this study are cleared and stained (c&s) for both cartilage and bone following a procedure described in ARRATIA & SCHULTZE (1992). Others are prepared as dry skeletons (skl). Most of the studied material has been prepared by G. ARRATIA. All photographed specimens of extant species

are complete, i. e., they have not been dissected and only the scales have been removed. Small specimens were studied and photographed with normal, phase-contrast and polarized light under an Olympus microscope with a Nikon camera attachment. When a particular structure was to be photographed under the compound microscope, the focus was centered in that structure so that surrounding regions may be out of focus. Larger specimens were studied under a Leica MZ9 stereomicroscope with both a Leica digital camera attachment and a camera lucida attachment. The size of the specimens is given only for the extant material. The drawings of the specimens were done with the stereomicroscope equipped with camera lucida attachment; they are not traced over photographs.

Although we have used a large number of specimens in comparative studies, the tables include only those fossil species where we have been able to examine the ural neural arches and establish their presence. Unfortunately, the neural arches are covered laterally by the uroneurals so that we cannot be certain how many there are.

Institutional abbreviations and specimens studied

The study includes a vast number of specimens deposited in different museums all over the world. Only the material that is mentioned and/or used in descriptions and illustrations is listed.

The studied material is catalogued in the following institutions: **AMNH**, American Museum of Natural History, New York, U.S.A.; **ANSP**, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; **BGHan**, Bundesanstalt für Geowissenschaften und Rohstoffe, Niedersächsisches Landesamt für Bodenforschung, Hannover, Lower Saxonia, Germany; **BSPG**, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Bavaria, Germany; **CAS**, **CAS(SU)**, California Academy of Sciences, San Francisco, California, U.S.A.; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, Pensylvania, U.S.A.; **DMNH**, Denver Museum of Natural History, Denver, Colorado, U.S.A.; **FMNH**, Dept. of Geology and Dept. of Ichthyology, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **GOE**, Institut und Museum für Geologie und Paläontologie, Georg-August Universität, Göttingen, Lower Saxonia, Germany; **JFBM**, James Ford Bell Museum – Ichthyology Collection, St. Paul, Minnesota; **JME**, Jura-Museum, Eichstätt, Bavaria, Germany (the addition of ETT indicates that the specimen is from the Upper Jurassic of Ettling; Moe indicates that the specimen is from the Mörnsheim Formation, Tithonian Malm Zeta 3; SCHA indicates that the specimen is from the Upper Jurassic of Schamhaupten; SOS indicates that the specimen is from some of the localities in the Upper Jurassic Solnhofen Limestones; the names of the localities are given in the text because they may have different ages; see SCHWEIGERT 2007); **KUNHM**, University of Kansas, Natural History Museum, Division of Fishes, Lawrence, Kansas, U.S.A.; **KUVP**, University of Kansas, Natural History Museum, Division of Vertebrate Paleontology, Lawrence, Kansas, U.S.A.; **LACM**, Division of Paleontology, Los Angeles County Museum, Los Angeles, U.S.A.; **LBUCH**, Laboratorio de Biología, Universidad de Chile, Santiago-Sur, Chile (all of these specimens will be deposited in the National Museum of Natural History, Santiago, Chile); **MB f.**, Collection of Fossil Fishes, Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany; **MCSNB**, Museo Civico di Scienze Naturali "Enrico Caffi", Bergamo, Italy; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MNHN-Stg**, Museo Nacional de Historia Natural, Santiago, Chile; **MRAC**, Musée Royale de l'Afrique Centrale, Tervuren, Belgium; **NHM** (= BMNH), Natural History Museum, London, England; **OS**, Department of Fisheries and Wildlife, College of Agriculture Sciences, Oregon State University, Corvallis, Oregon, U.S.A.; **Pi**, Institut und Museum für Geologie und Paläontologie, Georg-August-Universität, Tübingen, Baden-Württemberg, Germany; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **SIO**, Scripps Institution of Oceanography, University of California, La Jolla, California, U.S.A.; **SMNH**, Section of Paleozoology, Swedish Museum of Natural History, Stockholm, Sweden; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Baden-Württemberg, Germany; **TCWC**, Texas Cooperative Wildlife Collection, Department of Wildlife and Fisheries Science, Texas A&M University, College Station, Texas, U.S.A.; **UALVP**, University of Alberta, Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; **UCLA**, Department of Biology, University of California at Los Angeles, Los Angeles, California, U.S.A; **UF**, Florida Museum of Natural History, Gainsville, Florida, U.S.A; **UMMZ**, University of Michigan, Museum of Zoology, Ann Arbor, Michigan, U.S.A.; **UNC**, University of North Carolina, Institute of Marine Sciences, Morehead City, North Carolina, U.S.A.; and **USNM**, United States National Museum, Smithsonian Institution, Washington D.C., U.S.A.

Specimens studied

Holosteans

Amiiformes: *Amia calva*: KUNHM 21290, 4 c&s, 76, 79, 85, 86 mm TL; KUNHM 21261, skl, about 450 mm TL. KUNHM 3883, 5 c&s, 41, 50, 53 mm total length (TL).

Lepisosteiformes: *Lepisosteus osseus*: KUNHM 3651, 3 c&s, 60, 6, 70 mm total length (TL); KUNHM 3677, 1 c&s, 241 mm TL; KUNHM 8530, 1 c&s, 139 mm TL; KUNHM 12645, 1 c&s, 710 mm TL; KUNHM 16246, 1 c&s, 50.5 mm TL; KUNHM 17935, 1 c&s, 730 mm TL. *Lepisosteus platostomus*: KUNHM 16142, 1 c&s, 455 mm TL; KUNHM, 1 c&s, 626 mm TL; KUNHM 003138, 1 c&s, 626 mm TL.

Neopterygians incertae sedis

†Pachycormiformes: See ARRATIA & SCHULTZE (this volume) for a list of specimens.

Teleosteomorphs

†Aspidorhynchiformes: †*Aspidorhynchus acutirostris*: MB. f.358, MB. f.3529, MB. f.3554; MB f. 3566. †*Aspidorhynchus* sp.: JME ETT 2006-2. †*Belonostomus muensteri*: MB. f.3544. †*Belonostomus tenuirostris*: JME SOS 2339, JME SOS 2844. †*Belonostomus* sp.: BSPG 1956 I 422.

†'Pholidophoriformes': †*Eurycormus speciosus*: BSPG AS V510 and BSPG 1960 XVIII 106; JME SOS 2339 and JME SOS 2341. †*Pholidophorus bechei*: FMNH 2137, MB f.3504, and SMNS P 944. †*Pholidophorus latiusculus*: MCSNB 4302, MCSNB 4303b, MCSNB 4346a, and MCSNB 4723; Slg. Innsb 115. †*Siemensichthys macrocephalus*: BSPG AS I 1134; JME SOS 2812; MB f.7007 and MB f.7008a, MB f.7008b.

"True" teleosts (†*Leptolepis coryphaenoides* plus more advanced teleosts)

†*Ascalabos voithi*: CMNH 9491; JME 537; JME SOS 2363, JME SOS 2497, and many other specimens from different localities deposited at the JME; NHM 3672, NHM 3673, NHM 37062.

†*Tharsis dubius*: BSPG 1964 XXIII 280; CMNH 4845; FMNH 25076; FMNH 25124; JME, many specimens from different localities.

†Leptolepididae: †*Leptolepis coryphaenoides*: BGHan 1931-4, BGHan 1956-8, BGHan 1957-2, BGHan 1957-5, and BGHan 1960 (acid-prepared specimens); GOE uncatalogued, many articulated and disarticulated specimens.

†Crossognathiformes: †*Bavarichthys incognitus*: JME SOS 4934a/b. †*Chongichthys dentatus*: LBUCH 021778a, LBUCH 021778b, LBUCH 15-010277a, and LBUCH 15-010277b. †*Domeykos profetaensis*: LBUCH 12-260972a, LBUCH 12-260972b, LBUCH 01277-13a, and LBUCH 01277-13b. †*Protoclupea atacamensis*: LBUCH 1-250277a. †*Protoclupea chilensis*: R-396a, R396b; LBUCH 190179a and LBUCH 190179b. †*Varasichthys ariasi*: LBUCH 16-260972a, LBUCH 16-260972b, LBUCH 012378a, LBUCH 020778a, and LBUCH 020778b.

†Ichthyodectiformes: †*Allothrissops mesogaster*: JME SOS 1941/17a; FMNH-PF UC 2021 and FMNH-PF UC 2082; SMNH P 976, SMNH P 2925, and SMNH P 7733. †*Pachythrissops propterus*: BSPG 1986 XXIII 154; JME SOS 741; MB. f. 3505. †*Thrissops* cf. †*T. formosus*: JME SOS 3024. †*Thrissops subovatus*: JME SOS 1953/14a. †*Thrissops* cf. *T. subovatus*: JME SOS 2557.

Elopomorphs

Elopiformes: †*Anaethalion angustus*: JME SOS 2271, JME SOS 2259, JME SOS 2260, JME SOS 2261a, and JME SOS 2261b. †*Anaethalion angustissimus*: JME SOS 2271, Pi F 891, Pi 1074/1, Pi 1074/2, and Pi Y 1930. †*Anaethalion knorri*: JME SOS 2267a, JME SOS 2267b, JME SOS 2270, and JME SOS 2282. *Elops affinis*: SIO 69-167, 1 c&s, 121 mm SL; UCLA W 50-29, 4 c&s., 121.3, 128.4, 157, and 165 mm SL. *Elops hawaiensis*: CAS(SU) 35105, partially disarticulated skl, braincase of about 90 mm length; OS 5105, 2 c&s leptocephalous larvae, 26.7 and 32.5 mm SL. *Elops saurus*: ANSP 147401, 2 c&s, 97.8 and 99.1 mm SL; CAS(SU) 10847, skl, ±395 mm SL; TCWC 0503.1, 5 c&s, 24.0, 24.0, 26, 30.0, and 35.0 mm SL; TCWC 0782.1, 3 c&s., 35.7, 43, and 46.4 mm SL; TCWC 2452.2, 5 c&s, 60.1, 97.3, 107, 110.4 and 154 mm SL; UNC 82/8, 2 c&s, 57 and 76 mm SL. †*Elopsomolos frickhingeri*: JME SOS 4393. †*Elopsomolos* sp.: NMH 37048. *Megalops atlanticus*: UF 171286, 5 c&s, 26.3, 27.8, 29.1, 29.8, 40.5 mm SL; UF 208605, 5 c&s, 25.5, 31, 32.7, 41.1, and 44.5 mm SL; UF 208780, 3 c&s, 85, 90.4, and 122.5 mm SL. *Megalops cyprinoides*: CAS 145216, 2 c&s, 17.5 mm and 34.5 mm SL.

Albuliformes: *Albula vulpes:* AMNH 56840, skl, ±292 mm SL; AMNH 56743, skl, ±300 mm SL; and AMNH 56878, skl, ±305 mm SL; UCLA W58-96, 2 c&s, 195 and 220 mm SL; UCLA W49-122, 5 c&s, 46.7, 54.6, 63.5, 72.7, and 88.8 mm SL; UCLA W 49-122, 4 c&s leptocephalous larvae.

Anguilliformes: *Anguilla rostrata*: KUNHM 5029, 6 c&s, 50, 50.4, 53.8, 55, 82.5, and 103 mm SL.

Osteoglossomorphs

†Lycopteridae: †*Lycoptera davidi*: LACM 4959-122316 and LACM 4959-122317; SMNH P 6553. †*Lycoptera* cf. *L. sinensis*: FMNH 1291a and FMNH 1291b.

Hiodontidae: *Hiodon alosoides*: JFBM 43312, 1 skl, ±400 mm SL; JFBM 43306, 1 skl, ±380 mm SL; KUNHM 7618, 7 c&s, from 22.0 to 56.0 mm SL; KUNHM 9618, 7 c&s, from 22 to 55 mm SL; KUNHM 3 c&s, 68, 70, and 72 mm SL; KUNHM 9661, 2 c&s, 59 and 67 mm SL; KUNHM 13993, 2 c&s, 200 and 305 mm SL. *Hiodon tergisus*: KUNHM 9662, 3 c&s, 48.6, 51.8, and 55.7 mm SL. *Osteoglossum ferrerai*: KUNHM 22650, 1 c&s, 52.3 mm SL. *Pantodon buchholzi*: KUNHM 22651, 1 c&s, 50 mm SL.

Clupeomorphs

Clupeiformes: *Alosa chrysochloris*: KUNHM 9634, 2 c&s, 43.7 and 54.3 mm SL. *Anchoa mitchilli*: KUNHM 7494, 2 c&s, disarticulated specimens; KUNHM 17183, 2 c&s, disarticulated specimens. *Brevoortia patronus*: KUNHM 15113, 5 c&s, disarticulated specimens. *Coilia nasus*: KUNHM 40362, 33 c&s (15 larvae between 10.2 and 22.7 mm SL; 9 between 16.6 and 30.1 mm SL; 9 specimens between 63.5 and 103.1 SL). *Dorosoma cepedianum*: KUNHM 12100, 3 c&s, 30.5, 67, and 71.6 mm SL; KUNHM 16167, 1 c&s, 46.9 mm SL; KUNHM 21801, 169 c&s (100 sps. from 8 mm notochordal length (NL) to 15 mm SL and 69 sps. from 13.9 to 29.5 mm SL). *Dorosoma petenense*: KUNHM 956994, 2 c&s, 27.3 and 34.5 mm SL. *Engraulis encrasicolus*: KUNHM19941, 8 c&s, 25 to 50 mm SL. *Engraulis ringens*: KUNHM 19347, 10 c&s, disarticulated specimens. *Ethmidium maculatus*: KUNHM 19349, 2 c&s, disarticulated large specimens. *Jenkinsia lamprotaenia*: KUNHM 40364, 10 c&s, from 34.5 to 49.1 mm SL. *Lile stolifera*: KUNHM 5411, 3 c&s, 29.5, 45.6, and 52.2 mm SL; UCLA 58-307, 3 c&s, 71.7, 80, and 88.1 mm SL. *Sardinops sagax*: KUNHM 19345, 6 c&s larvae, 14 to 19 mm Sl, and 4 c&s disarticulated large specimens.

Denticipitidae: *Denticeps clupeoides*: MRAC M.T. 76-32-P-4915-932, 1 c&s, 29.1 mm SL; MRAC M.T. 76-44-P-7, 1 c&s, 18.5 mm SL.

Ostariophysan incertae sedis: †*Tischlingerichthys viohli*: JME Moe 8.

Gonorynchiformes: *Chanos chanos*: CAS(SU) 35075, 1 skl, disarticulated, braincase of 148 mm length; KUNHM 39848 to 39894, day-to-day series of about 200 specimens from about 10 mm to 10 mm notochordal length and from 7.0 to 83.5 mm SL; KUNHM 40365, 2 skl, 370 and 376 mm SL and 4 c&s, 150, 180, 330, and 400 mm SL. SIO 80-199, 7 c&s, from 16.1 to 44.5 mm SL. *Gonorynchus abbreviatus*: CAS 30993, 1 c&s, 150 mm SL.

Cypriniformes: *Aspius aspius*: ROM 52742, 4 c&s, 26.7, 35.8, 51.8, and 59.8; NRM 56968, 5 c&s, 34.6, 39.8, 46.9, 49.3, and 50.3. *Barbatula barbatula:* ROM 49713, 5 c&s, 49.8, 60.9, 64.1, 66, and 75 mm SL. *Carpiodes carpio*: KUNHM 21807, 24 c&s, 13.3 to 42.3 mm SL. *Carpiodes microstomus*: FMNH 35171, 4 c&s, 34.8, 38.8, 40.5, and 45.7 mm SL. *Catostomus commersoni*: JFBM 11495, 7 c&s, from 22.3 to 31 mm SL; JFBM 41727, skl, ±278 mm SL; KUNHM 38655, +100 c&s, between 12 to 21.3 mm SL. *Chanodictis mongolicus:* USNM, 2 c&s, 112.6 and 136 mm SL. *Cobitis lutheri*: KUNHM 38976, 2 c&s, 55.6 and 81.5 mm SL. *Cycleptus elongatus*: KUNHM 40695, 1 c&s, 148 mm SL. *Cyprinus carpio*: FMNH 42392, 1 c&s, 85.5 mm SL; KUNHM 3739, 1 c&s, 80.0 mm SL; JFBM, skl, ±354 mm SL. *Danio rerio*: KUNHM uncat., 10 c&s; KUNHM 40245, day-to-day ontogenetic series of about 100 specimens, between 6 to 27.9 mm SL. *Hemiculter leuciscus*: MCZ 32394, 2 c&s, 90.8 and 97.2 mm SL. *Labeo batesi*: USNM 303704, 4 c&s, 89.7, 95, 195.5, and 197.4 mm SL. *Lepidomeda mollispinus*: KUNHM 11768, 20 c&s, from 54.8 to 68.7 mm SL. *Misgurnus anguillicaudatus*: FMNH 57343, 5 c&s, 47, 50.1, 50.7, 53, and 80.5 mm SL; KUNHM 21447, 2 c&s, 96.2 and 100.3 mm SL. *Notropis atherinoides*: FMNH 72149, 20 c&s, from 20.2 to 55.5 mm SL. *Opsariichthys bidens*: CAS(SU) 32512, 2 c&s, 81.9 and 117.6 mm SL. *Opsariichthys uncirostris*: KUNHM 21448, 4 c&s, 25, 29.6, 36.6, and 70.4 mm SL. *Parabramis pekinensis*: USNM 86494, 5 c&s, 49, 50.5, 54.7, 58.5, and 59.1 mm SL. *Sabanajewa balcanica*: FMNH 63814, 3 c&s, 33.9, 36.8, and 58 mm SL. *Semonotilus atromaculatus*: KUNHM 12594, 5 c&s, 39, 41, 42, 42, 45, and 47 mm SL. *Squalibarbus curriculus:* AMNH 10890, 2 c&s, 112.6 and 136 mm SL. Only a few cypriniforms are listed here from more than 150 species with c&s specimens included in the Tree of Life of Cypriniformes.

Characiformes: *Astyanax* sp.: KUNHM 20099, 6 c&s, between 19.9 and 18.8 mm SL. *Xenocharax spilurus*: CAS(SU) 15639, 2 c&s, 74.7 and 92 mm SL.

Siluriformes: *Diplomystes nahuelbutaensis*: MNHN-Stg uncat., 4 c&s, 150 to 180 mm SL. *Diplomystes viedmensis*: FMNH 58004, 2 c&s, 80.5 and 91.7 mm SL. *Noturus exilis*: KUNHM 17229a, 10 c&s larvae, from 10 to 12.0 mm SL.

Euteleostei

Esociformes: *Esox americanus*: KUNHM 5227, caudal skeleton only, c&s; KUNHM 17864, 4 c&s, 82.7, 89.5, 112, and 123 mm SL. *Esox lucius*: KUNHM 19092, disarticulated skull, lower jaw 120 mm length, and caudal skeleton.

Salmoniformes: †*Erichalcis arcta*: UALVP 8598, UALVP 8602, UALVP 8606, and UALVP 8612. †*Humbertia* sp.: DMNH 2518-1. †*Leptolepides haertesi*: JME SOS 2473, JME SOS 2474, and JME SOS 2554. †*Leptolepides sprattiformis*: FMNH-PF 10984 and FMNH-PF 10986; JM-E SOS 2956; KUVP 60722 and KUVP 96128; SMNH P 1891, SMNS P 1894, SMNS 55106, and SMNS 55928. †*Orthogonikleithrus hoelli*: JME ETT 2301, JME ETT 2632, JME ETT 3954, JME ETT 3955, and JME ETT 3956. †*Orthogonikleithrus leichi*: JME SOS 2301 and JME SOS 2632. †*Orthogonikleithrus* sp.: JME ETT 30 and JME ETT 216. *Oncorhynchus mykiss*: KUNHM 12463, 7 c&s, from 28.0 to 43 mm SL; KUNHM 21936, 20 c&s, 290 to 300 mm SL; OS uncat., day-to-day ontogenetic series of about 200 c&s, from 13 mm NL to 73 mm SL. *Prosopium cilindraceous*: KUNHM 15471, 2 c&s, 300 and 310 mm SL. *Prosopium williamsoni*: KUNHM 11817, 13 c&s, 12 larvae between 20 and 33.6 mm SL and 1 specimen of 230 mm SL. *Thymallus arcticus*: KUNHM 15419, 3 c&s, 151, 166, and 177 mm SL. *Umbra limi*: KUNHM 10370, 6 c&s, 22.5, 26.3, 27, 27.8, 52, and 54.4 mm SL.

Argentiniformes: *Argentina sialis*: SIO 66-4, 3 c&s, 119, 140, and 121.2 mm SL. SIO CR 5208, 4 c&s, 3 larvae of 9.0 to 14 mm NL, and 1 specimen of 13.5 mm SL.

Terminology

To help the reader to follow the descriptions, short explanations of certain terms used in the text, as well as in figures, are provided below. These definitions are elaborated further in the text.

When using the **diural terminology**, we identify the two ural centra of the caudal endoskeleton as first ($U1^{D}$) and second ural ($U2^{D}$) centra. When using the **polyural terminology** we identify the elements as ural centrum 1 ($U1^{P}$), ural centrum 2 ($U2^{P}$), ural centrum 3 ($U3^{P}$), etc.

Actinotrichia: Slender rods of a kind of collagen called elastoidin that are the main support of the finfolds in young stages and the most distal supporting elements in adults (for references see SCHULTZE & ARRATIA 1989 and ARRATIA et al. 2001).

Arcocentrum: Part of a vertebra that develops from the basidorsal or the basiventral arcualia, and will become the neural arch and also part of the centrum. Arcocentra are identified as dorsal and ventral, respectively. See page 204 for further explanation.

Arcocentral type of centrum: Vertebral centrum formed by the lateral growth of the dorsal and ventral (cartilaginous) arcocentra, which fuse to each other forming the lateral wall of the centrum. See page 204.

Autocentrum: Vertebral centrum formed by direct ossification (no cartilage precursor) outside the chordacentrum or outside the notochord, depending on the teleostean subgroup. See page 208.

Autocentral type of centrum: Vertebral centrum formed by direct ossification outside the chordacentrum or outside the notochord. See page 208.

Basal fulcra: Basal fulcra are large, laterally expanded, paired or unpaired scale-like structures that preceed the bases of the median fins or of both paired and median fins depending on the actinopterygian subgroup. Basal fulcra may be lanceolate, leaf-like or arrow-like in shape.

Centrum or vertebral centrum: A mineralized, or ossified, or partly cartilaginous/ossified element that surrounds the notochord. Depending on its origin, the centrum is termed arcocentrum, chordacentrum, or autocentrum (ARRATIA et al. 2001).

Chordacentrum: Vertebral centrum that forms as a result of mineralization of the middle fibrous part of the notochordal sheath. See page 206.

Compound terminal centrum: Posterior region of the caudal endoskeleton comprising preural centrum 1 and ural centra 1 and 2 ($PU1+U1^{D}+U2^{D}$), or preural centrum 1 plus a variable number of ural centra ($PU1+U1^{P}+U2^{P}+n$). It occurs in ostariophysans, some clupeomorphs and some euteleosts. See pages 222–224 for further explanation.

Diural caudal skeleton: Type of caudal skeleton commonly found in adult basal teleosts and characterized by the presence of only two ural centra ($U1^{D}$, $U2^{D}$). See page 195 for explanations.

Dorsal arcocentrum: Parts of a vertebra that develop from the basidorsal arcualia, surround the neural cord, and will become the neural arch and also may be part of the dorsal region of the vertebral centrum.

Epaxial or dorsal basal fulcra: Series of basal fulcra positioned at the dorsal or antero-dorsal margin of the caudal fin (ARRATIA 2008).

Epural: Detached neural spine of a preural or ural vertebra that may support fin rays. See page 234 for further explanation.

Fringing fulcra: Paired structures associated with the leading ray/edge of paired and/or unpaired fins. These may be swollen, spine-like, lanceolate, or distally arrow-like in shape (ARRATIA 2008).

Haemal arch: Ventral arcocentrum or arch of a caudal vertebra (including all preurals), enclosing the main arteries and veins of the caudal region of the body.

Hypaxial or ventral basal fulcra: Series of basal fulcra positioned at the ventral or antero-ventral margin of the caudal fin (ARRATIA 2008).

Hypural: Modified haemal spine (of an ural centrum) that has lost its haemal arch and canal. Hypurals may be articulated or fused with their respective ural centra. See page 226.

Hypuraphophysis: Lateral process, ridge, or crest on the arch of the parhypural where the hypochordal longitudinalis muscle attaches. Hypurapophysis-like processes can also be present on the haemal arches of preural vertebrae or on the proximal region of hypurals 1 and 2, depending on the teleostean subgroup.

Hypural diastema: Space positioned between hypurals 2 and 3, or a notch positioned at the distal regions of hypurals 2 and 3.

Neural arch: Dorsal arcocentrum or arch of a vertebra sorrounding the neural cord.

Parhypural: The parhypural is the haemal spine of preural centrum 1 (after MONOD 1967: fig. 1, 2: PH(HAP1) = hémacanthe = haemal spine) or the arch plus the haemal spine of preural centrum 1 (after MONOD (1968). [In our descriptions, we make the difference between arch and spine of the so-called parhypural, as well as we do for other arches and spines of the preural vertebrae]. The arch of the parhypural represents the exit point of the main caudal arteries and veins. See page 195.

Pleurostyle: Paired, postero-dorsal process of preural vertebra 1 according to MONOD (1968). Currently, the pleurostyle is interpreted as a modified pair of uroneurals that fuses to preural vertebra 1 early in ontogeny of some teleostean groups such as ostarioclupeomorphs. See pages 227, 231–233 for further information.

Polyural caudal skeleton: A type of caudal skeleton characterized by the presence of more than two ural centra ($U1^{P}$, $U2^{P}$, $U3^{P}$, etc.), each associated with its respective hypural. See pages 195, 210.

Preural centrum: Vertebral centrum of the caudal region preceding the ural centra, bearing both neural and haemal arches and usually both neural and haemal spines, each of which supports a caudal ray at its distal tip. A preural centrum does not support hypurals. Preural centra are numbered from the posterior-most to the anterior-most. See pages 194, 197.

Preural centrum 1: Last caudal vertebra with a haemal arch (the arch of the parhypural), posterior to which the caudal vessels leave the protection of the haemal arches of the caudal vertebrae and run lateral to the hypurals. See page 194.

Procurrent caudal ray: Procurrent rays are short rays, shorter than the principal ones, which form the anterior series of lepidotrichia of median fins and which are associated with endoskeletal elements (e. g., pterygiophores, neural and haemal spines, epurals, uroneurals) (ARRATIA 2008).

Principal caudal rays: Principal rays of the caudal fin are all the segmented and branched rays plus normally one unbranched but segmented ray located at the leading margin in each lobe of the fin (HUBBS & LAGLER 1947); they are associated with endoskeletal elements (e. g., hypurals, haemal spines of preural centra 1 and 2) (ARRATIA 2008).

Stegural: Modified anterior-most uroneural bearing a membranous bony extension at its antero-dorsal border (see ARRATIA & SCHULTZE 1992 for further explanations iabout the history of this element). See page 227.

Teleosteomorpha: A clade comprising the stem-groups of teleosts and the apomorphy-based Teleostei (ARRATIA 2001).

"True" teleosts: Clade in common usage, for the apomorphy-based Teleostei formed by †*Leptolepis coryphaenoides* plus more advanced fossil basal teleosts and the crown-group Elopocephala (including fossil and living members; sensu ARRATIA 1999). This clade is strongly supported by many synapomorphies such as absence of coronoid bones and of surangular in lower jaw; autocentrum present; leading margins of caudal fin formed by first and last principal rays; cycloid scales; etc. (ARRATIA 1999, 2008).

Ural centra: Posterior-most centra of the vertebral column characterized by the absence of haemal arches. Ural centra support hypurals ventrally. They are numbered beginning from the most anterior (1) to posterior ones (2, 3, 4, etc.).

Ural neural arch: Skeletal paired element that develops from basidorsal arcualia of ural centra.

Uroneurals: Modified ural neural arches, and consequently, paired, elongate bones that extend along the dorso-lateral surface of the last preural centra and/or ural centra and dorso-lateral to the notochord. See page 227.

Urostyle: Posterior region of the caudal endoskeleton interpreted as result from fusion of preural centrum 1 and ural centra I^D and II^D ($PU1+UI^D+UII^D$), or preural centrum 1 plus a variable number of ural centra ($PU1+U1^P+U2^P+n^P$). The name is often used as synonym of the so-called compound terminal centrum. See pages 222–225.

Vertebra: This term includes one set of all serially repeated, ossified, cartilaginous, and ligamentous elements around the notochord, consisting of centrum, neural arch and spine, and haemal arch and spine (SCHULTZE & ARRATIA 1988, ARRATIA et al. 2001).

Ventral arcocentrum: Paired skeletal element that develops from the basiventral arcualia, surrounds the caudal artery and vein, becomes the haemal arch, and also may be part of the ventral region of the vertebral centrum.

Concept of homology

Our understanding of homologous features follows ideas extensively discussed by different authors and that were clearly summarized by AX (1987): Homologous features are features in two or more evolutionary species, which go back to one and the same feature of a common stem species. They may have been taken over from the stem species unchanged or else with evolutionary transformations.

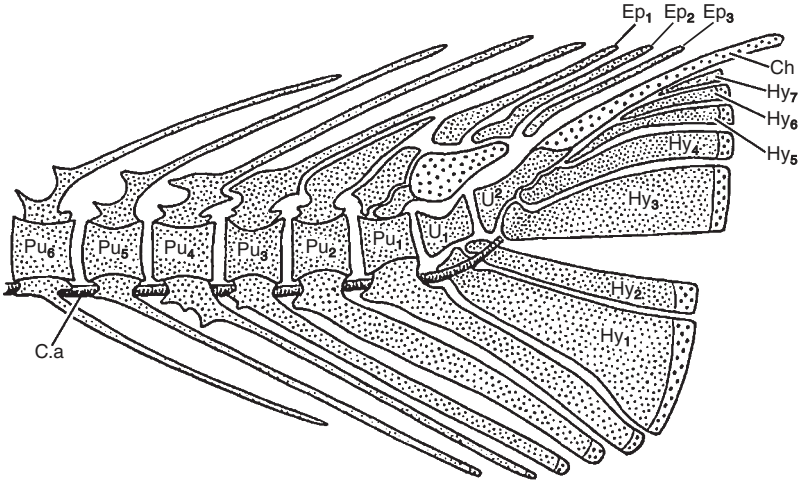
To investigate what features can be homologous or non-homologous we use the classic criteria set up by REMANE (1952, 1955 and followed later by others, e. g., RIEPPEL 1994, WILEY & LIEBERMAN 2011), as for instance, position or spatial relationships, origin, ontogenetic development and structure of the features under study. Our goals here, as clearly outlined in the Introduction, are not to test hypotheses of homology of specific features on certain teleostean phylogenies, but to communicate the results of our studies of different elements of the caudal skeleton of basal teleosts, ostarioclupeomorphs and certain euteleosts that question previous knowledge, open major questions on current interpretations of certain features traditionally considered as homologous, and, additionally, are an invitation for further research involving many more taxa including ontogenetic developmental studies, from early to late ontogeny.

Convention of NYBELIN (1963)

HOLLISTER (1936, 1937) was the first who recognized the value of the caudal skeleton as a taxonomic tool within teleosts. Almost 30 years later, NYBELIN (1963) and MONOD (1968) improved HOLLISTER's nomenclature for the caudal skeleton, and their terminology has been followed since.

Preural and ural centra: According to NYBELIN (1963), the important point in the identification of caudal endoskeletal elements is the fixation of a landmark – the exit of the caudal artery from the last haemal arch – to distinguish between preural and ural regions (Fig. 1). The caudal artery (dorsally positioned blood vessel) is enclosed by the haemal arches in the vertebral caudal region. The last haemal arch surrounding the caudal artery is that of preural centrum 1; beyond this haemal arch the artery runs outside the ventral elements, on the lateral surfaces of the hypurals (Fig. 2). NYBELIN named preural centra to be all centra preceding the ural centra **as long as they support caudal fin rays***. The course of the caudal artery is the landmark to distinguish between preural and ural centra, and between the arch and spine of

* The name preural centra or preural vertebrae of NYBELIN (1963) has a completely different meaning than that of GRANDE & BEMIS (1998: 27–28, pu) who did not adhere to NYBELIN's concept of preural centra when they defined them as follows: "**pu**, preural centrum (*pu1* = terminal vertebra of Gosline, 1961); we follow the terminology of Nybelin (1963); the first preural centrum is, by definition, the centrum that bears the parhypural (see *phy*); the preural centra include all of the abdominal centra, and most of the caudal centra (the preural caudal centra): unlike other vertebral counts, the preural centra and vertebrae are numbered from posterior to anterior; see Counts (Meristics)." However, NYBELIN (1963) proposed a functional definition of the preural centra as those bearing caudal rays, not a topological definition and numbering.



Die von mir vorgeschlagene Terminologie.

Präurale Wirbel				Urale Wirbel		
etc.	Präurale 3	Präurale 2	Präurale 1	Urale 1	Urale 2	etc.
				Hypuralia		

Fig. 1.
Terminology of the caudal skeleton after NYBELIN (1963: 489, fig. 1) identifying preural and ural regions. Abbreviations: **C.a**, caudal artery; **Ch**, notochord; **Ep**$_{1,2,3}$, epural; **Hy**$_{1-7}$, hypural 1–7; **Hypuralia**, hypural region; **Präurale Wirbel**, preural vertebrae; **Pu**$_{1-6}$, preural centrum 1–6; **U**$_{1,2}$, ural centrum I^{D}, II^{D}; **Urale Wirbel**, ural vertebrae.

preural centrum 1 and hypurals. (The haemal arch alone or the haemal arch plus haemal spine of preural centrum 1 were given the name parhypural by MONOD in subsequent publications in 1967 and 1968, respectively.) We make a distinction between the haemal arch and haemal spine (or parhypural) when describing hypaxial elements of preural centrum 1 (as well as of its epaxial elements). This is because in many teleosts the haemal arch of preural centrum 1 may be incomplete or only the spine is left or both the neural arch and spine may be missing (e. g., SCHULTZE & ARRATIA 1988, 1989; ARRATIA 1991, 1997, 1999, 2008, 2010; ARRATIA & SCHULTZE 1992).

NYBELIN (1963: figs. 1, 4, 6, 7, 8) distinguished the epurals and the uroneurals as those skeletal elements dorsal to the last vertebral centra; the hypurals are those endoskeletal elements ventral to the ural centra. Hypurals are modified haemal spines that may articulate or fuse with ural centra or may remain independent. He included among uroneurals the tendon-bone urodermals, a mistake that he corrected later (NYBELIN 1971; see below, section on Uroneurals). Monod confusingly labeled NYBELIN's uroneurals as urodermals.

Diural and polyural caudal skeletons: NYBELIN (1963: 488, and 1977) distinguished not only elements within the caudal skeleton, but also caudal skeletons of different fishes. He contrasted the polyural (with many ural centra) caudal skeleton of non-teleosts such as *Amia*, †*Ionoscopus* and †*Urocles* to the diural caudal skeleton (with two ural centra) of teleosts (e. g., †*Leptolepis*, *Elops*). The publication is in German, perhaps a reason that subsequent workers have ignored the following sentence concerning the two ural centra of the diural skeleton: "ich sehe hier davon ab, ob diese Elemente je einem einzigen Wirbelkörper entsprechen oder durch Verschmelzung zweier oder mehrerer ursprünglicher Wirbelkörper entstanden sind" (NYBELIN 1963: 487); a sentence that in English reads as follows:

> "I don't consider here, if these elements correspond each to one single centrum or originate from fusion of two or more original centra."

On page 488, NYBELIN (1963) compared the uralia (or ural region) of *Amia* (each ural centrum bearing one hypural) with the second ural centrum in *Elops* (bearing three hypurals): "Der Umstand, dass, mit

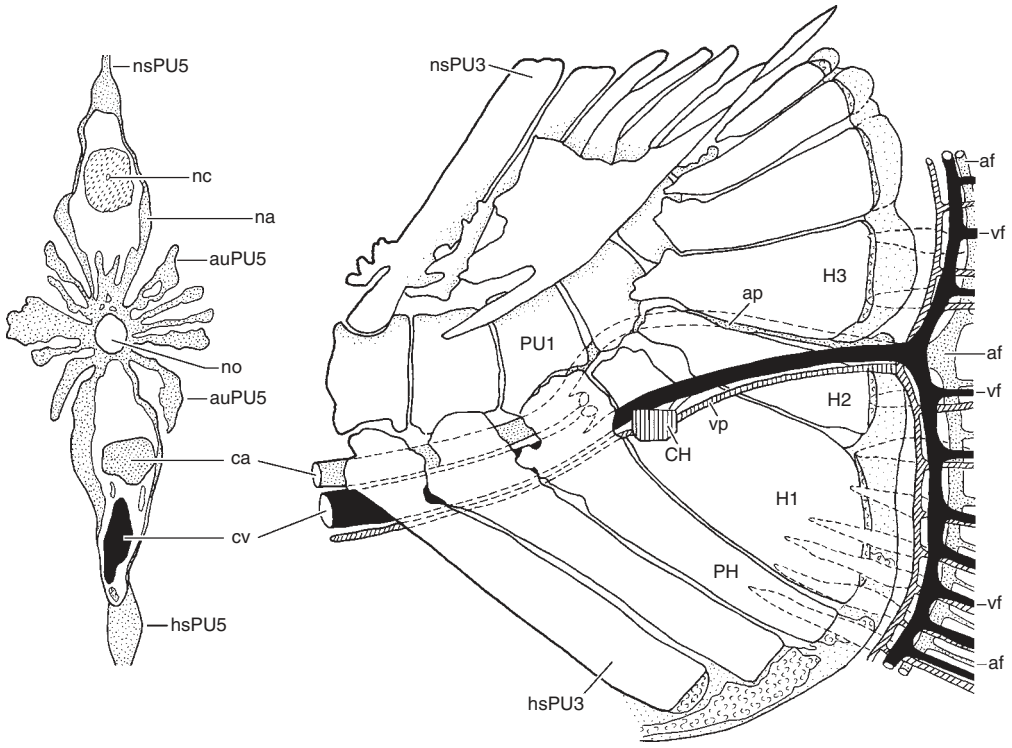


Fig. 2.
Main landmarks in the caudal skeleton of holosteans and teleosteans useful in diural and polyural conventions. Trajectory of the main blood vessels in the caudal region as illustrated for *Oncorhynchus mykiss* based on ethanol and cleared and stained specimens, and serial histological cross-sections (slightly modified from SCHULTZE & ARRATIA: 1989: fig. 20). **A,** vertical cross-section through preural vertebra 5. **B,** diagrammatic lateral view of caudal endoskeleton. Abbreviations: **af**, arteria flabellaria; **ap**, arteria pinnalis; **auPU5**, autocentrum of preural centrum 5; **ca**, caudal artery; **CH**, caudal heart; **cv**, caudal vein; **H1**, **2**, **3**, hypurals 1, 2, 3; **hsPU3**, **5**, haemal spine of preural centra 3 and 5; **na**, neural arch of preural centrum 5; **nc**, neural cord; **no**, notochord; **nsPU3**, **5**, neural spine of preural centra 3 and 5; **PH**, parhypural or haemal spine of preural centrum 1; **PU1**, preural centrum 1; **vf**, vena flabellaria; **vp**, vena pinnaria.

Ausnahme von Urale 1, ein jedes der Uralia bei *Amia* nur ein einziges Hypurale trägt, während Urale 2 bei *Elops* drei Hypuralia stützt, könnte darauf hinweisen, dass Urale 2 bei *Elops* aus drei ursprünglichen, während der phylogenetischen Entwicklung verwachsenen Elementen besteht. Die Lösung auf diese Frage ist aber noch nicht spruchreif." The English translation reads as follows:

> "The circumstance that, with the exception of ural 1, each ural in *Amia* carries a single hypural, whereas ural 2 of *Elops* supports three hypurals, could indicate that ural 2 of *Elops* is composed of three original elements, which are fused during phylogeny. The solution of this question is not yet ripe for a decision."

NYBELIN (1963, 1971) took the straighforward approach and numbered sequentially the elements present in adult teleosts. Many others followed his convention (e. g., MONOD 1968; PATTERSON 1968a,b; ROSEN 1973; TAVERNE 1977, 2011; FUJITA 1990; HILTON 2002, 2003), with the exceptions of studies by SCHULTZE & ARRATIA (1988, 1889), ARRATIA & SCHULTZE (1992), and ARRATIA (2010). Through ontogenetic studies, these later workers demonstrated the compound origin of the ural centra. Additionally, more than two ural elements also have been observed in fossils (e. g., PATTERSON & ROSEN 1977: fig. 24, and see below, ARRATIA 1991: fig. 14, pls. 8D, 14C, ZHANG 1998: fig. 12, BRITO 1999: figs. 2, 5; see Fig. 3A, and see description and illustration of *Eurycormus* below). However, the tradition and influence of diural terminology is pervasive even in the presence of observed multiple ural centra (e. g., PATTERSON

& ROSEN 1977: fig. 24; TAVERNE 2011: figs. 50–52, see Fig. 3C herein; BENSIMON-BRITO 2012: fig. 3). This situation, however, may be changing with new ontogenetic data from ostarioclupeomorphs from the Cypriniformes Tree of Life and euteleosts from the Euteleostei Tree of Life (research projects sponsored by NSF, U.S.A.) and with recent work by GRÜNBAUM & CLOUTIER (2010).

Numbering of elements: NYBELIN (1963) identified as preural centrum 1 (Fig. 1) the centrum bearing the last haemal arch to enclose the caudal blood vessels, and he identified as preural vertebrae all those anterior to it that support fin rays. Preural centra are numbered then from caudal to rostrad, whereas ural centra are numbered from rostral to caudad (see Fig. 1). Hypurals are numbered from rostral to caudad, hypural 1 being the next haemal element posterior to the parhypural. Epurals as well as uroneurals are numbered also from rostral to caudad.

The numbering in NYBELIN's terminology, with exception of preural centrum 1, **does not imply homology**, but rather position of elements, an approach that has been followed by most ichthyologists, but see PINNA (1996: 151–152).

Other caudal fin landmarks

Hypural diastema and trajectory of blood vessels

Detailed studies – based on ontogenetic series and histology – of extant *Hiodon*, *Elops* and salmonids permitted SCHULTZE & ARRATIA (1989) and ARRATIA & SCHULTZE (1992) to provide a more detailed picture of NYBELIN's convention concerning preural centrum 1 as a landmark, and also to add new landmarks.

Figure 2A illustrates a cross section through a preural vertebra showing that the neural arch surrounds the neural cord, and the haemal arch surrounds the main caudal artery and caudal vein. Figure 2B shows that the caudal blood vessels begin their bifurcation inside the haemal arch of preural centrum 1, exit the haemal arch, run outside hypurals 1 and 2 and then continue between hypurals 2 and 3 towards the caudal fin rays where the main artery and vein split into dorsal and ventral branches, respectively, at the base of the fin rays.

The split of the blood vessels (Fig. 2B) between hypurals 2 and 3, where the blood vessels diverge to irrigate the caudal fin rays, is another landmark that facilitates separation of hypurals 1 and 2 from hypural 3. A space or diastema (Figs. 3A–B, 4A–C) is observed between hypurals 2 and 3 in many extant teleosts from early ontogeny (see below, section on notochordal flexion) and the presence or absence of this space (Fig. 4D) or even its different shapes may be useful taxonomic characters in the identification of certain taxa. This space or diastema may also be helpful in the identification of hypurals 2 and 3 in certain fossil actinopterygians when the identification of the bases of the parhypural and of hypurals is difficult due to condition of preservation. This landmark is observed from early ontogeny and thus can be helpful in identifying tiny cartilaginous hypurals (see additional figures below).

Other landmarks – such as the dorsal-most principal ray or the ventral-most principal ray, and consequently their associated bones – can be helpful identifying different elements of the caudal skeleton. These landmarks may be especially useful with specimens that are incompletely preserved (see below).

Dorsal-most principal ray versus dorsal procurrent series of elements

The base of the posterior-most basal fulcrum (= basal fulcrum 1) or of the posterior-most epaxial procurrent ray (= procurrent ray 1) and of the first principal ray (segmented but unbranched) diverge from each other, lateral to the notochord, in a characteristic angle in "true" teleosts (Fig. 5A–C; ARRATIA 2008: figs. 6, 7A–C, 13, 22, 23). As a consequence, the posterior-most basal fulcrum or posterior-most procurrent ray is always dorso-lateral to the notochord, whereas the first principal ray is ventro-lateral (ARRATIA 2008). This landmark may be useful to identify these rays when the distal tips of the rays are damaged and also may be useful to locate the dorsal-most hypural.

Ventral-most principal ray and haemal spine of preural centrum 2

The first principal ray (segmented but unbranched) lies ventral to the notochord, but the last principal ray (segmented but unbranched) is associated with the haemal spine of preural centrum 2 in basal teleosts (SCHULTZE & ARRATIA 1989, ARRATIA 2008).

Understanding polyural and diural caudal skeletons is more than simply giving a name and number to the centra involved in the caudal region. It means understanding the formation of the vertebrae and their different elements in both ontogenetic and phylogenetic frameworks. Thus, before addressing our convention of the caudal endoskeleton, we discuss a few aspects such as body segmentation and possible elements involved in the formation of vertebral centra, especially in basal teleosts.

Segmentation or metamerization of caudal region

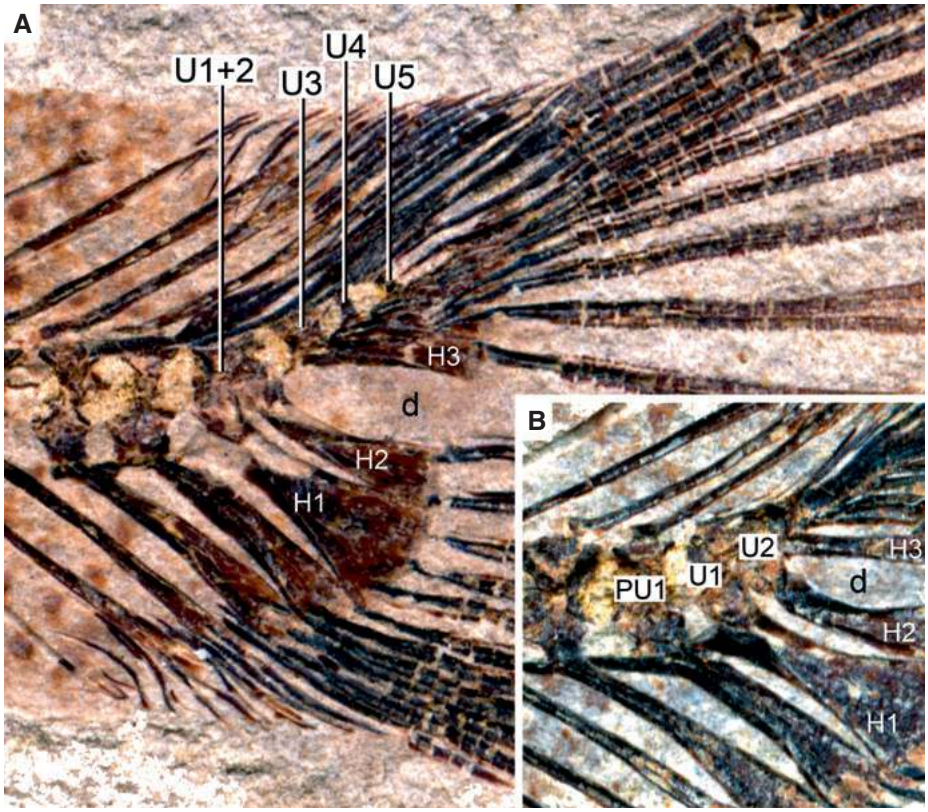
It is well accepted that there is a consistent relationship (usually interpreted as a one-to-one relationship) between the elements included in each body segment (e.g., muscles, bones and the peripheral nervous system). It is expected that this relationship is constant and can be followed along the body, including the tail, in most primitive, piscine body plans (e.g., GOODRICH 1930: 1–45; JOLLIE 1962). However, the regular metamerization between muscles, bones and peripheral nervous systems is lost in the elements supporting the adult caudal fins of actinopterygians, especially of teleosts (for instance see JOLLIE 1962: 420–421). The one-to-one relationship between a vertebral centrum per body segment, as well as muscles, nerves and blood vessels that is observed in the anterior body including the middle caudal region is lost in the elements supporting fins, especially the tail region. Figures 2B and 6A show the lack of a one-to-one relationship between bony elements and blood vessels; MONOD (1968: figs. 7–9, 11–14) also showed the lack of a one-to-one relationship between myomeres and caudal endoskeleton. This fact creates a problem when looking for relationships between some elements of the caudal region. Although there is no special mention of the lack of metamerization in the available literature, many authors have illustrated the loss in the last preural vertebral and ural region (e.g., elopiforms: RICHARDS 1984: fig. 28; notacanthiforms and anguilliforms: CASTLE 1984: fig. 50; ostariophysans: FUIMAN 1984: figs. 62, 63; osmerids: HEARNE 1984: fig. 81; argentinoids: AHLSTROM et al. 1984: figs. 85, 86; scombroids: COLLETTE et al. 1984: fig. 328, 329; and other papers in MOSER et. al. 1984). We have not observed muscle segmentation at the posterior tip of the body (Fig. 7A–C, and below) in larvae, juveniles, or adults of any actinopterygian species available to us.

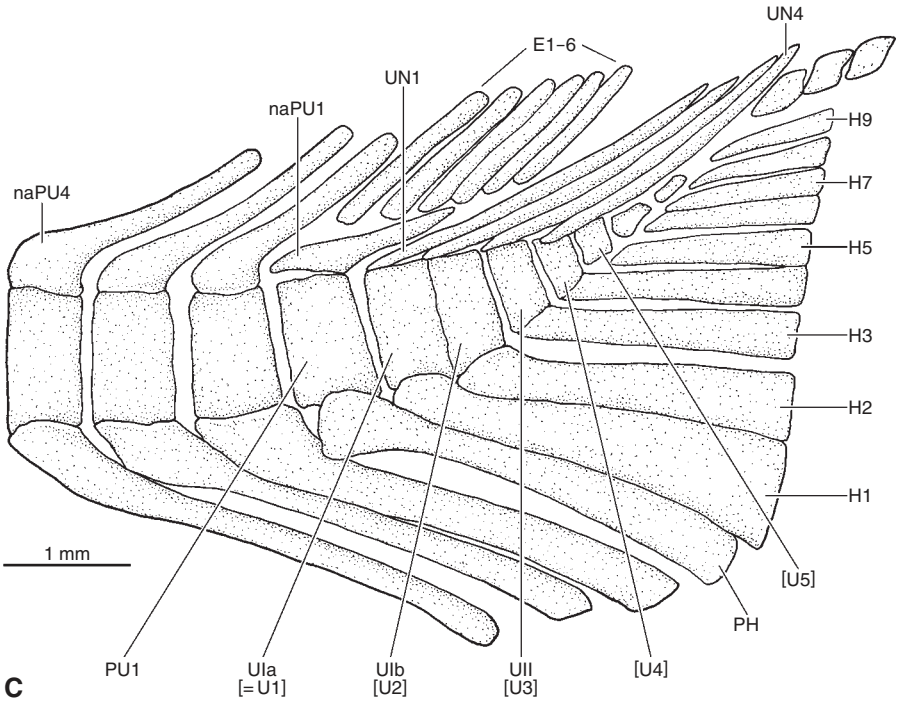
The loss of metamerization becomes a major problem when identifying serial homologues in the caudal region, establishing possible relationships of epurals and uroneurals to their ventral or hypaxial counterparts (hypurals), and their relationships to specific ural centra. A major problem arises from the loss of the one-to-one relationship between epaxial and hypaxial bony elements due to the fact that the number of vertebral ural centra in adult teleosts is reduced, a phenomenon that is associated with the upturning of the posterior vertebral centra in teleosts (see below). A few related questions can be put forward: To which ural centra belong the 9th, 8th, 7th or 6th hypurals present in †*Ascalabos*, †*Leptolepis*, *Elops*, *Hiodon* and other teleosts, respectively? To which ural centra belong the fourth, third, second, and first epural present in †*Domeykos*, †*Leptolepis*, *Elops*, *Albula*, *Hiodon* and other teleosts? Is it always the same centrum, or may the related centra be different in different teleostean groups? If so, what is the evolutionary significance of these differences?

Vertebral formation, mineralization, and ossification

Evidence shows that the type of vertebral centra varies depending on the phylogenetic position of a taxon within actinopterygians (ARRATIA et al. 2001). Thus, it is important to be aware of the type of vertebral formation found in different actinopterygians including teleosts.

Fig. 3.
Caudal skeletons in lateral view, illustrating preural versus ural regions. **A,** osteoglossomorph †*Asiatolepis muroii* (IVVP V11982.7b). × 7.4. **B,** osteoglossomorph †*Asiatolepis muroii* (IVVP V11982), courtesy of ZHANG J-Y. (IVVP, Beijing, China). **C,** Middle Jurassic 'pholidophoriform' †*Catervariolus hornemani* (slightly modified after TAVERNE 2011: fig. 50). Abbreviations: **d**, hypural diastema; **E1–6**, epurals 1–6 (position) → [epurals of ural centra 1–6^{P}]; **H1–9**, hypurals 1–9; **naPU4**, 1, neural arch of preural centra 4, 1; **PH**, parhypural; **PU1**, preural centrum 1; **UIa**, **Ib**, first ural centrum^{D} of diural terminology; **UII**, second ural centrum^{D} of diural terminology; **[U1–5]**, ural centra 1–5^{P} of the polyural terminology; **UN1**, **4**, uroneural 1, 4 (position) → [modified ural neural arches of ural centra 1 and 4^{P}]. ▷


A
U1+2
U3
U4
U5
H3
d
H2
H1
B
U2
H3
PU1
U1
d
H2
H1


UN4
E1–6
UN1
naPU1
H9
naPU4
H7
H5
H3
H2
H1
1 mm
[U5]
PH
PU1
UIa
[= U1]
UIb
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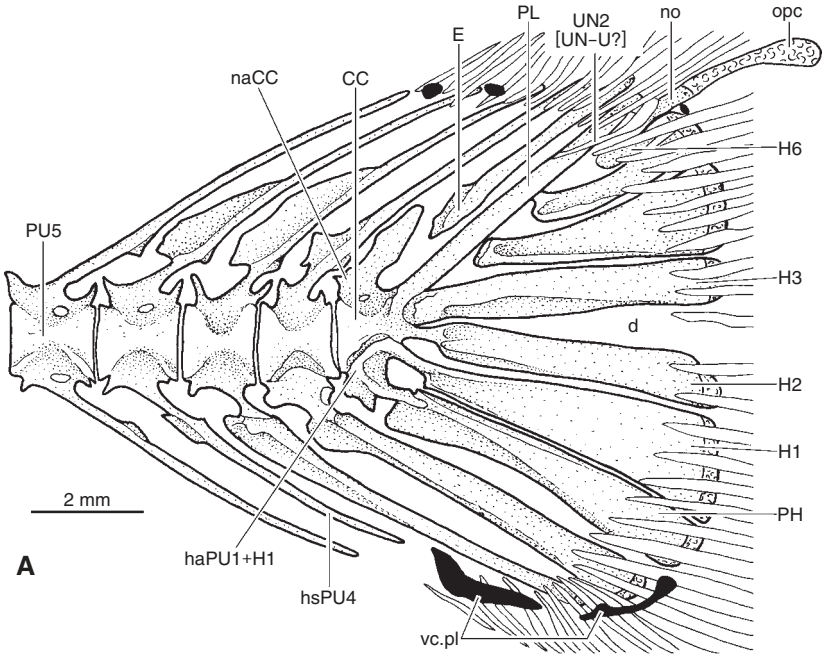
UII
[U3]
[U4]
C



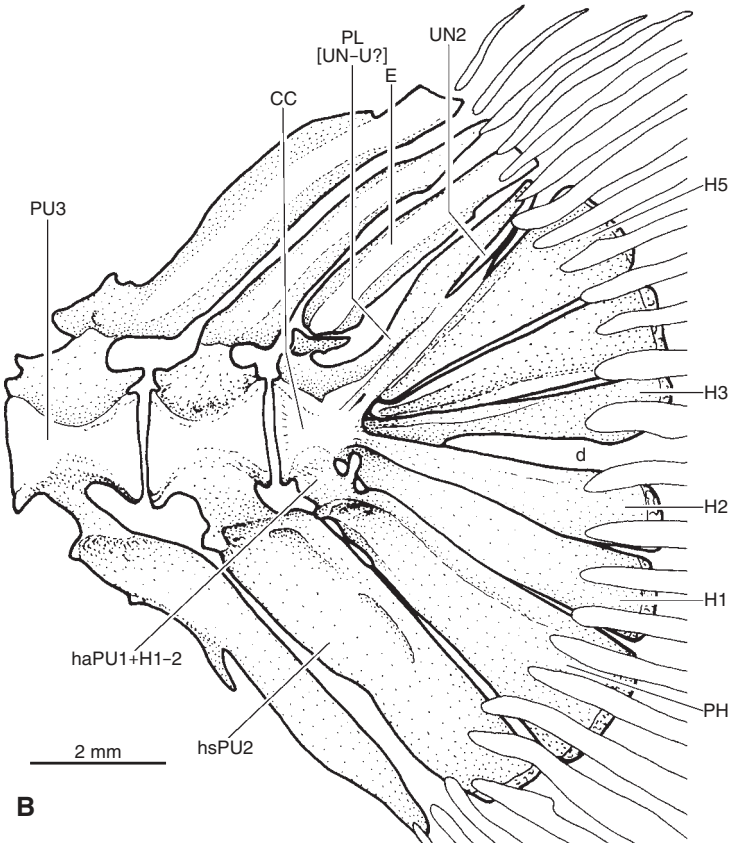
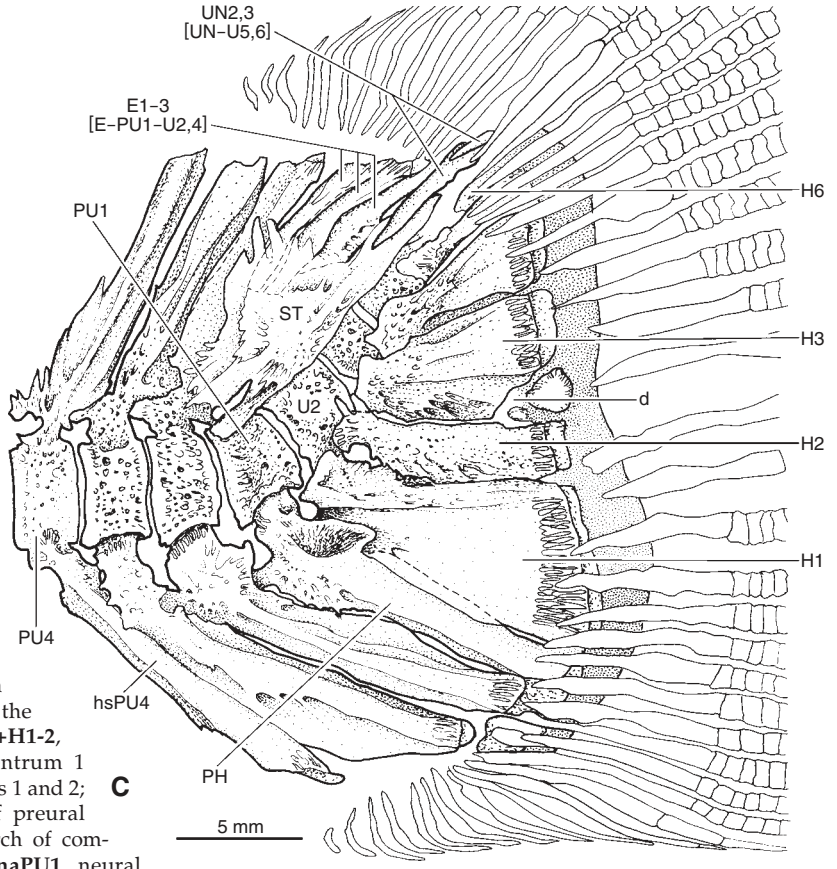
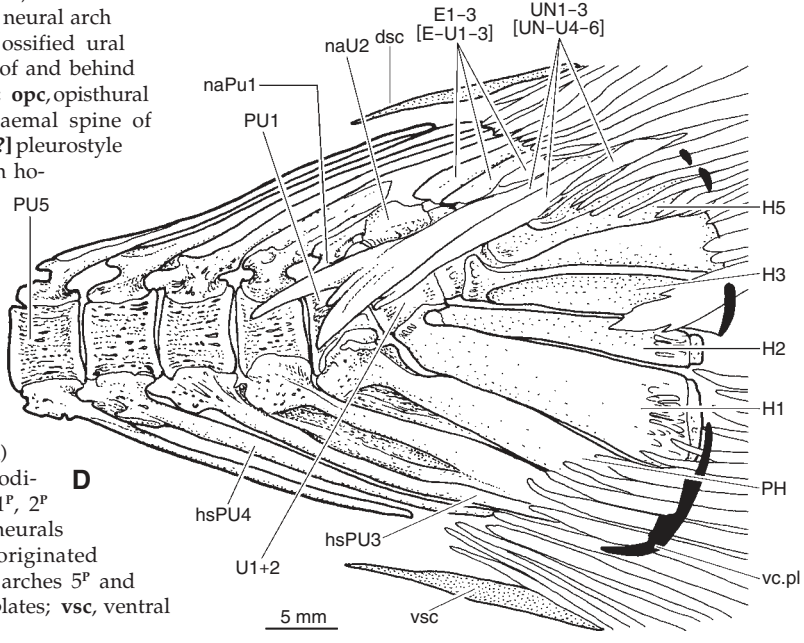


Fig. 4.
Caudal skeletons of some teleosts in lateral views illustrating the position of the hypural diastema [A–C] between hypurals 2 and 3 and its absence [D] and differences in the flexion of the caudal skeleton in adult specimens. **A,** cypriniform *Opsariichthys uncirostris* (KUNHM 21448; Recent). **B,** cypriniform *Cobitis biwae* (modified from FUJITA 1990; Recent). **C,** salmoniform *Oncorhynchus mykiss* (modified from ARRATIA & SCHULTZE 1992: fig. 3; Recent). **D,** elopiform *Elops saurus* (modified from SCHULTZE & ARRATIA 1988: fig. 15; Recent). Abbreviations: **CC**, compound terminal centrum–including an unknown number of centra–fused with the proximal regions of pleurostyle and hypural 2 [A] or pleurostyle and haemal arch of preural centrum 1 and hypurals 1–2 [B]; **d**, hypural diastema; **dsc**, dorsal caudal scute; **E,** epural (unknown homology); **E1–3[E-U1**, **2**, **4]**, epurals 1–3 (position) →[epurals originated as neural spines of ural centra 1^{P}, 2^{P} and 4^{P} in salmonids]; **E1–3[E-U1–3]**, epurals 1–3 (position) →[epurals originated as neural spines of ural



centra 1^P, 2^P and 3^P in elopiforms]; **H1–6**, hypurals 1–6; **haPU1+H1**, haemal arch of preural centrum 1 fused to the base of hypural 1; **haPU1+H1-2**, haemal arch of preural centrum 1 fused to the bases of hypurals 1 and 2; **hsPU4-2**, haemal spines of preural centra 4-2; **naCC**, neural arch of compound terminal centrum; **naPU1**, neural arch of PU1; **naU2**, ossified ural neural arch 2^P; note the presence of small ossified ural neural arches 1^P and 3^P in front of and behind ural neural arch 2^P; **no**, notochord; **opc**, opisthural cartilage; **PH**, parhypural or haemal spine of preural centrum 1; **PL**, **PL[UN-U?]** pleurostyle (modified uroneural of unknown homology); **PU5–1**, preural centra 5–1; **ST**, stegural (modified ural neural arch 4^P); **U2**, ural centrum 2^P that grows anteriorly partially supporting hypural 1; **U1+2**, ural centrum formed by the early ontogenetic fusion of ural centra 1^P and 2^P; **UN2**, **UN2[UN-U?]**, uroneural 2 [unknown homology]; **UN1–3[UN-U4–6]**, uroneurals 1–3 (position) → [uroneurals originated as modifications of ural neural arches 1^P, 2^P and 3^P]; **UN2,3[UN-U5,6]**, uroneurals 2, 3 (position) → [uroneurals originated as modifications of ural neural arches 5^P and 6^P]; **vc.pl**, ventral cartilaginous plates; **vsc**, ventral caudal scute.



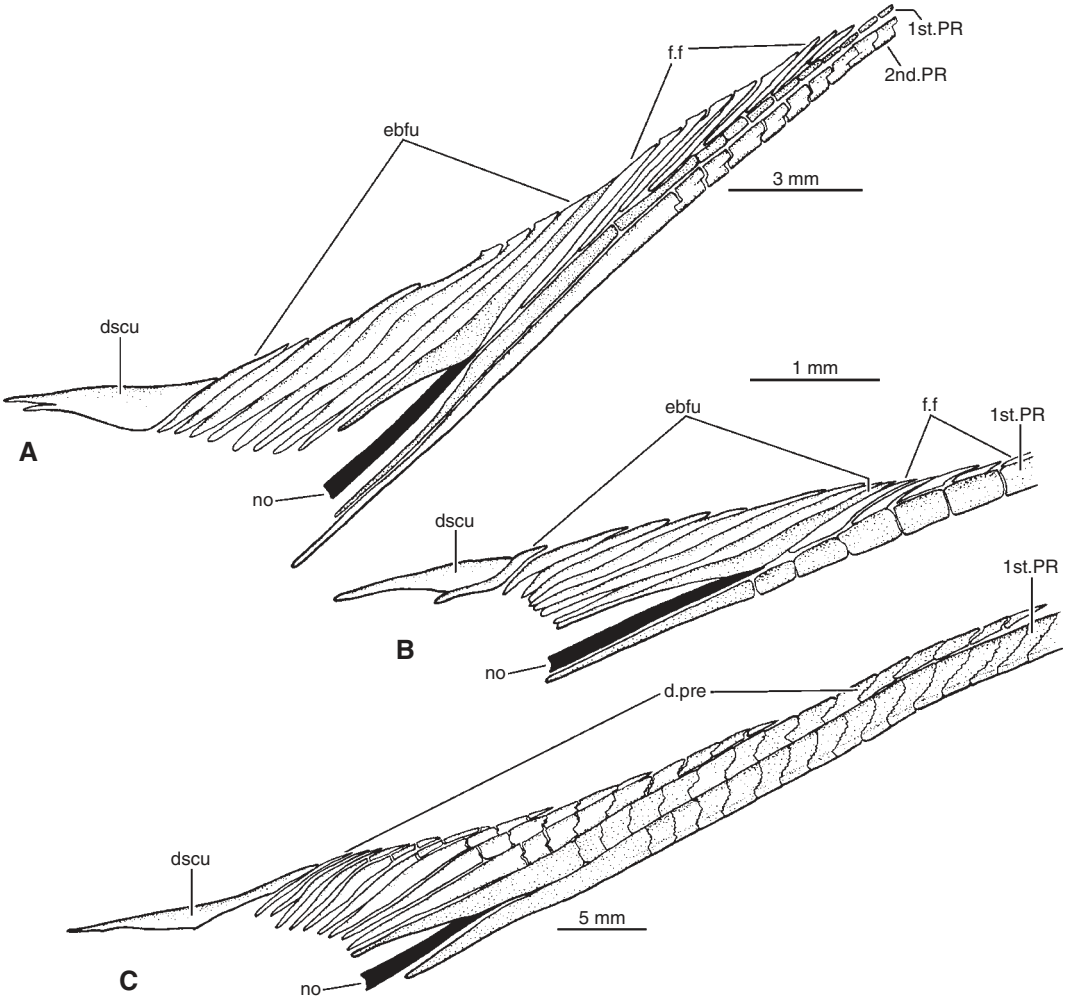
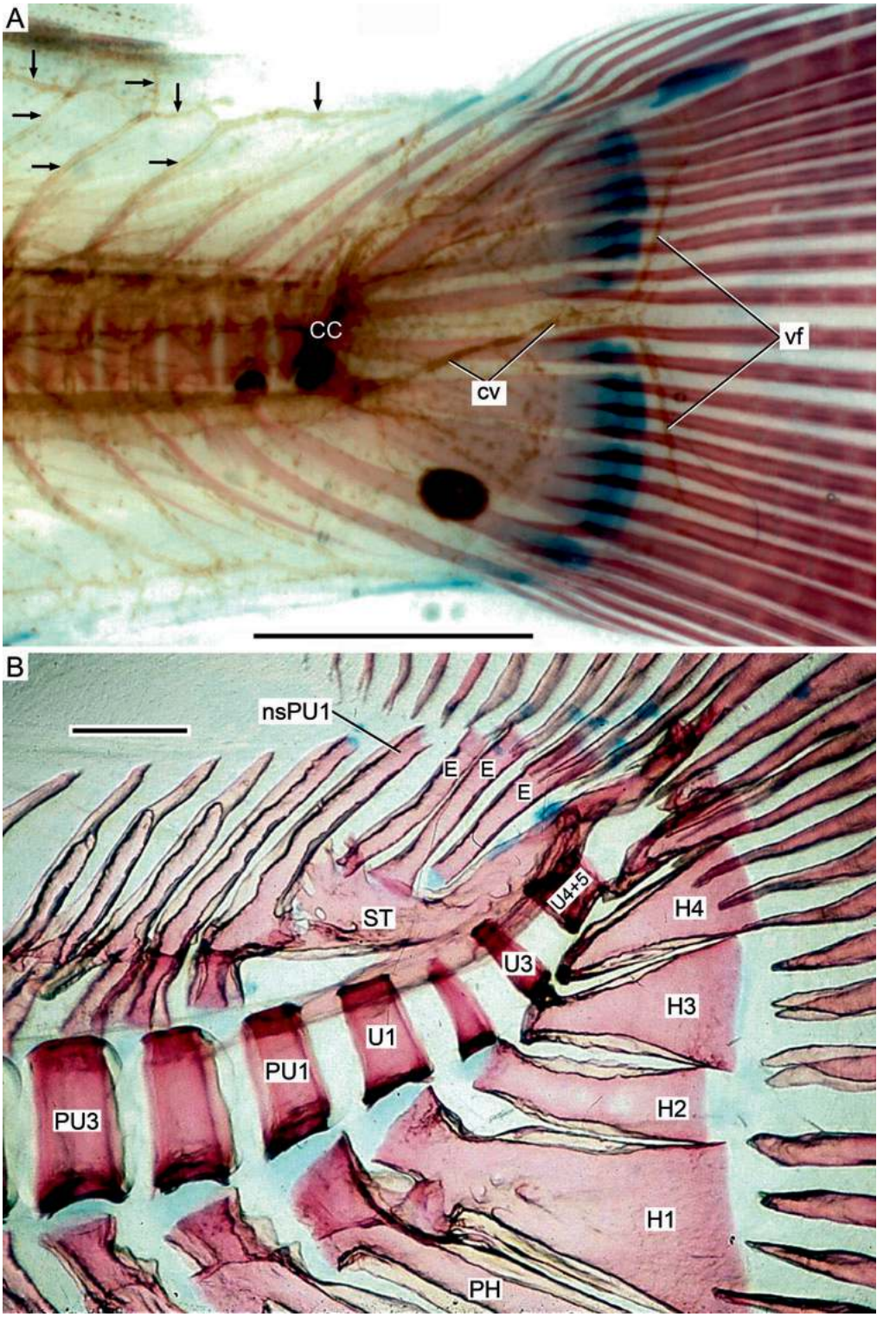


Fig. 5.
Diagrammatic representation of an additional landmark for identification of certain structures of the caudal fin. Note the gap or space left at the bases of the most posterior basal fulcrum and the first principal ray [A,B] and between the posterior-most precurrent ray and first principal ray [C]. The gap is partially occupied by the notochord. **A,** 'pholidophoriform' †*Eurycormus speciosus* (based on specimen MB f.7019; Upper Jurassic). **B,** basal teleost †*Leptolepis coryphaenoides* (BGHan 1957-5 and others; Lower Jurassic). **C,** basal elopiform *Elops saurus* (CAS(SU) 45172; Recent). (After ARRATIA 2008: fig. 7). Abbreviations: **d.pre**, change in figure too dorsal precurrent rays; **dscu**, dorsal caudal scute; **ebfu**, epaxial basal fulcra; **f.f**, fringing fulcra; **no**, notochord; **1st.PR**, first principal ray; **2nd.PR**, second principal ray.

Fig. 6.
Teleostean caudal skeletons in lateral views. **A,** cypriniform *Catostomus commersoni* (KUNHM 38655; Recent). Note the segmental position of body veins (indicated by small arrows) and the lack of a 1:1 relationship between blood vessels and the endoskeletal caudal fin region (first preurals and terminal centrum). **B,** caudal skeleton of a young salmonid, *Oncorhynchus mykiss*, showing the polyural condition of the caudal skeleton (KUNHM 12463, 28 mm SL; Recent). Abbreviations: **CC**, compound terminal centrum including preural centrum 1 and ural centra 1–3^{p} (see text for an explanation); **cv**, caudal vein; **E,** epurals 1–3 (position) →[epurals of preural centrum 1 and of ural centra 1^{p} and 2^{p}]; **H1–4**, hypurals 1–4; **nsPU1**, neural spine of preural centrum 1; **PU3,1**, preural centra 3, 1; **U1,3**, ural centra 1^{p}, 3^{p}; **U4+5**, ural centrum 4+5^{p} (or it could be only one or the other); **PH**, parhypural or haemal spine of preural centrum 1; **ST**, stegural →[modified uroneural 4]; **vf**, vena flabellaria. ▷


A
CC
cv
vf
B
nsPU1
E
E
E
U4+5
ST
H4
U3
H3
U1
PU1
H2
PU3
H1
PH

As we have shown in previous papers, the **adult** actinopterygian vertebrae may be diplospondylous (e.g., two centra per body segment, e.g., in some amiiforms, some 'pholidophoriforms'; Fig. 8A,B) or monospondylous (one centrum per body segment, e.g., lepisosteiforms, and most teleosts; Figs. 2B, 4A–D, 6A,B, 7C, 9A,B). The kinds of centra forming the diplospondylous or monospondylous condition may be different in different groups. However, and independently of the taxonomic group, one type of centrum, the arcocentrum – either dorsal or ventral – is always present (ARRATIA 1991, SCHULTZE & ARRATIA 1989, ARRATIA et al. 2001). Nevertheless, most of the basidorsal arcualia (and dorsal arcocentra) are lost in the ural region, whereas the basiventral arcualia that will become hypurals are developed in the hypural region of the tail.

A notochord that is partially surrounded by the dorsal and ventral arcualia is present at the earliest stage of development in all actinopterygians. During growth, mineralized or ossified centra may form; however, a persistent notochord remains for the whole life of the animal in certain actinopterygians (e.g., some †pycnodontiforms, some †pachycormiforms). The notochord plays a major role in "marking" the place where a centrum will form, independent of the type of centrum that will form during the course of development. This role was shown and discussed first by ARRATIA (1991) and later by ARRATIA (2003: 127–129, fig. 4.3), ARRATIA et al. (2001: 151, figs. 42A–C, 43), and ARRATIA & BAGARINAO (2010: figs. 3.2, 3.3) (see also NELSON 2010: 26), and has been noted without attribution by some developmental workers (e.g., FLEMING et al. 2004, STEMPLE 2005).

We distinguish three kinds of vertebral centra, the arcocentra, the chordacentra and the autocentra. One, two or three of these elements may form the adult actinopterygian centra.

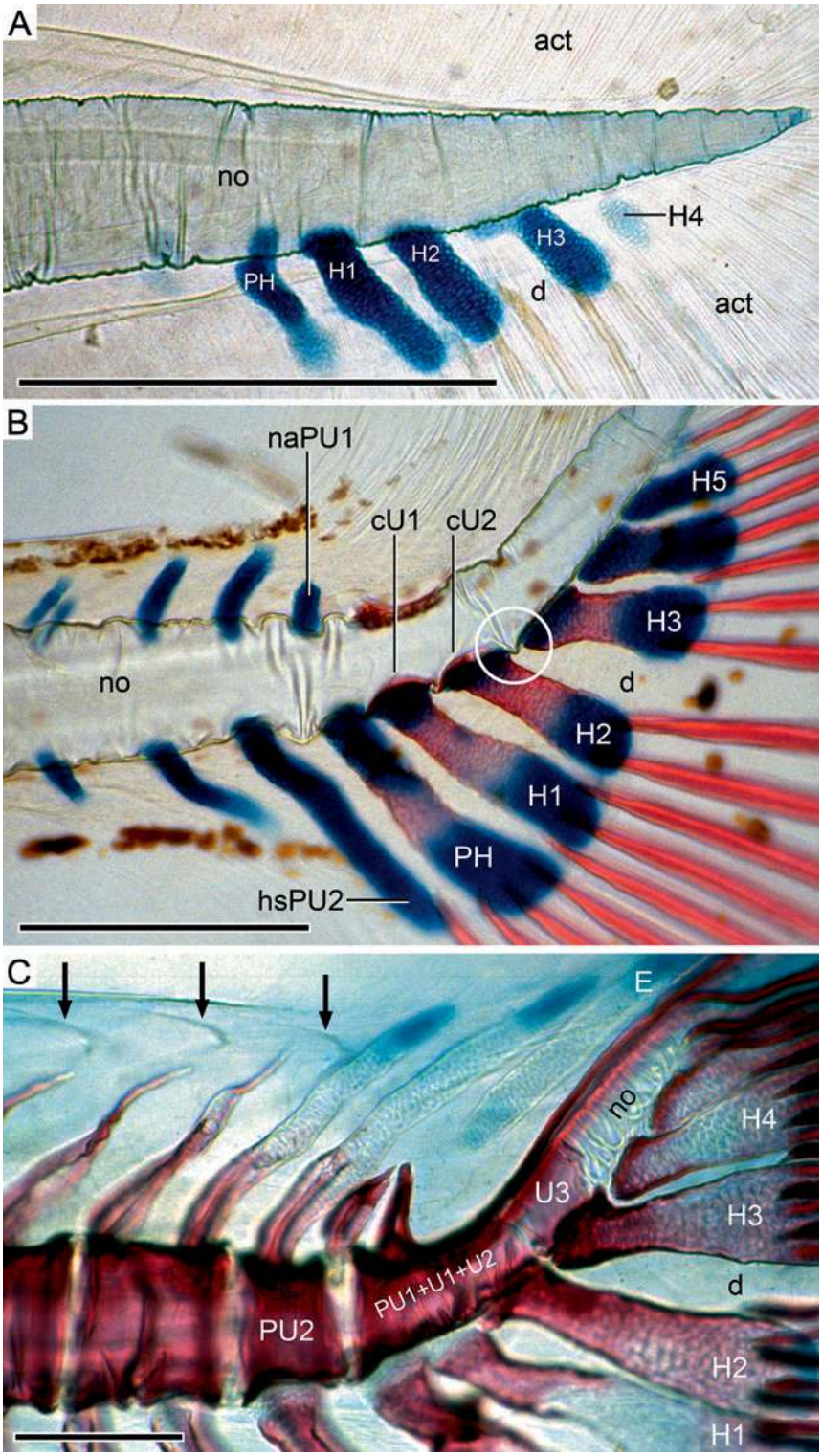
Arcocentrum: The arcocentra are the elements that develop from the basidorsal and basiventral arcualia (GADOW & ABBOTT 1895, ARRATIA et al. 2001). They ossify perichondrally and may retain partially ossified or unossified cartilage at the base of the arches in some teleosts (e.g., *Hiodon* and *Elops*: ARRATIA & SCHULTZE 1988: figs. 8, 9A, 10A,B, 12A; salmonids: ARRATIA & SCHULTZE 1992: figs. 11B, 12C,D; ARRATIA et al. 2001: fig. 40A), whereas they may ossify as compact bone in other groups (e.g., trichomycterid catfishes: ARRATIA et al. 2001: fig. 40B,C).

There is one pair of dorsal and one pair of ventral arcocentra per body segment in the vertebral column, except in the region of the caudal skeleton. The dorsal arcocentra are placed dorso-lateral to the notochord and surround the neural cord; each arcocentrum extends dorsally in the neural spine. The ventral arcocentra are placed ventro-lateral to the notochord and surround the blood vessels in the caudal region, e.g., the dorsal aorta and vein; each ventral arcocentrum extends ventrally in the haemal spine. Consequently, dorsal and ventral arcocentra form the dorso-lateral and ventro-lateral ossified part of each vertebral centrum, and they include the neural and haemal arches, respectively. Differences in the growth of the arcocentra characterize two special kinds of centra (the opisthocoelous and the arcocentral type).

In lepisosteiforms the basidorsal arcual cartilage grows and begins to ossify as the dorsal arcocentrum. Each dorsal arcocentrum grows ventrally until it reaches the basiventral cartilage, ossifies, and forms a vertebral centrum (see SCHULTZE & ARRATIA 1986: figs. 2–4, 1989: figs. 16, 17). These vertebral centra are opisthocoelous as seems to be unique to Lepisosteiformes.

In other actinopterygians, such as some †pycnodontiforms, †aspidorhynchiforms and †'pholidophoriforms' (e.g., †*Siemensichthys macrocephalus*), the lateral growth of the dorsal and ventral arcocentra may form an ossified layer of bone outside each chordacentrum, so that there is a bony continuation and fusion between both arcocentra. This is the arcocentral type of centrum formation, and it should not be confused with an autocentrum (ARRATIA et al. 2001: 147).

Fig. 7.
Lack of metamerization and flexion of the tail in the cypriniform *Catostomus commersoni* (KUNHM 38655; Recent). **A,** specimen of 11 mm notochordal length. **B,** specimen of 14.3 mm standard length (SL). The white circle encloses the region where the notochord extends between the bases of hypurals 2 and 3 marking the region of its flexion. **C,** specimen of 17.8 mm SL. The arrows indicate the position of muscle segments, which are not observed at the beginning of the preural and ural regions. Scales = 0.5 mm. Abbreviations: **act**, actinotrichia; **cU1**,**2**, ventral ural chordacentra 1^{P}, 2^{P}; **d**, hypural diastema; **E,** epural (unknown homology); **H1–5**, hypurals 1–5; **hsPU2**, haemal spine of preural centrum 2; **naPU1**, neural arch of preural centrum 1; **no**, notochord; **PH**, parhypural; **PU2**, preural centrum 2; **PU1+U1^{P}+U2^{P}**, compound terminal centrum formed by preural centrum 1 and ural centra 1^{P} and 2^{P}; **U3**, ural centrum 3^{P}. ▷


A
act
no
H4
H3
H2
H1
PH
d
act
B
naPU1
cU1
cU2
H5
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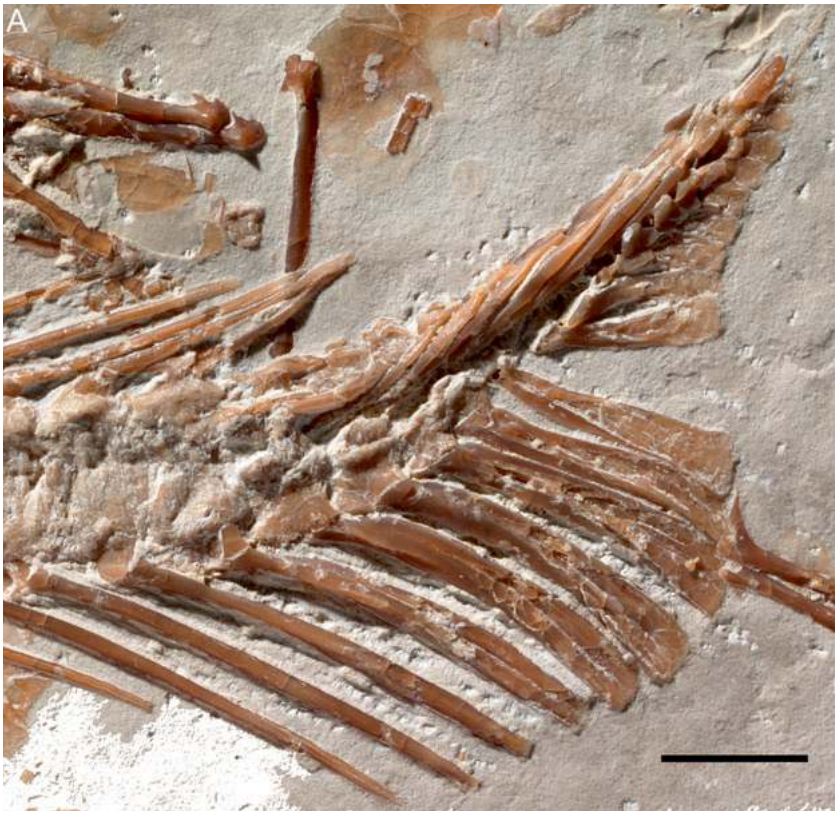
no
d
H2
H1
PH
hsPU2
C
E
no
H4
U3
H3
d
PU1+U1+U2
PU2
H2
H1

The neural spines ossify differently depending on the body region (see ARRATIA et al. 2001: 157 for general information). In the mid-caudal region the neural and haemal spines in extant teleosts are commonly dorsal and ventral membranous ossifications, respectively, of the distal portions of the arcocentra. Thus, they can be considered as membrane bone. However, the neural spines of the preural and ural regions, including the epurals, and the haemal spines of the preural region and the hypurals are expanded in comparison to the preceding spines and are perichondrally ossified (e.g., Figs. 6A,B, 7C). However, this is not the condition observed in basal teleosts such as †*Leptolepis coryphaenoides* (see Fig. 9A,B) and †*Tharsis dubius*, in which there is not an obvious, clear-cut difference between the preural neural and haemal spines and the spines of preceding vertebrae. In addition, in such teleosts all spines ossify perichondrally. It is unclear at what level of the teleostean phylogeny the spines anterior to those of the preural vertebrae ossify only as membrane bone. It is interesting that in an advanced euteleost, the gasterosteiform *Indostomus paradoxus*, the neural arches and spines and haemal arches and spines preceeding preural centrum 2 seem to be formed exclusively by membrane bone (BRITZ & JOHNSON 2002). A similar condition has been observed in gobies (pers. comm. G. D. JOHNSON, 2012).

Chordacentrum: Mineralization in the middle notochordal sheath forms the chordacentrum (SCHULTZE & ARRATIA 1988: figs. 6, 8, 10, 12, 13, 1989: fig. 9A–D; ARRATIA & SCHULTZE 1992: figs. 10, 12A, 16A, 17B, 23). The beginning of the mineralization process differs in actinopterygians. The chordacentra may begin to form in (1) the dorsal region or (2) in the dorsal and ventral regions almost simultaneously or (3) in the ventral region of the middle notochordal sheath.

1. A chordacentrum may originate at the dorsal region of the notochord, and then grow ventrally to form a complete ring-like chordacentrum. This kind of formation apparently is not common in actinopterygians but it is present at least in Recent lepisosteids (e.g., *Lepisosteus*: SCHULTZE & ARRATIA 1986: figs. 2A, 3A, 4; SCHULTZE & ARRATIA 1989: fig. 17; GRANDE 2010: fig. 88B). We have also observed this type of dorsal chordacentral formation in some Triassic actinopterygians interpreted as †'pholidophoriforms'.
2. The mineralization process of the notochord starts almost simultaneously at its dorsal and ventral regions and then progresses laterally (Fig. 10A–C). An example of this pattern is present in the Middle Jurassic teleost incertae sedis †*Todiltia*, where ventral and dorsal hemichordacentra take part in the formation of the chordacentrum. In the Recent esociforms *Esox lucius* and *Esox masquinongy* both ventral and dorsal hemichordacentra grow, forming a ring-like chordacentrum that later is surrounded by the autocentrum (BURDI & GRANDE 2010: fig. 3E,F).
3. The mineralization process of the notochord starts at the ventral region of the notochord and then grows dorsally to form a complete ring-like chordacentrum (Fig. 10D–F, 11A–D). This chordacentrum, which appears early in ontogeny, may stay as chordacentrum during the entire life of some actinopterygians (e.g., †*Pholidophorus bechei*), or it may be covered or obliterated by arcocentral and autocentral ossifications during growth (e.g., †*Leptolepis coryphaenoides*, †*Tharsis*, elopiforms, albuliforms, hiodontids, basal cypriniforms, salmonids, etc.). We have shown the participation of the chordacentrum in the formation of the vertebral centrum in several papers (e.g., ARRATIA 2001; SCHULTZE & ARRATIA 1986, 1988, 1989; ARRATIA & SCHULTZE 1992; ARRATIA et al. 2001), whereas chordacentra and their role are overlooked in many papers dealing with fossils and also in papers dealing with ontogenetic development of certain taxa. For instance, chordacentra in the ural region of *Amia calva* were figured in a specimen of 51 mm standard length, but they were not mentioned in the text (GRANDE & BEMIS 1998: fig. 80, photograph). In a description of the caudal skeleton of *Hiodon tergisus*, the ventral chordacentra starting in front of haemal arches of preural centra 5-2 and in front of hypurals 4 and 5 were not recognized or labeled as such (HILTON & BRITZ 2010: fig. 2A). GRÜNBAUM & CLOUTIER (2010) reported one ventral chordacentrum forming in front of hypural 2 in *Salvelinus alpinus*.

Chordacentra and their initiation can be observed in properly cleared and stained extant very young actinopterygians (e.g., see Fig. 11B and below) by just using a high-quality compound microscope. Not only is it possible to observe the chordacentra, but also the notochord, its changes in density and aspect, and its obliterations (e.g., Figs. 7A–C, 11B and other figures below). The chordacentra can be observed without the requirement of histological cross-sections; certainly, such preparations can confirm previous observations done under a microscope. In fossils, chordacentra (Figs. 12A, 13A,B) are easily recognizable because they have a different aspect and may have a different color (e.g., usually whitish or pale yellow; however they can be darker in the special preservation of the Upper Jurassic of Ettling; see TISCHLINGER & ARRATIA this volume: figs. 1b, 2a,b) than the arcocentra and other bony elements.



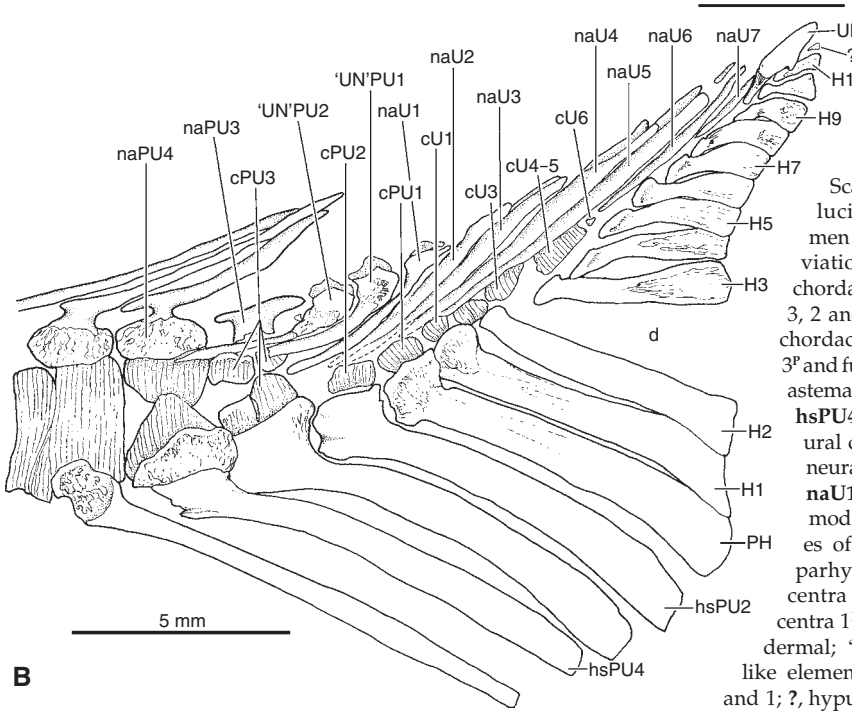


Fig. 8.
Caudal skeleton in lateral view of the 'pholidophoriform' †*Eurycormus speciosus* (BSPG 1956 I 422; Zandt near Denkendorf, Bavaria; Upper Jurassic, Tithonian). **A,** photograph. Scale = 5 mm. **B,** camera lucida drawing of specimen illustrated in A. Abbreviations: **cPU3**, **2**, **1**, ventral chordacentra of preural centra 3, 2 and 1; **cU1**, **3**, **4–5**, ventral chordacentra of ural centra 1^{P}, 3^{P} and fused $4+5^{P}$; **d**, hypural diastema; **H1–11**, hypurals 1–11; **hsPU4**, **2**, haemal spine of preural centrum 4, 2; **naPU3**, **4**, neural arch of preural 3 and 4; **naU1–7**, uroneural $1–7^{P}$ or modifications of neural arches of ural centra $1–7^{P}$; **PH**, parhypural; **PU3–1**, preural centra 3-1; **U1**, **2**, **4+5**, **6**, ural centra 1^{P}, 2^{P}, $4+5^{P}$, 6^{P}; **UD**, urodermal; '**UN'PU2**, **1**, uroneural-like elements of preural centra 2 and 1; **?**, hypural 12?.

Autocentrum: The autocentrum is the direct ossification that appears outside the chordacentrum (e.g., basal teleosts) or outside the notochord (advanced teleosts). The presence of an autocentrum is a synapomorphy of "true" teleosts; ARRATIA 1999: fig. 19, character 75). The autocentrum is thin, smooth, and ring-like in †leptolepidids (ARRATIA 1997: fig. 89A,B; ARRATIA & HIKUROA 2010: figs. 5A,B, 6A,B), but the notochord is strongly constricted by the autocentrum in more advanced teleosts with a thick autocentrum. Grooves, fossae and ridges may ornament the lateral walls of the autocentrum, and its lateral cavities are filled with adipose tissue.

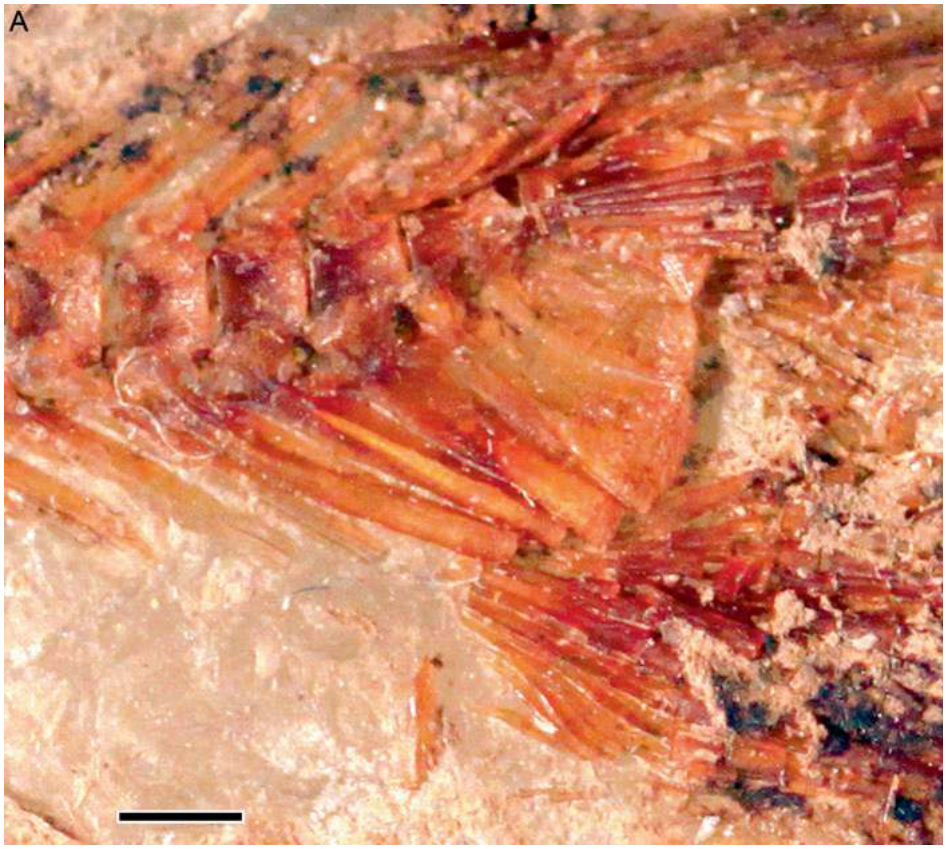
Flexion of the notochord and dorsal flexion of caudal endoskeletal elements

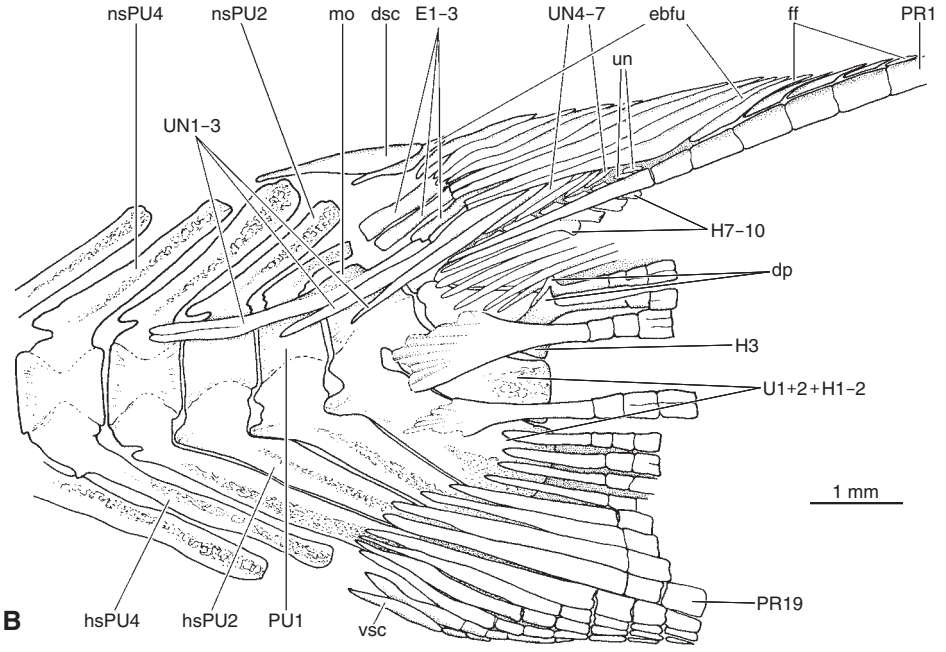
There is a gentle dorsal upturn of the preural and ural regions in actinopterygians such as lepisosteiforms, amiiforms, †aspidorhynchiforms, and some †'pholidophoriforms' (see Figs. 3C, 7B,C, 8A,B, 12A,B). The dorsal upturn is also very gentle and progresses caudally smoothly in basal "true" teleosts such as †*Leptolepis coryphaenoides* (Fig. 9A,B) and †*Tharsis dubius* (PATTERSON & ROSEN 1977: fig. 35; ARRATIA 1991: fig. 13), some elopiforms (e.g., *Elops*; Fig. 4D) and some osteoglossomorphs (e.g., †*Lycoptera*). A marked, abrupt dorsal upturn of the posterior part of the caudal skeleton is observed in members of the †varasichthyid group such as †*Protoclup*ea and †*Luisichthys* (ARRATIA 1997: fig. 9B,D), in †ichthyodectiforms such †*Allothrissops* and †*Pachythrissops* (e.g., ARRATIA 1997: fig. 24, 25), and in extant basal teleosts such as in some osteoglossomorphs (e.g., *Hiodon*), most ostarioclupeomorphs, and in salmonids (e.g., *Oncorhynchus;* Fig. 4C).

In the early development of teleosts, the notochord is straight, even in its most caudal region (e.g., Fig. 7A; McGOWAN & BERRY 1984: 59, 60; OLNEY 1984: fig. 195; FRITZSCHE 1984: fig. 215; COLLETTE et al. 1984: figs. 331, 332, and many others). Suddenly, a change of angle in the ventral region of the notochord between the bases of cartilaginous hypurals 2 and 3 (where the hypural diastema is situated and where the caudal blood vessels run) marks the beginning of the upturn of the posterior part of the notochord in some teleosts such as clupeiforms and cypriniforms (Fig. 7B), whereas in others the change of the angle of the notochord is at the bases of the cartilaginous arch of the parhypural and of the cartilaginous hypural 1 (e.g., salmonids; Figs. 4C, 6B). Our observations of early stages of development of elopomorphs, hiodontids, clupeiforms, ostariophysans, salmonids, and others, show that the notochord itself initiates its upturn between preural centrum 1 and ural centrum1/hypural 1 or between hypurals 2 and 3 and is consequently responsible for the re-arrangement in position of ventral and dorsal elements of the ural region. In this way, the ural centra form a marked angle with respect to preural centrum 1 (e.g., Fig. 4C), or ural centrum 3^{P} forms a marked angle with respect to ural centrum 2^{P} or to ural centrum $1+2^{P}$ (Fig. 7B,C). The space remaining dorsal to the notochord between the neural spine of preural centrum 2 (when preural centrum 1 does not have a spine), or of preural centrum 1 and the distal tip(s) of the first uroneural(s), becomes reduced compared to the area ventral to the notochord occupied by the hypurals.

The dorsal flexion of the notochord changes the position of the hypurals with respect to the horizontal body axis and results in a distinct separation between two sets of hypurals: the ventral set including hypurals 1 and 2 and the dorsal set including hypurals 3-to-n. While this change is occurring in the ventral region of the tail, epurals and uroneurals have not appeared yet, so that there is an asynchrony in timing between the appearance of the hypaxial (hypurals) and epaxial series of elements (epurals and/or uroneurals) (Fig. 7A,B). This turns out to be a major difficulty in understanding the relationships of the ural centra with corresponding epurals and uroneurals dorsally and hypurals ventrally.

Fig. 9.
Caudal skeleton of the basal teleost †*Leptolepis coryphaenoides* (northern Germany; Lower Jurassic, Toarcian). **A,** acid prepared specimen BGHan 1957-5. Scale = 1 mm. **B,** drawing of specimen illustrated in A (slightly modified from ARRATIA 1991: fig. 7). Abbreviations: **dp**, dorsal process of innermost principal caudal rays of upper lobe; **dsc**, dorsal caudal scute; **E1–3**, epurals 1–3 (position) →[epurals of ural centra $1–3^{P}$]; **ebfu**, epaxial basal fulcra; **ff**, fringing fulcra; **H3**, **H7–10**, hypurals 3 and 7–10; **hsPU4**,**2**, haemal spine of preural centra 4 and 2; **mo**, membraneous outgrowth on anterodorsal margin of first uroneural; **nsPU4**,**2**, neural spine of preural centra 4 and 2; **PU1**, preural centrum 1; **U1+2+H1–2**, fused ural centra $1+2^{P}$ + hypurals 2 and 3; **UN1–3**,**4–7**, uroneurals $1–3^{D}$ and $4–7^{D}$ (position) →[uroneurals originating as modifications of neural arches of ural centra $3–5^{P}$ and $6–9^{P}$, respectively]; **un**, uroneural-like element; **PR1**,**PR19**, first (uppermost) and last (lowermost) principal caudal rays; **vsc**, caudal scute of lower lobe of caudal fin. Note: the specimen was acid prepared in 1985 and the drawing was done at that time. The photograph was taken a few months ago and shows that after more than 25 years the fossil has some slight damage. ▷


A


nsPU4
nsPU2
mo
dsc
E1–3
UN4–7
ebfu
ff
PR1
un
UN1–3
H7–10
dp
H3
U1+2+H1–2
1 mm
PR19
B
hsPU4
hsPU2
PU1
vsc

As our investigations of the caudal skeleton of fossil and basal extant adult teleosts reveal, the upturn that initially begins anterior to hypurals 2 and 3 or between ural centra 2^{P} and 3^{P} can affect also the ural centrum (or centra) in front of hypurals 1 and 2, and these elements become also involved in the upturn of the last vertebral centra.

We believe that the change of the main angle (Fig. 7B,C) started in early ontogeny in the ventral part of the notochord – at the base of the hypurals 2 and 3. It can be accompanied by other changes to increase the upturn of the posterior part of the tail, especially of the ural region in advanced teleosts. The fusion of ural centra $1+2^{P}$ (= ural 1^{D}), or $3+4^{P}$ or $3+4+5^{P}$ (= ural 2^{D}), or the loss of ural centra (e.g., ural centrum 1^{P} in clupeiforms; ARRATIA 2010: fig. 13C,D, or ural centra 4^{P} and 5^{P} in cypriniforms; see below) or the loss of uroneurals (e.g., elopiforms, clupeomorphs, ostariophysans; see below section on Uroneurals) may increase the upturn of the tail and consequently its function or, alternatively, the losses are the result of the upturning of the tail. To the best of our knowledge, these changes have not been investigated in teleosts until now.

Polyural caudal skeleton and SCHULTZE and ARRATIA's convention

Within holosteans, NYBELIN (1963) compared the polyural skeleton of *Amia* (Fig. 11A,B), *Lepisosteus* and other fossil actinopterygians to the diural caudal skeleton of adult teleosts. Two centra support the hypurals in the diural skeleton (Figs. 1, 11C,D). In the diural caudal skeleton, the first centrum supports hypurals 1 and 2, and the second centrum supports three or more hypurals (Fig. 12C,D) depending on the teleostean group. The ural centra are typically labeled as ural 1 and 2 (Fig. 1) in the diural skeleton in the literature because of their number and topological arrangement, but not according to their ontogenetic origin. In contrast, in the polyural caudal skeleton each hypural is connected with its corresponding ural centrum, and they are named ural 1^{P}/hypural 1, ural 2^{P}/hypural 2, etc. (e.g., Figs. 3A–C, 8A,B, 11A,B, 12A,B).

The morphology of the caudal skeleton of extant *Amia calva*, fossil amiiforms, the Late Jurassic †*Ionoscopus* and other actinopterygians supports NYBELIN's expectation that there is a constant relationship between hypurals and ural centra in the polyural caudal skeleton. NYBELIN (1963: fig. 16) figured the caudal skeleton of *Amia calva*, and discussed the possibility that several ural centra of *Amia calva* correspond to a single centrum, the second ural centrum, in the diural caudal skeleton of *Elops* (NYBELIN 1963: 488; see above). In *Amia calva* (Fig 11A,B), each ural centrum connects with its respective hypural.

Our studies of early ontogenetic stages of extant basal teleosts have revealed the presence of more than two ural centra, a condition that sometimes is retained in juveniles or adults. In many cases, the polyural interpretation can be based on the presence of more than two ural centra (e.g., Figs. 6B, 7B, 11E, see below) or indirectly based on the presence of additional ural neural arches (e.g., Fig. 4D, 12D; see SCHULTZE & ARRATIA 1988: figs. 3C, 4, 5, 6, 7, 11A–F; HILTON 2002: figs. 74A–D, 76E,F) above the so-called first ural centrum of the diural terminology ($U1^{D}$). We are aware that the appearance of chordacentra and their development, and also of autocentra are very fast processes, and that one has to study many specimens of each day of development to be lucky enough to observe the formation (and fusion) of different centra.

In basal teleosts, such as the elopiforms †*Anaethalion*, *Megalops* and *Elops*, in adult individuals there are two ural centra, which may develop in front of the cartilage at the bases of hypurals 1 and 2 (Fig. 14A) and of hypurals 3 or 3 and 4 (Fig. 14B). These are cartilaginous remnants of the basiventral arcualia that partially ossify as an abbreviated arcocentrum in adults. There can even be small additional chordacentra at the base of hypural 5 (Fig. 14C; see ARRATIA 1987: figs. 4B, 21; SCHULTZE & ARRATIA 1988: figs. 15, 16B–D, 17A; ARRATIA 2008: fig. 6). A mass of cartilage, the compound cartilaginous neural arch (Fig. 14A,B and see below) dorsal to the ural centra of elopomorphs, may ossify as three ural neural arches during growth (Figs. 4D, 15B; ARRATIA 1987: fig. 18; SCHULTZE & ARRATIA 1988: fig. 22). The notochord plays a major role in "marking" the place where a centrum will form (Figs. 7A, 11B,D, 14A, 19B). (Often, in fossil elopomorphs, the region above the uroneurals is observed as empty; this may represent the result of poor preparation that has removed the small arches of the specimen or it may be the result of the lack of preservation of the cartilage or the ossifying cartilage [e.g., Fig. 15A]). We have observed similar development in the albulid *Albula vulpes* (SCHULTZE & ARRATIA 1988). We interpret the two ural centra present in adult fossil and extant elopiforms as indications of ural centrum $1+2^{P}$ and ural centrum $3+n^{P}$, and the small ossified ural neural arches as ural neural arches $1–3^{P}$ (Figs. 4D, 15B).

Ural centra 1 and 2^{P} can be observed anterior to hypurals 1 and 2 (Fig. 16) in the fossil osteoglossomorph †*Lycoptera middendorfii* (e.g., PATTERSON & ROSEN 1977: fig. 24). Usually hypurals 1 and 2 connect to ural centrum 1^{D} of the diural terminology; PATTERSON & ROSEN had to label the two ural centra as

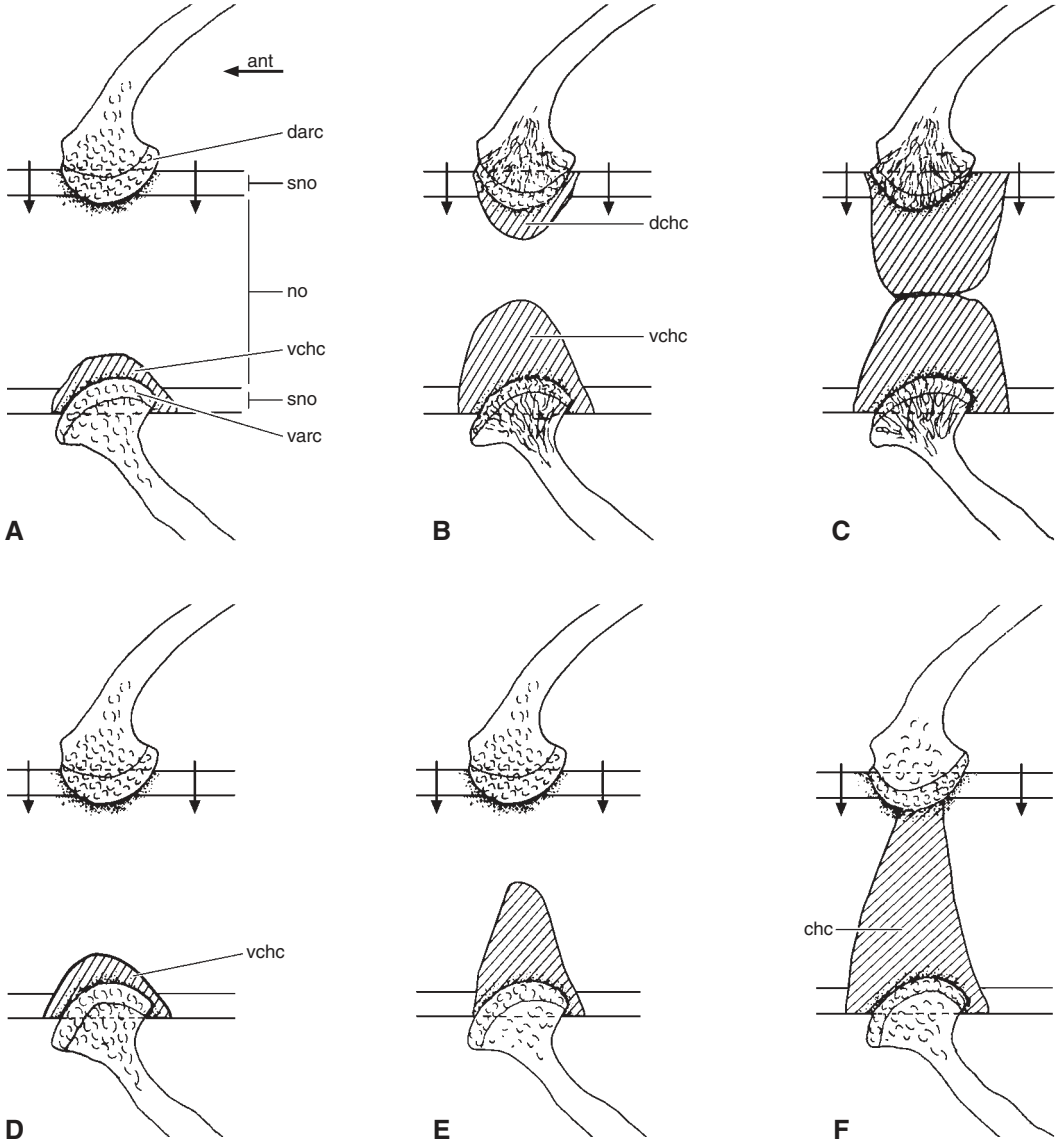
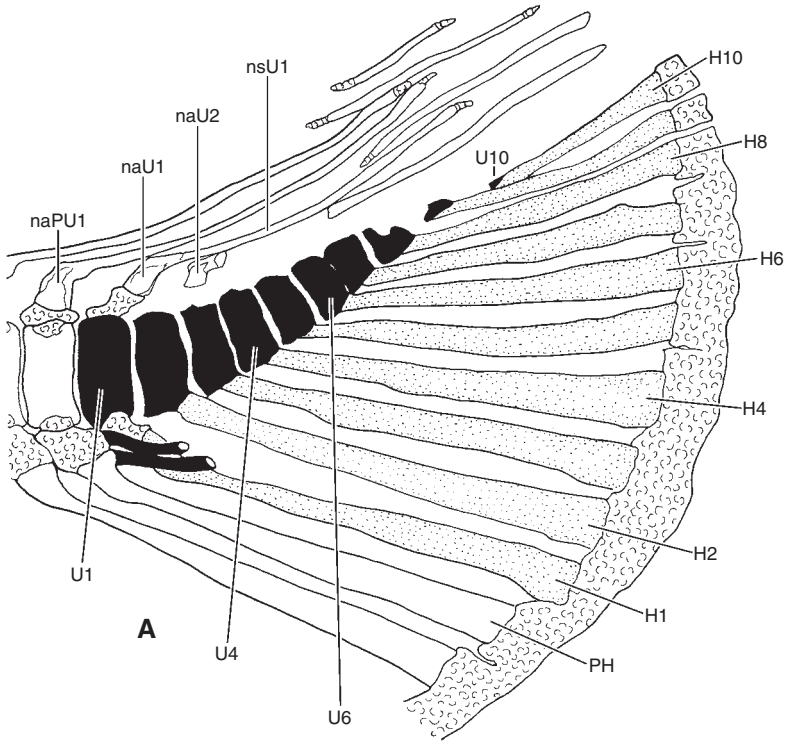


Fig. 10.
Diagrammatic representation of the formation of chordacentra (after ARRATIA 1991: fig. 2). **A–C**, chordacentra begin to form from dorsal and ventral regions of the notochord; e. g., teleost incertae sedis †*Todiltia schoewei*. **D–F**, chordacentra begin to form at the ventral region of the notochord; e. g., *Elops*, *Hiodon*, *Oncorhynchus*. Arrows indicate the region where obliterations of the notochord will set the limits where the chordacentra will grow. Abbreviations: **ant**, pointing in anterior direction; **chc**, chordacentrum; **darc**, dorsal arcocentrum; **dchc**, dorsal chordacentrum; **no**, notochord; **sno**, notochordal sheaths; **varc**, ventral arcocentrum; **vchc**, ventral chordacentrum.

UIa and UIb to accommodate the diural convention (Fig. 16; see also Fig. 3C for the †'pholidophoriform' †*Catervariolus*). Additional examples of a polyural skeleton in fossil teleosts are observed in the basal teleost †*Tharsis dubius* with separate ural centra 3^{p}, 4^{p} and 5^{p} in some specimens (ARRATIA 1991: fig. 14) and in other fossil osteoglossomorphs such as †*Kuntulunia longipterus* (ZHANG 1998: fig. 12B), and †*Asiatolepis muroii* (Fig. 3A,B). Ural centrum $1+2^{p}$ and ural centra $3+4^{p}$, 5^{p} and 6^{p} are present in some specimens of



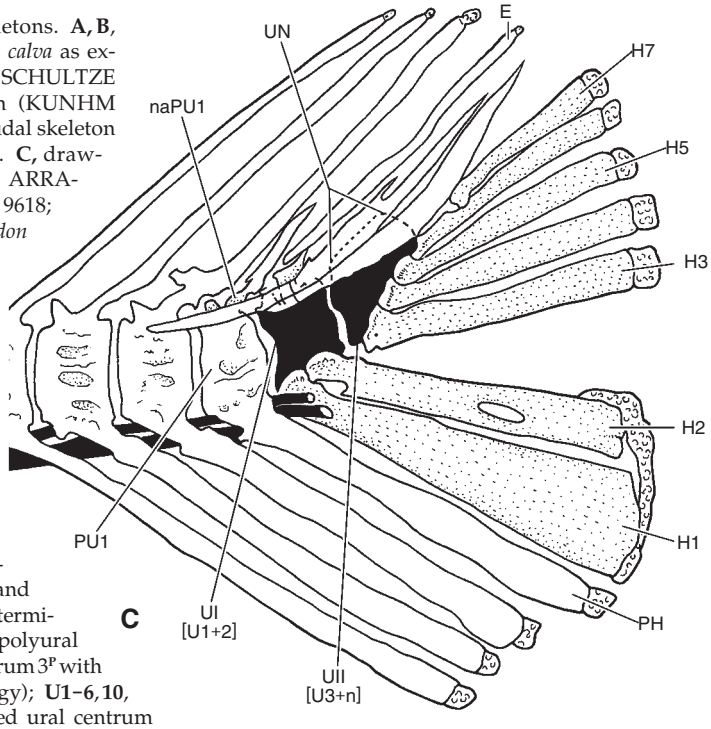
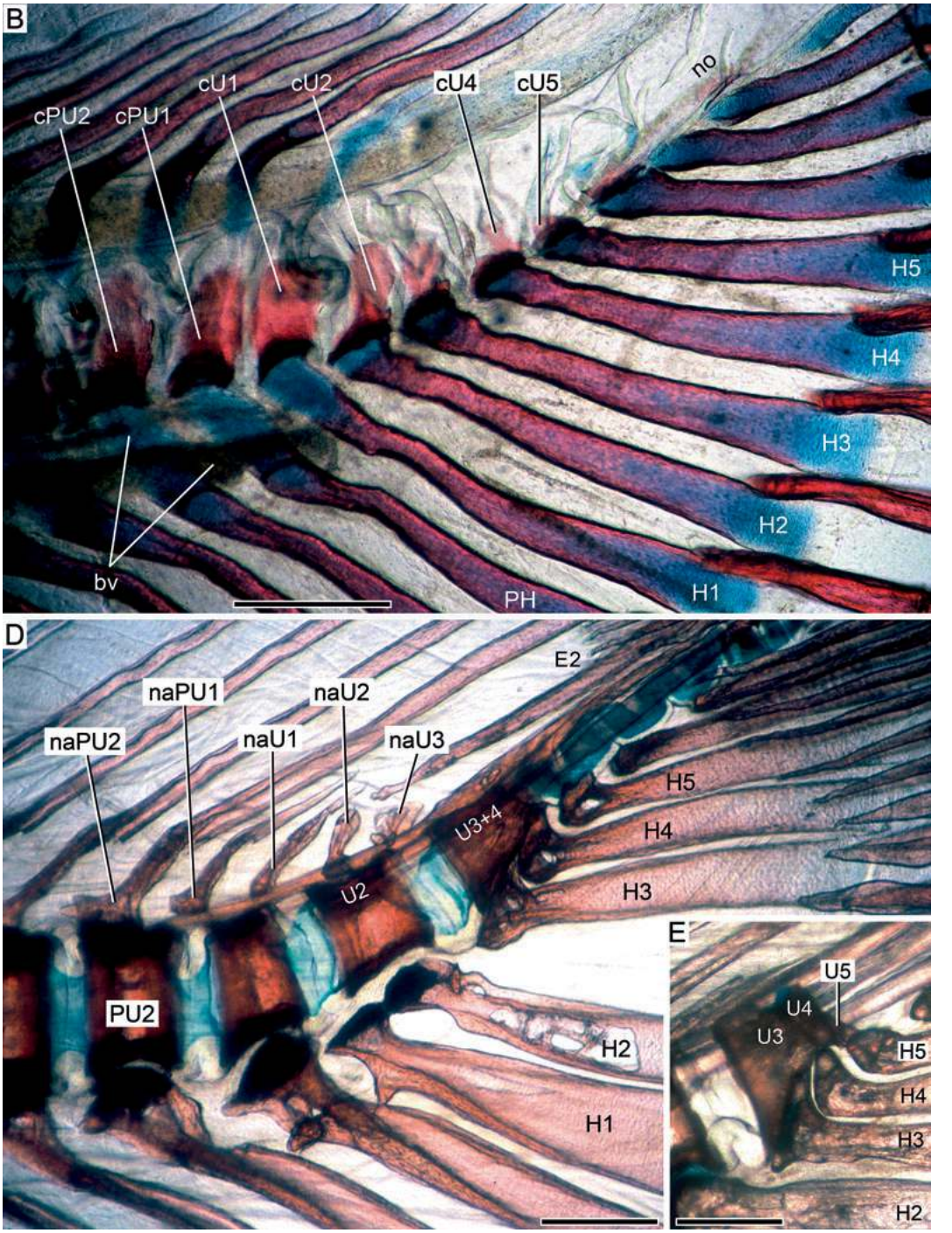
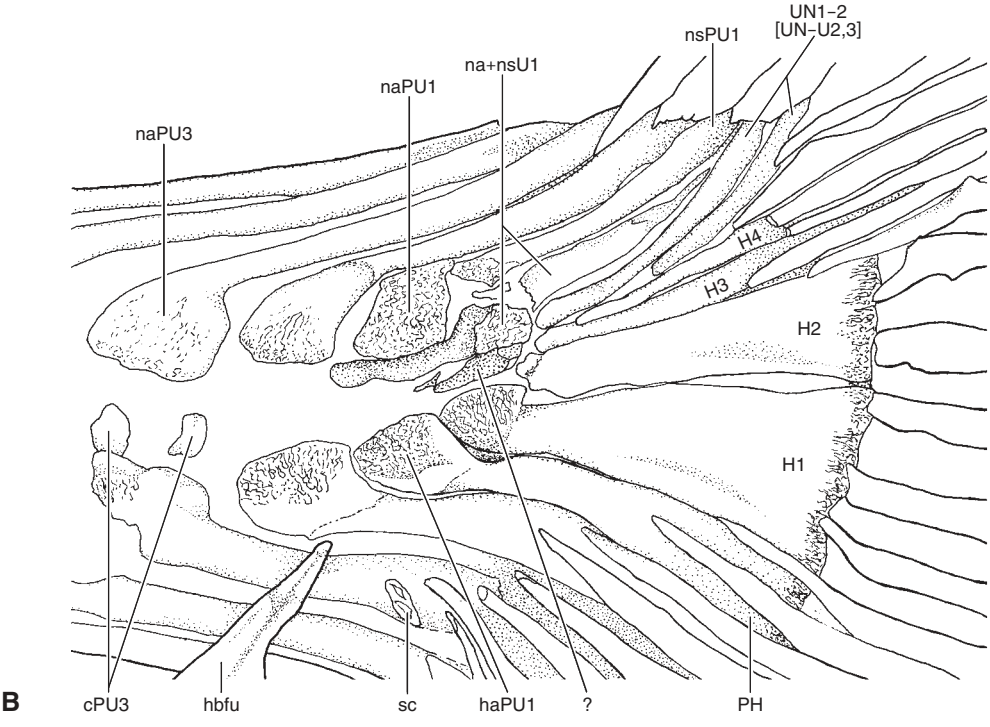


Fig. 11.
Polyural versus diural caudal skeletons. **A, B**, polyural caudal skeleton using *Amia calva* as example. **A,** drawing (modified from SCHULTZE & ARRATIA 1989). **B,** photograph (KUNHM 6883). Scale = 1 mm. **C, D,** diural caudal skeleton using *Hiodon alosoides* as example. **C,** drawing (modified from SCHULTZE & ARRATIA 1989). **D,** photograph (KUNHM 9618; 24.02 mm SL). Scale = 1 mm. **E,** *Hiodon tergisus* (KUNHM 9662; 48.53 mm SL). Scale = 0.5 mm. Abbreviations: **bv**, blood vessels; **cPU2, 1**, ventral preural chordacentra 2 and 1; **cU1–5**, ventral ural chordacentra 1–5^{P}; **E, E2**, epural (position) →[possible epural of ural centrum 2^{P}]; **H1–10**, hypurals 1–10; **naPU1, 2**, neural arch of preural centrum 1 and 2; **naU1–3**, neural arch of ural centra 1–3^{P}; **no**, notochord; **nsU1**, neural spine of ural centrum 1^{P}; **PH**, parhypural; **PU2, 1**, preural centra 2 and 1; **UI, II**, ural centra I^{D}, II^{D} (diural terminology); **[U1+2]**, ural centrum 1+2^{P} (polyural terminology); **[U3+n]**, fused ural centrum 3^{P} with other ural centra^{P} (polyural terminology); **U1–6, 10**, ural centra 1–6^{P} and 10^{P}; **U3+4**, fused ural centrum 3+4^{P}; **UN**, uroneurals.


B
cPU2
cPU1
cU1
cU2
cU4
cU5
no
H5
H4
H3
H2
H1
bv
PH
D
naPU1
naU2
naPU2
naU1
naU3
E2
H5
U3+4
H4
U2
H3
PU2
H2
H1
E
U5
U4
U3
H5
H4
H3
H2


A


UN1–2
[UN–U2,3]
nsPU1
na+nsU1
naPU1
naPU3
H4
H3
H2
H1
B
cPU3
hbfu
sc
haPU1
?
PH

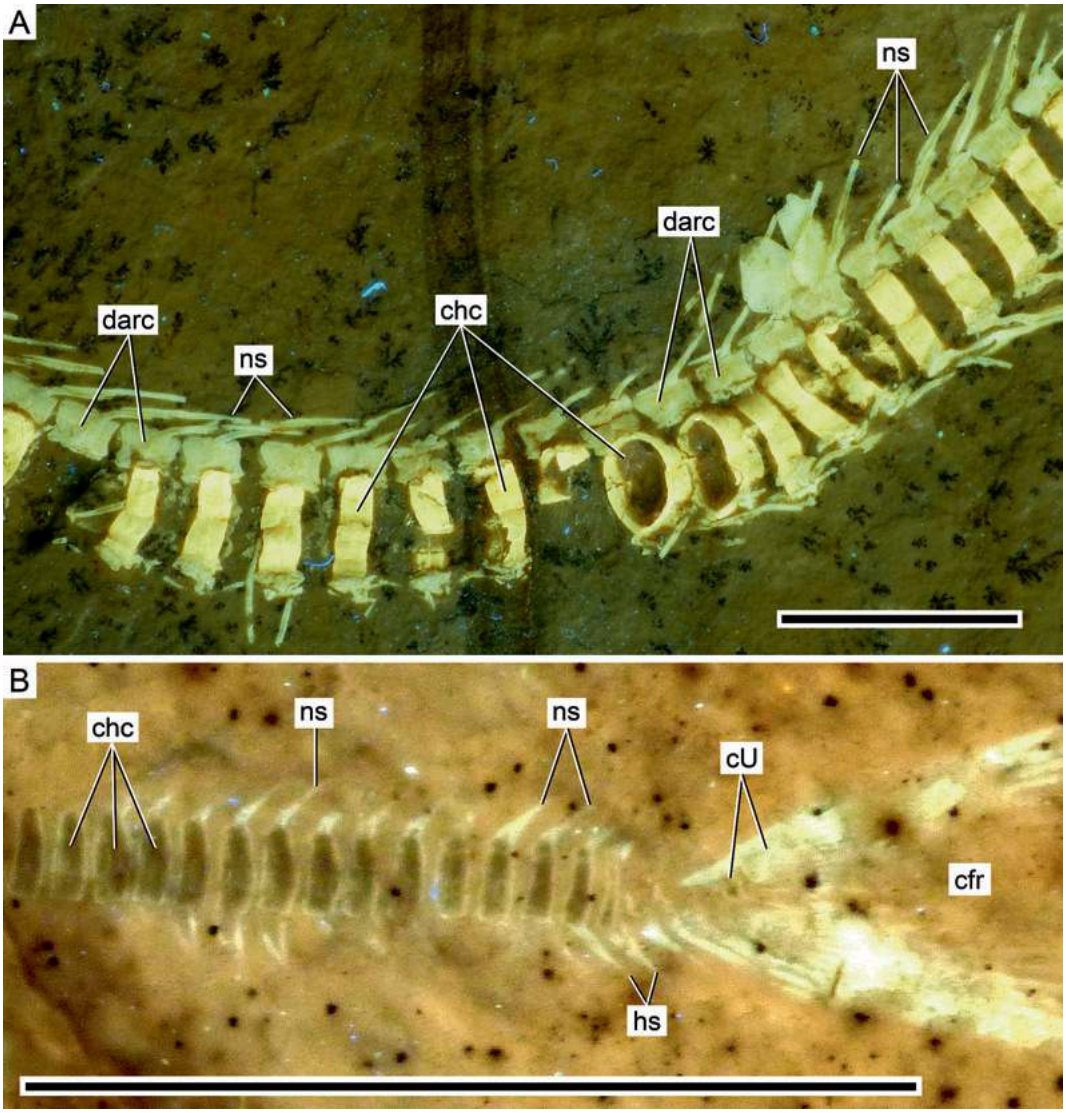


Fig. 13.
Chordacentra and arcocentra forming the caudal region in two fossil actinopterygians. Note the contrast between the aspect of the mineralization of the chordacentra and that of the bone (arcocentra and spines). **A,** aspidorhynchiform †*Belonostomus* sp. (BSPG 1956 I 422; Zandt near Denkendorf, Bavaria; Upper Jurassic, Tithonian). **B,** euteleost †*Orthogonikleithrus hoelli* (JME ETT 365; Ettling, Bavaria; Upper Jurassic). Scales = 5 mm. Abbreviations: **chc**, chordacentra; **cfr**, caudal fin rays; **cU**, ural chordacentra; **darc**, dorsal arcocentra; **hs**, haemal spine; **ns**, neural spine.

◁ **Fig. 12.**
Caudal skeleton of the aspidorhynchiform †*Belonostomus* sp. (BSPG 1956 I 422; Zandt near Denkendorf, Bavaria; Upper Jurassic, Tithonian). **A,** photograph under UV-light (courtesy of H. TISCHLINGER). Scale = 5 mm. **B,** camera lucida drawing. Abbreviations: **cPU3**, ventral chordacentrum of preural centrum 3; **H1–4**, hypurals 1–4; **haPU1**, neural arch of preural centrum 1; **hbfu**, hypaxial basal fulcrum; **naPU3,1**, neural arch of preural centrum 3 and 1; **na+nsU1**, neural arch plus neural spine of ural centrum 1^{P} (broken); **nsPU1**, neural spine of preural centrum 1; **PH**, parhypural or haemal spine of preural centrum 1; **sc**, small ornamented scale; **UN1–2[UN–U2,3]**, uroneurals 1–2^{D} (according to position) → [uroneurals originated as modifications of neural arches of ural centra 2^{P} and 3^{P}].

†*Kuntulunia*, whereas the first ural centrum is formed by fusion of ural centra 1^{P} and 2^{P}, followed by independent ural centra 3^{P}, 4^{P} and 5^{P} in †*Asiatolepis*. Each ural centrum is connected with its hypural.

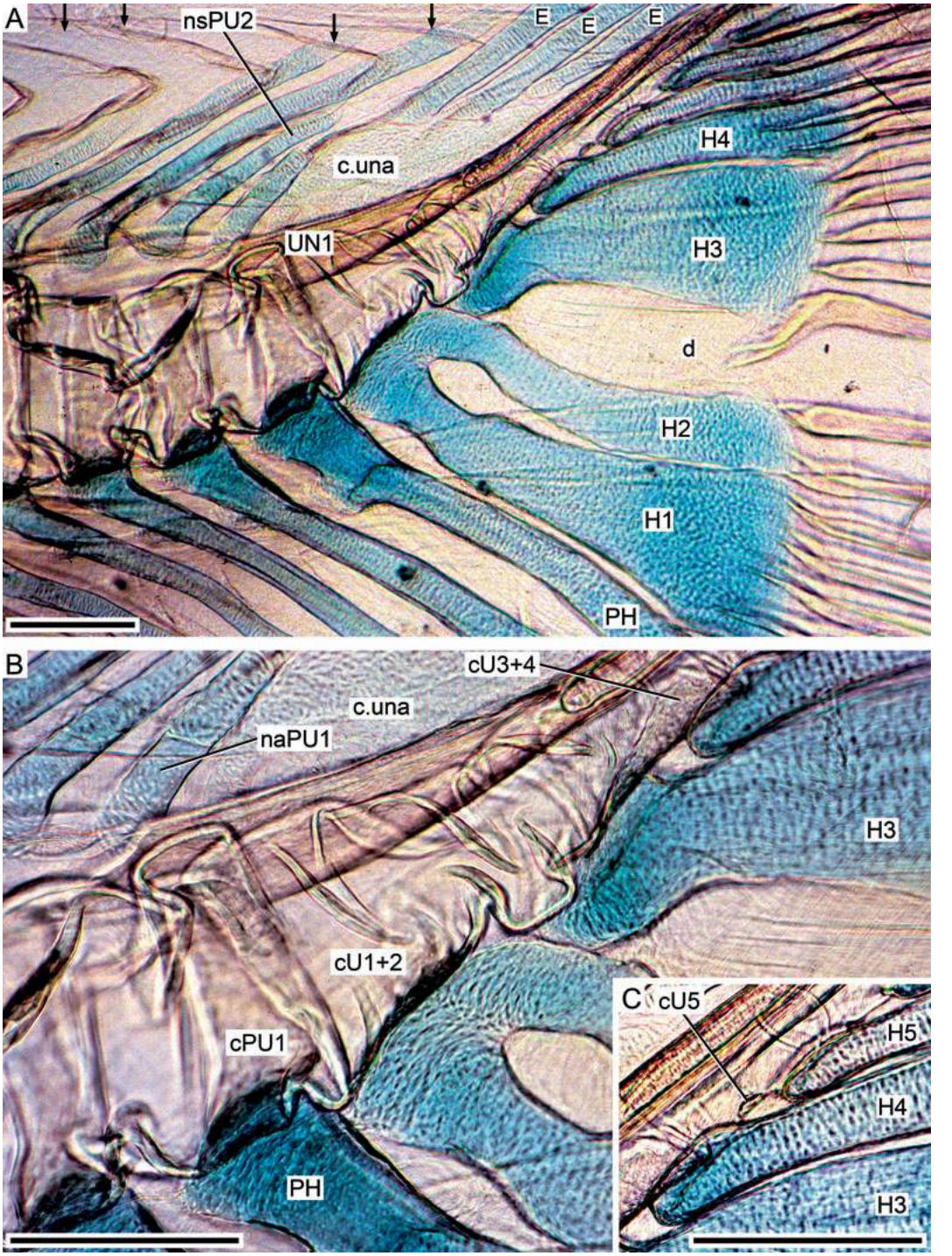
The smallest specimen of *Hiodon alosoides* that we have studied is 22 mm SL (SCHULTZE & ARRATIA 1988: fig. 4; and herein). At this stage of growth the teleost has already formed the second ural chordacentrum^{D} (= ural centrum $3+4+5+6^{P}$) in front of hypurals 3 to 6, and the first ural chordacentrum appears in front of hypural 2. No chordacentrum is observed in front of hypural 1, but a small ventral chordacentrum is beginning to form in front of the haemal arch of preural centrum 1. Only one ural chordacentrum is formed in front of hypurals 4 and 5 in a specimen of 23 mm SL of *Hiodon tergisus* (that seems ontogenetically younger than the 22 mm SL specimen of *H. alosoides* described above) (see also HILTON 2002: fig. 74). No other chordacentrum, not even that for preural centrum 1, is present in this specimen (the ural centrum as well as three ural neural arches present in this specimen were left unlabeled by HILTON & BRITZ 2010: fig. 2A,B). The chordacentrum in front of hypural 2 has grown and is now placed in front of the cartilage joining the bases of hypurals 1 and 2 in specimens of about 27 mm SL of *Hiodon alosoides*. Small ural centra 4^{P} and 5^{P} (Fig. 11E) in front of hypurals 4 and 5 are occasionally present in *Hiodon*. All specimens of *Hiodon* that we have studied, either *Hiodon alosoides* or *H. tergisus*, present two or three ural neural arches, some of them even bearing short neural spines (e. g., Fig. 11C,D; SCHULTZE & ARRATIA 1988: figs. 4, 6A, 7, 11C–D; HILTON 2002: fig. 74; HILTON & BRITZ 2010: fig. 2A,B). For a description of uroneurals and epurals see sections below.

We had given already in 1988 the interpretation of the early developmental situation in *Hiodon*. The so-called first ural centrum (U1^{D}) corresponds to U1+2^{P} or to the growth of ural centrum 2^{P} taking the space of ural centra 1 and 2, a situation also observed in clupeiforms such as *Clupea*, *Engraulis*, *Dorosoma*, and others (see ARRATIA 2010: fig. 13C,D and below). The second ural centrum (UII^{D}) is formed at least by ural centra $3+4^{P}$ or $3+4+5^{P}$ (Table 1).

In the osteoglossid *Arapaima gigas*, the first ural centrum (U1^{D}) supports only hypural 2, and hypural 1 is not associated with any ural centrum (see HILTON & BRITZ 2010: fig. 6B). A similar situation is shown by *Heterotis niloticus*, with hypural 1 not articulating with the first ural centrum^{D} (HILTON & BRITZ 2010: fig. 7A). The authors did not label the centra in their illustrations, but if we re-interpret these ural centra in the polyural fashion, then it is clear that the first ural centrum^{D} corresponds to ural centrum 2^{P} of the polyural terminology in a pattern similar to that shown by many clupeiforms (ARRATIA 2010: fig. 13C,D and see below). Then it is also evident that the so-called first ural centrum^{D} of *Arapaima* is not the same as the first ural centrum of †*Lycoptera* and *Hiodon* (see Table 1). The origin and composition of the first ural centrum in *Heterotis* and *Pantodon* is still unknown (HILTON & BRITZ 2010: figs. 7, 8). In these taxa, one ural centrum lies in front of hypurals 1 and 2; however, we do not know whether the first ural centrum results from the growth of ural centrum 1^{P} or ural centra 1^{P} and 2^{P}.

Two ural centra are present in adult individuals of fossil euteleosts such as the Late Jurassic †*Orthogonikleithrus leichi* and †*O. hoelli* (interpreted as basal 'salmoniforms' by ARRATIA 1997: 60–89, figs. 44, 48, 53, 60, 61; Fig. 17B herein), whereas more than two ural chordacentra have been observed in small specimens of †*O. hoelli* (Fig. 14B; see also KONWERT 2011: pl. 3B). It is interesting that the ural chordacentra and preural chordacentra appear late in this species, when almost all other vertebral centra are formed. ARRATIA & SCHULTZE (1992: fig. 15; Fig. 6B herein) have shown that some 28 mm SL specimens of the extant salmonid *Oncorhynchus mykiss* keep the polyural condition in the caudal skeleton, with four ural centra in front of hypural 1, 2, 3 and 4; i. e., each centrum carries its corresponding hypural. However, most specimens show the presence of two ural centra in the early ontogeny of *Oncorhynchus mykiss* (Table 1), the first one or ural centrum 2^{P} forming in front of hypural 2 and the second one or ural centrum 4^{P} forming in front of hypural 4 (ARRATIA & SCHULTZE 1992: figs. 3, 13) (in a fashion similar to that mentioned above

Fig. 14.
Caudal skeleton of a young specimen of *Elops saurus* (TCWC 05031, 24 mm SL; Recent). **A,** overview of the caudal endoskeleton. Note the muscle segments indicated by a series of small arrows. **B,** enlargement of the chordacentra and proximal regions of parhypural and hypurals. Note that the bases of hypurals 1 and 2 are joined by cartilage. **C,** small chordacentrum beginning to form in front of hypural 5. Scales = 0.25 mm. Abbreviations: **cPU1**, chordacentrum of preural centrum 1; **cU1+2**, **cU3+4**, **cU5**, chordacentra of ural centrum $1+2^{P}$, $3+4^{P}$, and 5^{P}; **c.una**, cartilaginous mass of ural neural arches or elopomorph ural neural arches 1–3; **d**, hypural diastema; **E,** epurals of ural centra 1^{P} to 3^{P}; **H1–5**, hypurals 1–5; **naPU1**, neural arch of preural centrum 1; **nsPU2**, neural spine of preural centrum 2; **PH**, parhypural or haemal spine of preural centrum 1; **UN1**, uroneural 1 (position) → [modified ural neural arch 4^{P}]. ▷


A
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H4
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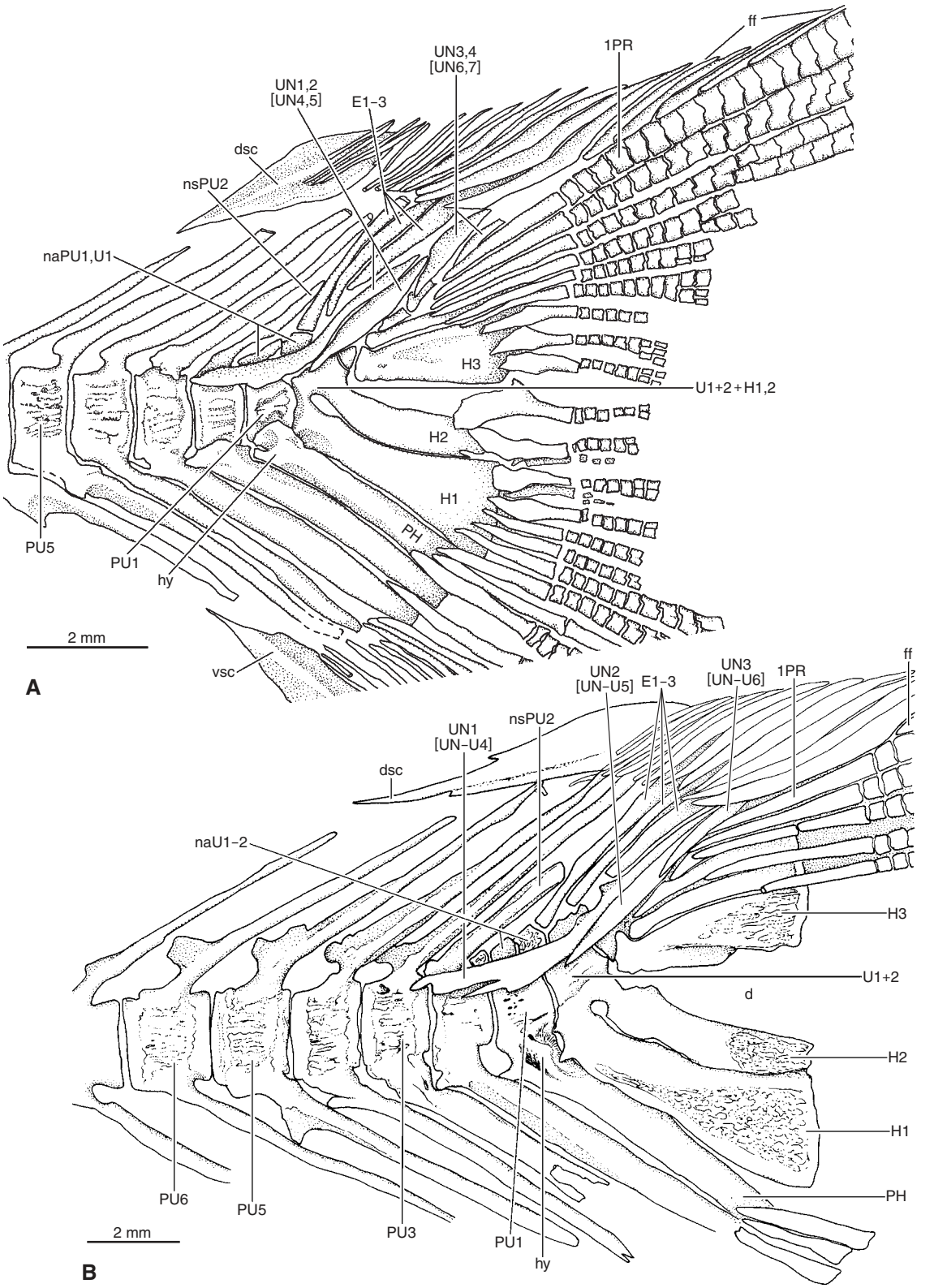
UN1
H3
d
H2
H1
PH
B
cU3+4
c.una
naPU1
H3
cU1+2
cPU1
PH
C
cU5
H5
H4
H3

Table 1.
Preural and ural centra in some fossil and extant holosteans, and some stem- and fossil and extant teleosts illustrating fusions and losses of centra. The information on extant fishes is based on developmental studies. Abbreviations: **U1–n**, ural centra 1^P to n^P; **PU1**, preural centrum 1. Arrows indicate direction of growth of a ural centrum.

Amia / Lepisosteus	PU1	U1	U2	U3	U4	U5	U6	Un
†*Pholidophorus*	PU1	U1	U2	U3	U4	Un		
†*Eurycormus*	PU1	U1	U2	U3	U4	U5	Un	
†*Catervariolus*	PU1	U1	U2	U3	U4			
"True" basal teleosts								
†*Leptolepis*	PU1	U1 + U2	U3 + U4 + U5					
†*Ascalabos*	PU1	U1 + U2	U3 + U4 + U5					
†*Tharsis*	PU1	U1 + U2	U3	U4	U5			
†*Tharsis PU1*	PU1	U1 + U2	U3 + U4 + U5					
Elopiforms								
†*Anaethalion*	PU1	U1 + U2	U3 + U4 + U5					
†*Elopsomolos*	PU1	U1 + U2	U3 + U4 + U5					
Elops	PU1	U1 + U2	U3 + U4 + U5					
Megalops	PU1	U1 + U2	U3 + U4 + U5					
Albula	PU1	←	U2	U3 + U4 + U5				
Osteoglossomorphs								
†*Lycoptera*	PU1	U1	U2	U3 + U4 + U5				
†*Asiatolepis*	PU1	U1	U2	U3	U4	U5		
Hiodon	PU1	U1 + U2	U3 + U4 + U5					
Hiodon	PU1	←	U2	U3 + U4 + U5				
Arapaima	PU1	←	U2	U3 + U4 + U5				
Ostarioclupeomorphs								
Dorosoma	PU1	←	U2	U3 + U4				
Coilia	PU1	+	U2 + U3 + U4					
Engraulis	PU1	+	U2 + U3 + U4					
Chanos	PU1 + Un ?							
Catostomus	PU1 + U1 + U2 + U3							
Danio	←	U1 + U2	U3					
Danio	←	U1 + U2 + U3						
Euteleosts								
†*Orthogonikleithrus*	PU1	U1 + U2	U3 + U4	?				
Oncorhynchus	PU1	U1	U2	U3	U4	U5		
Oncorhynchus	PU1	U1 + U2	←	U4	→			
Oncorhynchus	PU1	←	U2	←	U4	→		
Esox	PU1	U1	→	←	U4 + U5			

for *Arapaima gigas* and some specimens of *Hiodon*). No centrum appears in front of hypurals 1 or 3. Ural centrum 2^P grows anteriad and articulates with hypurals 1 and 2, whereas ural centrum 4^P grows anteriad and posteriad and articulates with hypurals 3, 4 and 5. Occasionally ural centra 1^P and 2^P may appear in front of hypurals 1 and 2 (see Fig. 6B). Consequently, the two centra commonly present in the adult *Oncorhynchus mykiss* represent ural centrum 2^P and 4^P. Additional ural centra may appear in later stages (Fig. 4C; see also ARRATIA & SCHULTZE 1992: fig. 3). This pattern – two ural centra of the caudal skeleton representing ural centra 2^P and 4^P – is not unique to *O. mykiss* because it is observed in other salmonids, e. g., *Thymallus arcticus* and *T. thymallus* (ARRATIA & SCHULTZE 1992: figs. 21, 22), *Salvelinus fontinalis* (ARRATIA & SCHULTZE 1992: fig. 24), and *Prosopium williamsoni* (ARRATIA & SCHULTZE 1992: fig. 25). The centra labeled as "U1" and "U2" in figures 66–71 of Salmonidae in FUJITA (1990) have the same position as ural 2^P and 4^P in front of hypurals 2 and 4 in our figures illustrating salmonids (ARRATIA & SCHULTZE 1992). Therefore, the diural skeleton of adult salmonids is formed by two ural centra, but these two ural centra (= 2^P and 4^P of

Fig. 15.
Caudal skeletons of fossil elopiforms. ▷ **A,** †*Anaethalion knorri* (JME SOS 2282; Upper Jurassic), figure reversed to the left. **B,** †*Elopsomolos* sp. (NHM 37048; Upper Jurassic). Scales = 2 mm. Abbreviations: **d**, hypural diastema; **dsc**, dorsal scute; **E1–3**, epurals of ural centra 1^P, 2^P and 3^P; **ff**, fringing fulcra; **H1–3**, hypurals 1–3; **hy**, hypuraphophysis; **naPU1**, **U1**, neural arches of preural 1 and ural 1^P; **naU1–2**, neural arch of ural centrum $1+2^P$; **nsPU2**, neural spine of preural centrum 2; **PH**, parhypural or haemal spine of preural centrum 1; **1PR**, first principal ray; **PU6–1**, preural centra 6–1; **U1+2**, ural centrum $1+2^P$; **U1+2+H1**, **2**, ural centrum 1^P+2^P+hypurals 1 and 2; **UN1–4 [UN4–7]**, uroneurals 1–4 (position) →[modified neural arches of ural centra 4 to 7^P]; **vscu**, ventral caudal scute.


ff
1PR
UN3,4
[UN6,7]
UN1,2
[UN4,5]
E1–3
dsc
nsPU2
naPU1,U1
H3
U1+2+H1,2
H2
H1
PH
PU5
PU1
hy
2 mm
vsc
A
ff
UN2
[UN–U5]
E1–3
UN3
[UN–U6]
1PR
UN1
[UN–U4]
nsPU2
dsc
naU1–2
H3
U1+2
d
H2
H1
PH
PU6
PU5
PU3
PU1
hy
2 mm
B

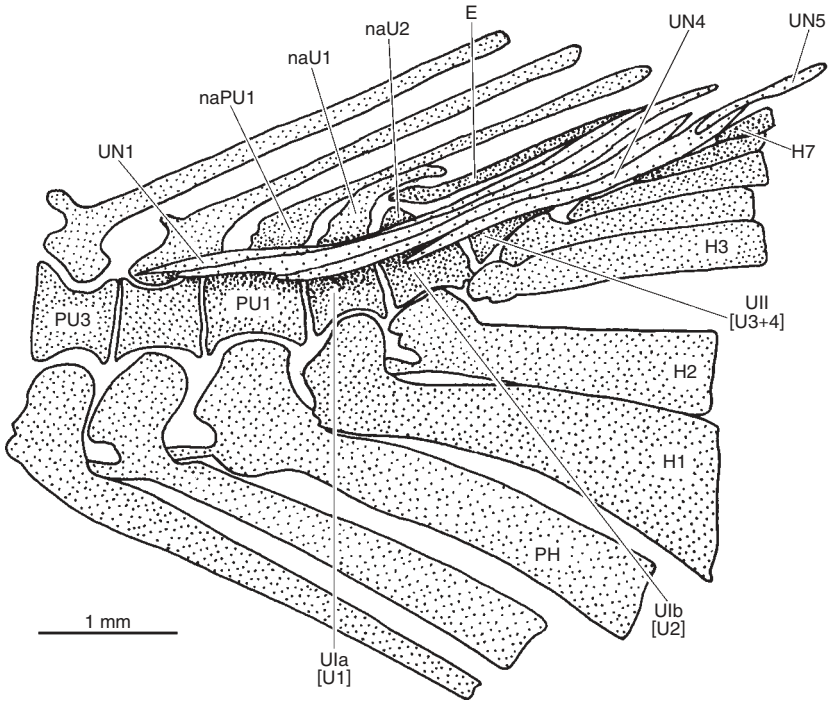
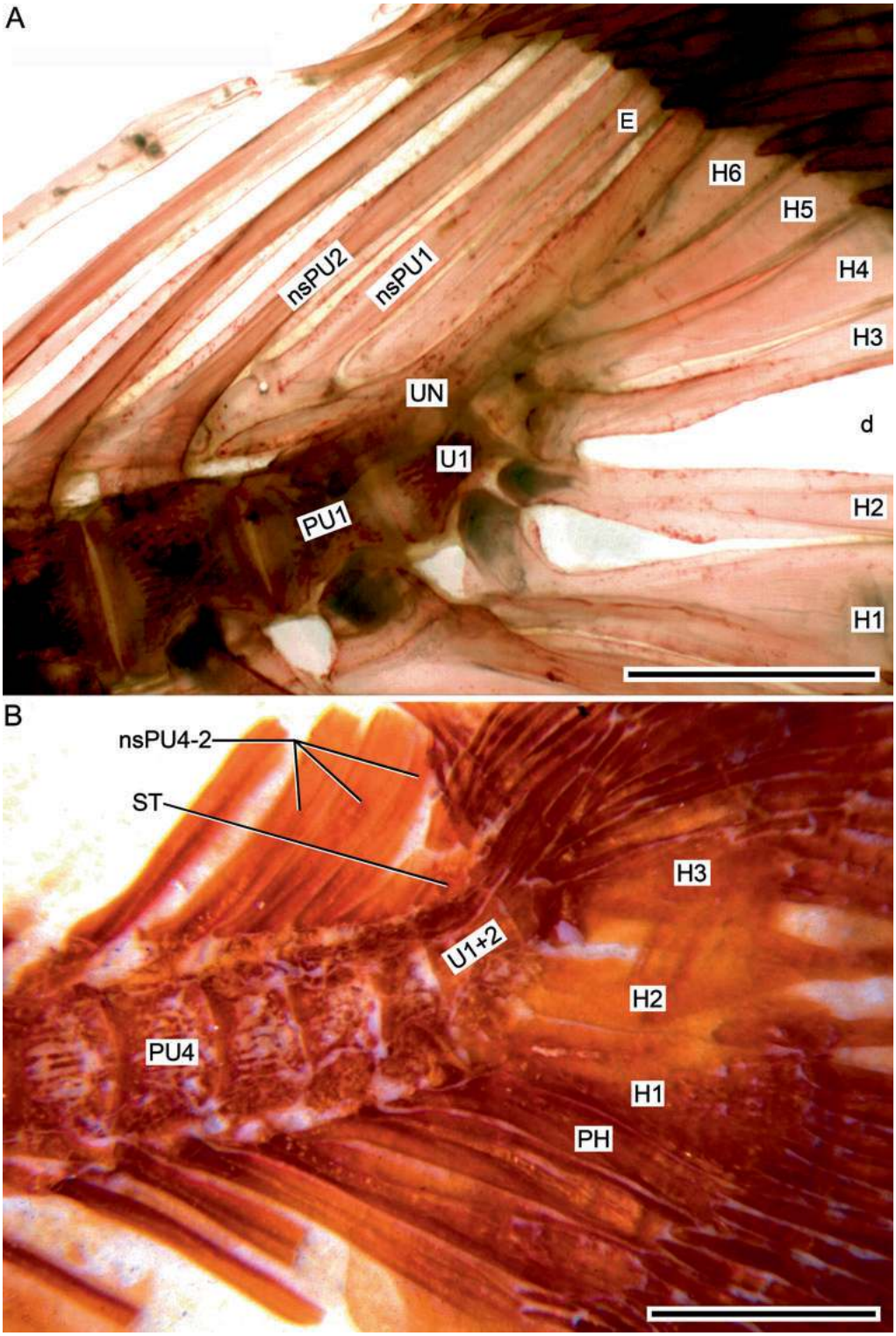


Fig. 16.
Caudal skeleton of the osteoglossomorph †*Lycoptera middendorfii* illustrating the polyural condition (slightly modified from PATTERSON & ROSEN 1977: fig. 24). Abbreviations: **E**, epural →[possible epural of ural centrum 2^{P}]; **H1–7**, hypurals 1–7; **naPU1**, neural arch of preural centrum 1; **naU1**,**2**, neural arch of ural centra 1^{P} and 2^{P}; **PH**, parhypural or haemal spine of preural centrum 1; **PU1**,**3**, preural centrum 1, 3; **UIa**,**Ib**, first ural centrum^{D} of the diural terminology; **UII**, second ural centrum^{D} of diural terminology; **[U1–2]**, ural centrum 1+2^{P}; **[U3+4]**, ural centrum 3+4^{P}; **UN1–5**, uroneurals 1–5 (position) →[modified neural arches of ural centra 3–7^{P}].

the polyural terminology) are not the same ural centra as found in elopiforms (U1+2^{P} or only U2^{P} and U3+4+5^{P}), osteoglossomorphs (U1^{P}, U2^{P} or U1+2^{P} or only U2^{P} and U3+4+5^{P}), clupeomorphs (U2^{P} and U3+4^{P} or U2+3+4^{P}), and others (Table 1 and below).

In esociforms the situation seems to be different. The first and second ural centrum (U1^{D} and U2^{D}) are reported to appear simultaneously at about 32 mm SL and 35 mm SL in *Esox lucius* and *E. masquinongy*, respectively (BURDI & GRANDE 2010: fig. 1C,D). Although figures 3E and 3F of *E. masquinongy* in BURDI & GRANDE (2010) are not labeled, they show a pattern of ural centra that differs from the patterns described here for other teleostean groups. The so-called first ural centrum^{D} forms in front of hypural 1 in specimens of *E. masquinongy* of 40.0 and 41.1 mm SL. No centrum is formed in front of hypural 2. We interpret therefore the first ural centrum^{D} as representing only ural centrum 1^{P} of the polyural terminology (Table 1). The so-called second ural centrum^{D} articulates with hypurals 4 and 5, and we interpret this centrum as formed by ural centra 4^{P} and 5^{P}. In a young specimen of *Esox americanus* (FUJITA 1990: fig. 54), hypurals 1 and 2 are united at their bases by cartilage and articulate with one centrum, appar-

Fig. 17.
Caudal endoskeleton of two basal euteleosts in lateral view. **A,** esociform *Esox americanus* (KUNHM 5227; Recent). Scale = 5 mm. **B,** euteleost †*Orthogonikleithrus leichi* (JME 2632; Zandt, Germany; Upper Jurassic, Tithonian). Scale = 3 mm. Abbreviations: **d**, hypural diastema; **E,** epural of unknown homology; **H1–6**, hypurals 1–6; **nsPU4–2**, neural spines of preural centra 4–2; **PH**, parhypural or haemal spine of preural centrum 1; **PU4**,**1**, preural centra 4, 1; **ST**, stegural →[modified neural arch of ural centrum 4^{P}]; **U1**, ural centrum 1^{P}; **U1+2**, fused ural centra 1+2^{P}; **UN**, uroneural of unknown homology. ▷


A
E
H6
H5
H4
H3
nsPU2
nsPU1
UN
d
U1
H2
PU1
H1
B
nsPU4-2
ST
H3
U1+2
H2
PU4
H1
PH

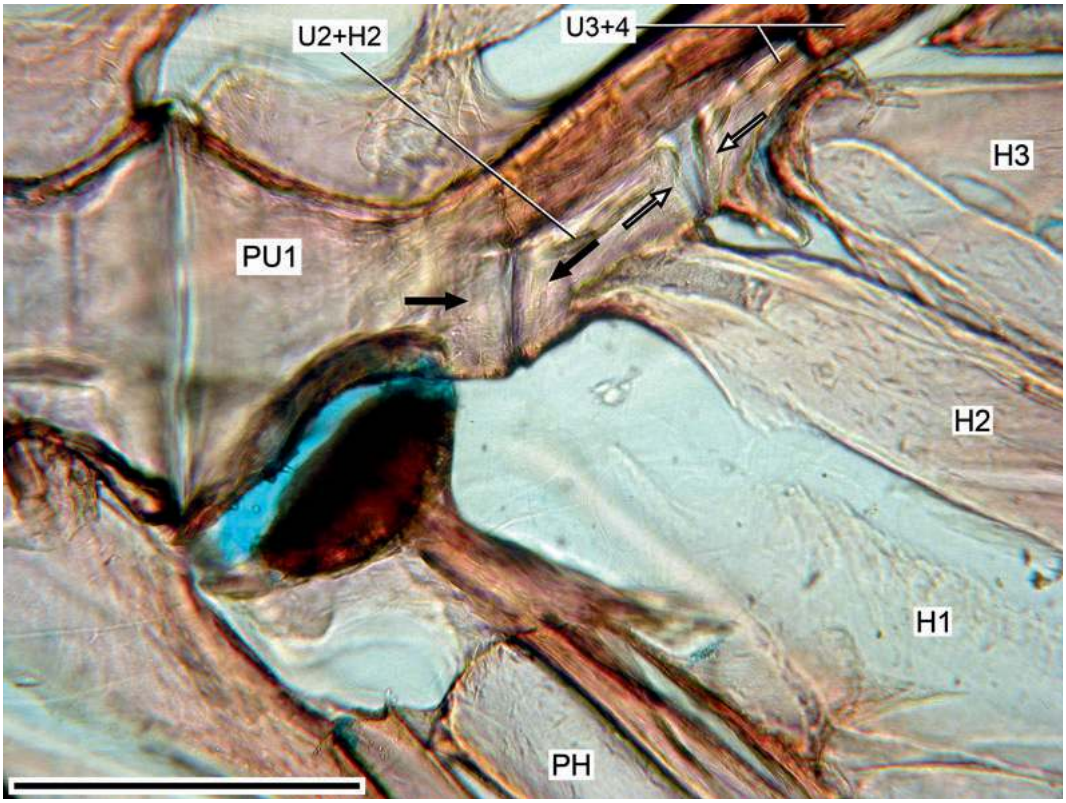


Fig. 18.
Enlargement of the compound terminal centrum of *Engraulis encrasicolus* (KUNHM 19941, 27.2 mm SL; Recent) illustrating the fusion of centra: preural centrum 1 with ural centrum 2^{P} and ural centrum $3+4^{P}$. Note that ural centrum 2^{P} is completely fused already with the base of hypural 2. Scale = 1 mm. Abbreviations: **H1–3**, hypurals 1–3; **PH**, parhypural or haemal spine of preural centrum 1; **PU1**, preural centrum 1; **U2+H2**, ural centrum 2^{P} + hypural 2; **U3+4**, ural centrum $3+4^{P}$.

ently, the enlarged ural centrum 1^{P} of the polyural terminology. In contrast, in a medium sized specimen of *E. americanus* (Fig. 17A), the proximal tip of hypural 2 articulates weakly at the postero-ventral region of the first ural centrum, whereas hypural 1 is the main element articulating with the first ural centrum. This observation supports the hypothesis that the first ural centrum^{D} corresponds to ural centrum 1^{P} of the polyural terminology. In large individuals of *Esox lucius*, hypural 1 articulates with ural centrum 1^{P}, whereas hypural 2 and hypural 3 do not articulate with any ural centrum, whereas hypurals 4, 5 and possibly 6 articulate with the ural centrum $4–5^{P}$ (see MONOD 1968: fig. 443). It would be desirable to re-visit the early development of different species of *Esox* and also large individuals to understand the variation observed.

The so-called compound terminal centrum or urostyle

The elements that we are able to identify as independent structures that articulate with other elements in the caudal skeleton of the most basal teleosts are reduced to fewer elements in more advanced teleosts. In most cases, the reduction is assumed to be the result of fusions. Reduction may involve losses as well as fusions. However, to understand whether loss, fusion, or both are involved requires study of the development of the actinopterygians from early ontogenetic stages.

A single terminal centrum supporting the haemal arch of the parhypural and hypurals 1 and 2, 1 to 3,

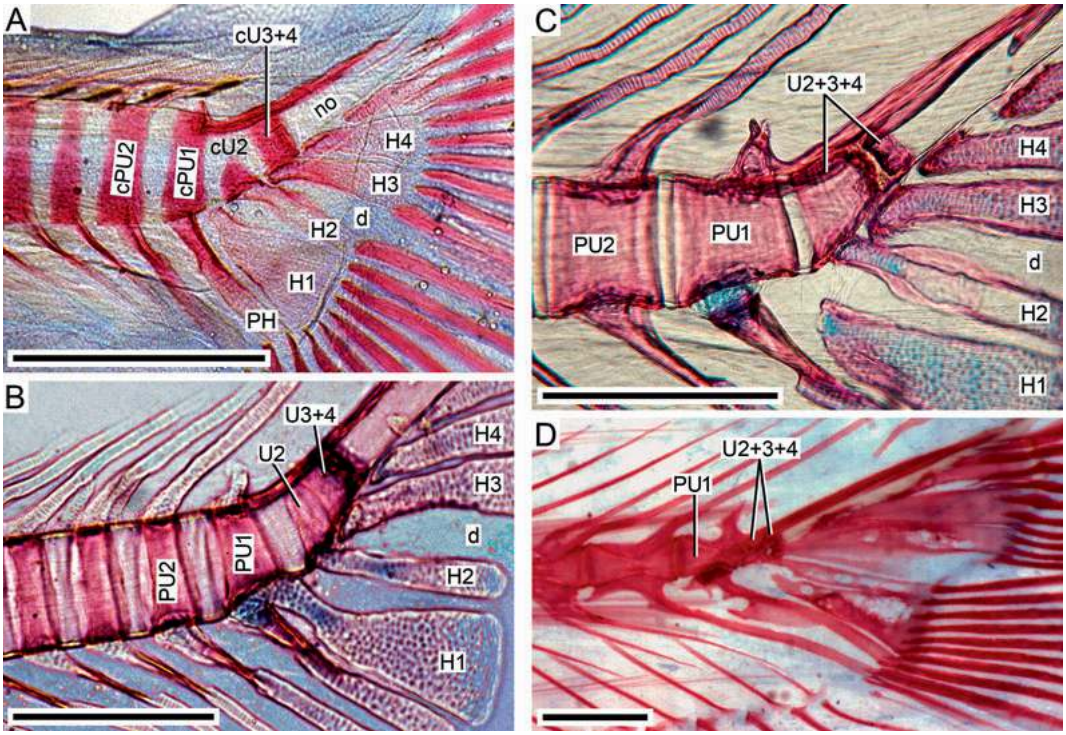


Fig. 19.
Caudal skeleton of the clupeomorph *Coilia nasus* illustrating changes of the preural region and the formation of the compound terminal centrum. **A,** specimen of 18 mm SL (KUNHM 40245; Recent). Scale = 1 mm. **B,** specimen of 19 mm SL (KUNHM 40245; Recent). **C,** specimen of 19.5 mm SL (KUNHM 40245; Recent). Scale of B, C = 0.25 mm. **D,** specimen of 80 mm SL (KUNHM 29144; Recent). Scales of A, D = 1 mm. Abbreviations: **cU2**, chordacentrum of ural 2^P; **cU3+4**, chordacentrum of ural $3+4^P$; **d**, hypural diastema; **H1–4**, hypurals 1–4; **no**, notochord; **PH**, parhypural or haemal spine of preural centrum 1; **PU2**, **1**, preural centra 2, 1; **U2**, ural centrum 2^P; **U3+4**, ural centrum $3+4^P$; **U2+3+4**, ural centrum formed by the fusion of ural centra 2^P, 3^P and 4^P.

or 1 to 4 is observed in adult ostariophysans and also in some clupeiforms such as engraulids (Figs. 7C, 18) as well as many euteleosts (e. g., lampriforms, paracanthopterygians, stomiiforms, cyprinodontiforms). This structure has been traditionally interpreted as a fusion comprising preural centrum 1 and the first ural centrum^D or preural centrum 1 and the first and second ural centra^D (see for instance GOSLINE 1961; PATTERSON 1968a, 1970; ROSEN 1973; FINK & FINK 1981; GRANDE 1985; FUJITA 1990; GRANDE et al. this volume). However, MONOD (1968: figs. 2, 3, 113–116, 118, 140, 141, 224, 247, 258, 259, and many others) interpreted this structure as formed by one centrum that he labeled CP1 (his "centrum pré-ural 1"). The same label (CP1) was used for preural centrum 1 of elopids, albulids, osteoglossomorphs (MONOD 1968: figs. 20–24, 94, 96–101, 108) (see also CHAPLEAU 1994: fig. 6A who labeled the terminal centrum as preural centrum 1 in pleuronectiforms). A distinction between terminal centra was made by FUJITA (1990). He labeled "PU1+U1" the terminal centrum present in most ostariophysans (e. g., his figures 32–46, 49), but "US" the terminal centrum present in the gonorynchiforms *Chanos* and *Gonorynchus*, a few other ostariophysans (his figures 31, 47, 48, 52), and many euteleosts (e. g., his figures 60, 78–83, 156–169, and many others). Thus, FUJITA (1990) visualized that there was a difference among some of these terminal centra, and he represented his interpretation using two different names. However, he was not able to solve the problem of homologization involved because he did not include early ontogenetic stages in his work. In addition, he also did not include large adults (as revealed by the scale bars accompanying his illustrations). His main goal was to show caudal skeleton diversity, not to address the problem of homologies involved. FINK & FINK (1981) suggested that the terminal caudal centrum in some adult catfishes seem

to be formed by a half centrum. Other authors, being aware that a problem of homologization is involved, avoided labeling the terminal centrum in gonorynchiforms (e.g., GRANDE & GRANDE 2008, GRANDE & ARRATIA 2010); others have used the names compound terminal centrum or compound centrum (e.g., in catfishes: FINK & FINK 1981, 1996; ARRATIA 2003) or urostyle (= terminal vertebra plus the first uroneural: GOSLINE 1961; e.g., cypriniforms: BRITZ & CONWAY 2009) or terminal centrum (e.g., stomiiforms: WEITZMAN 1967).

The single terminal centrum found in adults belonging to certain teleostean groups may involve fusions of epaxial and hypaxial elements, as for instance a pleurostyle (currently interpreted as a modification of a uroneural), hypural 2 (e.g., clupeiforms), hypurals 2 and 3 (some cyprinids), parhypural and hypurals 1 and 2, parhypural and hypurals 1-to-n in different ostariophysans and different euteleosts. We will analyze a couple of these caudal skeletons to illustrate the different patterns hidden behind those assumed fusions.

In extant clupeiforms of the families Clupeidae and Engraulidae, the first ural centrum^{D} corresponds to ural centrum 2^{P}, which grows anteriad in front of the base of hypural 1, which is partially resorbed during the growth process (ARRATIA 2010: fig. 13C,D; Table 1), whereas the second ural centrum^{D} develops in front of hypurals 3 and 4 and is interpreted here as ural centrum 3+4^{P} because it is formed by two distinct parts in early development. The first ural centrum to appear is ural centrum 3+4^{P}, whereas ural centrum 2^{P} appears later. Although ural centrum 1^{P} is not formed, a neural arch is placed above the empty space belonging to ural centrum 1. Ural centrum 2^{P} grows anteriad and articulates with the posterior region of preural centrum 1 in large specimens of clupeiforms such as *Dorosoma* and *Sardinops*. In contrast, in engraulids, ural centrum 2^{P} grows posteriad and fuses with ural centrum 3+4^{P} (Figs. 18, 19A,B). Ural centrum 2+3+4^{P} moves anteriad and fuses with preural centrum 1 during the growth. Consequently, the compound centrum includes preural centrum 1, ural centrum 2^{P}, and ural centrum 3+4^{P} (see Figs. 18, 19A–D; Table 1). In clupeids and engraulids, ural centrum 2^{P} fuses to the base of hypural 2 early in ontogeny. (A detailed description of the caudal skeleton of ostarioclupeomorphs will be published elsewhere).

The formation of the caudal skeleton in the gonorynchiform *Chanos chanos* is unclear, because we have not been able to observe the formation of chordacentra in front of any hypural; there is only a change in the density of the notochord in front of the arch of the parhypural and hypurals 1 to 4. The change of density of the notochord is followed by the rapid appearance of an autocentral ossification surrounding the notochord and forming a compound element that extends from the haemal arch of the parhypural to the base of hypural 4 and involves also the early fusion of the so-called first uroneural or pleurostyle to the terminal centrum (ARRATIA 2010: fig. 13A,B). Two or three cartilaginous neural arches are associated with this elongate autocentral element in early ontogeny (see below section on Epurals). The origin and formation of the caudal endoskeleton of *Chanos chanos* will be described in detail elsewhere.

Another example of the confusing use of the diural terminology is found in studies of the model teleost zebrafish *(Danio rerio)* where preural centrum 1 was interpreted as formed by two preural centra 1, and the second ural centrum was interpreted as being formed by two ural centra 2 (see BENSIMON-BRITO 2012: figs. 1, 3). Furthermore, there was a confusion of centra. Preural centrum 1 became preural centrum 2 and was included in the terminal centrum (their fig. 3G), a condition that we have not observed in any of our ontogenetic series of *Danio rerio* (Fig. 20). In contrast, a preural centrum 1 is missing in *Danio rerio* according to BIRD & MABEE (2003). According to our evidence, the terminal centrum of *Danio rerio* involves the early appearance of ural centrum 2^{P} in front of hypural 2, then another centrum (ural centrum 1^{P}) develops in front of the haemal arch of hypural 1 and grows anteriorly occupying the position of preural centrum 1 plus ural centrum 1^{P}. Ural centrum 1^{P} then fuses to ural centrum 2^{P} and the two centra fuse into a single elongate chordacentrum at about 6 mm standard length (Fig. 20). In some specimens ural centrum 2^{P} remains separate from ural centrum 1 (Fig. 20A). The parhypural and hypural 1 are joined at their bases by cartilage from early ontogeny on, whereas the base of hypural 2 fuses to ural centrum 2^{P}. The chordacentrum of ural centrum 3^{P} forms in front of hypural 3 and both may become fused early in ontogeny or stay separated. During early development ural centrum 3 + hypural 3 move anteriad, and the centrum abuts the compound centrum but it does not fuse to it. Thus, according to our material, the compound terminal centrum of *Danio rerio* includes two caudal centra (U1^{P}+U2^{P}; Table 3), and occasionally ural centrum 3^{P} is included in the fusion.

In summary, the composition of the single terminal centrum is unknown for most teleosts bearing a compound terminal centrum or urostyle due to the absence of developmental data.

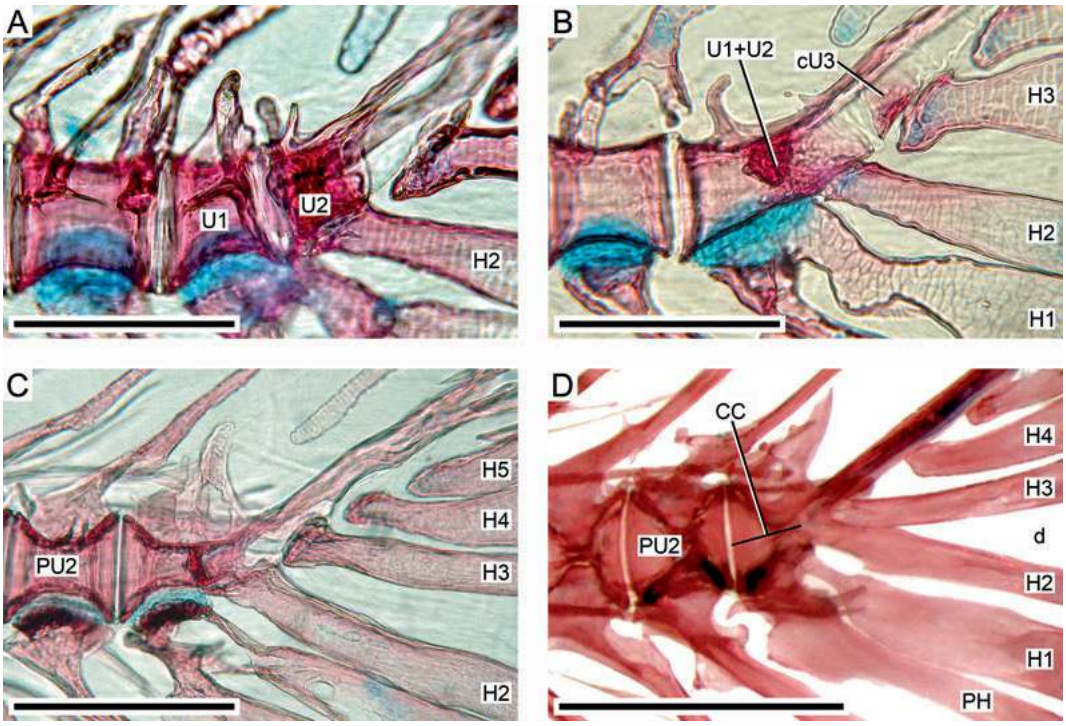


Fig. 20.
Caudal skeleton of the cypriniform *Danio rario* illustrating changes in the preural region and the formation of the compound terminal centrum. **A,** specimen of 7.2 mm SL (KUNHM 40245; Recent). **B,** specimen of 8.2 mm SL (KUNHM 40245; Recent). **C,** specimen of 10 mm SL (KUNHM 40245; Recent). Scales in A–C = 0.25 mm. **D,** specimen of 31.8 mm SL (KUNHM 29144; Recent). Scale = 1 mm. Abbreviations: **CC**, compound terminal centrum formed by the fusion of ural centra 1^{P} and $2^{P;}$ **cU3**, chordacentrum of ural 3^{P}; **PU2**, preural centrum 2; **U1**,**2**, ural centra 1^{P} and 2^{P}; **U1+U2**, fusion of ural centra $1+2^{P}$; **H1–5**, hypurals 1–5; **PH**, parhypural or haemal spine of preural centrum 1; note that the haemal arch of the parhypural and the base of hypural 1 are fused to each other; **U1+2**, ural centrum $1+2^{P}$.

Ural centra – Interpreting homologies

The ontogenetic development of different taxa reveals that the presence and composition of the ural centra differs in teleostean groups (see Table 1). In other words, the so-called diural caudal skeleton in basal extant teleosts is not always formed by the same elements.

The above examples demonstrate that there is no clear-cut difference between the polyural caudal skeleton in non-teleosts and the diural caudal skeleton in teleosts. According to the available information, the diural caudal endoskeleton of teleosts develops via a variety of developmental pathways from a polyural basis (Table 1). Day-to-day series including many specimens of most advanced teleosts have not been studied yet to understand the formation of the so-called compound terminal centrum or urostyle that is present. It has been a convention to identify them as preural centrum 1 plus first and second ural centra (= $PU1+U1^{D}$ or $PU1+U1^{D}+U2^{D}$), but it has never been proven that these specific three centra of the diural terminology are included in the single terminal centrum. Exceptions are the recent publications by HILTON & JOHNSON (2007) on carangids and KONSTANTINIDIS & JOHNSON (2010) on tetraodontiforms. Using the diural terminology, all taxa shown in Table 3 would be interpreted as possessing first and second ural centra. However, ontogenetic studies of these actinopterygians give a completely different scenario regarding the formation and composition of the ural centra and also of the compound terminal centra of some ostarioclupeomorphs (see Table 1). Naming the centra of the caudal skeleton of teleosts in the diural fashion – the common usage – and without studying its developmental origin in different

taxa belonging to different evolutionary levels can imply that all of them share the same two centra. This has further consequences for coding of characters in phylogenetic analysis and homology interpretations. The evidence documented here as well as the evidence offered in our previous publications on the caudal skeleton of basal teleosts do not support such an assumption. Such an assumption is not also supported by the results shown in ontogenetic studies done by others (e.g., BURDI & GRANDE 2010, HILTON & BRITZ 2010, GRÜNBAUM & CLOUTIER 2010, BENSIMON-BRITO et al. 2012).

As is shown here, the composition of the so-called compound terminal centrum or urostyle or preural centrum 1 + ural centra is different among various taxa bearing such elements. Consequently, we predict that the compound terminal centrum is also not formed in the same way in advanced euteleosts, e.g., paracanthopterygians, scorpaeniforms, cyprinodontiforms, and many others. As SCHULTZE & ARRATIA (1989) argued, we will not be able to understand the homologies involved without developmental studies.

Hypurals

The hypurals are modified haemal spines of ural centra that may retain part of their cartilaginous (Figs. 6B, 7B,C) or ossified arcocentra (Figs. 4C,D, 8A,B, 12A,B) at their bases; their distal part supports only principal rays (ARRATIA & SCHULTZE 1992: 244). For a review of other hypotheses concerning the origin of the hypurals see ARRATIA & SCHULTZE (1992: 244–245).

The hypurals differ in number, shape, and alignment among †'pholidophoriforms' and "true" teleosts. To determine the total count of the hypurals may be problematic in fossils when the dorsal-most principal rays are in situ and obscure the presence of the last and smallest hypurals. In some †'pholidophoriforms' such as †*Pholidophorus bechei* and †*Eurycormus speciosus*, 13 to 11 hypurals are present (see ARRATIA 1991: tb. 2, fig. 15A; Fig. 8B and Table 2 herein). A high number (11 or 10) is also found in †*Ascalabos voithii* among "true" teleosts (ARRATIA 1991: fig. 9, 1997: fig. 20), and †*Leptolepis coryphaenoides* (Fig. 9B). Nine or eight hypurals (ARRATIA 1991: table 2; Table 2) have been reported from †*Tharsis dubius*, but the number could be higher considering that the reported specimens have the hypural series partially hidden by the principal rays (for other counts in fossils teleosts see ARRATIA 1991: table 2). The number of independent hypurals decreases in extant teleosts (Table 2). For instance, seven hypurals have been reported in elopiforms and six in albulids (e.g., SCHULTZE & ARRATIA 1988); seven or eight in hiodontiforms (e.g., TAVERNE 1977; SCHULTZE & ARRATIA 1988; HILTON 2002, 2003); occasionally seven in some specimens of *Arapaima* (HILTON & BRITZ 2010); six or five have been reported for ostarioclupeomorphs (e.g., MONOD 1968, LUNDBERG & BASKIN 1969, GRANDE 1985, FUJITA 1900, GRANDE & ARRATIA 2010); six hypurals have been reported in salmonids (e.g., ARRATIA & SCHULTZE 1992), but a seventh cartilaginous hypural was described for *Salvelinus alpinus* (GRÜNBAUM & CLOUTIER 2010); and five hypurals are figured for the perciform families Carangidae (HILTON & JOHNSON 2007, HILTON et al. 2010) and Moronidae and for the tetraodontiform family Triacanthodidae (KONSTANTINIDIS & JOHNSTON 2012). Percomorphs have five or fewer hypurals; with a few exceptions non-percomorph eurypterygians have six (JOHNSON & PATTERSON 1993: 613). In conclusion, the number of hypurals decreases from a high number (13 to 10) of independent hypurals in fossil forms such as some †'pholidophoriforms' and basal "true" teleosts to a reduced number (8 to 5) of independent hypurals in extant teleosts (Table 2). The reduction in number of hypurals in "true" teleosts is considered to be the result of the loss of the most postero-dorsal elements of the series. This is supported by using the landmark of the hypural diastema between hypurals 2 and 3 and the trajectory of blood vessels (as documented by recent forms).

In †pachycormiforms and †aspidorhynchiforms, the number and pattern of hypurals are different (Table 2). Four hypurals are present in †aspidorhynchiforms (e.g., MAISEY 1991; BRITO 1997, 1999; ARRATIA 1999, 2008; see Fig. 6A,B), whereas most hypurals are included into a hypural plate in †pachycormiforms (PATTERSON 1973, ARRATIA & LAMBERS 1996, see ARRATIA & SCHULTZE this volume: figs. 9, 17).

Fossil and extant teleosts (e.g., †*Leptolepis coryphaenoides*, †*Tharsis dubius*, †*Ascalabos voithii*, various species of †*Anaethalion* and †*Elopsomolos*, various species of *Elops* and *Megalops*) may have hypurals 1 and 2 fused at their bases (Figs. 4D, 9B, 15A,B, Table 1); others may have some or all upper hypurals fused (e.g., some trichomycterid catfishes; ARRATIA 1993); and others may have all hypurals fused (e.g., Gasterosteiformes, Syngnathiformes: FUJITA 1990: figs. 194–202, and many other advanced euteleosts, BRITZ & JOHNSON 2002: figs. 14A,B, pl. 3E–H, named the single hypural plate in the gasterosteiform *Indostomus paradoxus* as a hypural). Some of these assumed fusions may not represent fusion at all, but instead the

losses of elements. Thus, from a set of independent hypurals, the evolutionary trend seems to be fusion of hypurals along their lengths, e.g., of hypurals 1 and 2, and a further fusion of dorsal hypurals, followed by a further fusion into two hypural plates or into a single hypural plate involving all hypurals.

Recent studies on the development of a few advanced teleosts (e.g., Carangidae, Balistidae, Tetraodontidae) illustrate a different scenario in the early development of the hypurals. Young specimens show three hypural plates that represent direct ossifications of three cartilaginous plates (KONSTANTINIDIS & JOHNSON 2012: Balistidae, Monacanthidae, Tetraodontidae) that were identified as hypural 1, hypural 2 and hyural 3 according to their positions. Hypurals 1 and 2 are separated by the hypural diastema, which is positioned between hypurals 2 and 3 in all basal teleosts**.** Using the diastema as a landmark, we interpret the three plates to be homologous to hypurals 1+2 (ventral plate, i.e., their hypural 1) and hypurals 3+4 and 5 (dorsal plate, i.e., their hypural 2 and their hypural 3). KONSTANTINIDIS & JOHNSON (2012) mentioned that MATSUURA & KATSURAGAWA (1985) observed four hypural anlagen, which form the two (ventral and dorsal) plates. Thus the hypurals 1+2 of Moronidae (KONSTANTINIDIS & JOHNSON 2012: fig. 2) and Triacanthodidae (ibidem: fig. 3) correspond to "hypural 1" (= ventral plate) of Balistidae and Monacanthidae (ibidem: fig. 5) and Tetraodontidae (ibidem: fig. 7). Hypurals 3–5 of Moronidae (ibidem: fig. 2) and Triacanthodidae (ibidem: fig. 3) correspond to hypurals dorsal to the hypural diastema, i.e., "hypural 2" (= dorsal plate) of Balistidae and Monacanthidae (ibidem: fig. 5) and Tetraodontidae (ibidem: fig. 7). We doubt that the use of the same name for different structures is the best approach. For example, ROSEN (1973) expressed the homologies of the two hypural plates in *Gigantura vorax* by labeling them as 'PHYP+HYP1+2' (homology with or fusion of parhypural + hypural 1+2) and 'HYP3-x' (homology with or fusion of hypural 3 with an unknown number of hypurals). We suggest the use of different names when developmental patterns seem to be different from those of basal teleosts.

Uroneurals

NYBELIN (1963) devoted about 26 of his 30-page paper to a discussion of the "Uroneuralia" without realizing that they are restricted in a true sense to teleosts. That was LUND's (1967) contribution to the understanding of the teleostean caudal skeleton (p. 211: "The uroneurals of the teleosts arise de novo, and are exclusively a teleostean innovation."), even though HECKEL (1850: 145) had already used the feature to define teleosts by this skeletal character, which was completely forgotten ("… dachförmige Gerüste ganz eigenthümlicher Knochen, welche auf die vorletzten Wirbelknochen gestützt und rückwärts über dieselben hinausragend …" [… roof-like frames of very peculiar bones, which lie on the second last centrum and reach backwards over them …]).

Uroneurals are modified, elongated ural neural arches that extend along the dorso-lateral surface of the last preural centra and/or ural centra. They are positioned dorso-lateral to the notochord (see ARRATIA 1999: 307) or only to ural centra. According to the fossil record, uroneurals have a long history in teleosts. Elements resembling uroneurals have been observed as elongate modified posterior-most ural neural arches (and without remnants of arcocentra at their bases) in some Early Jurassic †'pholidophoriforms' such as †*Pholidophorus bechei*. In contrast, the anterior elements are just ural neural arches with their spines. A series of true uroneurals occurs first in basal "true" teleosts, e.g, the Early Jurassic †*Leptolepis coryphaenoides* (see Fig. 9B). Uroneurals exhibit some major differences in shape, number, and position in different teleostean subgroups (Table 3). Here we will analyse first the condition present in fossil basal teleosts and then compare it with the condition observed in some extant teleosts.

Kind of uroneurals or modified elements

The uroneurals generally are elongate fusiform elements (e.g., Figs. 4D, 8B, 9B, 11C,D, 15A,B, 16), but the shape of the anterior-most element can be modified, producing an anteriorly expanded tip (e.g., *Elops*, *Megalops*, *Albula*; Figs. 4D, 14A,B, 15A,B), or producing an expanded membranous outgrowth at the dorsal margin of the bone so that the whole element is identified as a stegural (e.g., †*Orthogonikleithrus*, *Salmo*, *Oncorhynchus*: Figs. 4C, 6B, 17B), or losing its anterior tip and becoming fused to the terminal centrum (e.g., ostariophysans and extant clupeiforms with the exception of *Denticeps*; Figs. 4A,B, 7C, 19A–D, 20A–D). This last element was named the pleurostyle by MONOD (1968), who did not interpret it as a modified uroneural, but as a postero-dorsal process of preural centrum 1. A membranous expansion associated with the anterior-most uroneural in *Albula vulpes* and *Pterothrissus belloei* was labeled as a stegural ("ST") by MONOD (1968: figs. 97–103, 108).

Table 2.
Number of hypurals. Abbreviations: **H1–13,** hypurals 1–13; **H1 + H2,** hypurals 1 and 2 fused at their bases; **H1H2,** hypurals 1 and 2 form a hypural plate; **PH,** parhypural; **U1+2 + H1+H2,** bases of hypurals 1 and 2 fused to ural centrum 1+2; →, arrow indicates that there are more elements posteriorly. The repetition of a taxon indicates that more than one pattern is present in that particular group. – See SCHULTZE & ARRATIA (1989: table 1) and ARRATIA (1991: table 2) for more data.

Genus/hypurals	PH	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13
Lepisosteus	+	+	+	+	+	+	+	+	+	+	+	+	→	
Amia	+	+	+	+	+	+	+	+	+	+	+	→		
Neopterygii inc. sedis														
†*Pachycormus*	+	+	H2+H3+H4+H5+n											
†*Orthocormus*	–	H1+H2+H3+n												
Teleosteomorphs														
†*Aspidorhynchus*	+	+	+	+	+									
†*Belonostomus*	+	+	+	+	+									
†*Belonostomus*	+	H1+H2		+	+									
†*Vinctifer*	+	+	+	+	+									
†*Vinctifer*	+	H1+H2		+	+									
†*Eurycormus*	+	+	+	+	+	+	+	+	+	+	+	+	?	
†*Pleuropholis*	+	+	+	+	+	+	+	+	+	→				
†*Catervariolus*	+	+	+	+	+	+	+	+	+	+				
Basal teleosts														
†*Pholidophorus bechei*	+	+	+	+	+	+	+	+	+	+	+	+	+	+
†*Leptolepis coryph.*	+	U1+2+H1+H2		+	+	+	+	+	+	+	+			
†*Tharsis*	+	H1+H2		+	+	+	+	+	+	+				
†*Ascalabos*	+	U1+2+H1+H2		+	+	+	+	+	+	+	+	+		
†*Domeykos*	+	U1+2+H1+H2		+	+	+	+	+	+	+	+	+		
†*Protoclupea*	+	+	+	+	+	+	+	+	+	+				
†*Luisichthys*	+	+	U2+H2	+	+	+	+	+	+	+	+			
†*Pachythrissops*	+	U1,2+H1+H2		+	+	+	+	+	+					
Elopomorphs														
†*Anaethalion angustus*	+	H1+H2		+	+	+	+	+	+					
†*Anaethalion knorri*	+	U1+2+H1+H2		+	+	+	+	+						
†*Elopsomolos* sp.	+	H1+H2		+	+	+	+	+	+					
Elops spp.	+	H1+H2		+	+	+	+	+						
Megalops	+	H1+H2		+	+	+	+	+						
Albula	+	+	+	+	+	+	+							
Osteoglossomorphs														
†*Asiatolepis*	+	+	+	+	+	+								
†*Lycoptera*	+	+	+	+	+	+	+	+						
Hiodon	+	+	+	+	+	+	+	+	+					
Ostarioclupeomorphs														
†*Tischlingerichthys*	PU1+U1+2+PH+H1		+	+	+	+	?							
Chanos	+	+	+	+	+	+	+							
Dorosoma	+	+	U2+H2	+	+	+	+							
Coilias	+	+	U2+H2	+	+	+	+							
Engraulis	+	+	U2+H2	+	+	+	+							
Euteleosteomorphs														
†*Orthogonikleithrus*	+	H1+H2+		+	+	+	+							
†*Leptolepides*	+	U1+2+H1+H2		+	+	+	+	+	+	+				
Oncorhynchus	+	+	+	+	+	+	+							
Thymallus	+	+	+	+	+	+	+							

Table 3.
Neural arches versus uroneurals. Abbreviations: **na,** neural arch; **PL,** pleurostyle; **sp,** neural spine; **St,** stegural; **UN,** uroneural; **'UN'**, uroneural-like element; **?**, uncertain; **←,** arrow indicates that there are more elements in front. The repetition of a taxon indicates that more than one pattern is present in that particular group. The repetition of a taxon indicates that more than one pattern is present in that particular group.

Genus/caudal centra	PU3	PU2	PU1	U1	U2	U3	U4	U5	U6	U7	U8	U9
Neopterygii inc. sedis												
†*Pachycormus*	←'UN'	'UN'	'UN'	?	?	?	?	?	?	?		
Teleosteomorphs												
†*Aspidorhynchus*		na+sp	na+sp	UN	UN	UN						
†*Belonostomus* sp.		na+sp	na+sp	na+sp	UN	UN						
†*Belonost. tenuirostris*		na+sp	'UN'	UN	UN	UN	UN					
†*Vinctifer*		na+sp	na+sp	na+sp	UN	UN	UN					
†*Eurycormus*		'UN'	'UN'	UN	UN	UN	UN	UN	UN	UN		
†*Eurycormus*		na+sp	'UN'	UN	UN	UN	UN	UN	UN	UN		
†*Pleuropholis*			'UN'	UN	UN	UN	UN	UN	UN	UN		
†*Catervariolus*		na+sp	na+sp	UN	UN	UN	UN					
Basal teleosts												
†*Pholidophorus bechei*		na+sp	na+sp	na+sp	na+sp	na+sp	UN	UN	UN	UN	UN	
†*Leptolepis coryphaen.*		na+sp	na+sp	na+sp	?na	UN	UN	UN	UN	UN	UN	UN
†*Tharsis*		na+sp	na+sp	na+sp	na	UN	UN	UN	UN	UN	UN	UN
†*Ascalabos*		na+sp	na+sp	na+sp	UN	UN	UN	UN	UN	UN	UN	
†*Domeykos*		na+sp	na+sp	na	na	UN	UN	UN	UN	UN		
†*Protoclupea*		na+sp	na+sp	na	na	UN	UN	UN	UN	UN		
†*Luisichthys*		na+sp	na+sp	na	na	UN	UN	UN	UN	?		
Elopomorphs												
†*Anaethalion*		na+sp	na+sp	na	na	?	UN	UN	UN	UN		
†*Elopsomolos* sp.		na+sp	na+sp	na	na	na	UN	UN	UN			
Elops		na+sp	na+sp	na	na	na	UN	UN	UN			
Megalops		na+sp	na+sp	na	na	na	UN	UN	UN			
Osteoglossomorphs												
†*Asiatolepis*				na	na	?	UN	UN	UN	UN		
†*Lycoptera*				na	na	UN	UN	UN	UN	UN		
Hiodon				na	na	na	UN	UN	UN	UN		
Hiodon				na	na	UN	UN	UN	UN			
Ostarioclupeomorphs												
†*Tischlingerichthys*			na	?	?	PL	UN	UN	UN			
Chanos			na	na	na	PL?	?	UN?				
Chanos			na	na	PL?	?	?	UN?				
Catostomus			na	na	PL?	?	?	UN?				
Danio			na	PL?	?	?	UN?	?				
Coilia					PL?	?	?	UN?				
Engraulis					PL?	?	?	UN?				
Dorosoma			na	na	PL?	?	?	UN?				
Euteleosts												
†*Orthogonikleithrus*			na	na	?		ST	UN	UN	UN		
†*Leptolepides*			na	na	?	–	ST	UN	UN	UN		
Oncorhynchus			na	–	–	–	ST	UN	UN			
Thymallus			na	na	na	–	ST	UN	UN			

Origin and ossification of uroneurals

Seven long uroneurals are present in the most basal "true" teleosts such as †*Leptolepis coryphaenoides* (see Fig. 9A,B) and †*Tharsis dubius* (Table 3). According to their preservation and remnants of a cartilaginous core inside each uroneural, we interpret the uroneurals as chondral bones that ossify perichondrally. The uroneurals of basal teleosts such as †*Leptolepis coryphaenoides*, †*Tharsis dubius* and †*Ascalabos voithii* are moderately thin and slender anteriorly and lack membranous outgrowths, except †*Leptolepis coryphaenoides* that has a small outgrowth at the middle region of uroneural 1 (Fig. 9, mo).

In extant elopiforms such as *Elops* and *Megalops*, as well as in the extant osteoglossomorphs *Hiodon* (SCHULTZE & ARRATIA 1988), mormyrids, osteoglossids and *Arapaima* (HILTON & BRITZ 2010), the uroneurals develop from cartilaginous precursors. In *Elops* and *Megalops* the posterior part of the first uroneural ossifies perichondrally, the bone grows anteriad, and its anterior part expands in a modest membranous outgrowth (Fig. 14A, see below). The other two uroneurals present in elopiforms are perichondrally ossified and do not have membranous ossifications. A similar situation is observed in the fossil elopomorphs †*Anaethalion knorri* (Fig. 15A) and †*Elopsomolos* sp. (Fig. 15B) with the first uroneural slightly expanded anteriorly. In contrast, all uroneurals are perichondrally ossified and no anterior membranous extension is present in *Hiodon* (Fig. 11C,D). According to our observations, and due to the fact that in adult *Elops* the "cartilaginous elopomorph arch" ossifies into three ural neural arches that surround the neural cord, the first uroneural in *Elops* would develop from the next arch, the fourth ural neural arch (Table 3).

Salmonids have three uroneurals (Figs. 4C, 6B). The three uroneurals are first present as small masses of cartilage that ossify perichondrally. According to developmental studies, the first uroneural in salmonids corresponds to the modification of ural neural arch 4^p (ARRATIA & SCHULTZE 1992). The first uroneural (Fig. 6B) in salmonids ossifies perichondrally antero-ventrally and posteriorly, and a membranous bony extension ossifies at the antero-dorsal border of the bone, producing a modified uroneural named the stegural. The Late Jurassic euteleosts †*Orthogonikleithrus leichi* and †*O. hoelli* also have a well-developed stegural (Fig. 17B, Table 3).

The anterior-most uroneural or so-called uroneural 1 or pleurostyle present in ostarioclupeomorphs develops from a cartilaginous mass that is usually observed at the antero-ventral tip of the small bone that ossifies as membrane bone in some of the ostarioclupeomorphs (e.g., *Moxostoma*; GRÜNBAUM et al. 2003), but in others the bone develops completely as a membrane bone (e.g., *Dario rerio*; present study). The membranous pleurostyle has one or more dorsal projections that ressemble the cartilaginous neural arches present in other ostarioclupeomorphs. Additionally, the region where the pleurostyle fuses to the centrum seems to differ among ostarioclupeomorphs. Therefore, the origin and development of the pleurostyle in ostarioclupeomorphs seem to be different among subgroups (Table 3), but this structure is in need of careful research.

Number of uroneurals

Seven elongate uroneurals (Table 3) are present in the most basal "true" teleosts such as the Early Jurassic †*Leptolepis coryphaenoides* (Fig. 9A,B) and the Late Jurassic †*Tharsis dubius* (ARRATIA 1991: fig. 13) and †*Ascalabos voithii* (e.g., ARRATIA 1991: fig. 9, 1997: fig. 20). Seven uroneurals are also observed in the Late Jurassic †ichthyodectiform †*Allothrissops* (PATTERSON & ROSEN 1977: fig. 17). In contrast, only the three to five most posterior ural neural arches are modified into elongate uroneurals (without remnants of arcocentra at their proximal tips) in the Early Jurassic †*Pholidophorus bechei* (ARRATIA & TINTORI 1999: fig. 8A–C). The number of uroneurals or elongated ural neural arches is reduced to 3 (and occasionally 4) in †aspidorhynchiforms (Table 3).

According to our survey, the presence of seven elongate, modified ural neural arches or uroneurals represents the primitive condition in teleosts, and this is followed by a reduction in the number of elements in different groups (see Table 3). For instance, six uroneurals are found in some Late Jurassic †ichthyodectiforms (ARRATIA 2000: fig. 10A), whereas some Jurassic †crossognathiforms may have five uroneurals (e.g., †*Protoclupea*: ARRATIA 1991: fig. 12, ARRATIA 1997: fig. 9C) or four (e.g., †*Bavarichthys*; ARRATIA & TISCHLINGER 2010: fig. 11), some fossil euteleosts may have four or five (†*Leptolepides*; ARRATIA 1997: figs. 44, 48), and fossil elopiforms may have four or three (e.g., ARRATIA 1997: fig. 29, 2000: p. 156, figs. 15, 19; Fig. 15A,B herein), whereas extant elopiforms have three (e.g., Fig. 4D). Apparently, these reductions are due to losses of elements at different phylogenetic levels of the Teleostei (see section Homologies of uroneurals).

Position of uroneurals

In most basal "true" teleosts the elongate uroneural 1 extends anteriorly, reaching the lateral surface of preural centrum 3 (see Fig. 9A,B). The length of the first uroneural changes in basal teleosts, becoming shorter anteriorly so that in some teleosts the anterior tip of the first uroneural only reaches preural centrum 2 and in others only preural centrum 1.

The anterior tip of the first uroneural in the Late Jurassic elopiforms †*Anaethalion* and †*Elopsomolos* reaches preural 3 (e. g., ARRATIA 1997: fig. 29, 35; Fig. 15A,B). The first uroneural grows anteriad, reaching the dorso-lateral surface of preural centrum 2 in *Elops* and *Megalops* (e. g., MONOD 1968: figs. 20–24, 94, SCHULTZE & ARRATIA 1988: figs. 15–17, 22, FUJITA 1990: figs. 6, 7; Figs. 4D herein) and in the osteoglossomorph *Hiodon* (MONOD 1968: fig. 108bis and ter, SCHULTZE & ARRATIA 1988: figs. 2, 7, 11). The first uroneural reaches preural centrum 2 in fossil basal teleosts (e. g., †*Leptolepides* and †*Orthogonikleithrus*: ARRATIA 1997: figs. 48, 53), in †*Lycoptera middendorfii* (Fig. 16), and in extant salmoniforms (e. g., *Salmo*: MONOD 1968: figs. 279–280; *Oncorhynchus*, *Thymallus*, *Prosopium*: ARRATIA & SCHULTZE 1992: figs. 3, 9, 21, 22, FUJITA 1990: figs. 66–71). The first uroneural reaches preural centrum 1 in the albulids *Albula vulpes* (MONOD 1968: figs. 99–101, SCHULTZE & ARRATIA 1988: fig. 26), in *Pterothrissus belloci* (MONOD 1968: fig. 108, FUJITA 1990: fig. 8), and in the salmonid *Salvelinus* (ARRATIA & SCHULTZE 1992: fig. 25).

The uroneurals in †'pholidophoriforms' and fossil "true" basal teleosts are aligned one next to the other and gently decrease in length posteriorly (see Figs. 3C, 8A,B, 9A,B, 15, 16). Although there is a marked reduction in the number of uroneurals to only a few (3 or less) in extant teleosts, the most posterior element(s) of the series is (are) positioned at a different angle with respect to the first element; this feature was interpreted as a synapomorphy of the Clupeocephala by ARRATIA (2010: 653: fig. 15) (e. g., Fig. 4C).

Homologies of uroneurals

ARRATIA (1996: fig. 6A–F; Fig. 21 herein) assumed that all seven uroneurals in fossil basal teleosts are always present as in †*Ascalabos*, †*Leptolepis coryphaenoides* and †*Tharsis dubius*. Starting from a constant position of uroneural 4 (starting always at ural centrum 1^{P} or ural centrum $1+2^{P}$), she assumed that some single uroneurals represent an ontogenetic or phylogenetic fusion of many uroneurals (see Fig. 21). Without postulated fusion – but transformation of ural neural arches – the shaded uroneural in ARRATIA (1996; Fig. 21A–F herein) is the modified neural arch of ural centrum 5^{P}. In †*Ascalabos* (Fig. 21A), we have discovered only one neural arch on ural centrum $1+2^{P}$ so that the first free ural neural arch to become modified as a uroneural is ural neural arch 2^{P}, then ural neural arch 3^{P}, and so on. Since that paper was published, ontogenetic studies of extant teleosts (e. g., ARRATIA & SCHULTZE 1992, GRÜNBAUM & CLOUTIER 2010 and herein) have shown that the first enlarged uroneural (or stegural) is a uroneural belonging to ural centrum 4^{P} in extant salmonids. It does not represent a fusion of elements as was previously thought (e. g., CAVENDER 1970), but the growth of only one element. Consequently, the second uroneural^{D} corresponds to a modified arch of the neural arch of ural centrum 5^{P}, and the third uroneural^{D} to the neural arch of ural centrum 6^{P} in salmonids. According to our evidence (see Table 3) the reduction in number of uroneurals in basal teleosts is due to a loss of elements, not to a phylogenetic fusion as previously hypothesized by ARRATIA (1996). We have not been able to observe fusion between uroneurals among the studied species; however we are able to observe fusion among centra. Thus, the first three uroneurals of the series of seven found in primitive teleosts are lost in salmonids if one assumes that the first uroneurals correspond to ural neural arches 1^{P}, 2^{P} and 3^{P} in fossil basal teleosts (see Table 3).

Traditionally, uroneurals are identified by their numbers (e. g., UN1, UN2, etc.) in teleosts, but in reality we do not know the homology of these elements in most extant teleosts, especially in those with a reduction in number. The homology of each individual uroneural can only be established by ontogenetic studies, a difficult goal with fossil actinopterygians where very young specimens are rarely recovered. Our studies of extant basal teleosts have shown us that the first uroneural arises from ural neural arch 4^{P} (Table 3). This is a condition more widespread than we initially thought and it is also found in elopiforms, including †*Elopsomolos*. The condition is unclear for †*Anaethalion* because it is uncertain whether 2 or 3 ural neural arches are present. In *Hiodon*, the first uroneural may result as a modification of the neural arch of ural centrum 3^{P} or 4^{P}.

The origin of the modified uroneural or so-called pleurostyle found in ostarioclupeomorphs and some euteleosts is unclear and needs extensive research in different teleostean subgroups (see above). According to our evidence, the pleurostyle seems to have different origins in different groups. For instance, in the

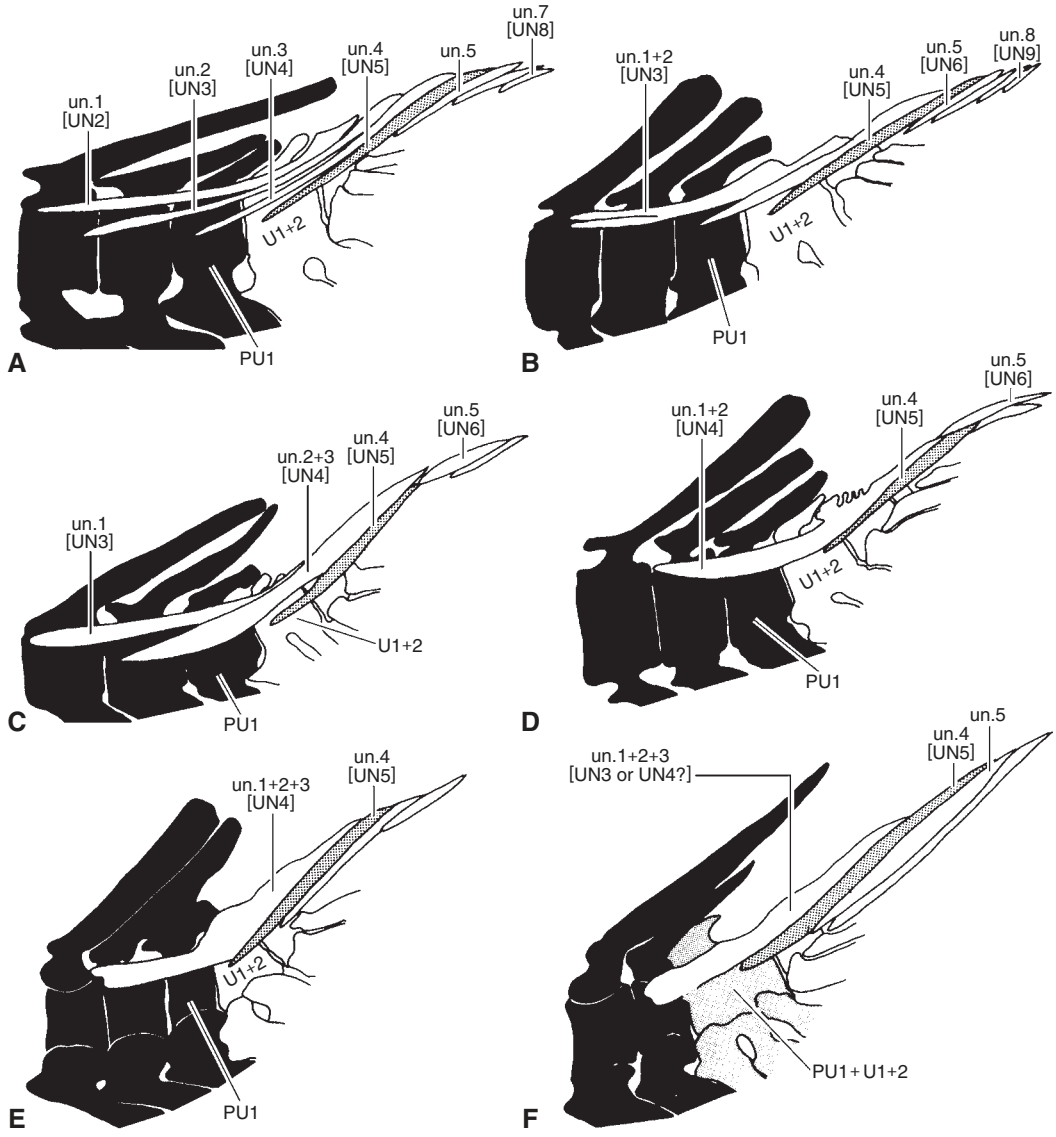


Fig. 21.
Diagrams illustrating some evolutionary changes of the uroneurals based on their positions versus their derivation from specific ural neural arches [represented in brackets] in certain Jurassic teleosts. Note that the uroneurals that are interpreted as fusion of uroneurals based on topological relationships have a different numbering, including losses of uroneurals, when the origin of the uroneural arch from an ural neural arch is considered. **A,** †*Ascalabos voithii*. **B,** †*Leptolepis coryphaenoides*. **C,** †*Domeykos profetaensis*. **D,** †*Leptolepides sprattiformis*. **E,** †*Orthogonikleithrus leichi*. **F,** †*Tischlingerichthys viohli*. (Modified from ARRATIA 1996). Abbreviations: **PU1**, preural centrum 1; **PU1+U1+2**, preural centrum 1 fused with ural centra 1+2^{P}; **U1+2**, fused ural centrum 1+2^{P}; **un.1–8[UN3–9]**, serially numbered uroneurals 1–8 (position) →[modified neural arches of ural centra 3–9^{P}]; **shaded uroneural**, corresponds to modified neural arch of ural centrum 5^{P}.

clupeiform *Dorosoma* and in the cypriniform *Catostomus* the pleurostyle seems to originate as a modification of an ural neural arch posterior to ural neural arch 1 (a small cartilage is observed at the anterior-most tip of the pleurostyle, and the rest of the element is solid membrane bone). It is unclear which neural

arch is the one transforming into a pleurostyle in these teleosts. In contrast, in *Danio rerio* an elongate pleurostyle is already present in specimens of about 5 mm SL extending dorsolateral to the notochord in front of hypurals 1 to 5. We have not been able to find a remnant of a cartilaginous ural neural arch associated with this element; it seems to be developed as a membrane bone exclusively. We have expressed our uncertainty concerning the pleurostyle (PL) using question marks in Table 3.

Numbering the uroneurals as 1, 2, 3, etc., as traditionally done, will not help to answer questions about their homologies in teleosts. Possible answers only will be found in detailed ontogenetic studies of different teleost groups, especially of basal teleosts, and by interpreting the caudal skeleton in a polyural fashion.

Hypothetical relationship between number of hypurals and uroneurals after PATTERSON (1973)

Naming elements of the caudal skeleton may have major consequences in the identification and classification of teleosts. The classical examples are actinopterygians such as †pachycormiforms and some †'pholidophoriforms' for which long-standing interpretations of them suddenly changed from being holosteans to become teleosts following PATTERSON (1973). The main character used by PATTERSON to consider †pachycormiforms and some †'pholidophoriforms' within the Teleostei was his interpretation that ural neural arches modified as uroneurals were found in those fishes. To justify the presence of uroneurals in the caudal skeleton of †pachycormiforms, PATTERSON (1973: fig. 19) used a restoration of a specimen of †*Pachycormus curtus* (see figure 17 in ARRATIA & SCHULTZE this volume) and the assumption that there is a one-to-one relationship between the presence of seven uroneurals and seven hypurals primitively in teleosts such as †pholidophorids and †leptolepids (after PATTERSON 1968b). We have been unable to find any specimen of a †pachycormiform or †'pholidophoriform' or †leptolepidid in which this hypothetical condition could be observed (see ARRATIA & LAMBERS 1996, ARRATIA & SCHULTZE this volume, and above).

Instead, †pachycormiforms have, on the posterior-most vertebrae of the caudal region, expanded median neural spines that look like uroneurals (see ARRATIA & LAMBERS 1996: figs. 2, 3A, 4A,B, 6, ARRATIA & SCHULTZE this volume: figs. 8, 9). The laterally expanded neural spines have been confused with ural neural arches modified as uroneurals and just named (and coded in phylogenetic studies) as uroneurals (e. g., PATTERSON 1977, GARDINER et al. 1996, HURLEY et al. 2007, FRIEDMAN et al. 2010). This is a strange overinterpretation because PATTERSON himself (1973: 275, 276) named these elements as "uroneurals of a peculiar type" or "uroneurals of a sort". Thus, the caudal skeleton of †pachycormiforms does not have uroneurals (= modified ural neural arches), and also does not show the supposed †pholidophorid and †leptolepidid primitive condition of a one-to-one relationship between seven uroneurals and seven hypurals proposed by PATTERSON (1973: 275). Until now it is unknown how many hypurals may be included in the hypural plate present in these actinopterygians, and it is unknown whether any modified ural neural arch is present at the posterior-most tip of the caudal endoskeleton.

In actinopterygians such as †aspidorhynchiforms, also interpreted as basal teleosts by PATTERSON (1977), the number of uroneurals versus hypurals is completely different. †Aspidorhynchiforms may have one uroneural-like bone associated with preural centrum 1, two or three (occasionally four) uroneurals associated with the ural region, and four hypurals (e. g., †*Aspidorhynchus*: BRITO 1999: fig. 3, †*Belonostomus*: BRITO 1999: figs. 4, 5, ARRATIA 2008: fig. 21). The first ural centrum may have a complete neural arch with a full spine in addition to there being two to three uroneurals and four hypurals (e. g., †*Vinctifer*: MAISEY 1991, BRITO 1999: figs. 1, 2, ARRATIA & SCHULTZE this volume: fig. 18A; Fig. 12A,B herein), with hypural 1 the largest of the series. The specimen of †*Belonostomus* sp. illustrated in Figure 13A, shows that the largest hypural is hypural 1, with hypural 2 smaller and hypurals 3 and 4 comparatively narrow. Hypural 1 has a large remnant of arcocentrum at its proximal base, whereas the arcocentrum is smaller in hypural 2. Because of the enlargement of the arcocentra, it is unclear whether chordacentra were present in preural vertebra 1 and the ural region. A similar pattern is found in *Amia calva*, where the identification of the last centrum bearing a haemal arch (preural centrum 1; see Fig. 11A,B) is easier than in a fossil because the exit of the blood vessels can be observed. The specimen of †*Belonostomus* sp. presents a complete, unmodified neural arch and spine on ural centrum 1, followed by two elongate uroneurals (not comma-like as in †*B. tenuirostris*), the first one the longest; the three uroneurals would correspond to transformations of ural neural arches 2 to 4 (see Table 3). The presence of large remnants of the arcocentra at the bases of hypurals of †aspidorhynchids makes it difficult to identify the last haemal arch of a preural vertebra where the blood vessels exit (PU1). The condition of the uroneurals seems to

be variable in †*Belonostomus* because in some specimens of †*B. tenuirostris* (= *muensteri* in ARRATIA 2008) a uroneural-like element is related to preural centrum 1, and the next four uroneurals are modifications of ural neural arches 1 to 4 (see BRITO 1999: fig. 4, ARRATIA 1999: fig. 21; Table 3). The first uroneurals are comma-like, but the last one is elongate. The †aspidorhynchiforms are also peculiar in their lack of epurals (see for instance, MAISEY 1991: 187; BRITO 1997: figs. 23, 35, 45, 1999: figs. 1, 2, 3, 4, 5; ARRATIA 1999: fig. 16A, 2008: fig. 21; ARRATIA & SCHULTZE this volume: fig. 18A; Fig. 6A,B).

†*Pholidophorus bechei* and †*Eurycormus speciosus* are two species used by PATTERSON (1973) to justify the new assignment of †'pholidophoriforms' within Teleostei. Both species were interpreted as having uroneurals, but neither of them shows the assumed primitive one-to-one relationship of seven uroneurals and hypurals. For instance, †*Pholidophorus bechei* has four or five modified, elongate ural neural arches or uroneurals and 12 hypurals (PATTERSON 1968b: fig. 2A). Some specimens of †*Eurycormus speciosus* may have one uroneural-like element associated with preural centrum 1 and a series of seven true uroneurals and more than 9 hypurals (see ARRATIA 1999: fig. 15; ARRATIA & SCHULTZE 2007: fig. 12A,B). In contrast, a very well-preserved specimen of †*Eurycormus* (Fig. 8A,B) presents two uroneural-like elements associated with preural centra 2 and 1, seven uroneurals as modifications of ural neural arches 1–7 (Table 3), and at least 11 hypurals (Table 2). The first two hypurals bear remnants of arcocentra at their proximal region in a pattern similar to that of *Amia calva* and †*Belonostomus* sp. (Fig. 12A,B).

Within "true" basal teleosts such as the taxa †*Leptolepis coryphaenoides* (Fig. 9A,B), †*Tharsis dubius* and †*Ascalabos voithii*, a one-to-one relationship between uroneurals and hypurals is not observed (compare Table 3 with 2). †*Leptolepis coryphaenoides* has at least seven uroneurals and 10 hypurals (e.g., ARRATIA 1991: fig. 7, ARRATIA & SCHULTZE this volume: fig. 18B), †*Tharsis dubius* has seven uroneurals and at least nine hypurals (ARRATIA 1991: fig. 13), and †*Ascalabos voithii* has seven uroneurals and 11 hypurals (ARRATIA 1997: fig. 20). To our best knowledge a one-to-one relationship between numbers of uroneurals and hypurals is not observed in any fossil or recent basal teleost, including †*Pholidophorus bechei* and †*Leptolepis coryphaenoides* (contra PATTERSON 1968b, 1973) (compare Table 3 with 2).

Consequently, and based on our data plus those of the available literature, we conclude that there is no support for the hypothetical one-to-one relationship between seven uroneurals and hypurals in teleosts, not even at the most basal level of Teleostei. Therefore, this hypothesis cannot be used to interpret the neural spines of preural elements present in †pachycormiforms, some †aspidorhynchiforms, and in some †'pholidophoriforms' as uroneurals. The assumption that true uroneurals are found in †pachycormiforms should be rejected and their interpretation as teleosts should be revised (see ARRATIA & SCHULTZE this volume).

Epurals

An epural is an epaxial, unpaired, free skeletal element or modified neural spine separated from its corresponding neural arch in the caudal region, commonly the ural region (see interpretations and literature about the possible origins of epurals in ARRATIA & SCHULTZE 1992: 240–242). To our best understanding, and based on our observations, we propose that epurals are epaxial elements belonging primarily to the ural centra, but that the first epural(s) may be associated with the preural region in certain actinopterygian groups. It is possible to establish the origin of a particular epural when we know from which neural arch an epural is detached. However, evidence of this can be extremely problematic in the absence of ontogenetic data or other indirect evidence, such as the continuous association between the epural with a specific preural or ural neural arch. It can be particularly problematic in teleosts showing loss or fusion of centra or with a markedly upturned caudal endoskeleton. In the latter case it may be almost impossible to follow the possible relationships between ural centra and epaxial elements.

Another major problem in understanding the epurals is their homologies. Epural 1 in one group is not necessarily epural 1 in another. The homologies of the epurals in certain taxa have been studied by ARRATIA & SCHULTZE (1992), ARRATIA (1997), and GRÜNBAUM & CLOUTIER (2010). ARRATIA & SCHULTZE (1992: table 7) named the epurals after the centra, to which they are related (E-PU1, E-U1, etc.). GRÜNBAUM & CLOUTIER (2010) proposed names on a one-to-one relationship between ural centra and epurals starting with E1 above $U1^{P}$ (E2 above $U2^{P}$, and so on) where the first epural on preural centrum 1 is labeled 'additional epural.' We prefer the naming that we proposed in 1992, because it gives the direct relationship of the epural to its centrum and avoids the confusion between epural 1 meaning the first epural and the use by GRÜNBAUM & CLOUTIER (2010) for epural 1 above ural 1^{P} (our E-U1).

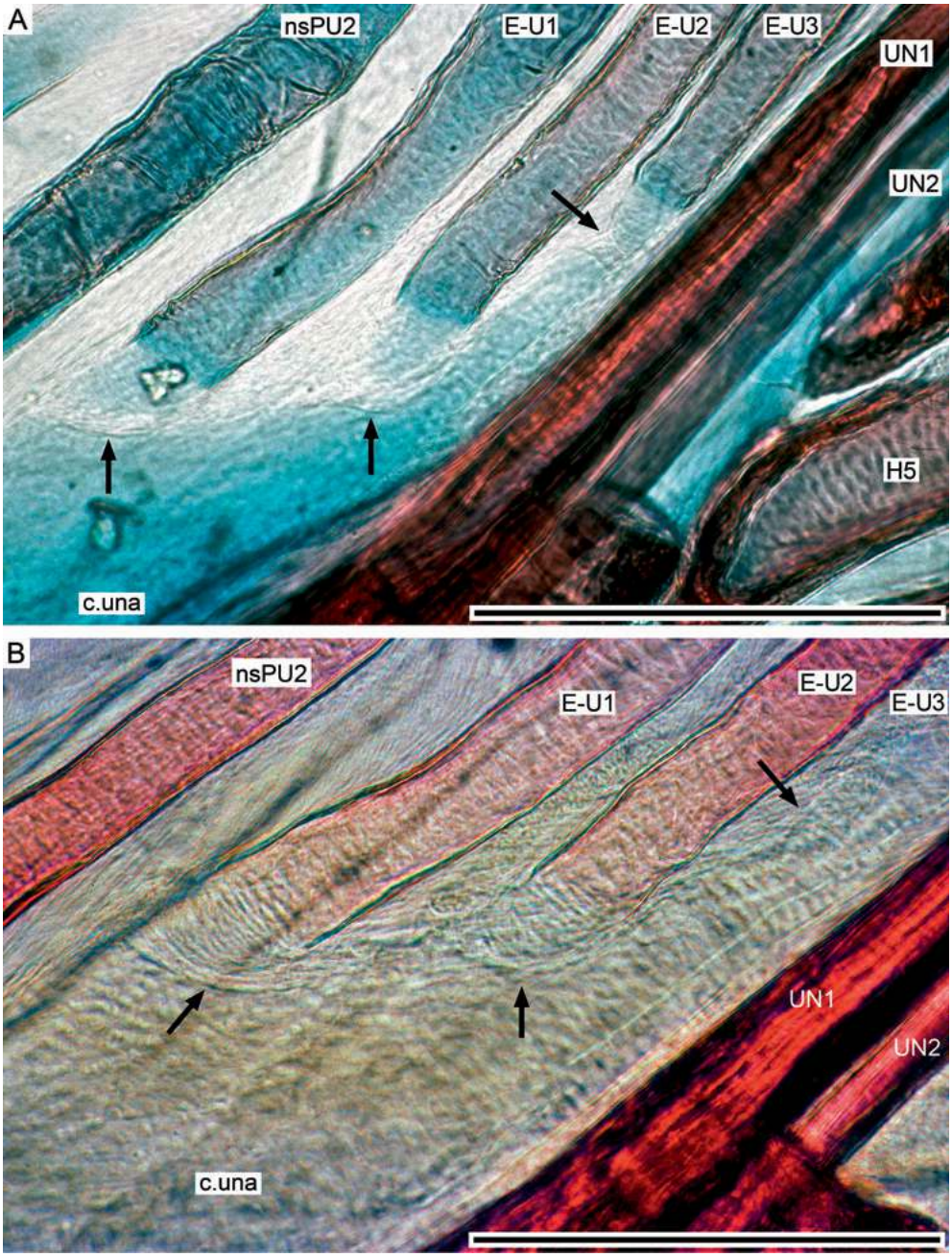


Fig. 22.
Cartilaginous mass of ural neural arches and its relationships with epurals in elopiforms. **A,** *Megalops atlanticus* (UF 208605; Recent). **B,** *Elops saurus* (TCWC 0503.1, 24 mm SL; Recent). Arrows point to the region where the cartilaginous connection between the mass of ural neural arch and epurals is beginning to separate. Note that the connection is still in place between the last epural and the ural cartilaginous mass. Scales = 0.25 mm. Abbreviations: **c.una**, cartilaginous mass of ural neural arches or the so-called cartilaginous elopomorph ural neural arch; **E-U1**,**2**,**3**, epurals of ural centra 1^{P}, 2^{P} and 3^{P}; **H5**, hypural 5; **nsPU2**, neural spine of preural centrum 2; **UN1–2**, uroneurals 1 and 2 (position) →[modified neural arches of ural centra 4^{P} and 5^{P}].

Our studies of the development of the caudal skeleton in the elopiforms *Megalops* and *Elops* reveal that the three epurals present in these teleosts arise from a mass of cartilage named "cartilaginous ural neural arch", which is characteristic of elopomorphs (e.g., FOREY 1973; PATTERSON & ROSEN 1977; ARRATIA 1987, 1997, 1999; SCHULTZE & ARRATIA 1988). This cartilaginous mass (Figs. 14A,B, 22A,B) positioned dorsal to the ural centra ossifies into independent ural neural arches (1, 2 and 3) during ontogeny (Figs. 4D, 15A,B; SCHULTZE & ARRATIA 1988: figs. 15, 22; ARRATIA 1997: fig. 29B). The cartilaginous continuity (Fig. 22A,B) between the distal region or dorsal margin of the elopomorph cartilaginous arch and the basal part of the epurals is observed in young individuals of *Megalops* and *Elops* studied by us. The last epural to separate from the cartilaginous arch is the posterior-most epural, epural 3. The changes in position of the cartilaginous cells and the appearance of connective tissue in the region of separation between both the

Table 4.
Distribution of epurals. Abbreviations: **'E',** epural-like structure; **E,** epural; **ns**, neural spine. The repetition of a taxon indicates that more than one pattern is present in that particular group.

Genus/caudal centra	PU4	PU3	PU2	PU1	U1	U2	U3	U4	U5	U6	U7
Teleosteomorphs											
†*Aspidorhynchus*		–	–	–	–	–					
†*Belonostomus*		–	–	–	–	–					
†*Vinctifer*		–	–	–	–	–					
†*Eurycormus*	E-PU4	E-PU3	E-PU2	E-PU1	E-U1						
†*Pleuropholis*		E-PU3	E-PU2	E-PU1	E-U1	E-U2	E-U3				
†*Catervariolus*					E-U1	E-U2	E-U3	E-U4	E-U5	E-U6	
Basal teleosts											
†*Pholidophorus bechei*	E-PU4	E-PU3	E-PU2	E-PU1	E-U1						
†*Leptolepis coryph.*					E-U1	E-U2	E-U3				
†*Tharsis*					E-U1	E-U2	E-U3				
†*Ascalabos*					E-U1	E-U2	E-U3				
†*Domeykos*				E-PU1	E-U1	E-U2	E-U3				
†*Protoclupea*				E-PU1?	E-U1	E-U2					
†*Luisichthys*				E=PU1?	E-U1	E-U2					
†*Pachythrissops*					E-U1	E-U2	E-U3				
Elopomorphs											
†*Anaethalion*					E-U1	E-U2	E-U3				
†*Elopsomolos*					E-U1	E-U2	E-U3				
Elops					E-U1	E-U2	E-U3				
Megalops					E-U1	E-U2	E-U3				
Osteoglossomorphs											
†*Lycoptera*						E-U2					
Hiodon						E-U2					
Ostarioclupeomorphs											
†*Tischlingerichthys*				E-PU1	E-U1	E-U2					
Chanos						E-U2					
Chanos					E-U1						
Catostomus					E-U1?						
Danio					?						
Dorosoma					E-U1?	?					
Coilia					E-U1?	?					
Engraulis					E-U1?	?					
Euteleosts											
†*Orthogonikleithrus*				E-PU1	E-U1	E-U2					
†*Leptolepides*				E-PU1	E-U1	E-U2					
Oncorhynchus				E-PU1		E-U2		E-U4			
Oncorhynchus				E-PU1	E-U1	E-U2					
Thymallus			E-PU2	E-PU1		E-U2		E-U4			

cartilaginous ural neural arch and the epurals can be clearly observed in different stages of development (see Fig. 22). Therefore we can identify the epurals of *Megalops* and *Elops* as epurals associated with the neural arches of ural centrum 1^{P} (E-U1 = first epural), of ural centrum 2^{P} (E-U2 = second epural), and ural centrum 3^{P} (E-U3 = third epural) following the derivation of a specific epural from a specific ural neural arch (Table 4).

A similar situation has been observed in young osteoglossomorphs such as *Hiodon*, but in this particular case the proximal region of the single epural is in contact with its ural neural arch in many individuals; this is commonly ural neural arch 2^{P} (naU2 in Figs. 11D, 23A). Thus, what is typically identified as epural or epural 1 in *Hiodon* in reality is the second epural (E-U2) because the epural is associated with ural centrum 2^{P} (Table 4). In *Arapaima gigas*, the element lying on ural centrum 1^{D} (or the enlarged ural centrum 2^{P} in our interpretation of HILTON & BRITZ 2010: fig. 6) keeps the neural arch and spine, and it has been interpreted as a neural arch and spine of the first ural centrum^{D} of the diural terminology by CASTRO LEAL & BRITO (2007: figs. 2a-f, 3a-f, 4a-d, 5a-d, 6a-c). However, the pattern in *Arapaima gigas* is consistent with that of *Hiodon*, in which this neural spine (= epural) belongs to ural centrum 2^{P} (see SCHULTZE & ARRATIA 1988: 5, 6, 7; Figs. 11D, 23A herein).

In early ontogeny of the basal gonorynchiform *Chanos chanos*, the single epural also is a detached neural spine from the cartilaginous neural arch that is positioned dorsal to the compound terminal centrum present in that species. In some larval specimens of *Chanos chanos*, the cartilaginous epural is still joined to the ural neural arch 1 of the compound cartilaginous neural arch of preural centrum 1 plus ural centrum 1^{P} (Fig. 23B); in other specimens, the compound neural arch includes also ural neural arch 2^{P} and the cartilaginous epural is attached to this arch. Since the epural separates from the most posterior part of the arch, it appears that the epural in *Chanos* may variably belong to ural neural arch 1^{P} (commonly) or neural arch 2^{P} (Table 4).

The detachment of the epural from a neural arch has been illustrated in some catfishes and some advanced euteleosts (SCHULTZE & ARRATIA 1989: fig. 11A–D). However, the neural arch, from which the epural separates, has not been studied yet in these fishes. Likewise, it has not been well studied in most euteleosts, with the exception of the salmonids (ARRATIA & SCHULTZE 1992, GRÜNBAUM & CLOUTIER 2010). For instance, the first epural (E-U1) is associated with preural centrum 1 in *Oncorhynchus*, the second (E-U2) with ural centrum 2^{P} and the third (E-U4) with ural 4^{P} (see ARRATIA & SCHULTZE 1992: tb. 7). *Thymallus* possesses three or four epurals, the first one (E-PU2) being a detached spine of preural centrum 2, the second one (E-PU1) a detached spine of preural centrum 1, and the third (E-U2) and fourth (E-U4) associated with ural centrum 2^{P} and 4^{P}, respectively (ARRATIA & SCHULTZE 1992: fig. 22C,D; Table 4). Whereas extant teleosts have commonly zero to three epurals. Some fossil teleosts and other actinopterygians that have been interpreted as teleosts or stem-group teleosts have a larger number of epurals (also in *Thymallus*), some of them are related to the preural region (Table 4). For instance, there are six epurals above the neural arches of preural centrum 3 to ural centrum 3^{P} in †*Pleuropholis*. Five epurals above the neural arches of preural centrum 4 (E-PU4) to ural centrum 1^{P} (E-U1) are present in †*Pholidophorus bechei* and †*Eurycormus speciosus* (ARRATIA & SCHULTZE 2007: fig. 12A,B). Three epurals above ural neural arch 1 and 2 (U1+2^{P}) and above ural centrum 3^{P} are present in the basal teleosts †*Leptolepis coryphaenoides* (Fig. 9A,B), †*Tharsis dubius*, and †*Ascalabos voithi*, similar to the condition observed in the fossil elopomorphs †*Anaethalion*, †*Elopsomolos* (Fig. 15A,B) and in extant *Elops* and *Megalops* (Fig. 4D, 14A, 22A,B). Despite the information presented above, the origin and homology of the epural(s) remain unknown in most teleosts.

Major evolutionary changes of the caudal endoskeleton in teleosts

It sounds contradictory that while the presence of a diural caudal skeleton has been interpreted as a teleostean synapomorphy (e.g., PINNA 1996), actinopterygians such as the Early Jurassic †*Pholidophorus bechei* and the Late Jurassic †*Eurycormus speciosus* that were removed from the Holostei and interpreted as basal teleosts by PATTERSON (1968b, 1973) do not present a diural caudal skeleton, but a polyural caudal skeleton (Fig. 8A,B). As we have explained and illustrated here, the caudal skeleton of basal teleosts is far more complex than one with two ural centra, seven uroneurals and seven hypurals. It displays a significant but incompletely understood diversity among basal teleosts involving transformations including fusions and/or losses of centra and hypurals, and losses of other structures such some uroneurals.

The tail of some †'pholidophoriforms' interpreted as teleosts, such as †*Pholidophorus latiusculus*,

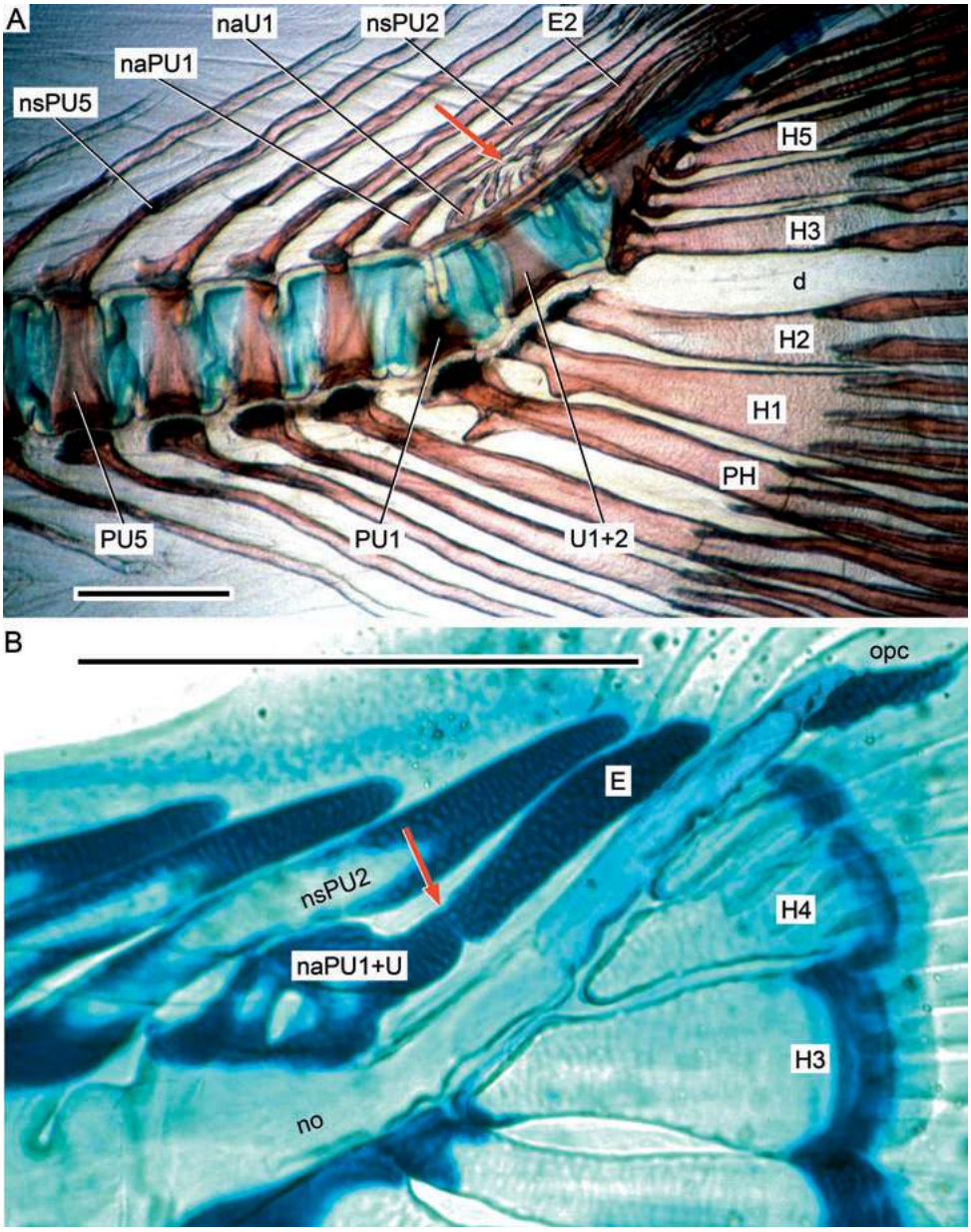


Fig. 23.
Caudal skeletons of *Hiodon* and *Chanos* in lateral view. **A,** osteoglossomorph *Hiodon alosoides* (KUNHM 7618, 27 mm SL; Recent). Small arrow points to the place where the epural is still joined to ural neural arch 2. **B,** part of the caudal endoskeleton of the gonorynchiform *Chanos chanos* (KUNHM 39857, 11 mm SL; Recent). Note the compound cartilaginous neural arch formed by the neural arch of preural centrum 1 and ural centrum 1^{P} (naPU1+U1^{P}), and the beginning of the separation of the epural (E) from the cartilaginous compound neural arch. Scales = 0.5 mm. Abbreviations: **d**, hypural diastema; **E,** epural of ural centrum 1^{P}; **E2**, epural of ural centrum 2^{P}; **H1**, **5**, hypurals 1 and 5; **no**, notochord; **naPU1**, neural arch of preural centrum1; **naPU1+U**, neural arch of preural centrum1 + ural centrum 1^{P}; **naU1**, neural arch of ural centrum 1^{P}; **no**, notochord; **nsPU5**, **2**, neural spine of preural centra 5, 2; **opc**, opisthural cartilage; **PH**, parhypural or haemal spine of preural centrum 1; **PU5**, **1**, preural centra 5 and 1; **U1+2**, fused ural centrum $1+2^{P}$.

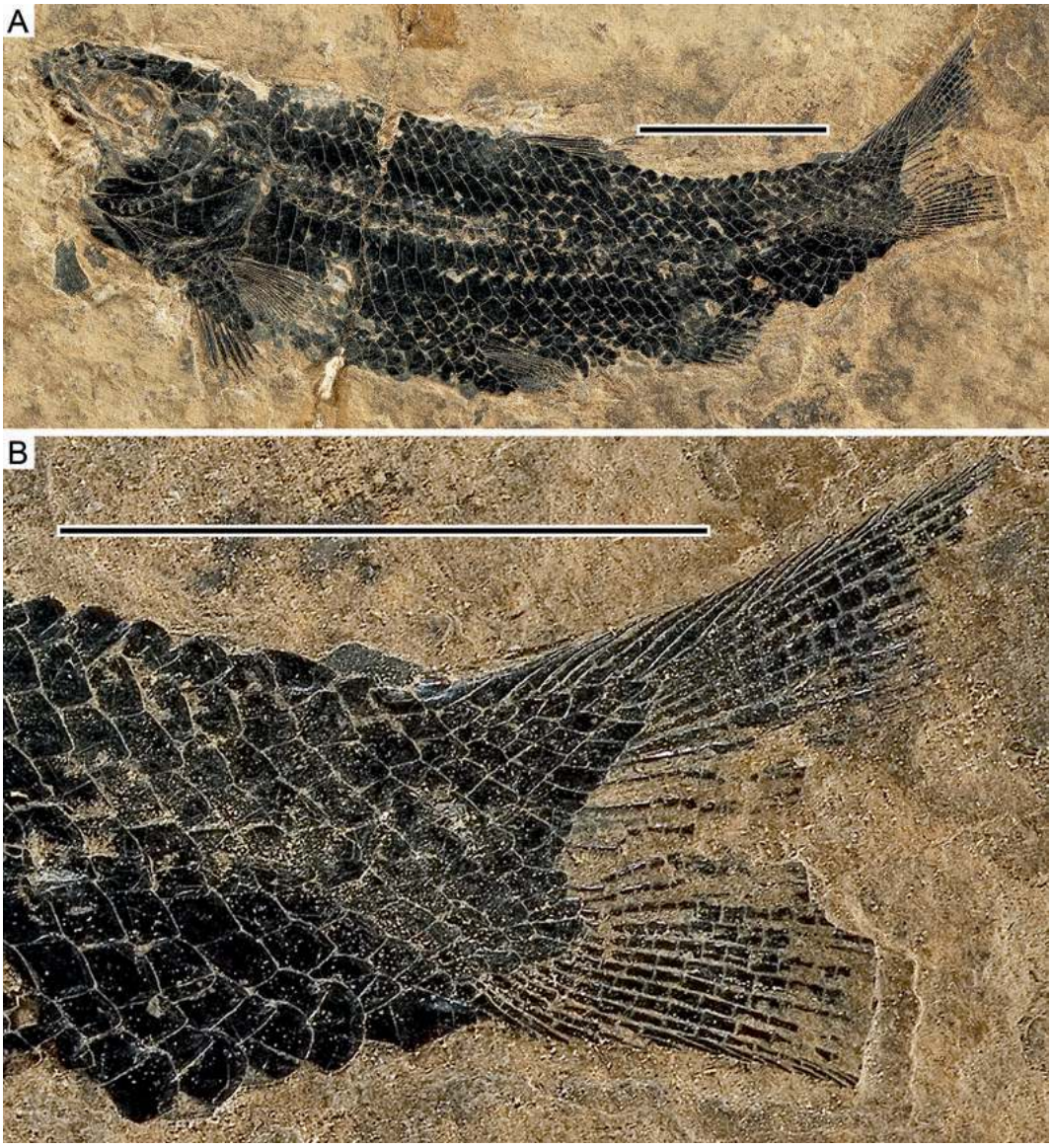


Fig. 24
Lateral view of the 'pholidophoriform' †*Parapholidophorus nybelini* (MCSNB 2897; Upper Triassic, Norian) and enlargement of the caudal region illustration the extension of the ganoid rhombic scales in the dorsal lobe of the (hemiheterocercal) tail. Scales = 1 cm.

†*Ph. nybelini* (ARRATIA 2000, 2001, 2004) and †*Catervariolus* (TAVERNE 2011: figs. 1, 7), is hemiheterocercal (Fig. 24A,B), with a series of rhombic scales extending into the dorsal lobe of the fin and covering the bases of the dorsal-most principal rays. The tail of †*Pholidophorus bechei* has a shorter extension of rhombic scales laterally covering the dorsal lobe of the tail (ARRATIA 2008: fig. 10). In contrast, the tail of †*Leptolepis coryphaenoides* and more advanced teleosts is commonly homocercal, with two well-defined and externally symmetrical lobes. However, in †*Pholidophorus bechei* as well as †*Eurycormus speciosus* and †*Catervariolus hornemani*, and despite the external shape of the tail and the extension of the cover of rhombic scales, the

series of dorsal, posterior-most hypurals extends posteriorly into the dorsal lobe of the caudal fin. A similar condition is retained in the internal disposition of the uroneurals and hypurals in †*Leptolepis coryphaenoides* (Fig. 9B).

However, in more advanced teleosts (e. g., Fig. 4A–C), the hypurals do not extend into the dorsal lobe but have a more fan-shaped arrangement. The dorsal-most hypurals are lost, and there is a strong flexion of the posterior-most vertebrae that is lacking in basal teleosts. The acquisition of a dorsal flexion of the last portion of the notochord is an important step in the evolutionary history of teleosts that marks major changes from a terminal vertebral column that is almost straight or slightly bent dorsally to an abrupt upturning of the notochord accompanied by internal asymmetry of the homocercal tail and other related changes.

At the most basal level of the teleostean phylogeny, including stem-groups, caudal vertebral centra are usually diplospondylous (e. g., †*Pholidophorus bechei*, †*Eurycormus speciosus*), whereas monospondylous caudal centra are consistently present in "true" teleosts. The ossification of the caudal centra also differs. †*Pholidophorus latiusculus*, †*Ph. bechei*, and †*Eurycormus speciosus* have only arcocentral plus chordacentral types of caudal centra, including those of the preural and ural region. In contrast, "true" teleosts have an autocentrum surrounding each chordacentrum and the bases of the arcocentra.

Conclusions

1. NYBELIN (1963) established a useful landmark for distinguishing between the parhypural and hypurals, and between preural and ural centra, namely, the exit of the caudal artery from the haemal arch. This landmark facilitates the homologization of elements in the caudal skeleton.

2. Additional landmarks, such as the trajectory of the main blood vessels and their division at the distal ends of hypurals 2 and 3, along with the presence of a space or hypural diastema between hypurals 2 and 3, facilitate the identification of those two hypurals from early in ontogeny (SCHULTZE & ARRATIA 1989; Figs. 2B, 4A,B).

3. The place where the notochord initiates its flexion is marked by a change in the aspect of its chordal sheaths, usually at the bases of hypurals 2 and 3, and sometimes in front of the arch of preural centrum 1 and hypural 1 (e. g., Fig. 7B).

4. Ontogenetic studies allow better understanding of the developmental process of the caudal skeleton of basal extant teleosts, including the changes from an early-stage polyural condition into a diural one or into a compound terminal centrum. The development of centra is so rapid that even day-to-day series may not be sufficient to reveal the composition of each ural centrum present in a diural skeleton. To reach such a goal, it is essential to have a large number of specimens per day.

5. The diural skeleton develops phylogenetically and ontogenetically from a polyural stage independently in different ways in different teleostean lineages, as demonstrated here, and we hypothesize that these differences indicate independent origins and developmental processes involved in the evolution of the diural skeletons in different groups. Thus, ural centrum 1^{D} may correspond to ural centrum 1^{P} or ural 2^{P} or ural $1+2^{P}$ of the polyural terminology, whereas ural centrum 2^{D} may correspond to ural centrum 3^{P} or ural centrum 4^{P} or ural centrum $3+4^{P}$ or ural centrum $3+4+5^{P}$, etc. (see Table 1).

6. The compound terminal centrum or urostyle that is generally assumed to be the result of a fusion of preural centrum 1 and ural centrum 1^{D} or preural ural centrum 1 and ural centra 1^{D} and 2^{D}, in reality may have different origins in teleosts, even in closely related teleosts (e. g., within ostarioclupeomorphs). For instance, the compound centrum of adult specimens is the result of the early fusion of four centra in the cypriniform *Catostomus*, but it is the result of only two, or occasionally three centra in the cypriniform *Danio* (see Table 1). Ontogenetic studies of different ostarioclupeomorphs and euteleosts are important to understand the origin, the evolutionary transformations, and the homologies involved in different ostarioclupeomorphs and also in many euteleost subgroups.

7. From the highest number of 13 hypurals in †*Pholidophorus bechei* there is a decrease in number of elements among the basal teleosts (Table 2). Groups such as the elopomorphs, with eight, seven or six independent hypurals in, e. g., elopiforms and albulids, have complex caudal skeletons in notacanthiforms and anguilliforms showing a compound terminal centrum and fused hypurals. Basal osteoglossomorphs may have eight or seven hypurals, a number that is reduced in osteoglossomorphs such as

Osteoglossum and *Pantodon*. Basal clupeocephalans have six or fewer ossified independent hypurals (ARRATIA 2010), although different kinds of fusions are observed, such as for instance hypural 2 fuses to ural centrum 2^{P} in recent clupeiforms, or the parhypural and hypural 1 fuses at their bases in, e. g., cyprinids, or hypural 1 and 2 fuse to each other and to the parhypural in most siluriforms. In addition, hypurals 3 to 6 may remain independent or they may exhibit different degrees of fusion, e. g., hypurals 3+4, or hypurals 3+4+5, or all hypurals fuse into one plate. In many cases, the reduction in number of hypurals has been interpreted as a result of fusion, but these hypothesized fusions are not based on ontogenetic studies yet.

8. A complete series of true uroneurals as modified neural arches of ural centra occurs first in all "true" teleosts, beginning with †*Leptolepis coryphaenoides* as the most basal taxon. The homologies of uroneurals are still not understood for most fossil and extant teleosts, with a reduction in number of uroneurals from the seven found in †*Leptolepis coryphaenoides* and a few other basal teleosts to three to none in different extant teleost lineages. In fossil basal "true" teleosts, the first uroneural seems to be a modification of ural neural arch 3^{P} (UN-U3; see Table 1), whereas in elopiforms, in some osteoglossomorphs, and in salmonids, the first uroneural is a modification of ural neural arch 4^{P} (UN-U4). The situation remains unknown for the so-called pleurostyle found in ostarioclupeomorphs and many euteleosts. Consequently, the homologization of uroneurals is not fully understood yet, even in all basal teleosts (see Table 3).

9. Elongate elements or "uroneurals of a peculiar sort" may develop as modified epaxial elements of many preural centra in, e. g., †pachycormiforms, or only of preural centra 1 and 2 or only preural centrum 1 in some †'pholidophoriforms' (e. g., Fig. 8A,B) and †aspidorhynchiforms.

10. The homologization of epurals is not fully understood for most teleosts, as shown by studies based on both early ontogenetic stages and fossils, because in most cases the developmental origin of the epural(s) characterizing a taxon is unknown. Epurals are neural spines separated from ural neural arches in teleosts. In contrast, some stem-teleosts and some euteleosts apparently can possess simultaneously epurals derived from neural spines of both preural and ural vertebrae (Table 4). However, †aspidorhynchiforms lack an epural. In fossil basal "true" teleosts, the first epural corresponds to the neural spine of ural centrum 1^{P} (E-U1), the second epural to the neural spine of ural 2^{P} (E-U2) and the third epural to the neural spine of ural 3^{P} (E-U3). This pattern is also found in fossil and recent elopiforms, but not in basal osteoglossomorphs. The origin of the epurals in most ostarioclupeomorphs is currently unknown.

Summarizing, and based on our evidence, we propose that the diural caudal skeleton of Teleostei develops ontogenetically and phylogenetically from a polyural skeleton. Consequently, we suggest devoting future studies to the origin and composition of the ural region of different teleostean subgroups – using the polyural terminology that assumes a one-to-one relationship between ural centra and their respective epaxial and hypaxial elements. This will allow us to understand and interpret the composition of the ural centra present in adult teleosts and their relationships to other epaxial (e. g., epurals and uroneurals) and hypaxial (hypurals) elements of the caudal fin. By using the polyural convention, and the different landmarks discussed here, we will reach a better understanding of the possible homologies involved, and probably we will achieve a better understanding of the patterns found in more advanced teleosts, e. g., the neoteleosts.

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