Papéis Avulsos de Zoologia

Museu de Zoologia da Universidade de São Paulo

Volume 46(10):107-123, 2006 www.scielo.br/paz ISSN impresso: 0031-1049
ISSN *on-line*: 1807-0205

The supratemporal system and the pattern of ramification of cephalic sensory canals in *Denticeps clupeoides* (Denticipitoidei, Teleostei): additional evidence for monophyly of Clupeiformes and Clupeoidei

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ABSTRACT

The cephalic portions of the latero-sensory canal system in Denticeps clupeoides *are described and analyzed. The species, a small herring-like fish from relictual West African streams, is the most primitive living clupeomorph and sole Recent representative of suborder Denticipitoidei. As sister group to over 360 species in Clupeoidei,* Denticeps *is a key taxon in understanding clupeomorph and lower teleostean relationships. Observations on recently-collected specimens of* Denticeps clupeoides *revealed comparatively-important and previously-unrecorded details of the cephalic latero-sensory canals which are relevant for understanding relationships at different levels in clupeomorph phylogeny. The infraorbital, supraorbital, preopercular, extrascapular and post-temporal canals of* Denticeps *have unbranched tubules in soft tissue, as in the hypothesized plesiomorphic condition for lower teleosts. Contrastingly, the presence of a complex network formed by a high order of branching of cephalic canals is hypothesized as a synapomorphy of the Clupeoidei.* Denticeps *and the Clupeoidei share an exclusive sensory branch that originates at the junction between the extrascapular bone and the* recessus lateralis, *here hypothesized as an additional synapomorphy of Clupeiformes. A supratemporal system is newly recorded in* Denticeps, *and the character is proposed as a synapomorphy of Clupeiformes, and not of Clupeoidei as previously thought. The hypothesis that the supratemporal system is homologous to the supraorbital cavern is refuted, and the latter is corroborated as an autapomorphy of* Denticeps. *Another autapomorphy of* Denticeps *(or Denticipitoidei) is the presence of the postorbital bulla, a hitherto unrecorded specialization of the infraorbital canal associated with infraorbitals 4 and 5. Homologies of other tubules of the cephalic sensory canals in* Denticeps *are also discussed, with emphasis on their bearing on the recognition of homologies of infraorbital bones in* Denticeps *and other lower teleosts. In general, data from the cephalic latero-sensory system corroborate* Denticeps *as the sister group to all other Recent clupeomorphs, and provide additional support for the monophyly of Clupeoidei and Clupeiformes.*

Keywords: Clupeiformes, *Denticeps clupeoides,* latero-sensory system, lower teleosts, phylogenetic relationships, postorbital bulla, sensory biology.

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INTRODUCTION

Denticeps clupeoides Clausen, 1959 (Fig. 1) is a peculiar little herring-like fish that inhabits a few isolated coastal streams in West Africa, from Eastern Benin to Cameroon (Teugels, 2003). The species is sole Recent representative of its genus, family Denticipitidae, and suborder Denticipitoidei. The Denticipitidae also includes the strikingly similar *Paleodenticeps tanganikae* from the Tertiary of Tanzania, East Africa (Greenwood, 1960). Denticipitoidei is sister-group to about 360 species of the fishes commonly known as sardines, herrings, and anchovies, grouped in the Clupeoidei (Greenwood *et al.,* 1966; Greenwood, 1968a, 1968b; Grande, 1985; Nelson, 2006). The Denticipitoidei and the Clupeoidei together comprise the Clupeiformes, which includes all living species of the Clupeomorpha (Grande, 1985). Despite their abundance and importance, the anatomy and relationships of clupeomorphs are still poorly known. Comparative or phylogenetically-oriented works on the group or its subunits have been relatively few, both on the basis of morphological and molecular data. It seems to us that current disputes about the relationships among Osteoglossomorpha, Elopomorpha, Otocephala and basal euteleosts (e.g., Johnson & Patterson, 1996; Arratia, 1997, 1999; Ishiguro *et al.,* 2003; Lavoué *et al.,* 2005) would benefit from a deeper understanding of character variation in clupeomorphs in general. *Denticeps clupeoides* in particular, because of its basal position among clupeomorphs, is a key taxon for understanding relationships among lower teleosts.

The acusticolateralis system has a series of unique features in different clupeomorph subgroups, particularly in the head region (Tracy, 1920; Wohlfahrt, 1936, 1937; O'Connell, 1955). The *recessus lateralis* is a complex that probably acts as a center for integration of stimuli perceived by the lateral line. Its presence is hypothesized as a synapomorphy of the Clupeiformes (Grande, 1985; Di Dario, 2004). The *recessus lateralis* is an intracranial space in the otic region into which the main branches of cephalic sensory canals converge, namely the supraorbital, infraorbital, preopercular, and extrascapular/post-temporal (Grande, 1985; Di Dario, 2004; Figs. 2 and 3). The exact mechanism and function of the *recessus lateralis* are not yet understood, although it is probably related to detection and analysis of small vibrational pressures and displacements (Hoss & Blaxter, 1982).

In species of the Clupeoidei, there is an ontogenetic increase in the branching of the main cephalic canals that results in a highly complex network formed by superficial soft-tissue tubules (Stephens, 1985; Fig. 2). The branches lack neuromasts and always end in a pore (Greenwood, 1968a; Coombs *et al.,* 1988). The pattern of ramification in representative species of the Clupeoidei has been accurately described and illustrated in a series of papers (Wohlfahrt, 1937; Bamford, 1941; Gunter & Demoran, 1961; Hoss & Blaxter, 1982; Nelson, 1983; Stephens, 1985; Blaxter, 1987). The network formed by the branches covers virtually the whole head of the fish (Fig. 2), and is likely responsible for an increase in the detection of mechanical waves (Stephens, 1985). Another distinct structure of the sensory apparatus of some clupeomorphs is the supratemporal system, originally described by Wohlfahrt (1937: "supratemporale System"). The supratemporal system is a complex structure formed by branched canals at the temporal region that originate from a sac-like expanded sensory canal that fills the temporal foramen (Patterson, 1970). A limited connection between the supratemporal system and the rest of the latero-sensory system persists via the supraorbital canal in most adult clupeomorphs (Bamford, 1941; Di Dario, 2004), although according to Wohlfahrt (1937) those systems are completely independent in *Sardina pilchardus* and possibly other clupeomorphs. The modified, sac-like, sensory canal or vesicle that fills the temporal foramen is the *sinus temporalis* (Wohlfahrt, 1937; Fig. 3). The temporal foramen is apparently exclusive to the Clupeiformes (Lauder & Liem, 1983). Typically, it consists of a roughly oval foramen dorsal to the *recessus lateralis* in the region of articulation between the frontal and parietal bones (Grande, 1985; Fig. 3). Bamford (1941) speculated that the supratemporal system is a sensory organ that detects differences of pressure around the head, caused by movements of the fish. Association between the supratemporal system, the *recessus lateralis,* and the highly branched head canal system have been proposed as one of the main factors responsible for the extraordinary ecological success of clupeomorphs, assisting in a variety of functions such as the precise perception of the position of the fish in a school, and in pressure balance during vertical migration (Blaxter, 1987; Webb, 1989).

The acusticolateralis system of *Denticeps clupeoides* is still poorly known. It is clear, nevertheless, that it is composed of an expected mosaic of autapomorphic and primitive features (Di Dario, 2004). One hypothesized autapomorphic structure of the acusticolateralis system of *Denticeps* is the supraorbital cavern (Figs. 4A and 5, cv), which is a sac-like canal that occupies a relatively large region between two bony bridges of the frontal, which are themselves also autapomorphic for *Denticeps* (Greenwood, 1968a; Fig. 4B, fbs). Other

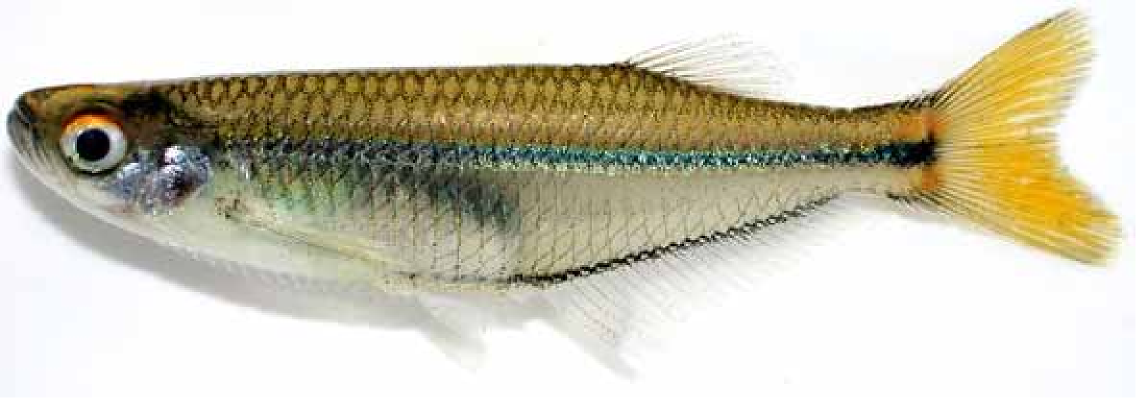

FIGURE 1. Freshly-preserved specimen of *Denticeps clupeoides* (SAIAB 74877; same collection as MZUSP 84776), 42.1 mm S.L. Photo by R. Bills.

features of the cephalic sensory canals of *Denticeps* have been noted, although their phylogenetic significance remains nebulous. Clausen (1959) observed five to seven soft unbranched aborbital tubules crossing the opercle of *Denticeps* in an oblique posteroventral direction. These tubules originate "from the postemporal and extrascapular portions of the main trunk, and (…) from the near junction between the infraorbital and preopercular branches." (Clausen, 1959:144). Similarity between those tubules and the branched sensory canals in the head of species of the Clupeoidei led Greenwood (1968a) to consider their presence as evidence that *Denticeps* is indeed a clupeomorph, at a time when characters from other complexes indicative of such a relationship were unknown or speculative.

Collecting efforts in the Republic of Benin recently yielded a large number of specimens of *Denticeps clupeoides* for study (Fig. 1). Observations on well-preserved specimens cleared and stained for bone, cartilage, and nerves, revealed details of the cephalic sensory canals unrecorded or not precisely described so far. The exact patterns and points of ramification of sensory tubules from main cephalic trunks could thus be identified and described for the first time. On the basis of new data, specific hypotheses of homologies between those tubules and sensory branches of members of the Clupeoidei are proposed. The aim of this paper is to report on these new findings and to interpret their phylogenetic significance.

MATERIAL AND METHODS

A total of 21 specimens of *Denticeps clupeoides,* between 26.1 and 40.7 mm SL, were prepared according to the clearing and counter-staining techniques of Taylor & van Dyke (1985) and Song & Parenti (1995), which allow for visualization of bone and cartilage. The nerve staining phase of Song & Parenti (1995) was successfully done in six of those specimens. In order to facilitate visualization of the cephalic sensory canals in cleared and stained specimens, India ink diluted in 50% glycerin was injected into that system, through a small opening in the usually large preopercular sensory canal. A similar procedure was employed for seven alcohol preserved specimens bleached with hydrogen peroxide, but in this case, India ink was diluted in 70% alcohol. Dissection of cleared and stained specimens followed the protocol described in Weitzman (1974), which exposes most of the relevant skeletal structures while minimizing damage to articulations. Drawings were made with a camera lucida attached to a stereomicroscope. Anatomical terminology follows Weitzman (1962), and Grande (1985). Cephalic canal terminology follows Nelson (1972) and Di Dario (2004).

Institutional abbreviations

ANSP, Academy of Natural Sciences, Philadelphia
FMNH, Field Museum, Chicago
INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus
MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica, Porto Alegre
MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo
SAIAB, South African Institute for Aquatic Biodiversity, Grahamstown
UMMZ, University of Michigan Museum of Zoology, Ann Arbor

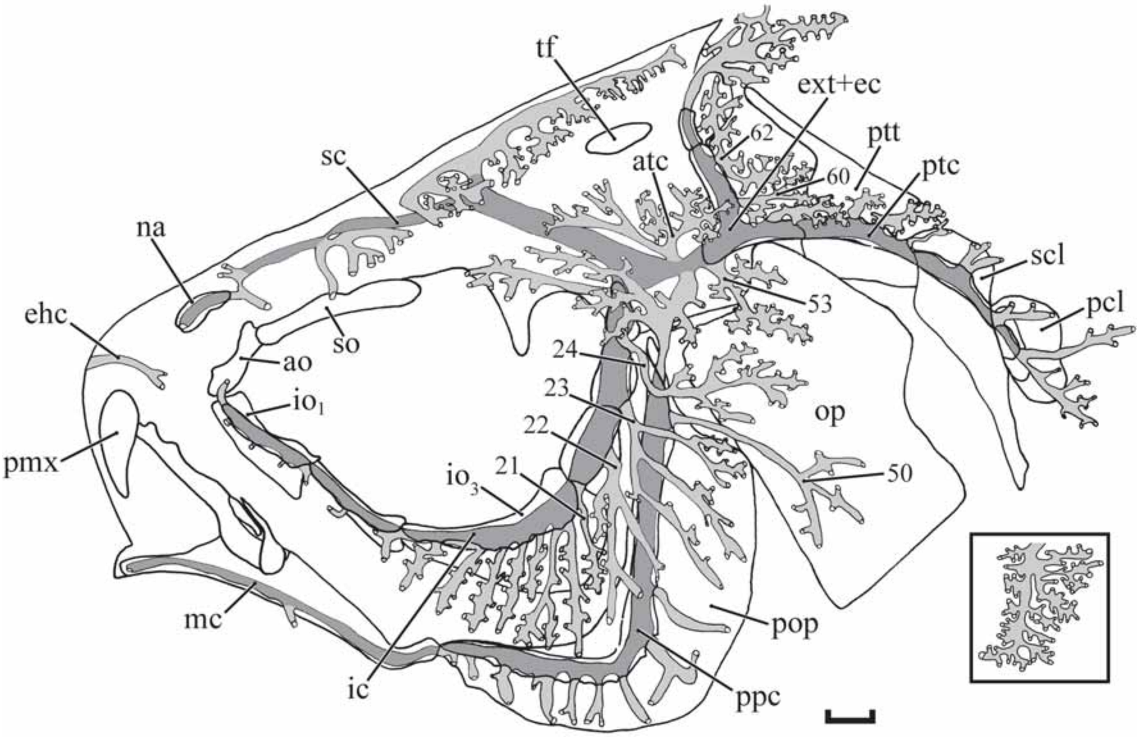

FIGURE 2. Cephalic latero-sensory canals and superficial bones of the head in *Dorosoma cepedianum* (82 mm S.L.), after Stephens (1985). Lateral view, left side. Inset shows extensive branching of the post-temporal canal based on a 290 mm S.L. specimen. Dark grey represents portions of cephalic canals enclosed or overlain by bone; light grey represents canals in soft tissue. Branches are numbered according to Stephens (1985). Supratemporal system not represented. Scale bar = 1 mm.

USNM, National Museum of Natural History, Smithsonian Institution, Washington DC

Anatomical abbreviations

ao, antorbital
aor, anterior opening to the chamber of *recessus lateralis*
atc, accessory temporal sensory canal
atio$_1$, anterior tubule of infraorbital 1
atpc, anterior tubule of post-temporal sensory canal
atss, anterior tubule of supratemporal system
bs, basisphenoid
cv, supraorbital cavern
dfp, dorsal opening of the pre-epiotic fossa
dmpb, dorsal middle tubule of postorbital bulla
dsp, dermosphenotic
dtpb, dorsal tubule of postorbital bulla
dtpp, dorsal tubule of preopercular sensory canal
ec, extrascapular sensory canal
ehc, ethmoidal sensory canal
epo, epioccipital
exo, exoccipital
ext, extrascapular
fbs, parasagittal frontal bridge
fp, pre-epiotic fossa
fr, frontal
gr, groove on the lateral wing of the frontal
ic, infraorbital sensory canal
io$_{1-5}$, infraorbital bones 1-5
iop, interopercle
lopoc, ventral opening for main preopecular sensory canal
mc, mandibular sensory canal
mor, middle opening to the chamber of *recessus lateralis*
mx, maxilla
na, nasal
op, opercle
optt, middle opening of the post-temporal
os, orbitosphenoid
oscl, posterior opening of the supracleithrum
pa, parietal
pcl, postcleithrum
pio$_4$, posterodorsal process of laminar region of infraorbital 4
pmx, premaxilla

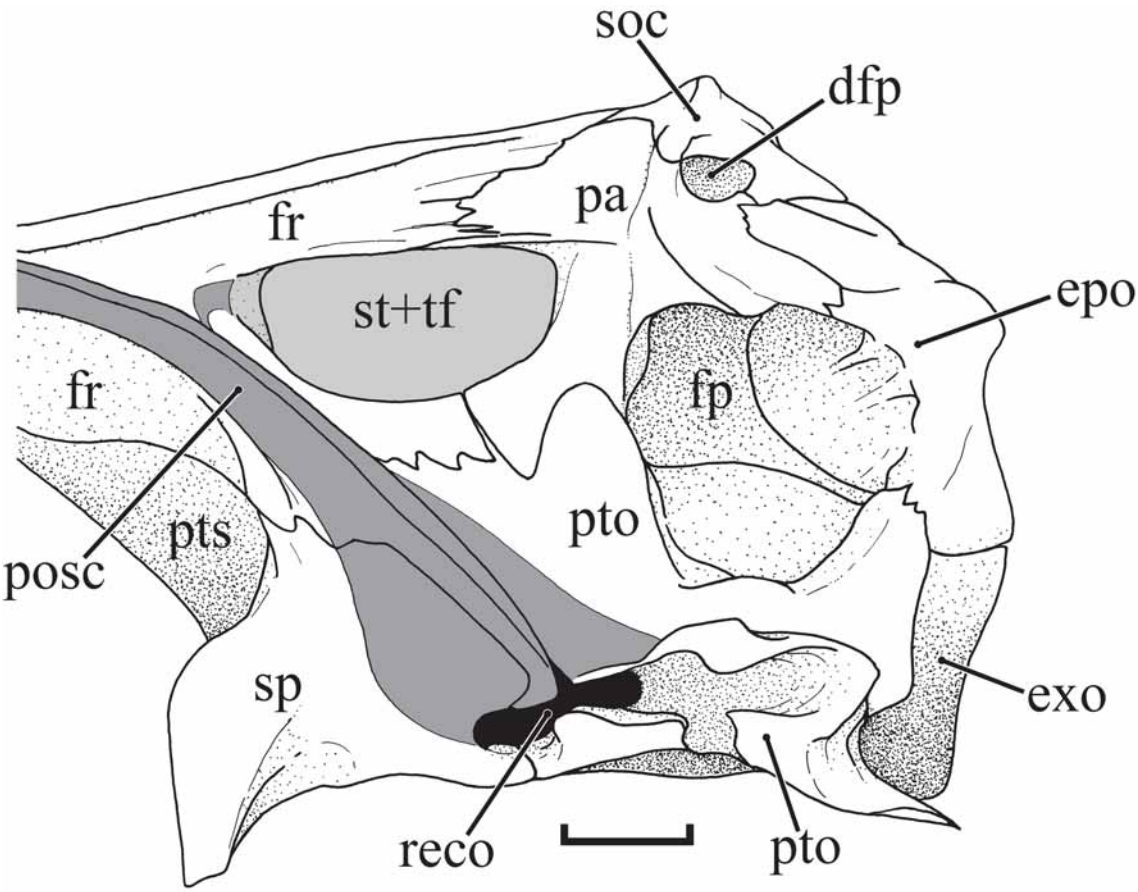

FIGURE 3. Temporal region of the cranium in *Clupea harengus* (ANSP 157065). Lateral view, left side. The *sinus temporalis* (st) fills the temporal foramen (tf). Branching of the *sinus temporalis* not represented. Dark grey represents portions of cephalic canals enclosed by bone; light grey represents canals in soft tissue. Scale bar = 1 mm.

pop, preopercle
por, posterior opening to the chamber of *recessus lateralis*
posc, postorbital branch of supraorbital sensory canal
ppc, preopercular sensory canal
pro, prootic
ptc, post-temporal sensory canal
ptec, parietal tubule of extrascapular sensory canal
ptio$_1$, posterior tubule of infraorbital 1
pto, pterotic
ptpc, posterior tubule of post-temporal sensory canal
ptrc, posterior tubule of *recessus lateralis*
pts, pterosphenoid
ptss$_1$, posterior tubule of supratemporal system 1
ptss$_2$, posterior tubule of supratemporal system 2
ptt, post-temporal
pvor, posteroventral opening to the chamber of *recessus lateralis*
rec, chamber of the *recessus lateralis*
reco, common opening to the chamber of the *recessus lateralis*
sc, supraorbital sensory canal
scl, supracleithrum
so, supraorbital
soc, supraoccipital
sop, subopercle
sp, sphenotic
ss, supratemporal system
st, *sinus temporalis*
stec, supraoccipital tubule of extrascapular sensory canal
tcv, tubule of supraorbital cavern
tf, temporal foramen.
tfc, chamber of temporal foramen
tlopoc, tubule of the ventral opening for main preopercular sensory canal
tpvr, tubule of the posteroventral opening of *recessus lateralis*

tuopoc, tubule of the dorsal opening for main preopercular sensory canal
uopoc, dorsal opening for main preopecular sensory canal
vmpb, ventral middle tubule of postorbital bulla
vtpb, ventral tubule of postorbital bulla

Comparative material examined

Number of examined specimens follows catalog number, and refers to number of cleared and stained specimens examined (unless noted: alc, alcohol preserved, unstained specimen; skl, skeleton), not to total number in lot:

Clupeiformes
Denticipitidae: *Denticeps clupeoides,* MZUSP 62480, 1; MZUSP 84776, 20 + 7(alc).
Chirocentridae: *Chirocentrus dorab,* MZUSP 62467, 1; MZUSP 72930, 1(skl).
Clupeidae: *Alosa caspia,* USNM 143891, 1; *A. pseudoharengus,* MZUSP 62471, 1; *Anodontostoma chacunda,* MZUSP 62476, 1; *Brevoortia aurea,* MZUSP 11729, 1; *B. pectinata,* MCP 7722, 1; MCP 7725, 1; MCP 7727, 1; *Clupea harengus,* ANSP 157065, 1; *Clupeichthys aesarnensis,* MZUSP 62465, 3; *C. bleekeri,* MZUSP 63114, 1; *C. perakensis,* MZUSP 63104, 3; *Dorosoma cepedianum,* MZUSP 62481, 3; USNM 272899, 6; *Dussumieria acuta,* MZUSP 62468, 3; *Etrumeus teres,* MZUSP 62469, 3; USNM 188934, 3; *Gilchristella aestuaria,* MZUSP 64115, 3; *Harengula clupeola,* MZUSP 18672, 1; *H. jaguana,* MZUSP 11269, 2; MZUSP 10791, 1; *Herklotsichthys dispilonotus,* MZUSP 63115, 1; *Lile piquitinga,* MZUSP 11215, 1; *Ophistonema oglinum,* MZUSP 10844, 3; *Pellonula afzeliusi,* UMMZ 195029, 2; *Platanichthys platana,* MZUSP 10629, 3; MCP 19409, 3; *Rhinosardina amazonica,* MZUSP 11231, 2; MZUSP 11452, 1; *Sardina pilchardus,* MZUSP 37394, 3; MZUSP 12123, 1; *Sardinella albella,* MZUSP 63117, 2; *S. aurita,* USNM 272875, 2; *S. brasiliensis,* MZUSP 12124, 1; MZUSP 11418, 2; *S. maderensis,* MZUSP 37382, 1; *Tenualosa ilisha,* USNM 276407, 2; *Spratelloides delicatulus,* MZUSP 62470, 3.
Coiliidae: *Coilia neglecta,* USNM 357380, 6; *C. rebentischii,* MZUSP 62483, 1; *Lycothryssa crocodilus,* MZUSP 62482, 1; *Setipinna melanochir,* MZUSP 64119, 1; *Thryssa baelama,* ANSP 63228, 1; *T. hamiltoni,* USNM 364595, 1; *T. mystax,* ANSP 60578, 1.
Engraulidae: *Amazonsprattus scintilla,* MZUSP 28475, 2(alc); *Anchoa filifera,* MZUSP 18528, 2; *A. lamprotaenia,* MZUSP 11508, 2; *A. lyolepis,* MZUSP 11476, 2; *A. spinifer,* MZUSP 11454, 2; *A. tricolor,* MZUSP 11547, 2; *Anchovia clupeoides,* MZUSP 11559, 1; *Anchoviella brevirostris,* MZUSP 11578, 2; *A. carrikeri,* MZUSP 5728, 3; *A. guianensis,* MZUSP 5726, 1; *A. lepidentostole,* MZUSP 51826, 2; *Cetengraulis edentulus,* MZUSP 11634, 3; *Encrasicholina heteroloba,* MZUSP 63118, 2; *Engraulis anchoita,* MZUSP 18393, 10; *Pterengraulis atherinoides,* MZUSP 11723, 1; *Stolephorus indicus,* MZUSP 63112, 2; MZUSP 63113, 1; MZUSP 63106, 1.
Pristigasteridae: *Chirocentrodon bleekerianus,* MZUSP 11097, 3; *Ilisha africana,* MZUSP 62463, 4; *I. amazonica,* MZUSP 33266, 2; *I. elongata,* UMMZ 219537, 1; *I. kampeni,* MZUSP 62477, 2; *I. megaloptera,* MZUSP 62472, 2; *I. melastoma,* MZUSP 62473, 2; *Neoopisthopterus tropicus,* MZUSP 62478, 2; *Odontognathus mucronatus,* MZUSP 11264, 3; MZUSP 11267, 3; MZUSP 10835, 2; *Opisthopterus dovii,* MZUSP 62462, 3; *O. equitorialis,* MZUSP 62479, 2; *O. tardoore,* MZUSP 62475, 2; *Pellona castelnaeana,* INPA 4959, 1; MZUSP 5492, 1; *P. ditchela,* ANSP 63526, 1; USNM 189996, 1; *P. flavipinnis,* MZUSP 40063, 1; MZUSP 18728, 1; *P. harroweri,* MZUSP 11283, 3; MZUSP 11308, 1; MZUSP 11374, 3; *Pliosteostoma lutipinnis,* FMNH 2818, 2; *Pristigaster cayana,* MZUSP 30338, 3; *P. whiteheadi,* INPA 8555, 3; *Raconda russeliana,* MZUSP 62466, 4.

Gonorynchiformes
Chanidae: *Chanos chanos,* MZUSP 62601, 1; USNM 347536, 9.
Gonorynchidae: *Gonorynchus* sp., MZUSP 63663, 1.
Kneriidae: *Kneria auriculata,* MZUSP 63121, 4; USNM 290762, 2.

Cypriniformes
Catostomidae: *Catostomus commersoni,* USNM 238094, 2; USNM 238111, 2; USNM 340759, 2.
Cyprinidae: *Opsariichthys uncirostris,* USNM 87445, 2; *Zacco platypus,* MZUSP 62597, 1.
Gyrinocheilidae: *Gyrinocheilus aymonieri,* USNM 271692, 1.

Characiformes
Citharinidae: *Citharinus latus,* MZUSP 84480, 1.
Distichodontidae: *Xenocharax spilurus,* MZUSP 50358, 1.
Characidae: *Hollandichthys multifasciatus,* MZUSP uncataloged, 5.
Curimatidae: *Curimata roseni,* MZUSP 55740, 1.

Argentiniformes
Argentinidae: *Argentina striata,* USNM 188212, 2.
Alepocephalidae: *Searsia koefoedi,* USNM 206873, 1; *Talismania aphos,* USNM 215540, 1.

Salmoniformes
Galaxiidae: *Galaxias auratus,* USNM 344893, 3; USNM 344895, 1.
Osmeridae: *Osmerus mordax,* MZUSP 64116, 1.
Salmonidae: *Salmo* sp., MZUSP uncataloged.

Esociformes
Esocidae: *Esox americanus,* USNM 237257, 2; USNM 120051, 2.
Umbridae: *Dalia pectoralis,* USNM 034033, 1; *Umbra pygmaea,* USNM 333152, 3; USNM 345523, 1.

Elopomorpha
Albulidae: *Albula vulpes,* MZUSP 10625, 2.
Elopidae: *Elops* sp., MZUSP 60346, 1.
Megalopidae: *Megalops cyprinoides,* USNM 173580, 3.

Osteoglossomorpha
Hiodontidae: *Hiodon tergisus,* MZUSP 28450, 1; *H. alosoides,* USNM 350554, 1. Notopteridae: *Chitala* sp., MZUSP uncataloged, 1.

RESULTS

Supratemporal system

The temporal foramen of *Denticeps clupeoides* is overlain by a flange formed mostly by the frontal (Greenwood, 1968a; Patterson, 1970; Fig. 5). A small portion of the posterior region of that flange, and consequently of the temporal foramen, is of parietal origin. The flange is arched laterally, resulting in a somewhat bulged chamber with a ventrally directed aperture. As the temporal foramen of *Denticeps* is housed within that chamber, the ventral opening of the chamber may be regarded as the actual exit to the exterior of the *sinus temporalis*. That distinguishes *Denticeps* from other clupeiforms, where the opening of the temporal foramen is directed laterally (Fig. 3). In spite of major differences in the architecture of the temporal region, the relative sizes of the opening of the chamber of the temporal foramen in *Denticeps* and the temporal foramen of other clupeiforms are similar.

The *sinus temporalis* completely fills the chamber of the temporal foramen in *Denticeps clupeoides* (Figs. 4A and 5). Consequently, the structure is relatively larger in *Denticeps* than in species of the Clupeoidei. Additionally, a superficial connection between the *sinus temporalis* and the supraorbital canal, present in some members of the Clupeoidei (e.g., Fig. 3), is absent in *Denticeps*. The region between the *recessus lateralis* and the opening of the chamber of the temporal foramen is slightly concave, with a pronounced angle close to the middle of the opening. A small portion of the *sinus temporalis* projects from the ventral opening of the chamber and rests on that concavity.

A series of unbranched tubules with diameters approximately similar among themselves, but somewhat variable along their length, originate from the exposed portion of the *sinus temporalis* (Figs. 4A and 5). Each tubule crosses the temporal region in a posteroventral direction and end in a pore. Tubules of the supratemporal system in *Denticeps* are extremely delicate and are often damaged during preparation and dissection of specimens. Of 21 cleared and stained specimens examined here, only nine had intact tubules on both sides of the head. Of those, one specimen has four tubules on each side, whilst two other specimens have three tubules on each side. All other specimens show different numbers on the left and right sides, revealing rampant bilateral variation in supratemporal tubule number in *Denticeps*. Two of the same nine specimens have three right and four left tubules, and two other specimens have those values reversed. A single specimen has three right and five left tubules, but with the anteriormost of those five extremely short. Another single specimen has three right and two left tubules. In nine additional specimens, supratemporal tubules could be counted on one side only (usually the left one, due to normal dissection practice). Seven of those have three tubules and two have four tubules. Finally, three other specimens were extensively dissected in the head, and tubules could not be counted on either side, although their severed remains in the soft tissue definitely indicate their presence.

In spite of variation in numbers of tubules of the *sinus temporalis,* the length of tubules and the region of the cranium they cover are approximately constant. One or two of the anterior tubules are short and reach only to the anteroventral margin of the extrascapular (Figs. 4 and 5). The extrascapular bears sections of the extrascapular and post-temporal canals, and both canals converge to a single opening at the posterior region of the *recessus lateralis* (Di Dario, 2004). Remaining one to three posterior tubules of the supratemporal system are longer and overlie the extrascapular bone (and associated canal) and the anterior region of the post-temporal bone (Figs. 4 and 5). A tubule of the post-temporal canal projects from a somewhat oblique opening at the post-temporal bone (Fig. 4B, optt), which encloses that portion of the main trunk of the post-temporal canal. The oblique opening at the post-temporal bone marks the posterior limit reached by any tubule of the supratemporal system.

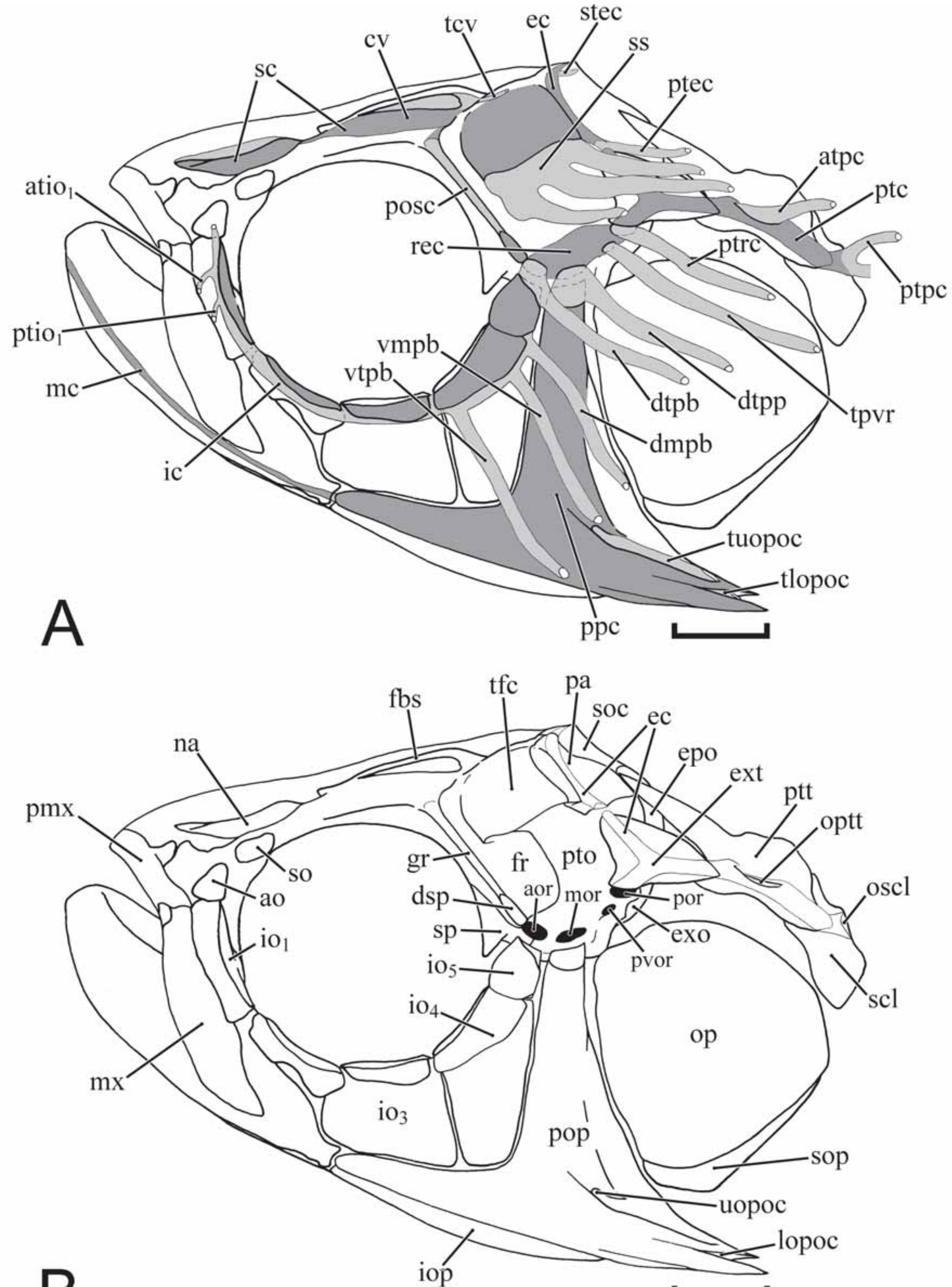

FIGURE 4. Cephalic latero-sensory canals (A) and superficial bones of the head (B) in *Denticeps clupeoides* (MZUSP 84776). Lateral view, left side. Dark grey represents portions of cephalic canals enclosed or overlain by bone; light grey represents canals in soft tissue. Dermal denticles not represented. Scale bars = 1 mm.

The region ventral to the opening of the chamber of the temporal foramen and portions of the dorsal regions of the extrascapular and post-temporal overlain by tubules of the supratemporal system are devoid of odontodes, which otherwise cover most bones of the head, the dorsal portion of the pectoral girdle, and associated scales (Clausen, 1959; Greenwood, 1968a; Sire *et al.,* 1998).

Postorbital bulla, and ramification of cephalic sensory canals

The pattern of ramification of cephalic sensory canals is remarkably constant among specimens of *Denticeps* examined, with just minor variation. The overall aspect is much less complex than that in members of the Clupeoidei. The infraorbital, supraorbital, preopercular, and post-temporal canals have primary tubules, which typically do not ramify (Fig. 4A).

A hitherto unrecorded specialization of the infraorbital canal of *Denticeps clupeoides* adds to the plethora of outstanding structures of the acusticolateralis system of clupeomorphs. The proximal portion of the infraorbital canal of *Denticeps* is markedly dilated, forming an elongated and clearly recognizable bulla, here called postorbital bulla (Figs. 4 and 6). Hypertrophy of that portion of the infraorbital canal reflects on the structure of associated infraorbital bones. Infraorbital 5 encloses the proximal region of the postorbital bulla and is therefore unusually inflated (Fig. 6), to such an extent that it is laterally the most prominent bone in the head. The mid- to anterior portion of the postorbital bulla is partially covered by the anterior margin of infraorbital 4 that gradually tapers distally. The posterodorsal region of the laminar component of infraorbital 4 in most examined specimens of *Denticeps* bears a delicate process that shores the posterior margin of the median section of the postorbital bulla (Fig. 6, pio$_4$). A major portion of the postorbital bulla, located between the projection of the anterior margin and the process at the posterodorsal region of the laminar component of infraorbital 4, is not enclosed by bone. The anterior end of the postorbital bulla is marked by an abrupt decrease in diameter of the infraorbital canal (Fig. 6), which then remains roughly the same for the rest of its length (Fig. 4).

Four tubules of the latero-sensory system of the head of *Denticeps* originate from the postorbital bulla. These tubules are not enclosed by bone, are approximately parallel, have the same length and diameter, and project from the postorbital bulla in roughly posteroventral direction (Fig. 4A). During their course, they overlie the preopercle and associated canal. As with tubules of the supratemporal system and those of other main cephalic canals, tubules of the postorbital bulla end in a pore. The dorsal tubule of the postorbital bulla originates near the connection between the infraorbital canal and the *recessus lateralis,* and ends approximately on the middle of the opercle (Figs. 4 and 6, dtpb).

Two tubules project from the middle region of the postorbital bulla. The dorsal one originates at the articulation between infraorbitals 4 and 5 (Figs. 4 and 6, dmpb). It is separated from the ventral middle tubule by a small bony process (Fig. 6, pio$_4$, described above). The two middle tubules of the postorbital bulla are closer to each other than each is to other tubules of the postorbital bulla. The dorsal middle tubule typically does not branch and ends in a region close to the middle of the posterior margin of the preopercle (Fig. 4). Variation in course and ramification was observed in the dorsal middle tubule of the postorbital bulla. In four examined specimens of *Denticeps,* the distal region of the dorsal middle tubule abruptly turns dorsally at a roughly 90° angle upon passing the posterior border of the preopercle and ends on the anterior third of the opercle. In one examined specimen, the dorsal middle tubule bifurcates. The dorsal branch of the bifurcation ends at a pore located approximately on the anterior third of the opercle, while the ventral one ends on the middle to ventral region of the posterior border of the preopercle. The ventral middle tubule never ramifies (Fig. 4A, vmpb), and ends in a pore at a region close to the dorsal opening for the main preopercular latero-sensory canal (Fig. 4B, uopoc).

The fourth tubule of the postorbital bulla originates ventrally at the anterior region of infraorbital 4 (Figs. 4A and 5, vtpb). It is oriented towards the angled posteroventral border of infraorbital 4, and ends at a region close to the middle of the ventral border of the preopercle.

Two short tubules of the infraorbital canal originate at the anterior region of the canal sector located in infraorbital 1. They are slightly curved posteriorly, and each ends in a pore at the ventral border of infraorbital 1 (Fig. 4A, atio$_1$ and ptio$_1$).

The main trunk of the preopercular canal is entirely enclosed in the somewhat inflate preopercle except for a relatively small region of connection with the *recessus lateralis,* where a posteroventrally-directed dorsal tubule of the preopercular canal originates (Figs.

4A and 6, dtpp). That tubule is dorsal to the dorsal tubule of the postorbital bulla. Both tubules are roughly parallel and have similar lengths and diameters, with the dorsal tubule of the preopercular canal ending in a pore located on the middle of the opercle (Fig. 4). Two additional tubules of the preopercular canal are located at the posteroventral region of the preopercle. The shape of the preopercle and the pattern of ramification of that portion of the preopercular canal were accurately described by Greenwood (1968a). He labeled the openings in the posteroventral region of the bone from which those tubules project as the upper and lower openings of the main preopercular sensory canal (Greenwood, 1968a:238-239; Fig. 4B, uopoc and lopoc, respectively). The upper opening of the preopercular canal leads to a narrow groove that houses its tubule (Fig. 4A, tuopoc). The lower opening of the preopercular canal is a long slit (Greenwood, 1968a). Both tubules end in pores at the margin of the posterior tip of the preopercle, which is extremely sharp (Greenwood, 1968a).

A total of four tubules are associated to the *recessus lateralis.* The two ventral ones have been described above in association with the preopercular canal and the postorbital bulla. A long tubule originates from the posteroventral opening of the *recessus lateralis,* located between its middle and posterior openings (Fig. 4B, pvor). Di Dario (2004) hypothesized that opening of the *recessus* as autapomorphic for *Denticeps clupeoides.* The tubule of the posteroventral opening of the *recessus lateralis* crosses in a ventral oblique direction the dorsal third of the opercle and ends in a pore at the posterior border of the bone (Fig. 4A, tpvr). The dorsal and last tubule associated to the *recessus lateralis* (Fig. 4A, ptrc) originates at the connection between the posterior opening of the *recessus* (Di Dario, 2004; Fig. 4B, por) and the canal enclosed in the anterior region of the extrascapular bone, which results from the merging of the proximal tips of the extrascapular and post-temporal canals. The posterior tubule of the *recessus lateralis* is dorsal and parallel to the tubule of the posteroventral opening of the *recessus,* runs along the proximal region

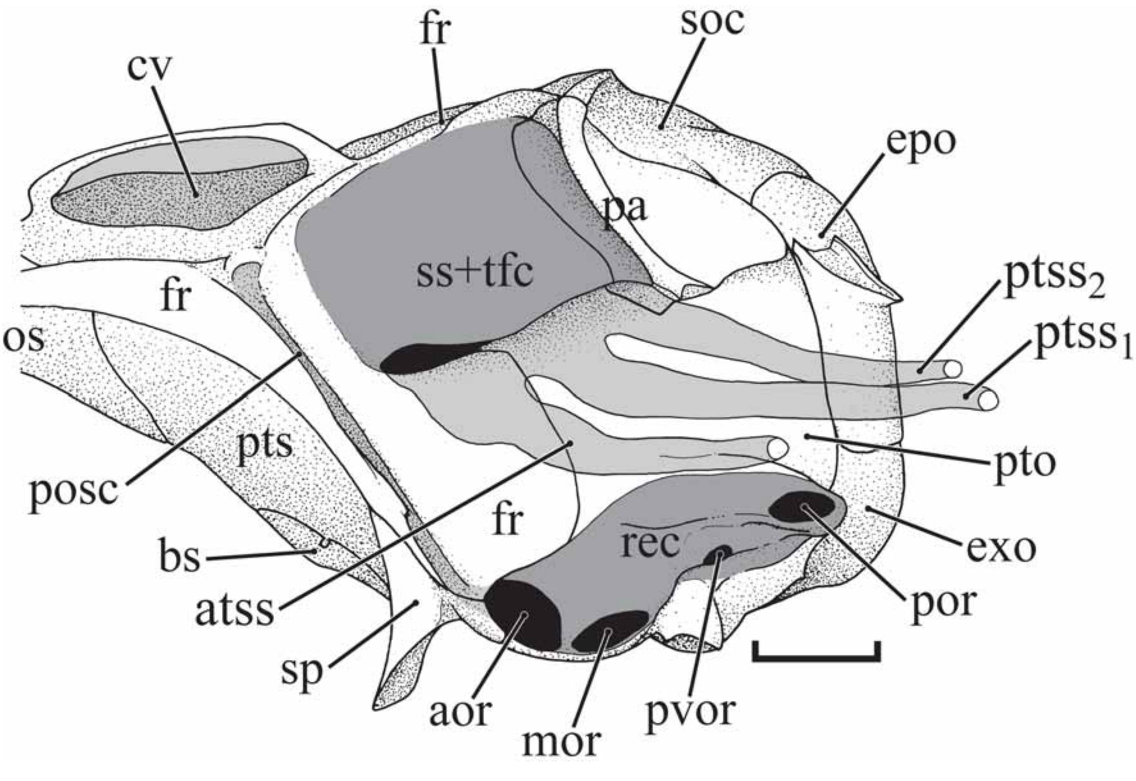

FIGURE 5. Main components of the latero-sensory system in the supraorbital and temporal regions of the cranium in *Denticeps clupeoides* (MZUSP 84776). Lateral view, left side. Extrascapular not represented. The *sinus temporalis* portion of the supratemporal system (ss) fills the temporal foramen chamber (tfc), which also houses the temporal foramen. Three tubules of the supratemporal system are present in this specimen (atss, ptss$_1$, and ptss$_2$), but 2 to 5 tubules are variably present in other specimens examined. Dark grey represents portions of cephalic canals enclosed or overlain by bone; light grey represents canals in soft tissue. Dermal denticles, tubule of supraorbital cavern, and extrascapular not represented. Scale bar = 0.5 mm.

of the opercle, and ends in a pore at the posterodorsal border of the bone.

Portions of the infraorbital bones, preopercle, and opercle overlain by superficial tubules of the *recessus lateralis* and of the infraorbital and preopercular canals lack odontodes (Fig. 6). That may have led Clausen (1959:144) to note that the tubules over the opercle of *Denticeps* are fringed by odontodes, when in fact odontodes cover the whole region except the paths of tubules. Greenwood (1960) noticed two large and well-defined odontode-free areas on the opercle of *Paleodenticeps tanganikae.* The position of those areas suggests that in life they were overlain by superficial tubules in a similar way as in *Denticeps clupeoides* (Greenwood, 1960).

Short tubules were also observed in the extrascapular, post-temporal, and supraorbital canals of *Denticeps clupeoides.* Two tubules are present in the post-temporal canal. The anterior one projects from a somewhat oblique dorsal opening at the middle of the post-temporal bone (Fig. 4B, optt). That tubule is oriented in a posterodorsal direction, and ends in a pore (Fig. 4A, atpc). The post-temporal canal bears another posterior tubule in the short space located between the supracleithrum and the first lateral-line scale (Fig. 4A, ptpc). As in the case of the anterior tubule, the posterior tubule of the post-temporal canal extends posterodorsally and ends in a pore. The extrascapular canal sends out two tubules during its course. The longer of those tubules (Fig. 4A, ptec) is present in the region of articulation between the extrascapular and the parietal, in the short space where the extrascapular canal is not enclosed by either of these two bones (Figs. 4B and 6). It is closely associated to and rests along the dorsal margin of the posteriormost tubule of the supratemporal system. The openings of both tubules are located in roughly the same region, which is slightly posterior to the posterior border of the extrascapular bone. Another short tubule originates at the space between the ossified segments of the extrascapular canal in the parietal and the supraoccipital (Fig. 4A, stec). That tubule projects posteriorly roughly perpendicular to the main axis of the body, and ends in a pore at a region close to the superficial border of the supraoccipital.

The last tubule of a cephalic sensory canal of *Denticeps* is a delicate structure located at the posterolateral region of the supraorbital cavern (Figs. 4A and 6, cv), which is a specialization of the supraorbital canal (Greenwood, 1968a). It extends over the top of the cranium, and opens in a small pore dorsal to the region between the anterior and posterior borders of the chamber of the temporal foramen (Fig. 4A, tcv).

DISCUSSION

Patterson (1970) suggested the presence of the supratemporal system as a synapomorphy of the Clupeoidei, and one which is absent in other teleosts including *Denticeps clupeoides* (Greenwood, 1968a). Our observations show that a supratemporal system is actually present in *Denticeps,* and that the structure is therefore a synapomorphy of the Clupeiformes. Differences in the anatomy of the supratemporal system, particularly of the *sinus temporalis,* between *Denticeps* and members of the Clupeoidei, explain the difficulties in identifying the structure in that genus previously. Such differences are probably related to the peculiar architecture of the temporal region in *Denticeps,* especially of its temporal foramen. The supratemporal system is a delicate structure, not preserved in fossils. Nevertheless, as the *sinus temporalis* is homologous to the parietal branch of the supraorbital canal (Wohlfahrt, 1937; Bamford, 1941; Di Dario, 2004), its absence can be inferred in fossils where that portion of the canal is unmodified (Patterson, 1970). Such is the case for all non-clupeiform clupeomorphs (Grande, 1985). The supratemporal system is also absent in all other known teleosts.

The identification of the supratemporal system in *Denticeps* also refutes the hypothesis of Di Dario (2004) that the supratemporal system of the Clupeoidei and the supraorbital cavern of *Denticeps* are homologous. The supraorbital cavern is exclusive to *Denticeps* among recent teleosts, as originally proposed by Greenwood (1968a). A particular feature of the supraorbital cavern, previously unnoticed, is the presence of an associated tubule (Fig. 4A, tcv). The pore at the distal end of that tubule is the only direct connection between the supraorbital cavern and the environment.

Another specialization of the cephalic sensory canals exclusive to *Denticeps clupeoides* is the postorbital bulla. The degree of inflation of that portion of the infraorbital canal and related bones, particularly of infraorbital 5, is unique among examined members of the Clupeoidei, other clupeomorphs and other lower teleosts (Grande, 1982a, 1982b, 1985; Chang & Grande, 1997; Chang & Maisey, 2003). This character cannot currently be observed in *Paleodenticeps tanganikae.* Tentatively, the postorbital bulla is hypothesized as a synapomorphy of the Denticipitoidei, based on the quite similar overall morphology of the circumorbital bones in *Denticeps* and *Palaeodenticeps* (Greenwood, 1960:8). Although the function of the postorbital bulla cannot be precisely determined at the moment, it is known that widening of portions of latero-sensory canals is associated with enhanced sensitivity to mechanical waves (Blaxter, 1987; Coombs *et al.,* 1988; Webb, 1989).

Four major patterns of cephalic sensory canals have been identified in teleosts, according to their general anatomy and degree of branching (Coombs *et al.,* 1988; Webb, 1989). *Denticeps clupeoides* has the simple canal pattern, where canals are typically cylindrical with bony walls, and only primary ramifications (tubules) are present. Such pattern is also present in representative basal teleosts, as in the osteoglossomorph *Hiodon* (Allis, 1904; Nelson, 1972; Hilton, 2002), and in ostariophysans such as *Chanos chanos,* cypriniforms (Lekander, 1949; Nelson, 1972; Siebert, 1987), primitive siluriforms (Arratia, 1987; Arratia & Huaquin, 1995), and characiforms (pers. obs.). The Clupeoidei is apomorphically characterized by the presence of a highly-branched canal pattern, forming an elaborate system composed of numerous pores at the end of secondary, tertiary, or even higher-order branching of sensory canals in the soft tissue of the head (Fig. 2). Such a pattern is most probably primitive for the suborder in view of its wide distribution among representative members of the clade, which spam most of the clades recognized for Pristigasteridae, Engraulidae and Clupeidae (Wohlfahrt, 1937; Bamford, 1941; Gunther & Demoran, 1961; Nelson, 1972; Hoss & Blaxter, 1982; Nelson, 1983; Stephens, 1985, 1996; Blaxter, 1987; Webb, 1989). Basal euteleosts typically have reduced, unbranched (i.e., simple) canal patterns (Nelson, 1972; Coombs *et al.,* 1988; Webb, 1989). Complex ramifications similar to the condition found in the Clupeoidei are rare among lower teleosts. Some such cases occur within Siluriformes, where the possession of a dendritic arrangement of latero-sensory canals in the skin of snout, cheek and nape is hypothesized as a

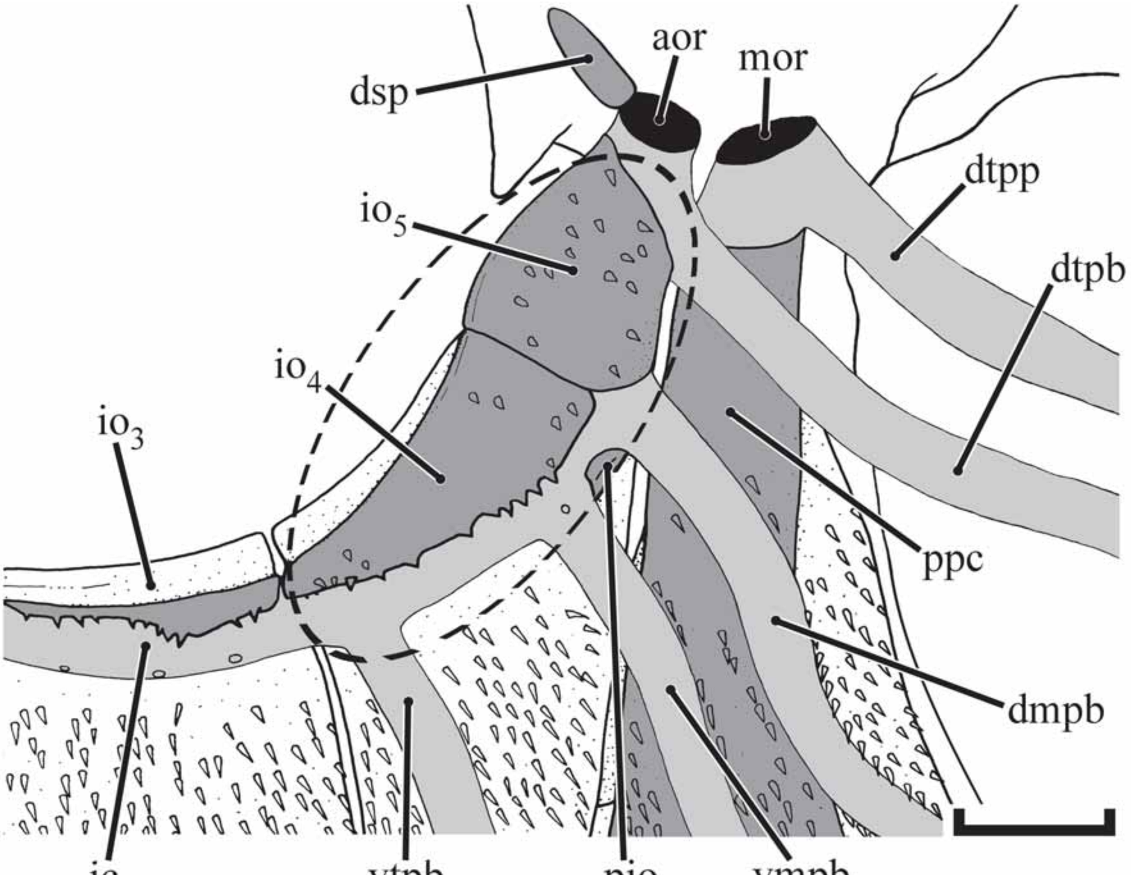

FIGURE 6. Postorbital bulla and surrounding structures in *Denticeps clupeoides* (MZUSP 84776). Lateral view, left side. Dark grey represents portions of cephalic canals enclosed or overlain by bone; light grey represents canals in soft tissue. Dashed ellipse shows the postorbital bulla. Scale bar = 0.5 mm.

synapomorphy of the Pimelodidae, sensu stricto (character 1 of Lundberg *et al.,* 1991), also occurring homoplastically in some other siluriform subclades (de Pinna, 1993). The elopiforms *Elops* and *Megalops* also have been reported to have a branched pattern of cephalic sensory canals (Webb, 1989). Nevertheless, the degree of ramification of those canals and the extent to which the network covers the head is much reduced when compared to members of the Clupeoidei (Nelson, 1972; Webb, 1989). Cephalic sensory canals in other elopomorphs are unbranched, except for a few shallow-water anguilliforms (Coombs *et al.,* 1988; Webb, 1989), indicating that the states in the Elopiformes and the Clupeoidei are convergent. Cephalic sensory canals with secondary and tertiary branches are found in basal actinopterygians, as in Lepisosteiformes (Allis, 1904) and Amiiformes (Allis, 1889), and in distal euteleosts, as sparids, exocoetids, labrids, and serranids (Coombs *et al.,* 1988; Webb, 1989). Based on current understanding of actinopterygian relationships, such occurrences are independent of that in Clupeoidei.

The repeated occurrence of superficial ramification of cephalic sensory canals in broadly divergent levels in actinopterygian phylogeny clearly shows that the character is prone to rampant homoplasy at higher levels. Within Clupeoidei, however, canal branching is constant in all species except highly paedomorphic ones, such as *Amazonsprattus* (pers. obs.) and *Sundasalanx* (Siebert, 1997). Cases of reversal in miniaturized species is not surprising, given that the latero-sensory canal system expands and branches off ontogenetically (Stephens, 1985; Weitzman & Vari, 1988; Webb, 1989; Arratia & Huaquin, 1995). We note, however, that the typical highly-branched pattern occurs in some other putatively paedomorphic small clupeoids, such as *Thrattidion noctivagus* (Roberts, 1972).

The condition of superficial sensory tubules on the head of *Denticeps clupeoides* is also elucidative at other levels of clupeiform phylogeny. The posteroventral opening of the *recessus lateralis* and its associated tubule are features exclusive of *Denticeps* among Recent teleosts (Di Dario, 2004). Whether this condition is a synapomorphy for *Denticeps* or Denticipitoidei cannot be resolved at present, because the relevant anatomical portions are not well-preserved in the *recessus lateralis* of available specimens of *Paleodenticeps tanganikae* (Greenwood, 1960).

Homologies between tubules of the latero-sensory system of the head of *Denticeps* and main trunks of the highly branched canals in members of the Clupeoidei can also be hypothesized, within the framework of a sister group relationship between the two taxa (Greenwood, 1968a; Greenwood *et al.,* 1966; Grande, 1985; Di Dario, 2002, 2004). The origin, angle of orientation, and extent of projection over the opercle, are all strongly suggestive of a homology between the posterior tubule of the *recessus lateralis* of *Denticeps* (Fig. 4A, ptrc) and branch 53 identified by Stephens (1985) in *Dorosoma* (Fig. 2). That branch, which originates between the extrascapular and the posterior opening of the *recessus lateralis,* also occurs in all members of the Clupeoidei so far studied (c.f. Stephens, 1985). No such tubule or branch is present in non-clupeiform teleosts. Thus, the presence of an unbranched tubule or a branched canal that originates at the junction between the extrascapular bone and the *recessus lateralis* and extends over the posterodorsal region of the opercle is hypothesized as a synapomorphy of Clupeiformes.

The posterior tubule of the *recessus lateralis* of *Denticeps* and branch 53 of the Clupeoidei are the only ramifications of the cephalic canals with identical origins in the bones in the cranium of members of both taxa. The lack of equivalent landmarks for other canal branches complicates futher hypotheses of homology. Two branches are typically present between the posterior opening of the *recessus lateralis* and the parietal of the Clupeoidei (Stephens, 1985), whereas a single tubule exists at that region in *Denticeps clupeoides.* The dorsal and more developed of the ramifications of the extrascapular canal in Clupeoidei is branch 62 of Stephens (1985), which further ramifies into branches 61 and 63 (Fig. 2). The dorsal position on the extrascapular bone and the similar degree of development shared between branch 62 in Clupeoidei and the parietal tubule of the extrascapular canal in *Denticeps* suggest that those ramifications are homologous. However, the alternative hypothesis of homology between the parietal tubule of the extrascapular canal of *Denticeps* and the ventral, reduced, branch of the extrascapular canal (branch 60) of Clupeoidei cannot be currently refuted. The presence of a different and, in case of members of Clupeoidei, variable number of ramifications of the post-temporal canal (Stephens, 1985) also prevents further proposal of homologies between ramifications of that portion of the latero-sensory system in *Denticeps* and the Clupeoidei.

Further homologizing of canal branches, however, are possible on the basis of one particular ramification in *Denticeps* and Clupeoidei which may serve as a useful landmark. In both taxa, only the dorsalmost ramification of the infraorbital canal overlies the opercle. In *Denticeps,* that ramification is the dorsal tubule of the postorbital bulla, which originates from the relatively small exposed canal area between infraorbital 5 and the *recessus lateralis* (Figs. 4A and 6, dtpb). In the Clupeoidei, branch 24 of Stephens (1985) originates at the junction between infraorbital 5 and the dermosphenotic (infraorbital 6). Branch 24 is the dorsalmost ramification of the infraorbital canal in clupeoids, and the only one which extends onto the opercle. The dorsal tubule of the postorbital bulla in *Denticeps* and branch 24 share various topological similarities. Both originate at the proximal region of infraorbital 5. Also, they are oriented in a posteroventral direction, and end in a region close to the middle of the opercle. Both ramifications overlie the preopercle and, consequently, the preopercular canal along their course. That set of attributes strongly indicates that the dorsal tubule of the postorbital bulla in *Denticeps* is homologous to branch 24 in Clupeoidei. Because branch 24 is constant in several species of Clupeoidei (Stephens, 1985) and probably primitive for the clade, it is a potentially useful anatomical landmark. The main difference between the two ramifications is the position of their origin. The dorsal tubule of the postorbital bulla in *Denticeps* originates relatively closer to the *recessus lateralis* than branch 24 does in Clupeoidei. That difference, nevertheless, is a result of the extremely reduced and displaced dermosphenotic of *Denticeps,* which is dorsal to the anterior opening of the *recessus lateralis* and covers the groove for the proximal portion of the supraorbital canal in the frontal (Greenwood, 1968a; Grande, 1985; Di Dario, 2004). Dermosphenotics in Clupeoidei, contrastingly, are relatively well developed, resting between infraorbital 5 and the *recessus lateralis* (Grande, 1985; Di Dario, 2004).

If homology is accepted between the dorsal tubule in *Denticeps* of the postorbital bulla and branch 24 in clupeoids, then other ramifications of the infraorbital canals in the two taxa are easily homologized. Branches 23 to 21, which originate sequentially in the region between the distal end of infraorbital 5 and the proximal end of infraorbital 3 (Fig. 2), are found in all members of the Clupeoidei so far studied (Stephens, 1985). The posteroventral orientation, degree of development, and relations to infraorbital bones and the preopercle of branches 23 to 21 and the dorsal middle, ventral middle, and ventral tubules of the postorbital bulla of *Denticeps* (Fig. 4A) are strikingly similar, indicating that those ramifications are sequentially homologous. Branches originating between infraorbitals 1 to 3 are variable in members of the Clupeoidei (Stephens, 1985), and therefore difficult to homologize at higher taxonomic levels.

The identification of homologies between branches 21 to 24 and tubules of the postorbital bulla helps to resolve the homology between dermosphenotic of *Denticeps* and that of other teleosts. The so-called dermosphenotic of *Denticeps* is so unusual that its homologies have long been controversial (Greenwood, 1968a; Grande, 1985; Di Dario, 2004). Greenwood (1968a) was the first to propose the homology of the bone in *Denticeps* with the dermosphenotic in other teleosts. Grande (1985) and Di Dario (2004) presented and discussed a series of evidence (e.g., shape of the bone, relations to cephalic canals, absence of neuromasts) contrary to that hypothesis. Di Dario (2004) suggested instead that the so-called dermosphenotic of *Denticeps* is a neomorph, and that infraorbital 5 of *Denticeps* is actually homologous to the dermosphenotic of other teleosts, including members of the Clupeoidei. The reduction in the number of infraorbital bones from six, which is the widespread condition among basal teleosts, to five in *Denticeps* would have resulted from the fusion between infraorbitals 3 and 4 in *Denticeps.* However, the pattern of ramification of the tubules of the postorbital bulla indicates that infraorbitals 3 to 5 in *Denticeps* are indeed homologous to similarly-numbered bones in members of the Clupeoidei and other basal teleosts with the primitive condition of six infraorbital bones. These considerations support Greenwood's (1968a) idea that the dermosphenotic in *Denticeps* is actually homologous to the bone bearing the same name in other lower teleosts.

A reduction in the proximal region of the infraorbital canal with the associated displacement of the dermosphenotic from its primitive position to a location dorsal to the *recessus* might explain the articulation between infraorbital 5 and the *recessus lateralis* in *Denticeps*. The distance between the proximal portion of the infraorbital and preopercular canals in all clupeiforms is markedly reduced, a trait hypothesized as a synapomorphy of the order (Di Dario, 2004). If the proximal portion of the infraorbital canal was shortened in *Denticeps,* such morphological change would be associated with a shortening of the proximal portion of the preopercular canal. The morphology of the preopercle of *Denticeps* favors that idea. The vertical distance between the preopercle and the temporal region which houses the *recessus lateralis* or the temporal canal is markedly smaller in *Denticeps* than in other clupeomorphs (Grande, 1982a, 1982b, 1985; Chang & Grande, 1997; Chang & Maisey, 2003; pers. obs.). In members of the Clupeoidei, the horizontal distance between the preopercular and infraorbital canals is markedly shorter than the vertical distance between the preopercle and the *recessus lateralis* (Fig. 2). In *Denticeps,* on the other hand, the horizontal distance between the proximal portions of the infraorbital and preopercular canals is only slightly shorter than the vertical distance between the preopercle and the *recessus lateralis* (Fig. 4B).

The proximity between the preopercle and the *recessus lateralis* in *Denticeps* may impede the presence of more than one tubule in that region, whereas three developed branches typically exist in the large space between the preopercle and the *recessus lateralis* in species of Clupeoidei (Stephens, 1985; Fig. 2). According to Stephens (1985), the most well-developed of the aborbital branches of the proximal portion of the preopercular canal is branch 50 (Fig. 2). That branch leaves the preopercular canal shortly after leaving the dorsal opening of the preopercle, and ends in the mid- to posterior region of the opercle. The dorsal tubule of the preopercle of *Denticeps* (Fig. 4A, dtpp) also originates at the dorsal opening of the preopercle, runs in a similar orientation over the opercle, and ends approximately in the middle of the bone, as does branch 50. These features are indirect evidence that the dorsal tubule of the preopercular canal of *Denticeps* and branch 50 of members of the Clupeoidei are homologous.

RESUMO

As porções cefálicas do sistema de canais látero-sensoriais em Denticeps clupeoides *são descritas e analisadas. A espécie, uma pequena sardinha com distribuição restrita a poucos riachos relictuais na África Ocidental, é o mais primitivo Clupeomorpha vivente, e único representante Recente da subordem Denticipitoidei. Como grupo irmão das mais de 360 espécies incluídas em Clupeoidei,* Denticeps *é um táxon-chave no entendimento das relações filogenéticas em Clupeomorpha e outros Teleostei inferiores. Observações com base em espécimes recentemente coletados de* Denticeps clupeoides *revelaram detalhes inéditos e comparativamente importantes dos canais látero-sensoriais cefálicos, relevantes para o entendimento de relações em diferentes níveis da filogenia de Clupeomorpha. Os canais infraorbital, supraorbital, preopercular, extrascapular e pós-temporal de* Denticeps *possuem túbulos simples nos tecidos moles, como na situação considerada plesiomórfica para teleósteos inferiores. Em contraste, a presença de uma rede complexa formada por ramificações múltiplas dos canais cefálicos é considerada uma sinapomorfia de Clupeoidei.* Denticeps *e Clupeoidei compartilham um ramo sensorial exclusivo que se origina na junção entre o osso extrascapular e o recessus lateralis, aqui proposto como uma sinapomorfia adicional de Clupeiformes. O sistema supratemporal é registrado pela primeira vez em* Denticeps, *e o caráter é consequentemente proposto como sinapomorfia de Clupeiformes, e não de Clupeoidei como se acreditava previamente. A hipótese de que o sistema supratemporal seria homólogo à caverna supraorbital é refutada, e a última é considerada autapomórfica para* Denticeps. *Uma outra autapomorfia de* Denticeps *(ou Denticipitoidei) é a presença da bula pós-orbital, uma especialização previamente desconhecida do canal infraorbital associada com os infraorbitais 4 e 5. As homologias de outros túbulos dos canais sensoriais cefálicos em* Denticeps *também são discutidas, com ênfase no reconhecimento de homologias dos ossos infraorbitais em* Denticeps *e em outros Teleostei inferiores. Em geral, os dados do sistema látero-sensorial cefálico corroboram a hipótese de* Denticeps *como grupo irmão de todos os outros clupeomorfos Recentes, e fornecem evidência adicional para o monofiletismo de Clupeoidei e Clupeiformes.*

Palavras-chave: Clupeiformes, *Denticeps clupeoides,* sistema látero-sensorial, teleósteos inferiores, relações filogenéticas, bula pós-orbital, biologia sensorial.

ACKNOWLEDGMENTS

We first thank Dr. Philippe Laleye (Université D'Abomey-Calavi, Faculté des Sciences Agronomiques, Cotonou), for logistic help and support during our visit to Benin. We are grateful to Roger Bills (South African Institute for Aquatic Biodiversity, Grahamstown), Timo Moritz (University of Würzburg, Würzburg), Charles Niyonkuru and Céline Dan (both from Université D'Abomey-Calavi) for help and companionship during fieldwork. Additional words of appreciation go to Roger Bills for allowing us to use photographs of *Denticeps clupeoides* taken during our joint expedition, one of which resulted in Figure 1. The manuscript benefited from comments and suggestions by C. Moreira, M. Toledo-Piza, and N. Menezes. For loans and exchanges of specimens we thank M. Rogers (FMNH), G. Burgess (UF), C. Lucena (MCP), M. Sabaj and J. Lundberg (ANSP), L. Py-Daniel (INPA), D. Nelson and W. Fink (UMMZ), S. Jewett and R. Vari (USNM). Research funding was provided by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo, proc. 99/09781-6 and 05/54162-5), Smithsonian Institution, and NSF (National Science Foundation).

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Recebido em: 23.08.2006
Aceito em: 10.10.2006

CNPq
Publicado com o apoio financeiro do
Conselho Nacional de Desenvolvimento
Científico e Tecnológico