Homology between the *recessus lateralis* and cephalic sensory canals, with the proposition of additional synapomorphies for the Clupeiformes and the Clupeoidei

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The *recessus lateralis*, a complex structure in the otic region of the skull that is probably associated with detection and analysis of small vibrational pressures and displacements, is widely recognized as a synapomorphy of the Clupeiformes. The Clupeiformes includes the Denticipitoidei, with one living species, *Denticeps clupeoides*, and the Clupeoidei, with about 360 living species commonly known as herrings and anchovies. Comparisons between details of the *recessus lateralis* of the Clupeoidei and Denticipitoidei, and the sensory cephalic canals of other teleosts, lead to hypotheses of a series of transformations of the cephalic sensory canals. Treating that complex as a single binary 'presence vs. absence' character as was traditional practice obscures important phylogenetically informative variation. Specific synapomorphies in that system exist for the Clupeiformes and the Clupeoidei. Hypothesized synapomorphies in the *recessus lateralis* for the Clupeiformes are the presence of a dilated internal temporal sensory canal in the pterotic, a postorbital branch of the supraorbital sensory canal located in a bony groove in the lateral wing of the frontal, and the terminal portions of preopercular and infraorbital sensory canals closely positioned. Hypothesized synapomorphies for the Clupeoidei are the presence of a postorbital branch of the supraorbital sensory canal located deep within the body of the lateral wing of the frontal, with the distal portion of that branch totally internal on the cranium, and the expanded distal portion of the postorbital branch of the supraorbital sensory canal. The homology of the *sinus temporalis* of Clupeoidei, and of the dermosphenotic of both *Denticeps* and the Clupeoidei, with those of other teleosts is also considered. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **141**, 257–270.

ADDITIONAL KEYWORDS: accessory temporal canal – basal teleosts – character complex – Denticipitoidei – dermosphenotics – *sinus temporalis*.

INTRODUCTION

The *recessus lateralis* is an intracranial space in the otic region of the skull into which the supraorbital, infraorbital, preopercular and temporal sensory canals open (Grande, 1985). The medial region of the *recessus lateralis* is separated from the inner ear by a thin elastic membrane (Tracy, 1920; Wohlfahrt, 1936; Bamford, 1941; O'Connell, 1955). Although the mechanism and function of the *recessus lateralis* is not yet well understood, it is probably related to detecting and analysing small vibrational pressures and displacements (Hoss & Blaxter, 1982).

As in the case of the Weberian apparatus of otophysans (Fink & Fink, 1996) and the tongue bite apparatus of osteoglossomorphs (Hilton, 2001), the *recessus lateralis* of the Clupeiformes is a staple character that is widely recognized and repeatedly listed in the literature. However, it is a character complex composed of a series of different morphological specializations. An often unsubstantiated assumption is that all components of a diagnostic character complex, such as the *recessus lateralis*, evolved simultaneously (Fink & Fink, 1996; Hilton, 2001). To treat these potentially multistate characters as a binary 'presence vs. absence' character overlooks possible sources of phylogenetic information (Hilton, 2001). The presence of the *recessus lateralis*, loss of the beryciform foramen and parietals completely separated by the supraoccip-

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ital have been considered as synapomorphies of the Clupeiformes (Grande, 1985). The separation of the parietals by the supraoccipital, however, has been subsequently proposed as a possible synapomorphy of the Otocephala, a group that includes the Clupeomorpha and Ostariophysi (Johnson & Patterson, 1996; Lecointre & Nelson, 1996). The Clupeiformes comprise all recent species of the Clupeomorpha, with approximately 360 living species (Nelson, 1994), divided between the Clupeoidei and Denticipitoidei, with *Denticeps clupeoides* the sole recent representative of the latter (Grande, 1985). Although the *recessus lateralis* is present in both the Clupeoidei and Denticipitoidei, its structure differs in each group (Greenwood, 1968; Patterson, 1970a; Arratia, 1997: fig. 77). The details of these differences have not been previously elucidated, due partly to the absence of comparative studies that focus on the homology between the *recessus lateralis* of the Clupeiformes and the cephalic sensory canals of other teleosts.

This study presents a short review of the generalized plesiomorphic structure of paired cephalic sensory canals in basal teleosts. Based on a comparison of this pattern with that of clupeiforms, precise homologies between the paired sensory canals and the chamber of the *recessus lateralis* of Clupeiformes are proposed. The results provide a precise definition of the levels of generality for particular patterns of that complex character. Two previously identified morphological modifications thought to be related to the development of the *recessus lateralis* are also discussed: the absence or reduction of the dermosphenotic (Patterson, 1967; Grande, 1985), and the approximation of the proximal portion of infraorbital and preopercular sensory canals (Nelson, 1972).

MATERIAL AND METHODS

Specimens were cleared and stained according to the procedure of Taylor & Van Dyke (1985). In order to facilitate visualization of the cephalic sensory canals in cleared and stained specimens, India ink diluted in 50% glycerine was injected into that system through a small opening in the usually large preopercular sensory canal. A similar technique was employed for alcohol-preserved specimens, wherein the India ink was diluted in 70% alcohol.

Drawings of the left side of specimens were made with the aid of a camera lucida. Cephalic canal and pit-line terminology follows Nelson (1972). Osteological terminology follows Weitzman (1962) and Grande (1985). Institutional abbreviations are as listed in Leviton *et al.* (1985). Osteological abbreviations are as follows: AC, antorbital sensory canal; *acr*, accessory temporal sensory canal opening to the chamber of the *recessus lateralis*; AIC, anterior extension of the infraorbital sensory canal; ao, antorbital; *aor*, anterior opening to the chamber of the *recessus lateralis*; ATC, accessory temporal sensory canal; CV, supraorbital cavern region; dsp, dermosphenotic; EC, extrascapular sensory canal; EHC, ethmoidal sensory canal; epo, epioccipital; ESC, epiphyseal branch of supraorbital sensory canal; exo, exoccipital; ext, extrascapular; fbo, oblique frontal bridge; fbs, parasagittal frontal bridge; fr, frontal; gr, groove on the lateral wing of the frontal; hm, hyomandibula; IC, infraorbital sensory canal; io_{1-5}, infraorbital bones 1–5; lfr, lateral wing of the frontal; MC, mandibular sensory canal; *mor*, middle opening to the chamber of the *recessus lateralis*; na, nasal; nc, canal for nerves supplying neuromasts of the supraorbital cavern; op, opercle; pa, parietal; pfh, fossa on the pterotic that articulates with the posterior condyle of the hyomandibula; pop, preopercle; *por*, posterior opening to the chamber of the *recessus lateralis*; PoSC, postorbital branch of the supraorbital sensory canal; PPC, preopercular sensory canal; pro, prootic; PSC, parietal branch of the supraorbital sensory canal; PTC, post-temporal sensory canal; pto, pterotic; ptt, post-temporal; *rec*, chamber of the *recessus lateralis*; *reco*, common opening to the chamber of the *recessus lateralis*; SC, supraorbital sensory canal; sfh, fossa on the sphenotic that articulates with the anterior condyle of the hyomandibula; so, supraoccipital; sp, sphenotic; TC, temporal sensory canal; tf, temporal foramen.

The distribution of character states among examined taxa were discussed and optimized on the currently accepted phylogenetic hypothesis for relationships of components of the Otocephala and basal teleosts (Grande, 1985; Fink & Fink, 1996; Johnson & Patterson, 1996; Arratia, 1999; Di Dario, 1999, 2002).

RESULTS

To evaluate the variations and potential *recessus lateralis* synapomorphies for and within the Clupeiformes, it is first necessary to review the structure of the paired cephalic sensory canals in basal teleocephalans. The paired cephalic sensory canals include the preopercular, which is usually continuous anteriorly with the mandibular, the supraorbital, the infraorbital, the temporal, the extrascapular and the post-temporal canals (Nelson, 1972; Fig. 1). The pattern of connection between these canals, their structure, and also their relationships with the bones in which they are housed, is remarkably consistent among basal teleocephalans and is accurately described or illustrated in a series of papers (e.g. Allis, 1904; Ridewood, 1904; Weitzman, 1962; Greenwood, 1970; Patterson, 1970a, b, 1975, 1984; Nelson, 1972; Weitzman & Fink, 1983; Siebert, 1987; Poyato-Ariza, 1996; Arratia, 1997 and references therein). Paired sensory canals in basal
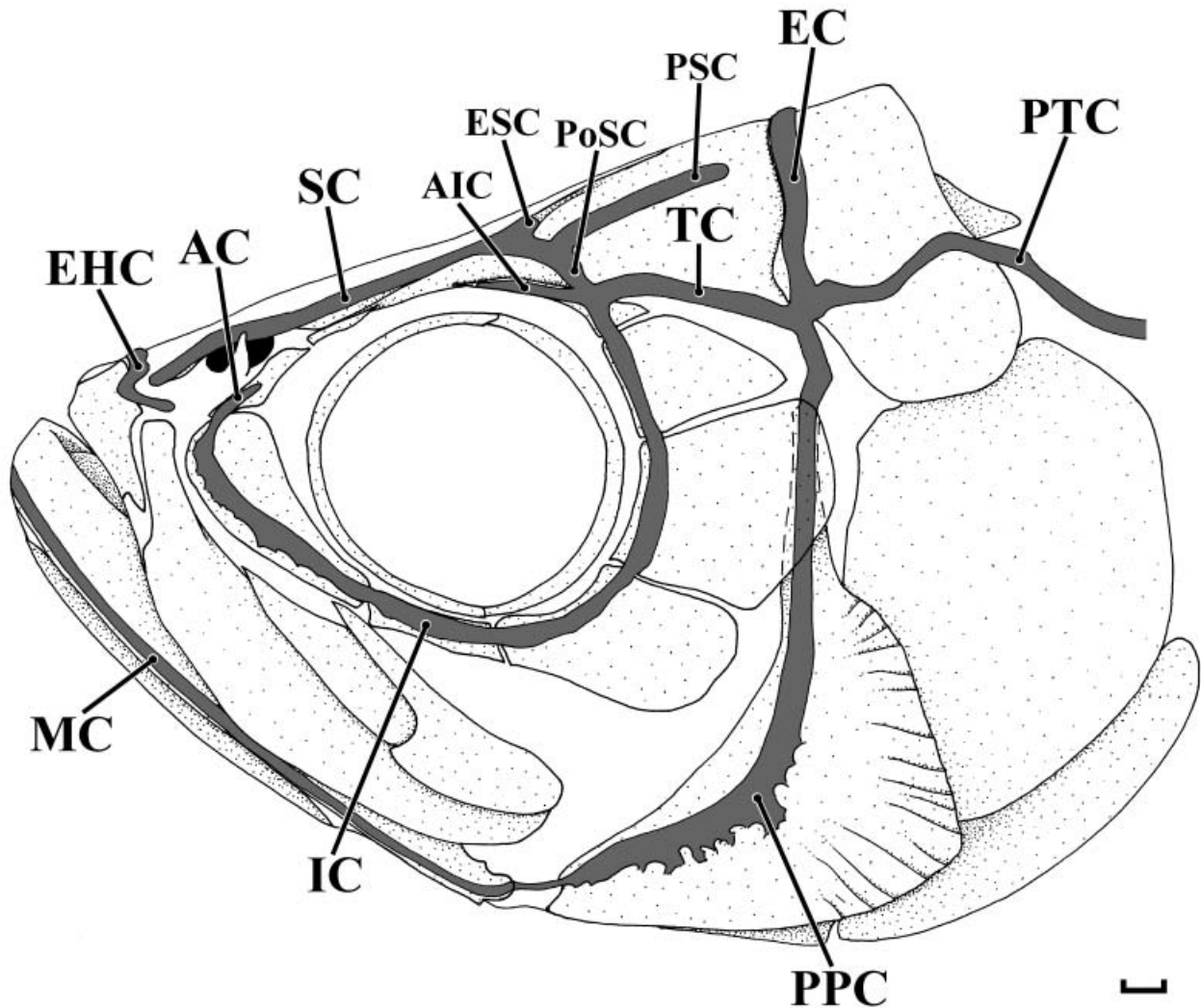
Figure 1. Pattern of connections among cephalic sensory canals in *Megalops cyprinoides* (USNM 173576) in left lateral view. Branching of sensory canals, other than those of supraorbital canal, not represented. Scale bar = 1 mm.

teleosts are typically tubular and superficial, positioned between a thin layer of epithelium and the dermal laminar bone underlying the canal (Webb, 2000). In lower teleosts, ossification of portions of the sensory canal seems to be independent of the dermal bone underlying it, usually fusing with it during early ontogeny. Distal teleosts, as perciforms, have a one component origin for canal-bearing bones, with canal ossification originating as expansions of the dermal bone underlying the canal (Tarby & Webb, 2003). Despite particular differences in development, the association between an ossified segment of the sensory canal and a particular dermal bone forms the 'lateral line bones' in the presumptive adult or semi-adult condition (Webb, 1999).

In most elopomorphs, osteoglossomorphs and ostariophysans, and in euteleosts such as *Salmo*, *Osmerus*, *Synodus* and *Thymallus*, the paired sensory canals

are connected in the otic region through the temporal canal (Nelson, 1972; Fig. 1). The interconnection through the temporal canal is a feature generally considered to be primitive for teleosts (Goodrich, 1958; Nelson, 1972; Siebert, 1987; Arratia, 1997), although *Hiodon*, *Chanos*, and some characiforms (e.g. *Hoplias*) and cypriniforms (e.g. *Opsariichthys*) lack a connection between supraorbital and temporal canals (Nelson, 1972; Patterson, 1975). Among representatives of basal teleocephalans, the temporal canal is orientated in a plane nearly parallel to the body axis. The temporal canal bone, as used herein, refers to the ossified temporal canal. The temporal canal bone is usually restricted to the pterotic in basal or 'generalized' teleosts and in this sense, is equivalent to the pterotic canal of Weitzman (1962). Its anterior margin contacts the sphenotic, and its posterior margin extends into the portion of the pterotic posterior to the fossa on that

bone for the articulation of the hyomandibula (Weitzman, 1962; Greenwood, 1970; Fig. 2). Although completely restricted to the pterotic, the anterior portion of the temporal canal bone dorsally contacts the lateral wing of the frontal, a projection, more or less developed, of the frontal bone that spreads laterally posterior to the postorbital region (Tracy, 1920).

Other paired sensory canals connect to the temporal canal through three openings in the temporal canal bone (Fig. 2). The supraorbital canal is almost completely restricted to the frontal. Its posteromedial portion has three main branches. The posterior, or parietal branch, extends along the top of the cranium to the parietals and middle pit-line (Nelson, 1972). The short epiphyseal branch of the supraorbital canal extends medially from above the orbits at the split between the parietal and postorbital supraorbital branches (Weitzman, 1962). The postorbital branch of the supraorbital canal is herein defined as the portion of the supraorbital canal between the splitting of the parietal branch from the main supraorbital canal and the temporal canal. The postorbital branch of the

supraorbital canal typically parallels the posterodorsal margin of the orbit and is associated with the anterior region of the lateral wing of the frontal. It is equivalent to the pterotic branch of the frontal laterosensory canal of Weitzman & Fink (1983). Nevertheless, as the term pterotic branch was previously and most frequently applied to a nonhomologous structure of the postotic sensory system of siluriforms (Fink & Fink, 1981; Schaefer & Aquino, 2000), it will not be adopted here. Except in cases where there is no direct connection between the supraorbital and temporal canals, the postorbital branch of the supraorbital canal joins the infraorbital canal close to, but outside of the dermosphenotic or infraorbital 6 (when this bone is present) to form a single tube continuous with the anterior opening of the temporal canal bone. The dermosphenotic carries only the infraorbital canal, except in the Distichodontidae (Characiformes) in which the large dermosphenotic apparently incorporates the supraorbital and/or the temporal canal, and sometimes also a portion of the preopercular canal (Vari, 1979). In addition, the infraorbital canal has an
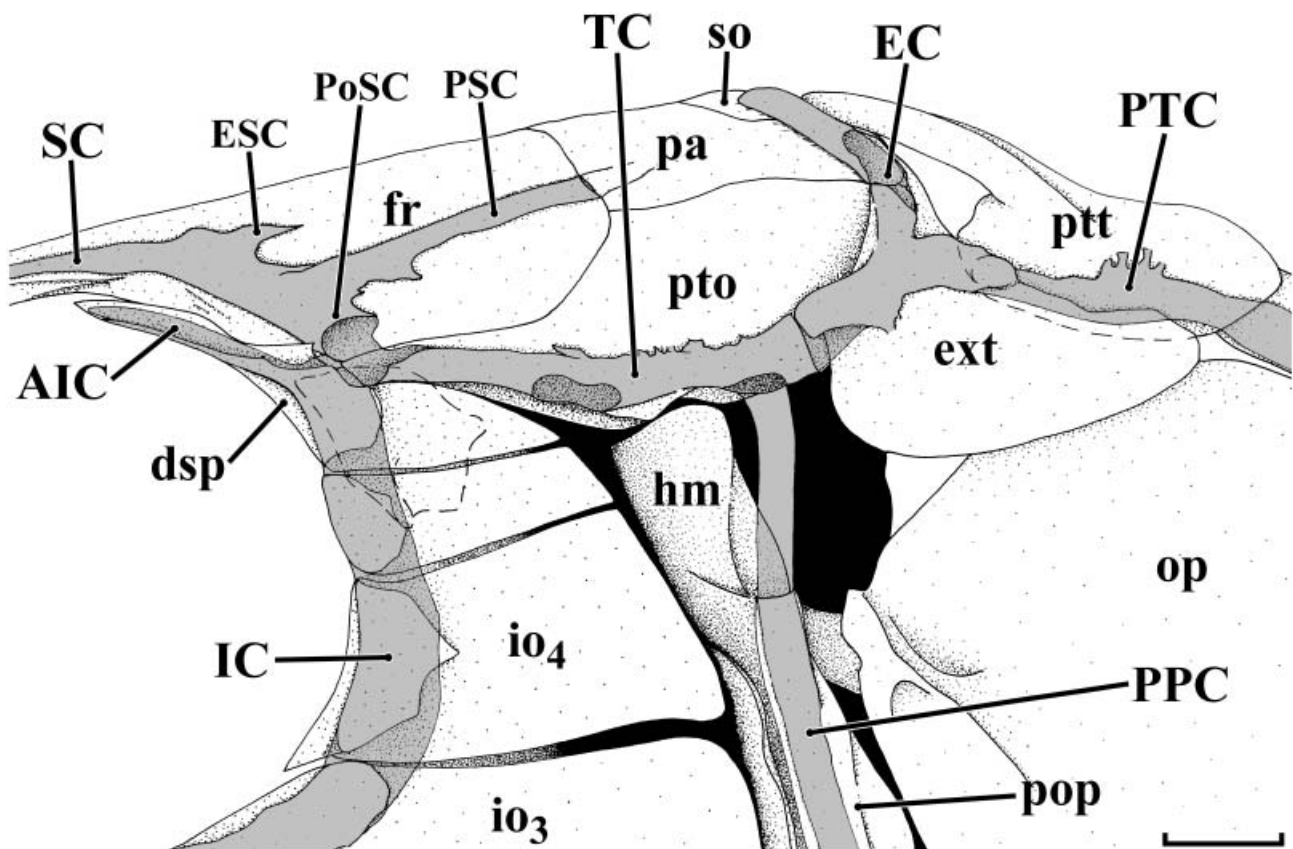

Figure 2. Relative position of the temporal canal (TC) and its connection to other cephalic sensory canals in *Elops saurus* (USNM 123629) in left lateral view. Outline of autosphenotic in dashed lines under dermosphenotic and infraorbital 5. Branching of sensory canals, other than those of supraorbital canal, not represented. Scale bar = 1 mm.

anterior extension through the anterior portion of the dermosphenotic dorsal to the orbit (Nelson, 1972; Fig. 2). Among the taxa examined, this extension was lacking in *Denticeps*, cypriniforms, some characiforms (e.g. *Xenocharax*) and euteleosts (*sensu* Johnson & Patterson, 1996), although its presence was reported in the fossil euteleosts *Gaudryella gaudryi* and *Humbertia operta* (Patterson, 1970b).

The preopercular, extrascapular and post-temporal canals contact the posteromedial region of the temporal canal at almost the same spot (Fig. 2). The preopercular canal and the proximal portion of the extrascapular canal are both orientated vertically near their junction with the temporal canal. The preopercular canal contacts the temporal canal through an opening on the posteroventral margin of the temporal canal bone. The extrascapular and the post-temporal canals share a common opening at the posterior limit of the temporal canal bone to which they connect via one or more extrascapulars.

CONNECTIONS OF CEPHALIC SENSORY CANALS IN THE CLUPEIFORMES

As described in the Introduction, the ventro-lateral region of the pterotic of clupeiforms is expanded and physically accomodates most of the *recessus lateralis*. As with the temporal canal, the longest axis of the chamber of the *recessus lateralis* of *Denticeps* is orientated nearly parallel to the axis of the body (Fig. 3). Furthermore, connections between the chamber of the *recessus* and the paired cephalic canals of *Denticeps* are the same as those between the temporal canal and the paired cephalic canals in the hypothesized plesiomorphic state for lower teleosts described above. The *recessus* of *Denticeps* has three main openings (Greenwood, 1968; Grande, 1985). The superficially situated supraorbital and infraorbital canals connect to the *recessus* through its single anterior opening (Greenwood, 1968; Fig. 3, *aor*). The anterior margin of this opening is partially bordered by the sphenotic, with
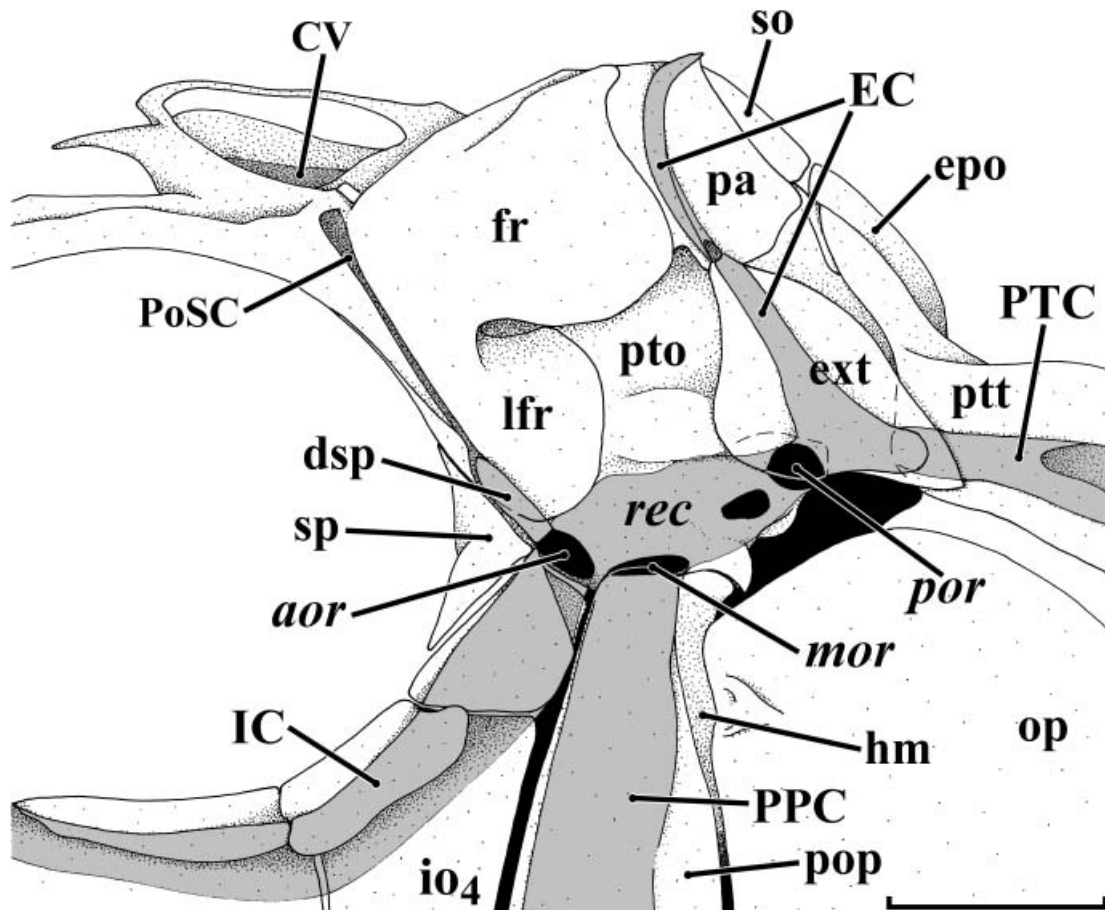

Figure 3. Relative position of the *recessus lateralis* chamber (*rec*) and its connections to sensory cephalic canals in *Denticeps clupeoides* (USNM 195992) in left lateral view. Dermal denticles not represented. Branching of sensory canals, other than those of supraorbital canal, not represented. Scale bar = 1 mm.

the main portion of the aperture formed by the pterotic. The anterior opening of the *recessus* is closely approached by the lateral wing of the frontal bone. The epiphyseal and parietal branches of the supraorbital canal are not apparent in the supraorbital region, which is, instead, occupied by the supraorbital cavern (Fig. 3, CV). The supraorbital cavern contains neuromasts and is a supraorbital canal specialization exclusive to *Denticeps* (Greenwood, 1968).

The middle opening of the *recessus* in *Denticeps* connects ventrally to the preopercular canal (Fig. 3, *mor*). The portion of the pterotic that forms the posterolateral wall of the *recessus* chamber has two openings. The dorsal and more developed of these openings connects to the single extrascapula, which carries the extrascapular and post-temporal canals (Greenwood, 1968; Fig. 3, *por*). The ventrally located opening is less

developed and does not connect to any major cephalic canal (Greenwood, 1968). Given its absence in the other teleosts examined, it is probably autapomorphic for *Denticeps*.

In marked contrast to the condition found in the Clupeoidei (Wohlfahrt, 1936), the *recessus* chamber of *Denticeps* does not gradually taper dorsally in depth and width. Instead, the upper margin of the chamber of *Denticeps* is straight and the overall shape of the chamber is that of a dilated tube. In *Denticeps*, the floor of the *recessus* chamber is provided by the prootic, its roof is entirely of pterotic material, and the anterior wall is formed by the pterotic and sphenotic (Greenwood, 1968).

The chamber of the *recessus lateralis* of the Clupeoidei is larger than that in *Denticeps* (Fig. 4, shorter dashed line). As in *Denticeps*, the floor of the chamber
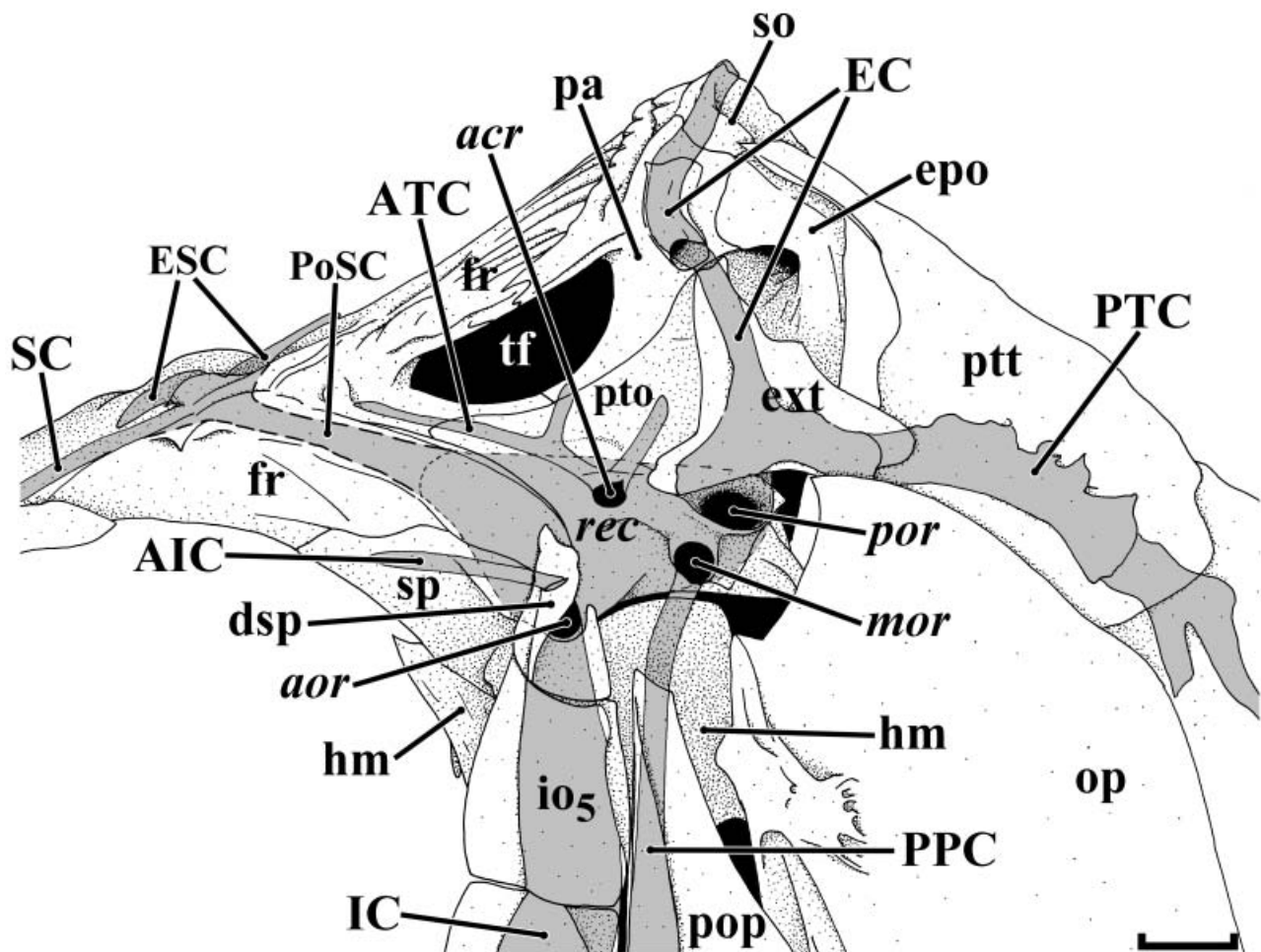

Figure 4. Relative position and shape of the *recessus lateralis* chamber (*rec*) and its connections to sensory cephalic canals in *Nematalosa erebi* (USNM 173587) in left lateral view. Larger dashed line representing postorbital branch of supraorbital canal, continuous to the *recessus lateralis* chamber; shorter dashed line representing the *recessus lateralis* chamber, internal to the cranium. Branching of sensory canals, other than supraorbital and accessory temporal, not represented; branching of the supraorbital and accessory temporal canals simplified. *Sinus temporalis* not represented. Scale bar = 1 mm.

is formed by the prootic and the anterior wall by the pterotic and sphenoid. The roof of the *recessus* chamber of Clupeoidei is typically provided by the pterotic and the lateral wing of the frontal bone, which also forms part of the lateral wall of the chamber (Tracy, 1920; Greenwood, 1968). For descriptive purposes, the chamber of the *recessus* can be divided into two portions, a ventral one, which is homologous to the whole chamber in *Denticeps* and a dorsal one, which is unique to the Clupeoidei. The ventral portion in Clupeoidei is dilated and continuous with the dorsal portion, which gradually tapers dorsally both in depth and width, resulting in a bell-shaped structure (Wohlfahrt, 1936: fig. 25; Grande, 1985). The upper tip of the dorsal portion of the chamber is continuous with the remaining postorbital branch of the supraorbital canal (Wohlfahrt, 1936; O'Connell, 1955; Grande, 1985; Fig. 4, PoSC).

The ventral portion of the chamber in examined representatives of Clupeoidei has three main openings (Fig. 5). The relative position of the ventral portion of the *recessus* on the cranium and the position of its openings relative to the paired sensory canals in the Clupeoidei are largely the same as in the *recessus* of *Denticeps*. One exception is that the postorbital branch of the supraorbital canal is not superficial on the cranium (Wohlfahrt, 1936; Patterson, 1970a). Also, the postorbital branch of the supraorbital canal does not share the external anterior opening of the temporal canal/*recessus* with the infraorbital canal. Instead, the anterior two-thirds of the supraorbital canal in the Clupeoidei is enclosed in the lateral wing of the frontal, while its distal third is completely internal to that bone (Tracy, 1920; Stephens, 1985: fig. 4). The distal third of the postorbital branch expands ventrally and develops into the dorsal portion of the *recessus* chamber.

As in *Denticeps*, there is little indication of a parietal branch of the supraorbital canal in adult clupeoids. This portion of the supraorbital canal is thought to be modified into the *sinus temporalis*, a sac-like expansion of the supraorbital canal that fills the temporal foramen in the Clupeoidei (Patterson, 1970a). Evidence of a homology between the *sinus temporalis* and the parietal branch of the supraorbital canal is derived from both innervation (Wohlfahrt, 1937) and ontogeny (Bamford, 1941). In specimens of *Dorosoma cepedianum* (USNM 272899) 16.1–25.4 mm
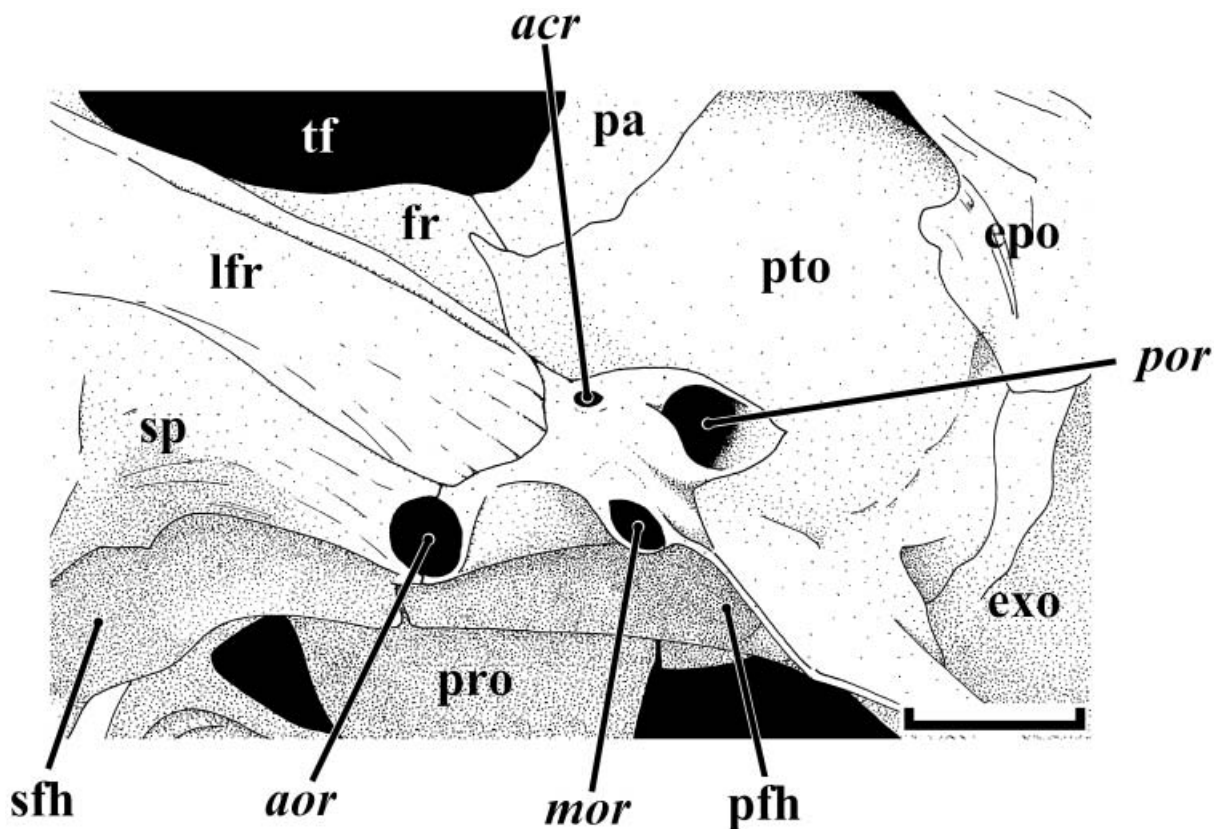

Figure 5. Openings of the *recessus lateralis* to superficial sensory cephalic canals in *Nematalosa erebi* (USNM 173587) in left lateral view. Scale bar = 1 mm.

and *Harengula pensacole* (USNM 272649) 23.0–28.1 mm, the parietal branch of the frontal is clearly discernible with its posterior margin associated with the temporal foramen, whereas in *Dorosoma smithi* (USNM 225024) 60.5 mm, the parietal branch is much reduced and similar in form to that in adult Clupeoidei (Fig. 6). The bony portion of the epiphyseal branch of the supraorbital canal of clupeoids conforms to the plesiomorphic condition. The epiphyseal branch does, however, spread posteriorly via a series of canals in the soft tissue that reach to the parietals and the middle pit-line (Patterson, 1970a) in a way similar to that of the parietal branch of the supraorbital canal in the nonclupeiform condition.

The Clupeoidei examined have one additional sensory canal connected to the *recessus lateralis* that is absent in *Denticeps*. Grande (1985: 279) described an opening of the *recessus lateralis* to a 'third unnamed canal' on the pterotic of some taxa in the Clupeoidei. That canal is positioned dorsal to the other three ventral openings of the *recessus lateralis* discussed above. Although Grande could not establish the precise relationship between this opening and a specific sensory canal, he stated that it probably connects a series of superficial head canals to the *recessus* chamber. The canal connected to this opening was described by Wohlfahrt (1936) as the 'accessorisches Temporalsystem', and by O'Connell (1955) as the accessory temporal (Fig. 4, ATC). This canal originates at the dorsal region of the *recessus*, projects dorsally toward the temporal foramen, and ramifies dorsally to form a tree-shaped set of superficially connected sensory
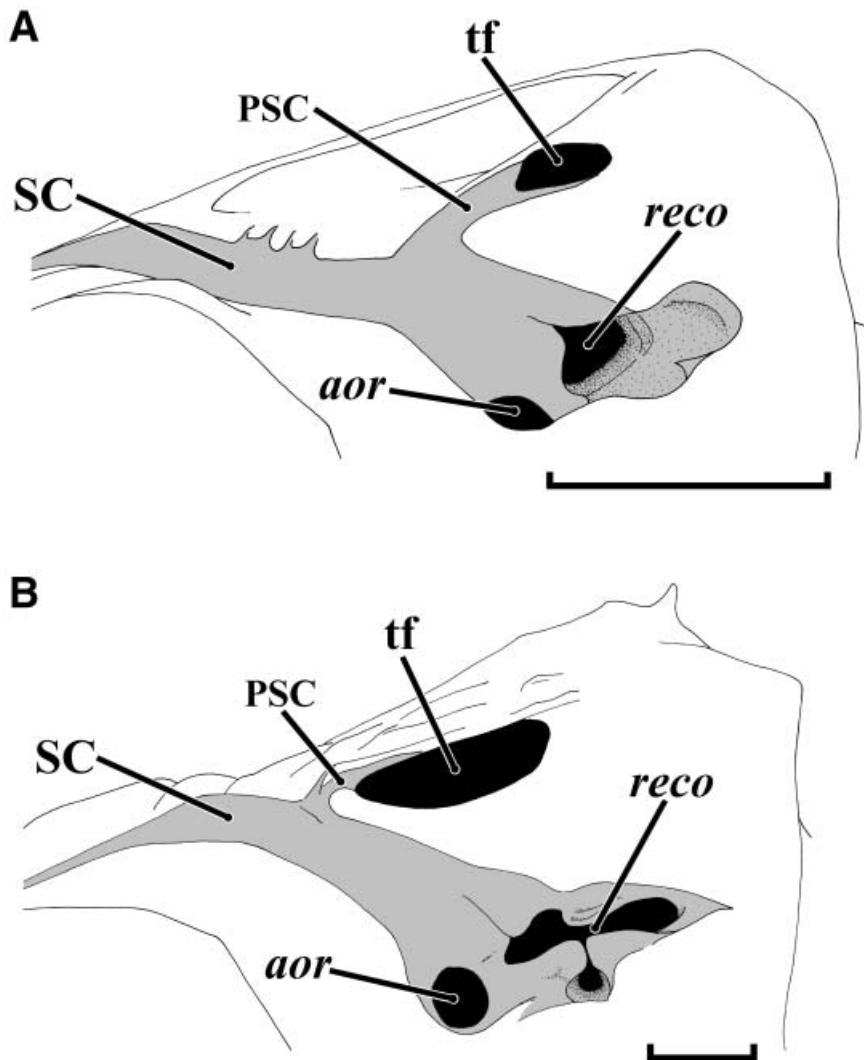

Figure 6. Outline of the temporal region in left lateral view, showing the relation between parietal branch of supraorbital canal and temporal foramen in (A) *Dorosoma cepedianum* 23.1 mm (USNM 272899) and (B) *Dorosoma smithi* (USNM 225024) 60.5 mm. Scale bars = 1 mm.

canals on the temporal region situated between the internal portion of the supraorbital canal and the extrascapular canal (Stephens, 1985). Although overlapping, the secondary and tertiary canals of the accessory temporal canal and the canals of the *sinus temporalis* do not anastomose.

DISCUSSION

The data presented above clearly support the hypothesis that the chamber of the *recessus lateralis* of *Denticeps clupeoides* is homologous to the temporal canal of nonclupeiform teleosts with which it shares the same topological relations with the supraorbital, preopercular, infraorbital, extrascapular and post-temporal sensory canals. The chamber of the *recessus lateralis* of *Denticeps* thus represents a temporal canal that is dilated and displaced into the pterotic bone. Additional evidence for this hypothesis is the similarity of the tube-like form, orientation of the chamber relative to the cranium, and the relation between the chamber of the *recessus* and cranial bones in *Denticeps*, which are similar to those of the temporal canal in nonclupeiform teleosts. Likewise, the ventral portion of the chamber of the *recessus lateralis* of the Clupeoidei, as described above, is hypothesized to be homologous to the chamber of the *recessus* in *Denticeps*. The internalization of the temporal canal is shared exclusively by *Denticeps* and the Clupeoidei, and a dilated and internal temporal canal is thus hypothesized to be a synapomorphy of the Clupeiformes. Nonclupeiform clupeomorphs (Ellimmichthyiformes and *Armigatus*) have superficial temporal and supraorbital canals as described above in the plesiomorphic condition (Patterson, 1970a; Grande, 1982a, b, 1985). The presence of a dorsally expanded *recessus* chamber in the Clupeoidei, with the distal portion of the lateral wing of the frontal providing both partial roof and lateral wall to the chamber, can be seen as resulting from two additional modifications exclusive to the Clupeoidei that are hypothesized as synapomorphies of that clade. The first of these modifications is the shift of the postorbital branch of the supraorbital canal into the body of the lateral wing of the frontal, particularly of its distal third, totally internal to that bone. The second is the expansion in diameter of the distal third of the postorbital branch of the supraorbital canal, continuous with the upper portion of the temporal canal (or the homologous *recessus lateralis* chamber of *Denticeps clupeoides*) which, in the hypothesized plesiomorphic state, is undifferentiated from the anterior two thirds of the postorbital branch of the supraorbital canal.

The condition of the postorbital branch of the supraorbital canal of *Denticeps clupeoides*, although located superficially on the cranium, does not exactly conform to the plesiomorphic state described for non-clupeiform teleosts. In the plesiomorphic state, this branch of the supraorbital canal is tubular and superficial to the underlying bone. In contrast, the postorbital branch of the supraorbital canal runs in a deep bony groove in *Denticeps* and is therefore not completely superficial but partially enclosed within the frontal bone (Greenwood, 1968; Fig. 7, gr). This condition is intermediate between the plesiomorphic state and that found in clupeoids. Ontogenetic evidence also supports the hypothesis of this transformation. In 16.1–18.1 mm (TL) specimens of *Dorosoma cepedianum* (USNM 272899), the postorbital branch of the supraorbital canal, or a portion of the supraorbital canal largely equivalent to that branch, runs in a groove around the posterior margin of the supraorbital canal. This condition is similar to that of *Denticeps*. Thus, the postorbital branch of the supraorbital canal partially enclosed in the lateral wing of the frontal, running in a deep groove on that bone, is hypothesized to be synapomorphic for the Clupeiformes.

The chamber of the *recessus lateralis* of *Denticeps*, engrauloids and most clupeoids examined is completely enclosed by bone, except for the openings that connect that structure to other cephalic canals and the medial nonossified membrane that connects the chamber to the gas-filled prootic bullae (Blaxter, 1987). In pristigasteroids, and in the clupeoids *Clupea*, *Hyperlophus*, *Pellonula*, *Platanichthys* and *Rhinosardinia*, the chamber of the *recessus lateralis*, although clearly internal to the cranium, is not completely enclosed by bone. In these taxa, all or most of the four openings of the *recessus* that connect that structure to the infraorbital, preopercular, accessory temporal and extrascapular-post-temporal canals, are closely positioned and confluent to each other, forming a large common opening to the *recessus* chamber. This character may be significant as evidence for grouping more restrictive clades within the Clupeoidei, but the proposal of such synapomorphies must await further study.

The presence of the accessory temporal canal and epiphyseal canals that extend posteriorly to the middle pit-line are not exclusive to the Clupeoidei; they are also present in other teleosts (such as *Megalops*) and, possibly, *Amia* outside the Teleostei (Allis, 1889; Stephens, 1985). Nevertheless, the fact that these conditions have a restricted distribution outside the Clupeoidei suggests that they might be optimized as additional synapomorphies for that group. The presence of the *sinus temporalis*, although apparently exclusive to the Clupeoidei (Stephens, 1985), also requires further corroboration as an additional synapomorphy of the Clupeoidei. Like the *sinus temporalis*, the supraorbital cavern of *Denticeps*, although not filling the temporal foramen, is also a
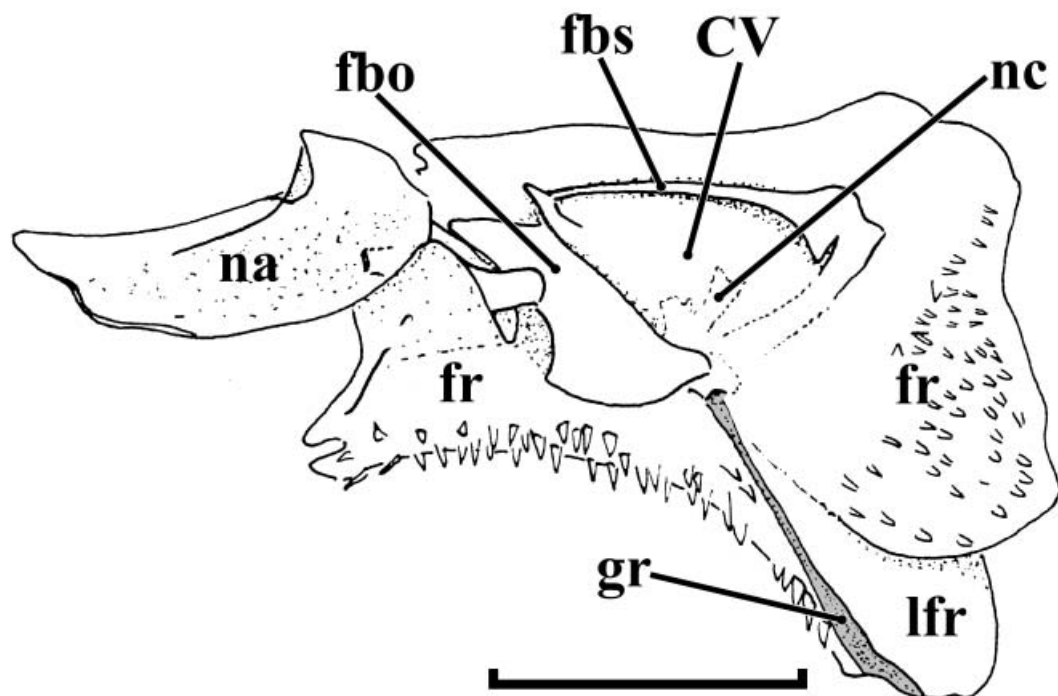
Figure 7. Temporal region in left lateral view of *Denticeps clupeoides* (after Greenwood, 1968) showing the groove (gr) for the postorbital branch of the supraorbital canal on the lateral wing of the frontal, and the supraorbital cavern. Scale bar = 1 mm.

sinus-like structure apparently derived from the supraorbital sensory canal (Greenwood, 1968). Furthermore, the fact that the epiphyseal and parietal branches of the supraorbital canal are not recognizable in *Denticeps*, and that the area on the cranium occupied by these structures in the plesiomorphic condition is occupied by the supraorbital cavern in *Denticeps*, strongly suggests that the supraorbital cavern is derived from the parietal and/or epiphyseal branches of the supraorbital canal. If this is the case, it seems likely that the *sinus temporalis*, derived from the parietal branch of the supraorbital according to both ontogenetic and morphologic evidence (see Discussion above and Fig. 6), and the supraorbital cavern, are homologous. As a consequence, the modification of the parietal branch of the supraorbital canal in a sac-like sensory structure located at the posterodorsal portion of the cranium may be an additional synapomorphy of the Clupeiformes. Further studies regarding the homology of the supraorbital cavern and components of the supraorbital sensory canal are required to confirm this hypothesis.

The proximity between the proximal portions of the preopercular and infraorbital canals (Nelson, 1972), and the absent or reduced dermosphenotics (Patterson, 1967; Grande, 1985), are additional features exclusive to the Clupeiformes. Perhaps due to a premise that the occurrence of these attributes is

somehow related to the presence of the *recessus lateralis*, these conditions have not been proposed as synapomorphies of the Clupeiformes. I do not agree with such an interpretation and herein propose that the proximity between preopercular and infraorbital canals is an additional synapomorphy of the Clupeiformes, based on the exclusive occurrence of this state in that group. In the plesiomorphic state, the proximal portions of the infraorbital and preopercular canals are widely separated at their connection to the temporal canal (Fig. 2) whereas in *Denticeps* and in members of the Clupeoidei, the infraorbital and preopercular canals are extremely close at that region (Figs 3 and 4).

As shown by outgroup comparisons including nonclupeiform clupeomorphs (Grande, 1982a, b, 1985), the plesiomorphic condition for clupeiforms is to have the dermosphenotics consisting of a proportionately well developed laminar base that partially covers the autosphenotic, and an ossified segment of the infraorbital canal. Additionally, the dermosphenotic is typically characterized by the forking of the supraorbital canal and the presence of one neuromast (Nelson, 1969). Patterson (1967) and Grande (1985) expressed doubt about the homology between the dermosphenotics of the Clupeoidei and that of nonclupeiform teleosts. According to Grande (1985), the clupeiform dermosphenotic lacks a branched

canal. Nevertheless, the anterodorsal margin of the dermosphenotic in the Clupeoidei usually has an opening into which the anteriorly directed extension of the infraorbital canal projects (Nelson, 1969; Stephens, 1985). The dermosphenotic of *Alosa*, for example, not only has such an opening but also, a completely ossified additional tube that wraps around the base of the anterior extension of the infraorbital canal. This results in a partial Y-shaped structure that strongly resembles the ossified canal component of the dermosphenotic in the plesiomorphic state. Additionally, the plate-like bone component of the dermosphenotic is still partly present in all examined members of the Clupeoidei. The dermosphenotic of *Dussumieria acuta*, for example, has a relatively well developed plate-like bone anteriorly. *Pellona harroweri*, a basal pristigasteroid (Di Dario, 1999), also has an ossified lamina that extends a short distance dorsal to the anterior upper margin of the canal component of the dermosphenotic. Furthermore, Nelson (1969) reported the presence of a neuromast in dermosphenotics of examined members of the Clupeoidei.

Thus, the dermosphenotic of the Clupeoidei is homologous to that of other teleosts, differing from the latter in having a reduced laminar component. Alternatively, the dermosphenotic of *Denticeps* is hypothesized as nonhomologous to that of other teleosts, including the Clupeoidei. Grande (1985) previously noted some striking differences between the dermosphenotics of *Denticeps* and the Clupeoidei, observations that are confirmed and expanded in the present study. The dermosphenotic of *Denticeps clupeoides* is not associated with the infraorbital canal, is situated dorsal to the *recessus* openings and wraps solely around the distal portion of the postorbital branch of the supraorbital canal, a condition not present in other teleosts. Among specimens examined, only the characiform *Xenocharax* has a connection of the supraorbital and temporal canals through the dermosphenotic (Vari, 1979), but it differs from the condition in *Denticeps* in having the dermosphenotic also associated with the infraorbital canal. As discussed by Grande (1985), the dermosphenotic of *Denticeps clupeoides* is apparently an ossification of the terminal portion of the supraorbital canal and completely lacks a laminar component, whereas the dermosphenotic of the Clupeoidei has a shape comparable to the infraorbital bone in outgroups. Finally, neuromasts are absent in dermosphenotics of examined *Denticeps*, contrary to the condition in the Clupeoidei and other teleosts.

If the structure which Greenwood (1968) identified as the dermosphenotic in *Denticeps* is indeed not that bone, it is possible that the infraorbital 5 of *Denticeps*, the posteriormost bone of the infraorbital series, is in fact the dermosphenotic. Since the anterior extension of the infraorbital canal is absent in *Denticeps*, the association between this portion of the sensory canal and the dermosphenotic in the plesiomorphic state is uninformative as evidence for homology or lack thereof between infraorbital 5 and the dermosphenotic of other teleosts. Other features, however, suggest that infraorbital 5 of *Denticeps* is actually a teleostean dermosphenotic. Infraorbital 5 of *Denticeps* connects the terminal portion of the infraorbital canal to the *recessus lateralis*, to which it is closely associated, as does the dermosphenotic in the Clupeoidei (Fig. 8). This ossification in *Denticeps* also has a reduced laminar anterior extension that resembles the condition found in the Clupeoidei, although this resemblance is also shared with other infraorbital bones additional to the dermosphenotic in that group. A fusion of infraorbitals 3 and 4 is relatively widespread at this level of the cladogram, being present in basal ostariophysans such as *Chanos* and Cypriniformes (Fink & Fink, 1996), and probably in all recent osteoglossomorphs (Nelson, 1969). Such a fusion of the third and fourth infraorbitals might explain the apparently reduced number of 5 instead of 6 infraorbitals in *Denticeps*. Although infraorbital 3 of *Denticeps* is relatively large, supporting the hypothesis of fusion between the third and fourth infraorbitals, it contains only one neuromast, whereas the usual condition for clupeomorphs is to have two neuromasts in infraorbital 3 and one neuromast in infraorbital 4 (Nelson, 1969). Further evidence, possibly derived from the ontogeny of *Denticeps*, is necessary to precisely define the homologies between the infraorbital bones of *Denticeps* and those of other teleosts. If infraorbital 5 of *Denticeps* is homologous with the dermosphenotic, then the reduction of the laminar bone component of dermosphenotics would be another synapomorphy of the Clupeiformes.
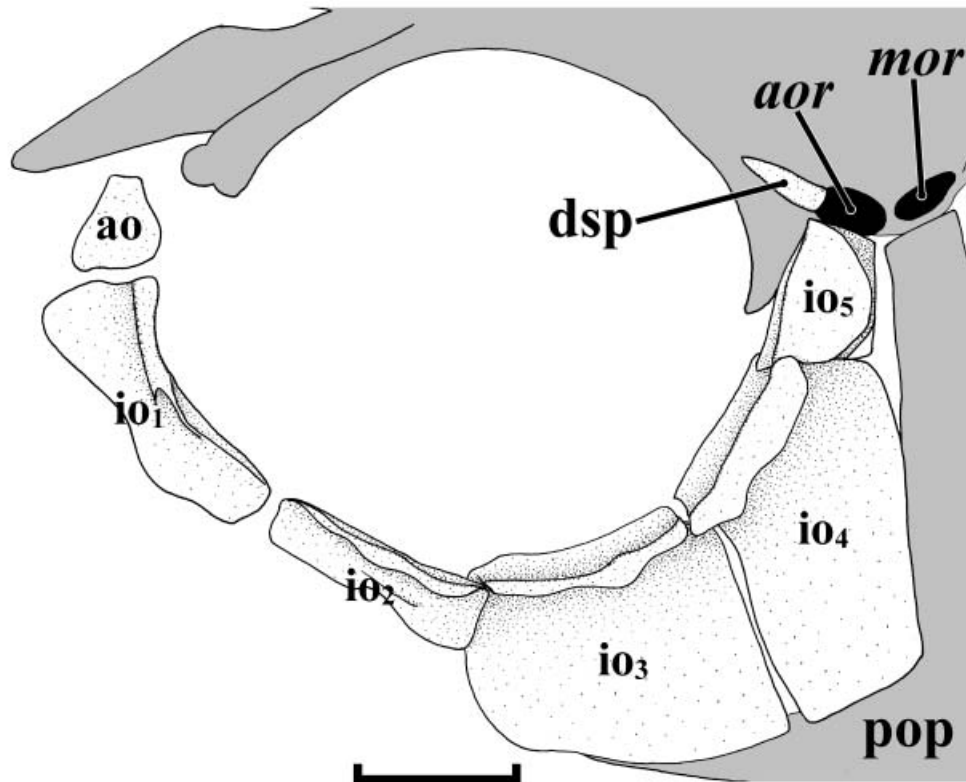
Figure 8. Outline of the orbital region and preopercular, and left infraorbital series in lateral view, of *Denticeps clupeoides* (USNM 195992), showing the relationship between infraorbital 5 and the *recessus lateralis*. Notice also the laminar anterior sheet of bone of infraorbital 5 and the large infraorbital 3. Dermal denticles not represented. Scale bar = 1 mm.

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APPENDIX

COMPARATIVE MATERIAL EXAMINED

Number of examined specimens follows catalogue number: *Albula vulpes*, MZUSP 10625, 2; *Alosa mediocris*, AMNH 88825, 1; *A. pseudoharengus*,

MZUSP 62471, 1; *Anchoa filifera*, MZUSP 18528, 2; *A. lamprotaenia*, MZUSP 11508, 2; *A. lyolepis*, MZUSP 11476, 3; *A. spinifer*, MZUSP 11454, 3; *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; *Anodontostoma chacunda*, MZUSP 62476, 1; *Brevoortia aurea*, MZUSP 11729, 1; *B. pectinata*, MCP 7722, 1; MCP 7725, 1; MCP 7727, 1; *Cetengraulis edentulus*, MZUSP 11634, 3; *Chanos chanos*, AMNH 95415, 1; MZUSP 62601, 1; *Chirocentrodon bleekerianus*, MZUSP 11097, 3; *Chirocentrus dorab*, MZUSP 62467, 2; *Citharinus* sp., USNM 231554, 2; *Clupeichthys aesarnensis*, MZUSP 62465, 3; *C. bleekeri*, MZUSP 63114, 1; *C. perakensis*, MZUSP 63104, 3; *Coilia rebentischii*, MZUSP 62483, 1; *Cyphocharax abramoides*, USNM 267953, 1; *Dalia pectoralis*, USNM 034033, 2; *Denticeps clupeoides*, MZUSP 62480, 1; USNM 174587, 1; USNM 195992, 1; *Dorosoma cepedianum*, MZUSP 62481, 3; USNM 272899, 6; *D. smithi*, USNM 225024, 1; *Dussumieria acuta*, MZUSP 62468, 3; *Elops saurus*, USNM 123629, 1; USNM 272928, 1; *Elops* sp., MZUSP 60346, 1; *Encrasicholina heteroloba*, MZUSP 63118, 2; *Engraulis anchoita*, MZUSP 18393, 10; *Etrumeus teres*, MZUSP 62469, 3; *Galaxias auratus*, USNM 344895, 3; *Gilchristella aestuaria*, MZUSP 64115, 3; *Harengula clupeola*, MZUSP 18672, 1; *H. jaguana*, MZUSP 11269, 2; MZUSP 10791, 1; *H. pensacole*, USNM 272649, 10; *Herklotsichthys dispilonotus*, MZUSP 63115, 1; *Hiodon tergisus*, MZUSP 28450, 1; *H. alosoides*, USNM 350554, 1; *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; *Kneria auriculata*, MZUSP 63121, 4; *Lile piquitinga*, MZUSP 11215, 1; *Lycothryssa crocodilus*, MZUSP 62482, 1; *Megalops cyprinoides* USNM 173576, 3; USNM 173580, 3; *Nematalosa erebi*, USNM 173587, 1; USNM 173590, 1; *Neoopisthopterus tropicus*, MZUSP 62478, 2; *Odontognathus mucronatus*, MZUSP 11264, 3; MZUSP 11267, 3; *Ophistonema oglinum*, MZUSP 10844, 3; MZUSP 10835, 2; *Opisthopterus dovii*, MZUSP 62462, 3; *O. equitorialis*, MZUSP 62479, 2; *O. tardoore*, MZUSP 62475, 2; *Opsariichthys uncirostris*, USNM 87445, 2; *Osmerus mordax*, MZUSP 64116, 1; MZUSP 64118, 2; *Pellona castelnaeana*, MZUSP 5492, 1; AMNH 93109, 1; AMNH 57916, 1; *P. ditchela*, ANSP 63526, 1; AMNH 98899, 1; USNM 189996, 2; *P. flavipinnis*, MZUSP 40063, 1; MZUSP 18728, 1; *P. harroweri*, MZUSP 11283, 3; MZUSP 11308, 1; MZUSP 11374, 3; *Pellonula afzeliusi*, UMMZ 195029, 2; *Platanichthys platana*, MZUSP 10629, 3; MCP 19409, 3; *Pliosteostoma lutipinnis*, FMNH 2818, 2; *Pristigaster cayana*, MZUSP 30338, 3; *P. whiteheadi*, INPA 8555, 3; *Pterengraulis atherinoides*, MZUSP 11723, 1; *Raconda russeliana*, MZUSP 62466, 4; *Rhinosardina amazonica*, MZUSP 11231, 2; MZUSP 11452, 1; *Salmo gairdneri*, USNM 62995, 2; USNM 348889, 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; *Setipinna melanochir*, MZUSP 64119, 1; *Spratelloides delicatulus*, MZUSP 62470, 3; *Stolephorus indicus*, MZUSP 63112, 2; MZUSP 63113, 1; MZUSP 63106, 1; *Tenualosa ilisha*, USNM 276407, 2; *Xenocharax spilurus*, MZUSP 50358, 1; USNM 227693, 1; *Zacco pachycephalus*, MZUSP 62598, 1; MZUSP 62599, 1.