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Source: American Museum Novitates, 2004(3455) : 1-21

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2004)455<0001:ROSDOC>2.0.CO;2

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AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3455, 21 pp., 10 figures, 1 table October 28, 2004

Redescription of *Santanichthys diasii* (Otophysi, Characiformes) from the Albian of the Santana Formation and Comments on Its Implications for Otophysan Relationships

ARNAUD FILLEUL[1] AND JOHN G. MAISEY[2]

ABSTRACT

A detailed redescription of *Santanichthys diasii* is presented, based on several new acid-prepared and very well-preserved specimens. *S. diasii* has a complete Weberian apparatus and is at present the earliest otophysan fish known (early Cretaceous, Albian). In addition, this fish displays at least one synapomorphy of modern characiforms (large and globular lagenar capsules that extend well lateral to the cranium) and we consequently suggest that it is a stem characiform. If this is correct, it represents a significant temporal extension for characiforms. We discuss the phylogenetic implications of its unique combination of features in light of earlier phylogenetic hypotheses.

INTRODUCTION

The Santana Formation of northeastern Brazil has been known for more than 150 years as a rich source of fossil fishes, yet the taxonomic diversity of its vertebrate fossil assemblages has only become appreciated in the past few decades. The best known of these assemblages come from carbonate concretions that occur at various horizons within the upper part of the sequence (Romualdo Member).

One of the smallest fossil fishes from the Romualdo Member (mostly under 30-mm total length) is a teleost originally described as *Leptolepis diasii* (Silva Santos, 1958). Little can be gleaned from that original description, other than the presence of generalized teleostean characters, and in most respects the description is applicable to almost any of the

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ISSN 0003-0082

taxa originally described as ‘‘leptolepids’’ from the Jurassic or Cretaceous. Historically, *Leptolepis diasii* was only the second ‘‘leptolepid’’ to be described from Brazil; the first was *Leptolepis bahiaensis* from the early Cretaceous of Bahia (Schaeffer, 1947). Silva Santos (1958) noted differences between these taxa in the proportions of the head, shape of the mouth, number of caudal vertebrae, and the relative positions of the anal and pelvic fins, but he did not find any evidence to suggest a close relationship between them.

Leptolepis bahiaensis was subsequently discussed by Patterson (1970), who noted similarities with *Scombroclupeoides scutata* (also from the early Cretaceous of Bahia). *L. bahiaensis* was also examined by Patterson and Rosen (1977), who concluded that its caudal fin skeleton was phylogenetically more advanced than in many other ‘‘leptolepids’’, and that this taxon should be classified as Clupeocephala incertae sedis; in addition, they recommended placing it within the genus *Scombroclupeoides*. Maisey (1991: 273) illustrated the incomplete caudal fin skeleton of an acid-prepared specimen of *Leptolepis diasii* and found two features suggesting that this taxon is more advanced than *Scombroclupeoides bahiaensis*: the parhypural and first two hypurals are attached to the fused preural and first ural centra, and a stegural is present. *Leptolepis diasii* was classified as Euteleostei incertae sedi by Maisey (1991).

The generic name *Santanichthys* was erected for ‘‘*Leptolepis*’’ *diasii* by Silva Santos (1991), who regarded it as a clupeomorph. Unfortunately, *Santanichthys* lacks all the synapomorphies of the Clupeomorpha sensu Grande (1985). In hindsight, Silva Santos’ conclusion was certainly the consequence of a confusion between specimens of *Santanichthys* and specimens of another undescribed species, which is of the same size as *Santanichthys* and is currently under study (Figueiredo and Gallo, 2002). Despite this confusion, the generic name *Santanichthys* is available for ‘‘*Leptolepis*’’ *diasii* (Maisey, 1993).

Silva Santos (1995) provided more information about *Santanichthys diasii*, confirming details of the caudal skeleton reported by Maisey (1991) and claiming the presence of two fontanelles in the skull roof similar to those identified in *Clupavus maroccanus* (Taverne, 1977) and *Lusitanichthys characiformis* (Gayet, 1981). On that basis Silva Santos (1995) suggested that these taxa might be related, but he was unclear whether *Santanichthys* belonged to the same family as *Clupavus*.

Lusitanichthys (originally referred to *Clupavus* aff. *neocomiensis*) and *Salminops ibericus*, both from the Cenomanian of Laveiras, Portugal (Fereira, 1961; Gayet, 1981, 1985a), have been the subject of heated and sometimes acrimonious debate in recent years, because of their putative phylogenetic position near the base of otophysans. The strongest support for that view is provided by specialized anterior vertebral elements that may represent a primitive Weberian apparatus (Gayet 1980, 1981, 1982a, 1982b, 1985a, 1985b; Fink et al., 1984; Fink and Fink, 1981, 1996). Similar modifications to the anterior vertebrae also have been reported in *Clupavus maroccanus* (Gayet, 1981; Taverne, 1995). Gayet (1981) removed *Lusitanichthys* from the genus *Clupavus* but retained both in the family Clupavidae, which she suggested may be a plesiomorph sister group to the Characidae. Fink et al. (1984: 1035) rejected that proposal sugessting instead that ‘‘there is some evidence of ostariophysan and possibly otophysan features, but substantial contradictory evidence also exists.’’ Patterson (1993) listed *Lusitanichthys* and *Salminops* as incertae sedis Otophysi, but commented that their status is controversial. Taverne (1995) included *Lusitanichthys*, *Salminops*, and *Clupavus* in the Otophysi, but concluded that *Clupavus* is evolutionarily more advanced than the others, sharing one of Fink and Fink’s (1981) characiphysan characters (presence of a single large supraneural between the braincase and fourth vertebra).

Some Brazilian fossils from the Marizal Formation of Bahia were referred to the genus *Clupavus* by Taverne (1977), with additional description by Silva Santos (1985), who named a new species *C. brasiliensis*. From these descriptions, *C. maroccanus* and *C. brasiliensis* appear to be similar, although they may differ in their caudal skeleton. It is uncertain whether they should be classified in the same genus, but the Brazilian form is here retained provisionally in *Clupavus*.

Although *Lusitanichthys*, *Salminops*, *Clupavus*, and *Santanichthys* share many primitive teleostean, ostariophysan, and otophysan characters, monophyly of these ''clupavid'' fishes has not been demonstrated convincingly, and in all likehood they do not constitute a monophyletic group. As is frequently the case in paleontology, however, poor preservation of critical specimens is a significant factor in the debate. In the case of *Clupavus maroccanus*, Grande (1985: 298) noted that different interpretations of particular fossils have led to contradictory phylogenetic conclusions; for example, based on the same fossils, according to Taverne (1977, 1995) the caudal skeleton has U1 fused to hypural 2 and has uroneural 1 fused to the first preural centrum (the condition in clupeoids), but according to Gayet these fusions are absent. Regarding *Lusitanichthys*, Fink et al. (1984: 1035) commented that ''its relationships may remain obscure until more information becomes available, and that may depend upon discovery of specimens in a better state of preservation''. *Salminops* is known only from a single, poorly preserved and miniscule specimen. Clearly, it would be advantageous to have better-preserved fossil representatives of basal ostariophysan fishes, and in this regard *Santanichthys diasii* seems to work well.

MATERIALS AND METHODS

HOLOTYPE: DGM-DNPM 647P, complete fish in matrix.

REFERRED MATERIAL: AMNH 20050–20075. Skeletons of 26 individuals were recovered by transfer preparation of a single concretion. Additional specimens were recovered during acid preparation of other fossil fish, including an exeptionally well-preserved individual (cataloged as AMNH 19439) with scales and dermal bones of the head intact, which was serendipitously freed by acid from the matrix of another much larger fish (Tharrias araripis, AMNH 13680). Many isolated bones of *Santanichthys* were also recovered as stomach contents during acid preparation of larger fishes.

All the specimens of *Santanichthys diasii* studied here are from the Santana Formation of the Araripe Basin, northeastern Brazil. The species is also reported from the Taquari Member of the Riachuelo Formation (Sergipe Basin) and the Codo Formation (Parnaiba Basin) (Silva Santos, 1985, 1991), but none of this material was available for examination. Line illustrations were made using a Nikon SMZ-U binocular microscope with camera lucida. Digital photographs were taken using a Nikon D1 camera connected to a dedicated PC and equipped with an Infinity Optics K-2 long-distance lens, with high intensity illumination provided by a Microptics ML-1000 fiber optic flash unit. Comparisons were made with Recent *Brycon* (a generalized characid; Weitzman, 1962) and various other Recent otophysans.

ABBREVIATIONS

Asp	autosphenotic
Bh	basihyal
Boc	basioccipital
Cb	ceratobranchial
Cl	cleithrum
Dn	dentary
Dsp	dermosphenotic
Ect	ectopterygoid
En	entopterygoid
Exo	exoccipital
F	fontanelle
Fr	frontal
H	hypural
Hm	hyomandibular
Hpu	hemal spine of preural vertebra
Ic	intercalarium
Io	infrorbital
Iop	interopercle
LC	lagenar capsule
Mes	mesethmoid
Mx	maxilla
NA	neural arch
Npu	neural spine of preural centrum
Op	opercle
P	parapophysis
Pa	parietal
Pcl	postcleithrum
Ph	parhypural
Pmx	premaxilla
Pop	preopercle
Ps	parasphenoid
Pto	pterotic
Ptt	posttemporal
PU	preural centrum

Qu	quadrate
R	rib
Sc	sclerotic bone
Sca	scaphium
Scl	supracleithrum
Smx	supramaxilla
Sn	supraneural
So	supraorbital
Soc	supraoccipital
Sop	subopercle
Sy	symplectic
Tp	tripus
U	ural centrum
Ur	uroneural
V	vertebra

SYSTEMATIC PALAEONTOLOGY

DIVISION TELEOSTEI SENSU PATTERSON AND ROSEN, 1977

SUPERORDER OSTARIOPHYSI SENSU ROSEN AND GREENWOOD, 1970

SERIES OTOPHYSI SENSU ROSEN AND GREENWOOD, 1970

SUBSERIES CHARACIPHYSI FINK AND FINK, 1981

ORDER CHARACIFORMES SENSU FINK AND FINK, 1981

Santanichthys diasii (Silva Santos, 1958).
Leptolepis diasii Silva Santos 1958: 3.
Leptolepis diasii Silva Santos; Silva Santos and Valença 1968: 349.
Leptolepis diasii Silva Santos; Patterson 1970: 289.
Leptolepis diasii Silva Santos; Maisey 1991: 272.
Santanichthys diasii Silva Santos 1991: 30.
Santanichthys diasii Silva Santos; Maisey 1993: 14.
Santanichthys diasii Silva Santos; Silva Santos 1995: 252.

TYPE: 647-P, DGM-DNPM, complete fish.

TYPE LOCALITY: Romualdo Member, Santana Formation, Araripe Basin, NE Brazil.

STRATIGRAPHIC AGE: Albian, Lower Cretaceous.

DIAGNOSIS: The following combination of primitive and derived characters is diagnostic for the species. Stem characiform with large and gobular lagenar capsules and no other characiform character; standard length 26–29 mm; dentary toothless with high and broad coronoid process; two supramaxillae; first supramaxilla elongate and narrow; second supramaxilla large and rounded; small mesethmoid; well-developed frontooccipital fontanelle; infraorbital series complete with triangular infraorbital 1 and narrow infraorbital 2; preopercular canal with projecting rounded tubules; supraoccipital limiting the frontooccipital fontanelle and bearing a small crest; pterotic with long posterior process; posttemporal with well-developed inner arm; Weberian apparatus developed; intercalarium articulates ventrally with the second vertebra; small tripus with both parapophysis and rib portions visible and weakly fused; neural arch of third centrum moderately expanded; 38–40 vertebrae; epineurals up to 18th centrum; neural and hemal arches fused to their respective centra throughout the column; compound centrum formed by fusion of PU1 and U1; separate long second ural centrum; parhypural, hypurals 1 and 2, and first uroneural all fused to compound centrum; at least 4 hypurals; cycloid scales covering the body.

TABLE 1
Measurements for *Santanichthys diasii*[a]

	mm	% standard length
Standard length	27	—
Total length	29	—
Head length	9	33
Mandible length	3	11
Body depth	7	26
Predorsal length	14	52
Preanal length	21	77
Prepectoral length	8	30
Prepelvic length	15	55
Caudal peduncle depth	2.5	9

[a] Based on specimen AMNH 20053.

DESCRIPTION

Santanichthys diasii is a small fish, with a total length rarely exceeding 30 mm. Measurements are summarized in table 1. Specimen numbers in the following description refer to individuals in which particular structures were best observed, but are not necessarily the only specimens in which the structures are recognizable.

ETHMOID REGION: A few specimens show a relatively well-preserved ethmoid region, but the mesethmoid is rarely visible. The bones of the snout are sometimes connected forming a small ossification of uncertain shape (e.g., AMNH 19439, 20050). This strongly suggests that the mesethmoid is reduced to a very small bone and was probably partially cartilaginous (fig. 1). By contrast, the frontals are long and extend very far anteriorly. The ethmoid region is moderately long and limited posteriorly by the lateral ethmoid (well preserved in AMNH 19439, 20068). This bone is characteristically triangular, with its upper arm long, slender, and backwardly directed. There is sometimes a rather square ossification behind the lateral ethmoid (e.g., AMNH 20068). It is not yet possible to determine whether this element is unpaired, but its position and shape recall those of a rhinosphenoid. A comparable ossification was not found in AMNH 19439. Other bones of the ethmoid region are not observable.

DERMAL BONES OF THE SKULL ROOF: Much of the skull is roofed by the frontals (figs. 1, 2). These bones are tapered anteriorly, where they meet the small mesethmoid, but become wider posteriorly and form the sides of a large oval frontooccipital fontanelle, best seen in AMNH 20050 (fig. 2). This fontanelle is present in many extant characiforms as well as in some other otophysans. A similar fontanelle is also reported in three fossil taxa, *Clupavus maroccanus* (Taverne, 1977, 1995), *Salminops ibericus* (Gayet, 1985), and *Lusitanichthys characiformis* (Gayet, 1981). The shape of the fontanelle in *Santanichthys*, *Salminops*, and *Lusitanichthys* differs from that of extant characiforms, where the fontanelle is less wide but much longer.

Silva Santos (1991) identified an additional frontomesethmoid fontanelle in *Santanichthys*, situated anteriorly between the frontals. A frontomesethmoid fontanelle is reported in *Clupavus maroccanus* and *Lusitanichtys characiformis* as well as in various otophysans. In our *Santanichthys* material, however, the contact between the frontals anterior to the epiphyseal canal is almost straight, although in specimens where the frontals have moved out their original position the displaced bones can sometimes appear to diverge anteriorly (e.g., AMNH 20068–20070). In specimens of *Santanichthys* where the frontals are still in contact with each other anteriorly, no frontomesethmoid fontanelle is evident. We conclude that no such fontanelle was originally present in this form.

The small and subrectangular parietals are separated by the frontooccipital fontanelle in *Santanichthys*, but the extent to which the parietals contribute to the margin of the fontanelle is variable. In AMNH 19439 the parietals reach the fontanelle and form a significant part of its margin, but in AMNH 20050 the supraoccipital extends anteriorly to contact the frontal, just occluding the parietal from the fontanelle margin.

The supraorbital canal runs through the entire length of the frontals and continues into the parietals. The parietal also contains part of the supratemporal commissure (AMNH 20065). The extrascapulars are not fused with the parietals, however, and are clearly visible in AMNH 19439. These elongate bones bear the sensory canal from the posttemporal to the parietals and are loosely applied to the posterolateral part of the cranium.

ENDOCRANIUM: The endochondral bones of the neurocranium are very loosely connected in *Santanichthys* and are rarely preserved in their original location except in the unusually well-preserved specimen AMNH 19439. Much of the endocranium was clearly cartilaginous, and chondral bones are difficult to recognize and may have been unossified. In most of the specimens we observed the ventral part of the neurocranium has become displaced, so the basioccipital is not in contact with the first vertebra, but lies more ventrally, and often the parasphenoid is also displaced with its anterior extremity meeting the frontals.

The orbitosphenoid is a small ossification forming the anterodorsal part of the endocranium. It is not well preserved in our material, and all that can be determined is that it lacks an interorbital septum and seems to project far anteriorly.

The autosphenotic is often preserved (e.g., AMNH 20050, 20055, 20062) and typically defines part of the orbital margin. The bone is subrectangular and bears a thin and spinous process directed slightly anteriorly (e.g., AMNH 20050). Its posterior portion is covered by the anterior part of the dermopterotic.

The dermopterotic is also commonly pre-

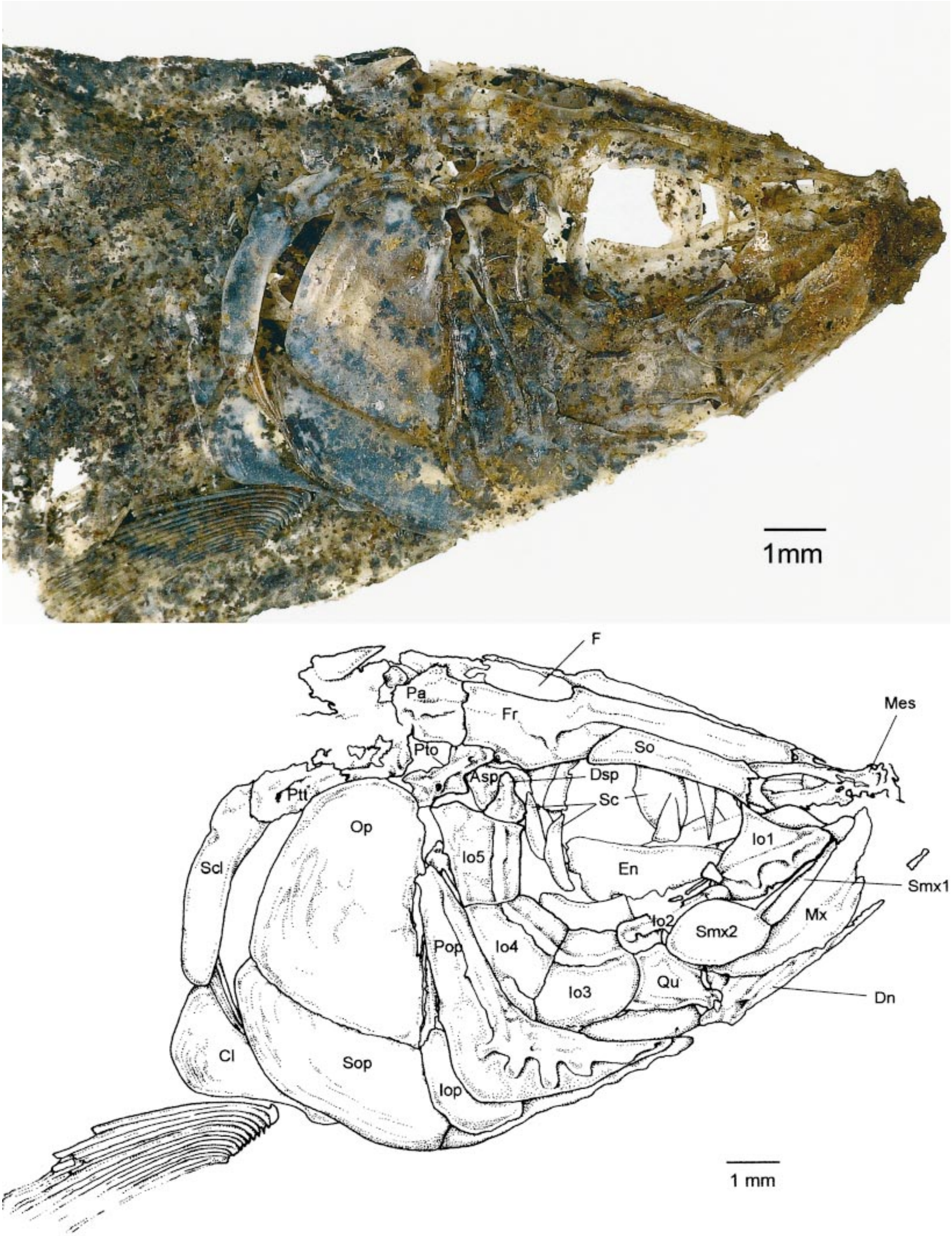

Fig. 1. *Santanichthys diasii*, specimen AMNH 19439, photograph and drawing of the head in lateral view.

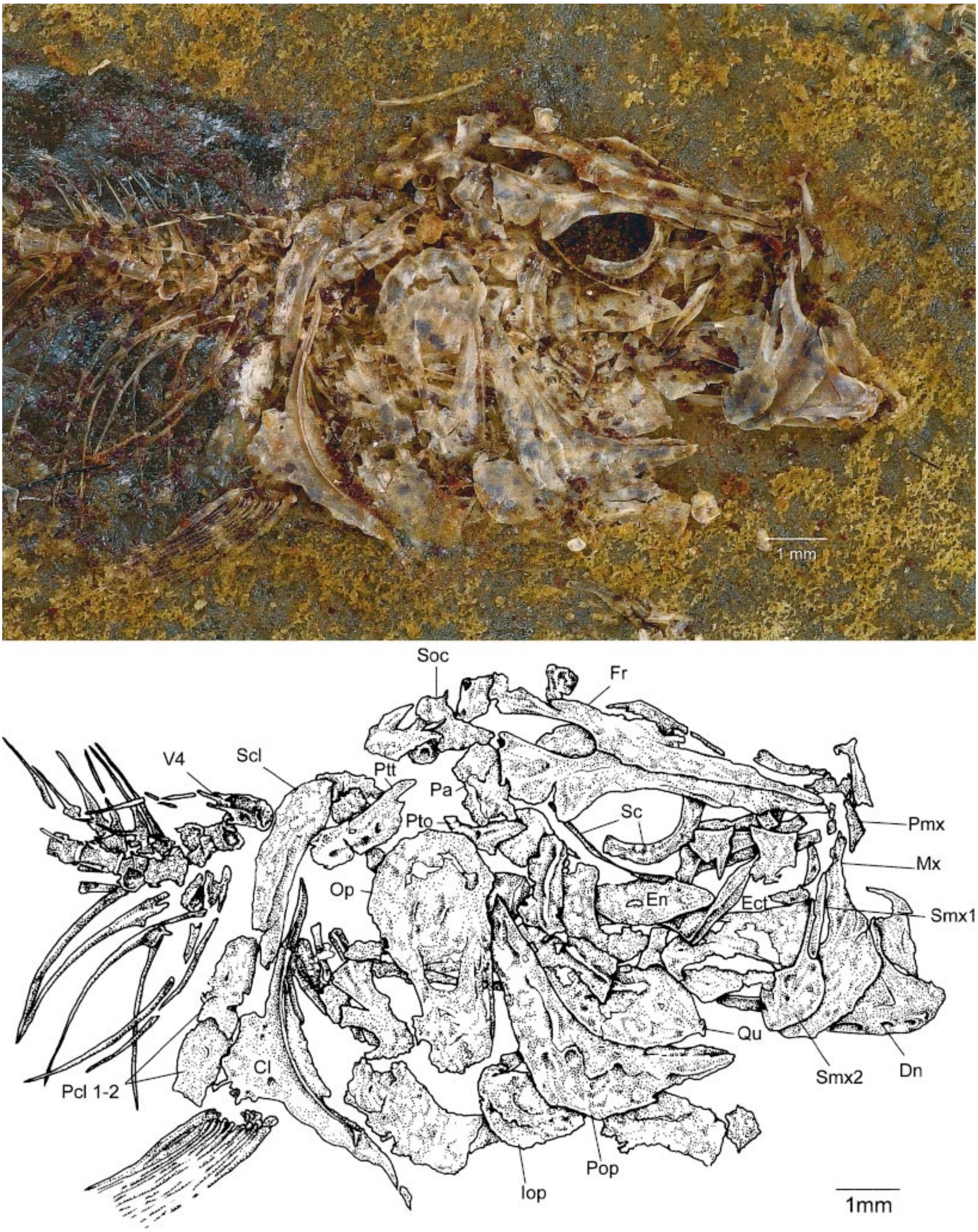

Fig. 2. *Santanichthys diasii*, specimen AMNH 20050, photograph and drawing of the head in lateral view.

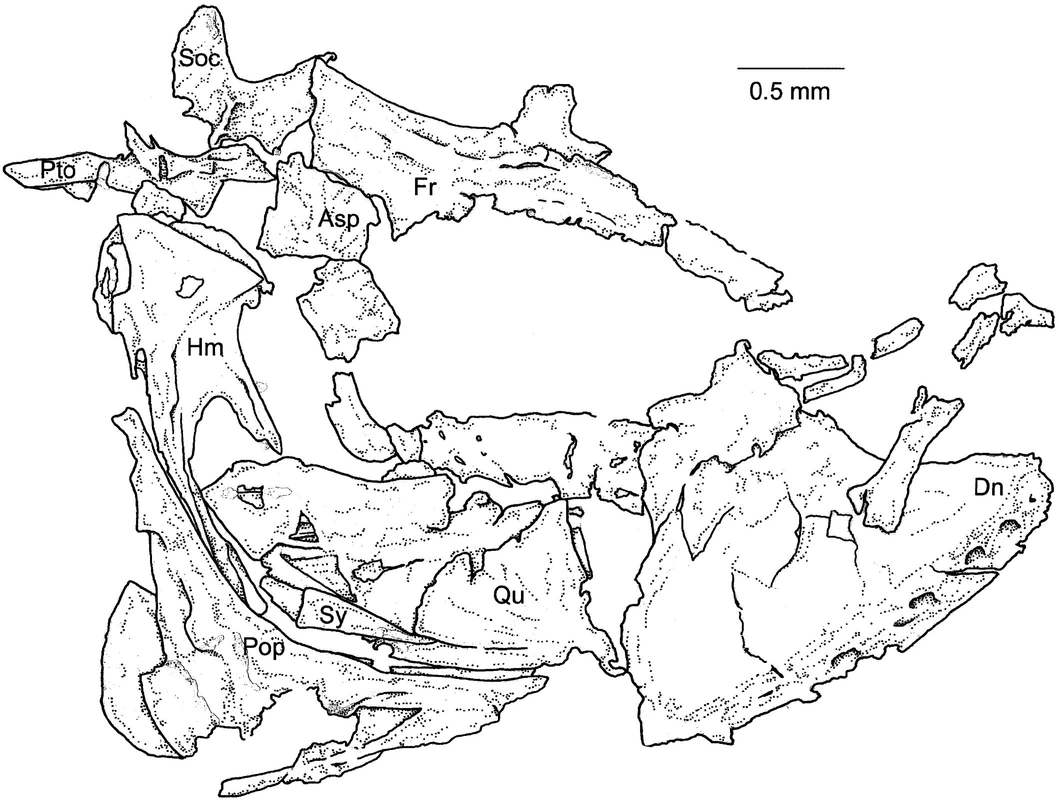

Fig. 3. *Santanichthys diasii*, specimen AMNH 20062, suspensorium, lower jaw, and part of the neurocranium.

served (figs. 3, 4), even though it is not sutured to any surrounding bones and presumably was held in place by soft tissues in life. It is very elongated anteroposteriorly and bears a strong posterior process, which recalls the condition seen in characiforms (e.g., *Brycon meeki*; Weitzman, 1962). This process seems to project well behind the posterior wall of the skull (e.g., AMNH 20062, 20063, 20068). The dermopterotic carried its sensory canal within a bony tube, with a ventral tubule extending from the middle part of the bone. Anteriorly, the dermopterotic meets the posterolateral corner of the frontal.

The supraoccipital is a flat bone with a deeply concave anterior margin forming the posterior limit of the frontooccipital fontanelle (e.g., AMNH 20050, 20060, 20062; fig. 3). Its posterior edge bears a very small crest as in many primitive teleosts, unlike the derived characiform condition (with a well-developed crest extending posteriorly).

Nothing can be said concerning the epiotics (which are badly preserved in all our specimens) or the prootic (which is either covered by the hyomandibular or poorly preserved; e.g., AMNH 20070). A basisphenoid has not been observed and may have been absent (it is unlikely to have been lost in all the specimens examined). Absence of a basisphenoid is regarded as a synapomorphy of ostariophysans (Fink and Fink, 1981: char. 7).

The exoccipitals and basioccipital are characteristic and form a large globular lagenar chamber that projects laterally (figs. 4, 5). This unique feature is regarded as a synapomorphy of characiforms (Fink and Fink, 1981). The basioccipital contributes to the lower part of the capsular wall (this is particularly clear in AMNH 20068 and can also be observed in AMNH 20052, 20053, 20064, 20069). In life, the lagenar chamber contained a large otolith (the astericus), but the otoliths are not preserved in acid-prepared fossils. The right and left lagenar chambers are separated posteriorly by a narrow septum (fig. 4) and open anteromedially into the saccular chamber (housing the sagitta in life). This cavity is slender compared with the posterior width of the bone. The anterior edge of the basioccipital is almost straight and vertical, and posteriorly this bone forms the entire occipital condyle. The exoccipital forms the dorsolateral parts of the capsular wall. Although this bone is often badly preserved, it clearly has concave posterior and dorsal surfaces. The lateral outer surface of this bone is subrectangular in shape and is pierced posteriorly by three foramina (e.g., AMNH 20071). The largest of these foramina is probably for the vagus nerve.

The parasphenoid differs from the generalized teleostean condition in being curved, as in characiforms. It is slender, lacks teeth, and extends posteriorly below the basioccipital as far as the lagenar chamber (a condition strongly resembling that of *Brycon meeki* as drawn by Weitzman, 1962).

SUSPENSORIUM: The hyomandibular is well preserved in many specimens (fig. 3). Its head is large and has two articular facets; one facet is elongated and directed dorsally to articulate with the cranium, and the other one is rounded and directed posteriorly for the opercle. The lower arm of the hyomandibular is slender in its median portion but becomes very wide and flattened farther ventrally. The bone has a very thin anterior wing whose size and extent seem to vary betweem individuals. The interhyal has not been observed.

The symplectic is elongate and triangular. As in teleosts generally, it sits within a deep notch in the quadrate. Its posterior portion extends beyond the quadrate while its anterior extremity almost reaches the quadrate lower margin.

The quadrate is typical of teleosts generally: it is triangular in shape, with a posterior arm for the symplectic and a condyle for the articulation with the lower jaw (fig. 3). Unlike in most basal teleosts, however, the bone is slightly inclined and the articular condyle is positioned somewhat anteriorly. The quadrate lacks a depression in its dorsal margin like that found in extant characiforms (e.g., *Brycon*).

The ectopterygoid is frequently lacking or poorly preserved in the available specimens. It is a thin, toothless bone that meets the metapterygoid posteriorly and projects anteriorly toward the ethmoid region, where it becomes even thinner.

The endopterygoid is also usually broken. It is a very thin toothless bone, oval in shape, stretched anteroposteriorly and lies dorsally against the ectopterygoid. Its dorsal surface can be seen in AMNH 20050.

The exact shape of the palatine is uncertain, and no dermopalatine has been observed. Absence of the dermopalatine is regarded as a synapomorphy of ostariophysans (Fink and Fink, 1981).

UPPER JAW: The premaxilla is thick, short, edentulous, and has no dorsal process. It has a condyle articulating with the small mesethmoid (AMNH 20050). The maxilla is seen best in AMNH 20050, 20065, and 20068. Its articulation is more complex than that of the premaxilla. The condyle for the mesethmoid is followed posteriorly by a rounded articular facet for the autopalatine. Although the maxilla is slender anteriorly, it becomes wider posteriorly and has an extremely deep and rounded ventral part. The maxilla is completely edentulous. Two supramaxillae are present. The anterior supramaxilla is elongated and pointed anteriorly, bordering the anterior part of the maxilla. The posterior one has a thin pointed arm projecting anteriorly above the posterior margin of the anterior supramaxilla. An unusually large oval posterior portion of the posterior supramaxilla lies against the maxilla.

LOWER JAW: It was not possible to determine exactly which bones articulate with the quadrate, since the pattern of fusion between the angular, articular, and retroarticular remains unclear. However, the socket for the quadrate condyle is often preserved and shows a short postarticular process. The limit between the angular and the dentary is visible in AMNH 20055, where the angulars have been dislodged, leaving the two preserved dentaries side by side. The angular penetrates the dentary very deeply, with the latter forming a long ventral arm that bears the mandibular canal and borders the ventral part of the angular. The dentary is edentulous and extremely deep, with a strong coronoid

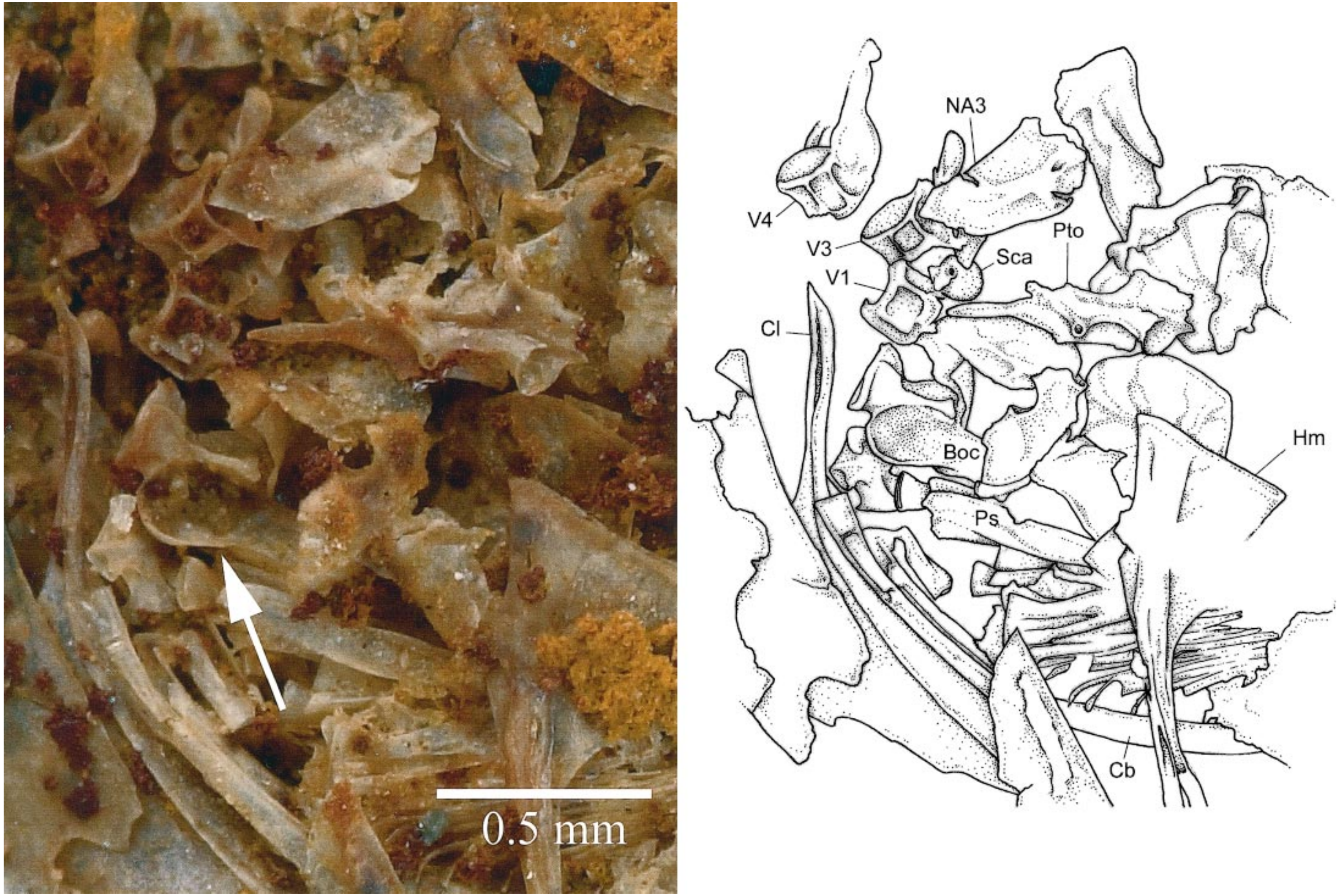

Fig. 4. *Santanichthys diasii*, photograph and drawing of the Weberian apparatus and posterior part of the skull in AMNH 20068. The lagenar capsules are indicated by the white arrow.

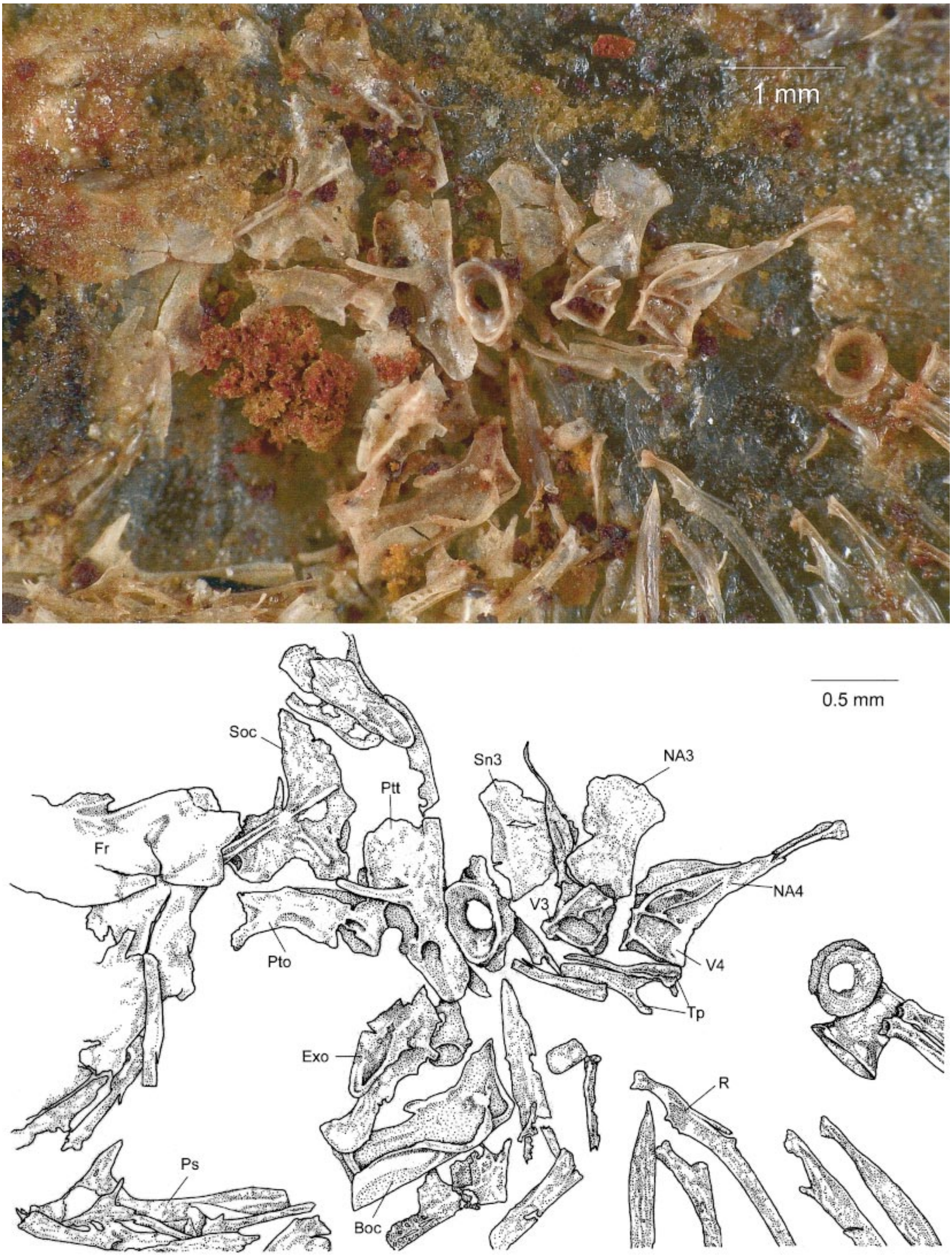

Fig. 5. *Santanichthys diasii*, AMNH 20052, photograph and drawing of the Weberian apparatus and some details of the skull.

process (e.g., AMNH 20062; fig. 3). The mandibular canal is wide, with several progressively larger oval openings posteriorly.

BRANCHIAL SKELETON: The branchial skeleton is incompletely preserved in many specimens, but parts are visible in AMNH 20058, 20059, 20064, 20068, and 20069. Unfortunately, the bones are never connected and a complete description of the branchial skeleton cannot be presented. Some ceratobranchials and epibranchials are recognizable, although most cannot be referred to a particular arch (the fourth epibranchials are both identifiable in AMNH 20059, thanks to their peculiar shape with two tubular arms projecting dorsally). The basihyal may be represented in AMNH 20064 by a small unpaired bone with a larger anterior portion bearing three processes on each side. In the same specimen, two tooth-bearing ceratobranchials are visible (fig. 6). In AMNH 20068, at least 12 gill rakers are preserved, inserted on their ceratobranchial. These rakers do not show any spicules.

OPERCULAR SERIES: The opercular series is perfectly preserved in AMNH 19439. The opercle is a fairly large bone, with a straight and almost vertical anterior margin. Its posterior margin is almost as straight but is more oblique, and the dorsal margin of the bone is rounded. The ventral part of the bone is the widest, with a sligthly rounded lower margin.

The preopercle comprises two branches. The dorsal branch (the longest) meets the ventral one at a slightly obtuse angle. The preopercular canal runs down the entire bone, along the anterior edge of the dorsal branch and the dorsal edge of the ventral one. This canal ramifies into five large tubules in the median and ventral parts of the bone, with the largest tubules in the median portion of the bone where the two main branches meet.

The interopercle lies beneath the ventral branch of the preopercle, but the interopercle is longer and its lower and posterior portions clearly extend beyond the preopercle. Its posterior margin is slightly rounded. Its depth equals that of the subopercle posteriorly but decreases anteriorly.

The subopercle is large and usually well exposed, since most of its surface is not covered by the opercle. Its anterior margin is almost straight and slightly oblique, and its ventral edge is strongly rounded posteriorly.

CIRCUMORBITAL SERIES: The circumorbital series (fig. 1) consists of several extremely delicate bones that would not normally be preserved in fossils, but they are perfectly preserved in AMNH 19439. The first infraorbital is triangular but elongated anteroposteriorly, and it is positioned above the first supramaxilla and also extends above part of the second one. The bone encloses the anterior termination of the infraorbital sensory canal and has two short ventral tubules extending from the main canal. The second infraorbital is elongate and narrow, with an unbranched canal. The third infraorbital is shorter than the second but is much deeper, with a deep rounded ventral wing reaching the preopercle. Its canal is confined to the upper portion of the bone and is unbranched. The fourth infraorbital is located at the posteroventral edge of the orbit and is also expanded ventrally, with its entire ventral margin meeting the preopercle. Its canal is confined to the margin bordering the orbit. The fifth infraorbital is almost square and contains the vertically oriented part of the sensory canal (again unbranched) behind the orbit. The dermosphenotic is a small ossification, consisting of little more than a bony tube enclosing the sensory canal, connecting the infraorbital supraorbital canals at the posterodorsal corner of the orbit. There is a single elongate supraorbital that edges the frontal all along the dorsal portion of the orbit. Nasals and antorbitals were not recognized in any of the material examined.

PECTORAL GIRDLE: The dorsal surface of the posttemporal is often preserved, but the inner concave surface of the bone is rarely observed (e.g., AMNH 20052). A long, well-developed arm projects perpendicular from the inner surface (fig. 5) and undoubtedly met the neurocranium to provide a firm attachment for the pectoral girdle. The posttemporal sensory canal passes along the midpart of the bone (e.g., AMNH 20059). The posttemporal also has a long anterior process although it is often broken; it can be seen in AMNH 20050, 20053, 20059, 20060, and 20064. According to Weitzman (1962) an identical arrangement is present in *Brycon meeki*.

The supracleithrum is an elongate, slightly curved, thin and narrow bone covering the upper part of the cleithrum but inserting under the posttemporal. The laterosensory canal enters the supracleithrum and extends through the upper length of this bone at the level of the upper tip of the cleithrum (e.g., AMNH 20060, 20068). The cleithrum is a large bone lying just posterior and medial to the opercle. Its upper arm is slender and very pointed, but its lower portion is expanded into a large posterior wing (e.g., AMNH 20050, 20052). The anteroventral part of the bone is also narrow.

The scapula and the coracoid can be seen in a few specimens (e.g., AMNH 20052, 20060, 20071), although few details can be discerned. The scapula is well developed, jutting out of the cleithrum ventrally. The coracoid is visible at the base of the fin rays, but its shape is uncertain. An extrascapula has not been positively identified. The bone is usually extremely small and thin in teleosts and in addition is often fused with the parietal. In AMNH 20050, a small bone which may contain a canal lies adjacent to the left posterior part of the braincase (fig. 2). This may represent a fused parietal–extrascapula but it is too poorly preserved for accurate identification.

Sixteen fin rays are present in AMNH 19439. No pectoral splint was observed.

WEBERIAN APPARATUS: In some specimens of *Santanichthys* there is evidence of a well-preserved Weberian apparatus. Most of the characteristic elements have been identified, although not all are observable in any one specimen. The general arrangement of this Weberian apparatus nevertheless seems to differ from that of all extant otophysans, but shares some similarities with the (presumably primitive) Weberian apparatus of *Chanoides* illustrated by Patterson (1984).

The first four vertebrae form elements of the Weberian apparatus, and are shorter and more elaborate than the following ones. An element interpreted as the scaphium is visible in AMNH 20064 and 20068. This bone has a ventral process that fits within a pit in the anterior border of the first centrum. It also has a shell-like concave anterior edge extending anteriorly beyond the end of the basioccipital, and an ascending process projecting posteriorly and dorsally (fig. 6). In extant otophysans, the concave portion of the bone (concha strapedis) is applied to the sinus impar. There is a foramen for the root of the spinal nerve passing through the bone above the articulating process. Just above this foramen is a knob, which is interpreted as the attachment of the ligament from the intercalarium.

A claustrum has not been identified in any of the specimens we examined, and an intercalarium has been identified in only two specimens (AMNH 20059 and 20064). Its shape is similar to that of *Chanoides* and unlike that of extant otophysans. The intercalarium of *Santanichthys* has a pedicel ventrally that articulates with the second vertebra. The bone is similar to the scaphium in shape, but its anterior edge is pointed (fig. 6). No foramen has been observed in the intercalarium, as in extant otophysans but not in *Chanoides*, where a foramen is present.

A manubrium has not yet been identified in *Santanichthys*, and the third vertebra is not reduced (unlike *Chanoides*). Nevertheless this vertebra bears a large transformed neural arch (e.g., AMNH 20052, 20068), resembling that of modern cypriniforms. The side of the third vertebral centrum also has a strong oblique crest, which we regard as evidence for the attachment of a tripus (figs. 5, 7). In support of this interpretation, AMNH 20052 has an element ventral to this vertebra that may represent a displaced tripus. This element is stretched and triangular with a convex posterior margin and is separated into two pieces. This configuration conforms to current hypotheses on the origin of the tripus as being formed from two different bones (parapophysis and rib). Rosen and Greenwood (1970) described a tripus in two pieces in a juvenile *Brycon*, suggesting that this is the primitive condition for the bone.

The fourth vertebra bears unfused and flattened neural arches, pointed and backwardly directed. In AMNH 20052 there is a large bone anterodorsal to the third vertebra that is regarded as a broken piece of a well-developed third supraneural.

PELVIC GIRDLE AND DORSAL FIN: The pelvic bones are triangular with a thick posterior portion, although their exact shape is unclear.

Fig. 6. *Santanichthys diasii*, AMNH 20064, photograph and drawing of the elements of the neurocranium, the branchial skeleton and the Weberian apparatus.

These bones are located under the vertebrae 15–8. The pelvic fin is composed of nine rays, whose length is equal to that of the pelvic bones. No pelvic splint has been seen.

The base of the dorsal fin is situated under vertebrae 16–19, but the first pterygiophore reaches the neural spine of the 12th vertebra. This pterygiophore has two branches (AMNH 20050) and bears at least two short rays (AMNH 20074) as well as the first long ray. At least nine pterygiophores can be counted (AMNH 20071), but the original number of fin-rays is unknown, although the dorsal fin was probably short anteroposteri-

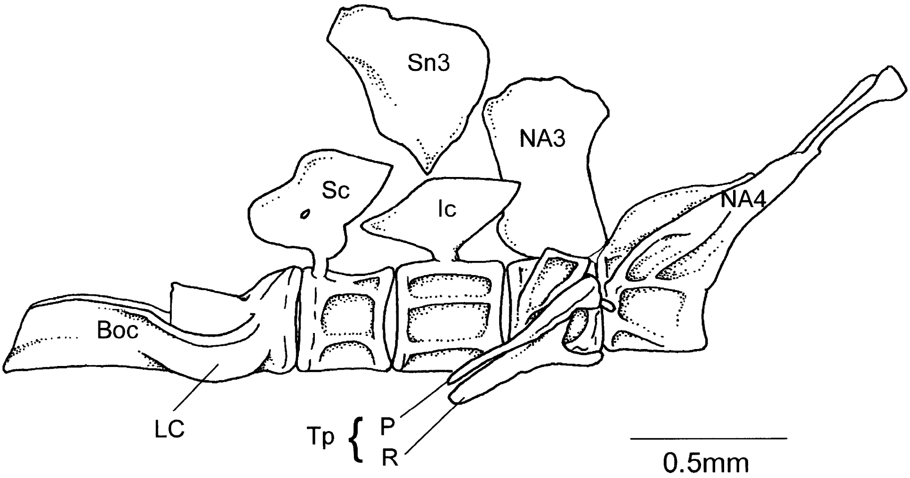

Fig. 7. *Santanichthys diasii*, restoration of what is known of the Weberian apparatus.

orly. It is unknown whether an adipose fin was present.

AXIAL SKELETON: There are between 38 and 40 vertebrae, including a compound ural centrum, the independent second ural centrum, and the anterior vertebrae bearing the Weberian apparatus (fig. 8). Most of the vertebrae are long, especially those from the midpart of the body, and all are moderately constricted. Their ornamentation is restricted to two crests on each side, and all the vertebrae generally have a smooth appearance. Unbranched epineurals are visible as far back as the 18th vertebra, attached at the base of the neural spine (AMNH 20050). No epicentral or epipleural elements were identified. Ribs are present up to the 25th vertebra, but on vertebrae 23–25 the hemapophyses are extended to form a small hemal spine supporting the rib. Hemal spines of the 26th and subsequent vertebrae are completely formed. Throughout the column, the neural and hemal spines are fused to their respective centrum in a very anterior position.

CAUDAL SKELETON: In *Santanichthys* the first ural and preural centra are fused to form a compound centrum, although the second ural centrum remains independent, is elongate in shape, and extends far posteriorly (fig. 9). The parhypural and first two hypurals are usually all fused to the compound centrum, as well as the first uroneural, but in AMNH 12826 the first two hypurals, parhypura,l and first two hemal spines appear to be unfused (fig. 10). However, this specimen is unusual in having been found in the stomach content of another fish (*Rhacolepis*) and is partially digested, so the surface of the bone and the crests of the vertebrae have been removed. Digestion may have secondarily separated caudal elements from the centra, and the specimen is of considerable interest because it suggests that these elements were fused only superficially with their centrum but remained unfused internally.

The hemal spines of preural centra 2 and 3 are expanded. The spine of preural centrum 2 has a large but thin anterodorsal wing and a flattened extremity. The neural spine of preural centrum 3 is not modified, whereas that of preural centrum 2 is short and slightly flattened. The neural spine of the compound centrum (first preural spine?) is even shorter and leaflike. Uroneural 1 is fused with the compound centrum only and forms a ridge on its surface. There is a space for a second uroneural, but this element has not been observed. Hypural 1 is enlarged and lies between the parhypural and hypural 2, which are similarly shaped. Hypural 3 is approximately as large as the first (e.g., AMNH 20055, 20058, 20059, 20062, 20068) and is unfused (it is missing in some specimens). It is clearly associated with the small and elongate independent second ural centrum in AMNH 20053, 20059, 20068, and 20072, which is similar to the arrangement in *Chanoides* (Patterson, 1984). There is no diastema between hypurals 3 and 4. The fourth hypural lies just above the third and is considerably smaller. There may have a fifth and sixth hypural but these have not been identified. An elongate and slightly sigmoid dorsal element (possibly an epural) is present in AMNH 20068. The exact number of caudal finrays is uncertain. The bases of the finrays are not expanded and ray segmentation is almost straight.

SQUAMATION: The scales are cycloid and arranged in oblique rows, although the arrangement has only been seen in AMNH 19439. In the abdominal region, each transverse row contains approximatively 15 scales. The total number of scale rows is unknown, as AMNH 19439 lacks the tail.

DISCUSSION

Of the 15 characters used by Fink and Fink (1981) to define the Ostariophysi, 8 are potentially observable in fossils. Five of these can be demonstrated in *Santanichthys*: absence of basisphenoid (their character 7), saccula and lagena situated more posteriorly and nearer in the midline (8), dermopalatine absent (20), dorsomedial portion of the anterior neural arches expanded (63), and all haemal spines anterior to that of the second preural centrum fused to their centrum (111). However, two of these characters are reportedly also found in clupeomorphs (8, 111; T. Grande, personal commun.). One of the features observable in *Santanichthys* clearly contradicts one of Fink and Fink's (1981) ostariophysan characters—absence of supramaxillary bone (41; *Santanichthys* clearly has two supramaxillary bones, which is the generalized condition for teleosts). This does not contradict the insertion of *Santanichthys* among ostariophysans, but it strongly suggests that this character should be reconsidered as an ostariophysan synapomorphy. If *Santanichthys* is an otophysan and a stem characiform (as we propose), the presence of two supramaxillae indicates that loss of these bones may not have occurred at the Ostariophysi level but more probably occurred independently in gonorhynchiforms and otophysans (perhaps several times). This possibility was partly acknowledged by Fink et al. (1984) because Patterson (1984) found a supramaxilla in the stem otophysan *Chanoides*, but Fink and Fink (1996) subsequently suggested that other reported supramaxillae in characiforms are neomorphic. Now, however, the presence of two supramaxillae in a putative stem characiform (which is also the oldest ostariophysan known to date) further weakens the possibility that characiforms primitively lacked these bones.

Fink and Fink (1996) found 14 characters to support a monophyletic Otophysi, many of which are related to the Weberian apparatus. We regard *Santanichthys* as having a complete Weberian apparatus, although the shape of some of its elements are unusual. We suggest that *Santanichthys* displays Fink and Fink's (1996) characters 60, 66, 69, 78, and 85 (anterior supraneural expanded; first neural arch modified to form a scaphium; second neural arch modified to form the intercalarium; first four centra shortened in comparison with the more posterior ones; and parapophysis and rib of the third centrum modified to form a tripus). The Weberian apparatus of *Santanichthys* differs from that of Recent teleosts in having an unusually shaped intercalarium, a small tripus, and a moderately expanded supraneural and neural arch of the third centrum. Instead, in some respects the Weberian apparatus of *Santanichthys* resembles that of *Chanoides* (Patterson, 1984), especially the shape of the intercalarium, fourth neural arch and possibly the supraneural (in *Santanichthys* the expanded supraneural is poorly known). On the other hand, the third centrum is not shortened in *Santanichthys* and extant otophysans, as opposed to *Chanoides* (Patterson, 1984) or *Lusitanichthys* (Gayet, 1981, 1982). Based on these observations alone it would be difficult to determine the relationships of *Santanichthys* to any particular group of otophysans, or to propose any hypothesis on the evolution of the Weberian apparatus.

Besides the Weberian apparatus, *Santanichthys* also displays other common characters in otophysans (though not necessarily otophysan synapomorphies), including the presence of a compound terminal centrum and fusion of the hypural 2 with the compound centrum (in most but not all specimens; see above). These features are also seen in clupeomorphs and numerous teleosts and therefore we do not consider them as prima facie evidence of an otophysan relationship.

In all modern otophysans, the compound terminal centrum represents a fusion of the first preural centrum plus the first and second ural centra. Fink and Fink (1996, char. 110) maintained that the compound centrum is a synapomorphy of the Otophysi. Gayet (1986) questioned this, suggesting instead that the character could be convergent. In *Santanichthys* the second ural centrum remains free although the first preural and first ural centra are fused together. This is also the situation in *Chanoides* (Patterson, 1984), suggesting that the compound terminal centrum has a discernible phylogenetic history in which different character states are recognizable (primitively unfused; fusion between U1 and PU1; and fusion of U2). Possibly these fusions between PU1, U1, and U2 have occurred independently in various otophysan subgroups, in which case fusion of all three elements does not necessarily constitute a synapomorphy for the whole group (especially if *Santanichthys* is a stem characiform as proposed here).

Another significant feature of the caudal skeleton in *Santanichthys* is fusion between the first hypural and the compound centrum, which is observed in many specimens, although the bones are only fused perichondrally and are easily separated (broken or partially digested individuals in stomach content often show a separate first hypural). Fusion between the first hypural and the compound centrum is a common condition among teleosts, but in otophysans the second hypural is usually fused to the centrum whereas the first hypural is separate (regarded as an apomorphic feature by Fink and Fink, 1996). This would not be problematic if *Santanichthys* is a basal otophysan, but our findings suggest that it actually occupies a higher position within the group (see below), in which case this character may represent a reversal.

Any attribution of *Santanichthys* to one of the recognized crown otophysan subgroups (Cypriniformes, Characiformes, Siluroidei, Gymnotoidei) is more controversial, although *Santanichthys* could be considered a characiform on the basis of the presence of large and globular lagenar chambers that project well laterally to the cranial condyle (Fink and Fink, 1996: char. 15). The fact that the basioccipital contributes to the ventrolateral part of the capsular wall is certainly a striking similarity between *Santanichthys* and characiforms, since this bone is primitively excluded from the capsule in teleosts by the exoccipitals. This character therefore involves important developmental transformations of the neurocranium (especially the basioccipital, but also the exoccipital, otoliths and membranous labyrinth) that would not be readily subject to convergence, and apparently the feature is unique, not only among ostariophysans, but among basal teleosts generally. We consider this to be the strongest evidence for a relationship between *Santanichthys* and characiforms.

Other otophysan characters proposed by Fink and Fink (1996) supporting monophyly of characiforms are either absent or are not observable in *Santanichthys* (e.g., presence of an auditory foramen in the prootic). Conversely, no features observable in this species seem to contradict its inclusion in otophysans, and certain features (e.g., the long posterior process of the dermopterotic and shape of the posttemporal) are unusual and recall those found in characiforms (e.g., *Brycon meeki*, Weitzman, 1962). The absence of jaw teeth in *Santanichthys* may represent an autapomorphy of the genus, since characiforms are characterized by multicuspid jaw teeth (these are absent in gonorhynchiforms and cypriniforms). *Santanichthys* diplays none of the characters supporting the Cypriniformes, Siluroidei, and Gymnotoidei. In our opinion *Santanichthys* is a stem characiform sharing at least one character with extant members of the group.

Our view that *Santanichthys* is a primitive characiform is admittedly incongruent with certain aspects of Fink and Fink's (1996) phylogenetic hypothesis. They grouped the Characiformes and Siluriformes together in the Characiphysi, with Cypriniformes forming a sister group of the Characiphysi and consequently more basal than the Characiformes. Their Characiphysi was supported by 15 characters, 5 of which we could not compare in *Santanichthys*. Of their 10 remaining characters, 7 are observable in *Santani-*

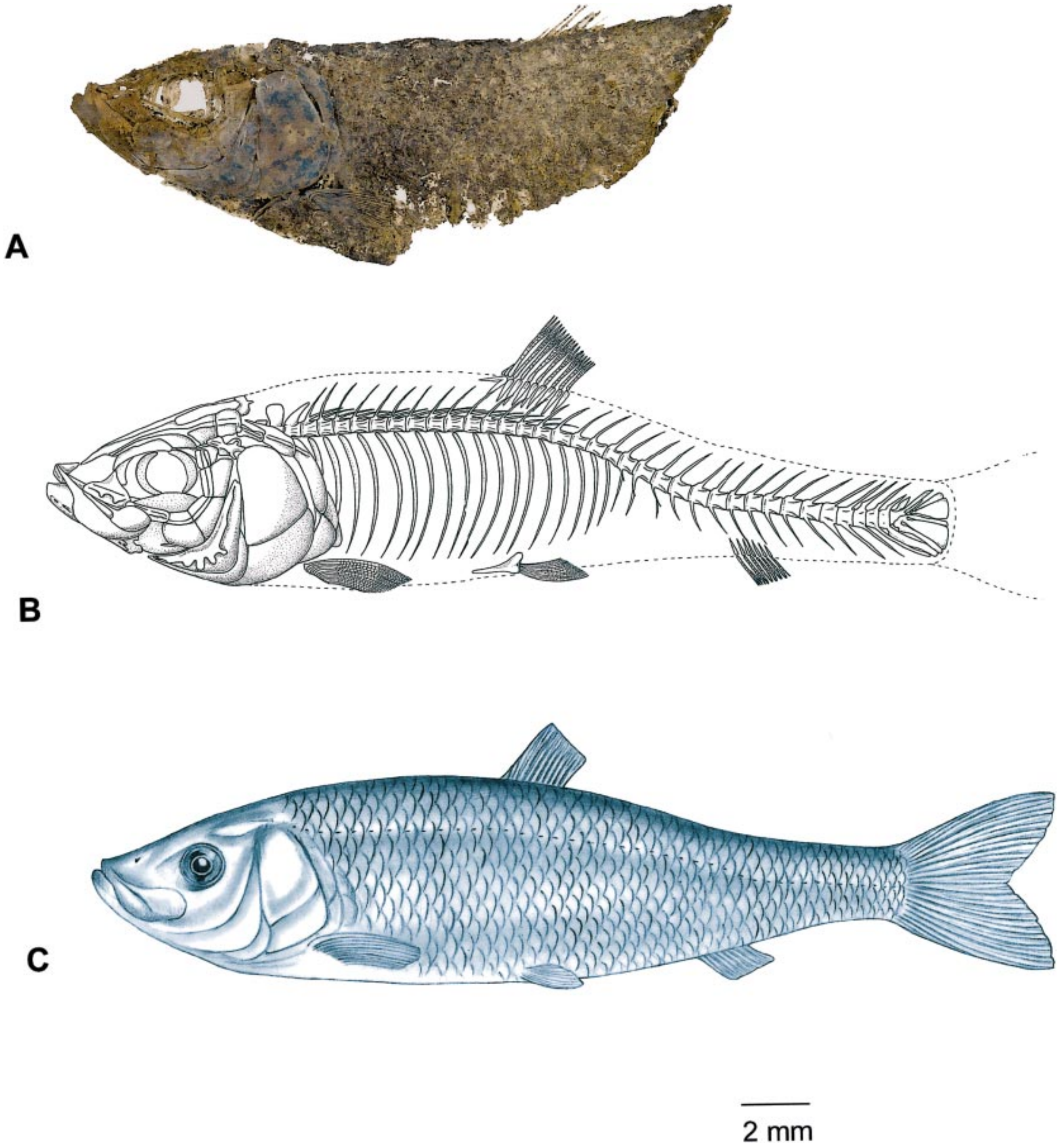

Fig. 8. *Santanichthys diasii*: (**A**) specimen AMNH 19439; (**B**) restoration of the entire skeleton, the head is slightly inclined to see the fontanelle; (**C**) restoration of the fish as living.

chthys, whereas a different state is present for three of their characters (72, 73, 75). These all involve the shape and the extension of the third neural arches and spines, which are more reduced in *Santanichthys* than in extant Characiphysans.

While these observations may weaken support for grouping characiforms together with other characiphysans, we cannot propose any alternative hypothesis or characters supporting another grouping based on our observations. Nevertheless, the inclusion of extinct taxa such as *Santanichthys* and *Chanoides* in future phylogenetic analyses of otophysan fishes might very well affect their outcome (and may especially affect those

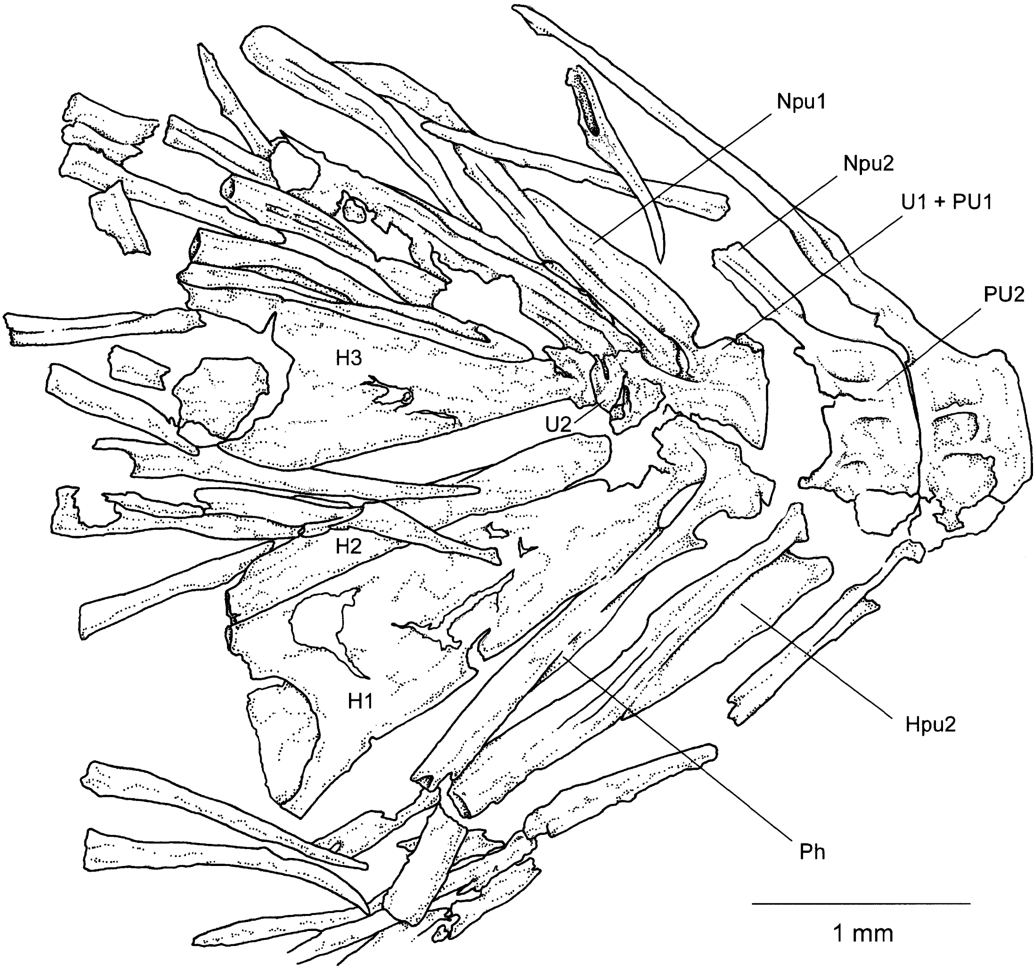

Fig. 9. *Santanichthys diasii*, AMNH 20068, caudal skeleton.

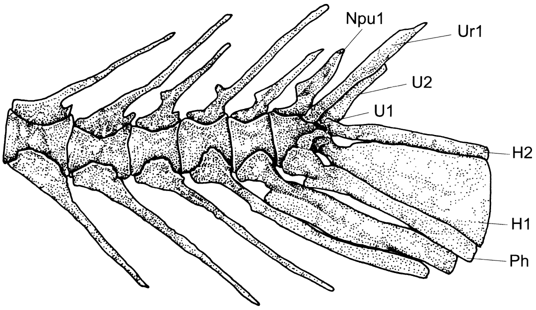

Fig. 10. *Santanichthys diasii*, AMNH 12826, caudal skeleton.

characters suspected here to be convergent). If we are correct that *Santanichthys* is a basal characiform with two supramaxillae, an unfused second ural centrum, and a large frontooccipital fontanelle, its inclusion in future phylogenetic analyses may well affect hypotheses of otophysan and characiphysan relationships.

We recognize that our identification of *Santanichthys* as a stem characiform will be controversial and that our observations of certain characters will only add fuel to existing controversies surrounding otophysan phylogeny (Fink and Fink, 1981, 1996; Gayet, 1981, 1982, 1985a, 1986; Gayet and Chardon, 1987). We will not try to revive this discussion here, but simply point out that other supposed otophysan fossils (e.g., *Lusitanichthys*) also do not rest comfortably within the phylogenies presented by Fink and Fink (1981, 1996). We agree with Fink et al. (1984) and Patterson (1984) that Gayet's proposals of independent dispersals of marine ''pre-characids'' and ''pre-cyprinids'' into South America, America, and Europe are not parsimonious, nor are they based on a well-supported phylogenetic hypothesis. However, as Patterson (1984) pointed out, many early ostariophysans were marine (including Gayet's taxa as well as *Chanoides*), and *Santanichthys* was probably also either marine or at least could tolerate brackish mangrovelike waters. If primitive characiforms are marine, it is difficult to explain why all cypriniforms (supposedly occupying a more basal phylogenetic position) are freshwater fishes. Hopefully, future phylogenetic analyses of otophysan fishes (including fossils) will clarify their biogeographic origins.

CONCLUSIONS

Santanichthys is considered here to be the oldest characiform (and otophysan) known to date, and together with *Chanoides* is one of the better preserved fossil otophysans. These and other extinct taxa deserve inclusion in future phylogenetic analyses of otophysan fishes, where they will undoubtedly affect some character distributions and polarity, and will perhaps also affect their outcome. Its Gondwanan occurrence certainly has biogeographic significance although no biogeographic conclusions will be offered in the absence of a detailed phylogenetic analysis.

ACKNOWLEDGMENTS

We thank Marie-Hélène Hamel who made the final versions of the line illustrations. We also thank Dr. David Grimaldi for allowing us to use his photographic system in this work, and Roy Larimer for taking the photographs. Funding for our investigation was provided by the Herbert and Evelyn Axelrod Research Chair in Vertebrate Paleontology at the AMNH. We also thank the reviewers for their useful remarks.

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