A New Clupeomorph Fish from the Santana Formation (Albian) of NE Brazil

JOHN G. MAISEY[1]

ABSTRACT

A new clupeomorph fish is reported from the Lower Cretaceous (Albian) Santana Formation of NE Brazil. It is of small size; the largest individual is approximately 120 mm standard length, and some are considerably smaller. The new fish displays several clupeomorph and clupeiform characters, but its placement within the Clupeiformes is problematic. It possesses obliquely inclined suspensorium and elongate jaws, which are reminiscent of the engrauloid condition. Several plesiomorphic character states conflict with that hypothesis, such as the autogenous parhypural, lack of fusion between the first uroneural and first preural centrum, unreduced first ural centrum, presence of a complete series of lateral line scales, and lack of dorsal scutes; therefore the fish is considered as a clupeiform incertae sedis.

INTRODUCTION

The Santana Formation of the Chapada do Araripe is a well-known source of fossil fishes representing a tremendously diverse ichthyofauna. Many of these fossils (including those studied here) occur in carbonate concretions of late diagenetic origin, within shales and marls of the Romualdo Member (the uppermost member of the Santana Formation). Recent palynological studies have determined the age of these fossils to be Middle or Late Albian (Pons et al., 1990).

The clupeomorph described here is a rare constituent of the assemblage, and is the first clupeomorph species to be described from the Santana Formation. Other undescribed and somewhat different clupeomorphs occur lower in the Romualdo Member, from pyrobituminous shales overlying gypsum deposits of the Ipubi Member.

This new clupeomorph was first reported by Maisey (1991b) from two small individuals in a single concretion belonging to the

[1] Curator, Department of Vertebrate Paleontology, American Museum of Natural History.

American Museum, associated with disarticulated bones of the primitive gonorynchiform *Tharrhias*. Subsequently, another specimen was identified in the AMNH collection, and some others were found among material in the collections of the Departamento Nacional de Producão Mineral (DNPM), Rio de Janeiro. One of these DNPM specimens has been selected to serve as the holotype (fig.1). Although the total sample is small, these clupeomorph specimens seem to represent a single taxon, which is treated here as a new genus and species.

ABBREVIATIONS

Institutional

AMNH	American Museum of Natural History
DNPM	Departamento Nacional de Producão Mineral, Rio de Janeiro

Anatomical

A	angular
af	auditory fenestra
Bo	basioccipital
D	dentary
Epo	epioccipital
Exo	exoccipital
Fr	frontal
fp	preepiotic fossa
H	hypural
Hm	hyomandibula
hmfa	anterior hyomandibular facet
hmfp	posterior hyomandibular facet
Ic	intercalar
Iop	interopercular
Le	lateral ethmoid
Me	mesethmoid
Mpt	metapterygoid
Mx	maxilla
Npu	preural neural arch
Op	opercle
or	foramen for orbital artery
Os	orbitosphenoid
Pa	parietal
Ph	parhypural
Pmx	premaxilla
Pop	preopercle
Pro	prootic
Psp	parasphenoid
Pto	pterotic
Pu	preural centrum
Q	quadrate
rec	openings for recessus lateralis
S	symplectic
Smxa	anterior supramaxilla
Smxp	posterior supramaxilla
Soc	supraoccipital
Sop	suboperacle
Spo	sphenotic
Steg	stegural
tf	temporal fenestra
U	ural centrum
Un	uroneural
VII, X, XII	foramina for cranial nerves

SYSTEMATICS

COHORT CLUPEOCEPHALA

SUBCOHORT CLUPEOMORPHA

ORDER CLUPEIFORMES

Clupeiformes incertae sedis

Santanaclupea, new genus

ETYMOLOGY: After Santana do Cariri, the town giving its name to the famous Santana Formation, and *Clupea* (Latin), small river fish.

DIAGNOSIS: Clupeomorph fish with parietals separated by supraoccipital, supratemporal sensory canal passing through parietals but external to supraoccipital; dilatator fossa shallow, without roof; preepiotic fossa large; temporal foramen large; no frontal fontanelle; hyomandibula with slight posterior inclination; complete series of lateral line scales extending back to caudal region; continuous series of ventral scutes present from behind pectoral fins as far as anal fin; 19 or 20 abdominal vertebrae plus 19 caudal and 2 ural centra. Proportions (as percent of standard length): head 22, maximum trunk depth 33, predorsal 45–47, prepelvic 51–53, preanal 75. Pelvic fins slightly posterior to dorsal; fin ray counts: D14; A11; P12; V8-9; C19 principal rays (10 upper, 9 lower), plus 5 dorsal and 4 ventral procurrent rays.

TYPE SPECIES: *Santanaclupea silvasantosi*.

Santanaclupea silvasantosi, new species

ETYMOLOGY: *silvasantosi* after Prof. Rubens de Silva Santos, preeminent Brazilian authority on paleoichthyology, who described many species of fossil fishes from the Santana Formation.

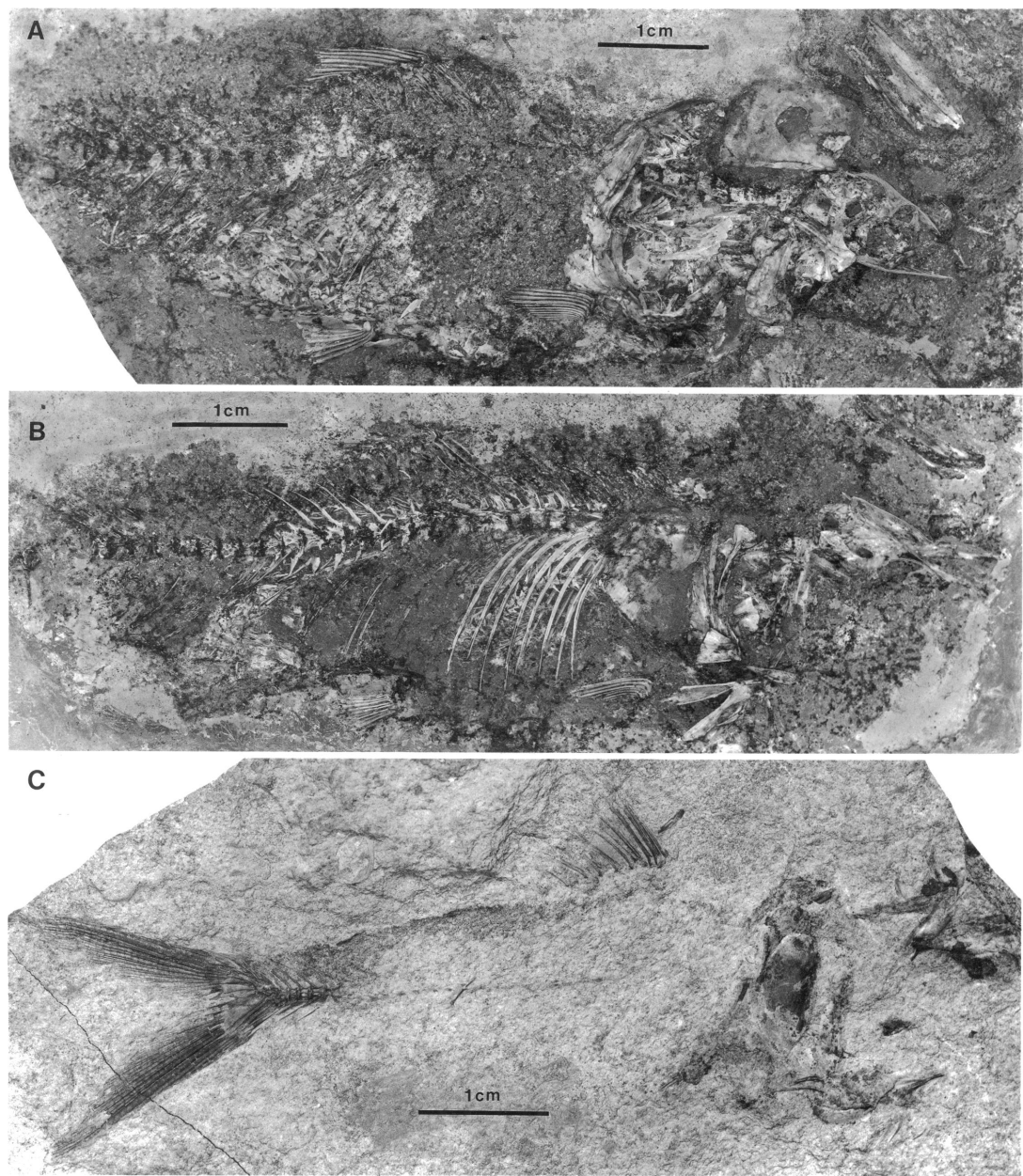HOLOTYPE: DNPM 515-P, fish lacking tail, in part and counterpart, preserved length ap-

Fig. 1. *Santanaclupea silvasantosi.* (A, B) The holotype DNPM DGM 515-P; (A) part and (B) counterpart after acid preparation; (C) DNPM DGM 1338-P (B and C reversed).

prox. 85 mm, estimated standard length approx. 100 mm, Santana Formation, Chapada do Araripe, now acid-prepared (figs. 1A, B, 4, 8).

REFERRED MATERIAL: **AMNH 18968,** the largest known individual, having an esti-

mated standard length of approx. 120 mm (figs. 2C, 3A). **AMNH 12789 and 12790,** two small associated individuals, both with a standard length of approx. 45 mm (figs. 2A, B, 3B, C, 6A). **DNPM 1338-P,** poorly preserved individual with good tail, part of dor-
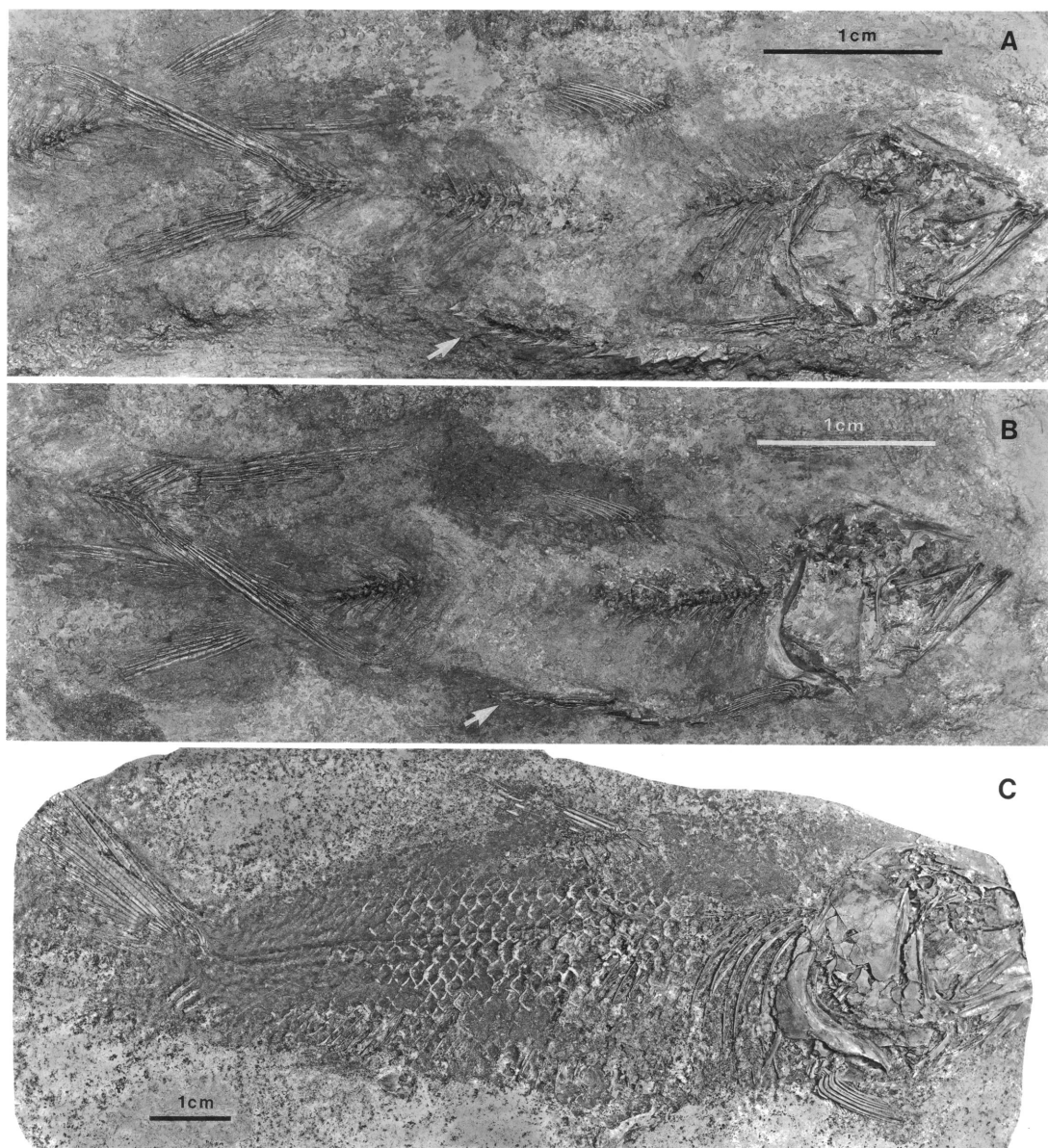
Fig. 2.   *Santanaclupea silvasantosi.* **(A)** AMNH 12790; **(B)** AMNH 12789; **(C)** AMNH 18968 (A and B reversed).

sal fin and opercular series, estimated standard length approx. 60 mm (fig. 6B). **DNPM 683-P,** complete fish approximately 60 mm standard length.

Specimens have been acid-prepared apart from DNPM 1338-P and 683-P. A part and a counterpart exist only in the holotype.

DIAGNOSIS: As for genus.

DESCRIPTION

The ethmoid region and anterior part of the orbit are incomplete in all the specimens examined except for the holotype, DNPM 515-P. Most of the postorbital region of the braincase is well preserved in this specimen and in AMNH 18968, which together pro-
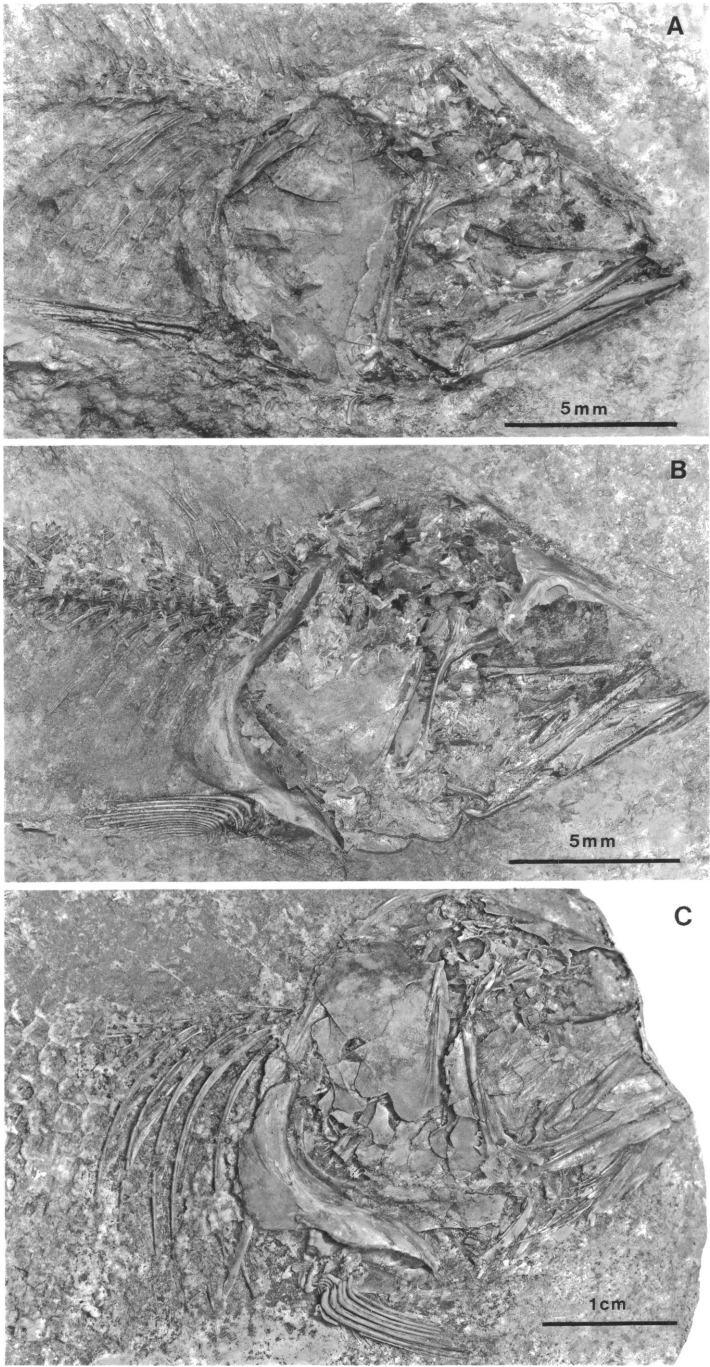
Fig. 3. Details of the head in **(A)** AMNH 12790; **(B)** AMNH 12789; **(C)** AMNH 18968 (B and C reversed).
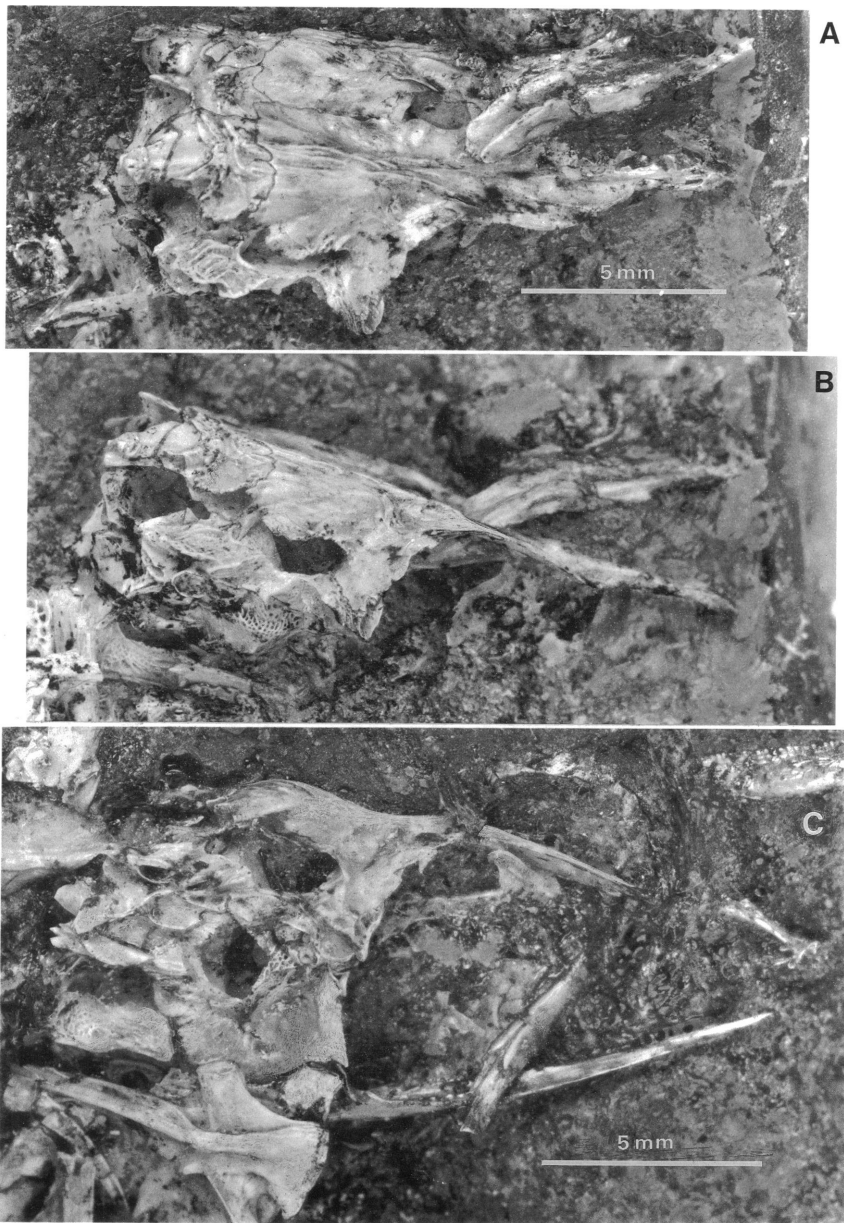
Fig. 4.   Braincase in DNPM DGM 515-P. **(A)** Oblique dorsal view showing supraoccipital separating parietals, commissural canal not entering supraoccipital; **(B)** lateral view of same, with pitted "strawberry appearance" of the prootic; **(C)** lateral view of the counterpart, with displaced hyomandibula (A and B reversed).

vide most of the information given here (figs. 4, 5). In the two small associated individuals, AMNH 12789 and 12790, the neurocranium is incompletely ossified and individual bones are disarticulated. Their size and degree of ossification suggest that these two specimens are juvenile. The head and jaws are well preserved in DNPM 683-P. Nothing of the head is preserved in DNPM 1338-P.

The parietals, supraoccipital, and posterior part of the frontals are ornamented by sinuous ridges and rounded processes. Farther
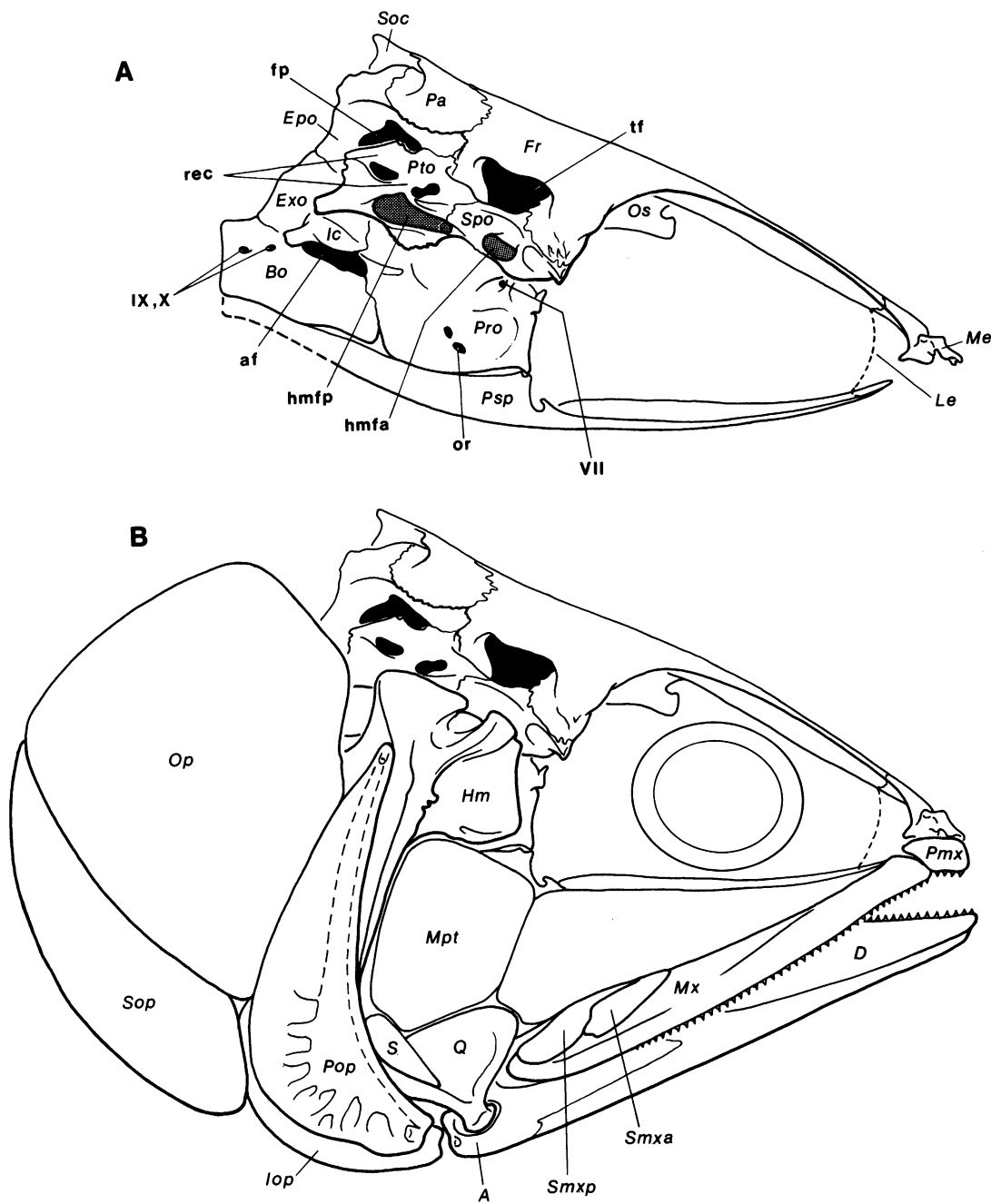
Fig. 5. Reconstruction of (A) braincase and (B) parts of head in *Santanaclupea*.

anteriorly the frontals are smoother. The supraoccipital completely separates the parietals. The supratemporal commissural canal is enclosed by the parietals, but is external to the supraoccipital (fig. 4A, B). The parietal has a broad contact with the frontal anteriorly and meets the epioccipital posteriorly. There is a lateral flange on the parietal above the
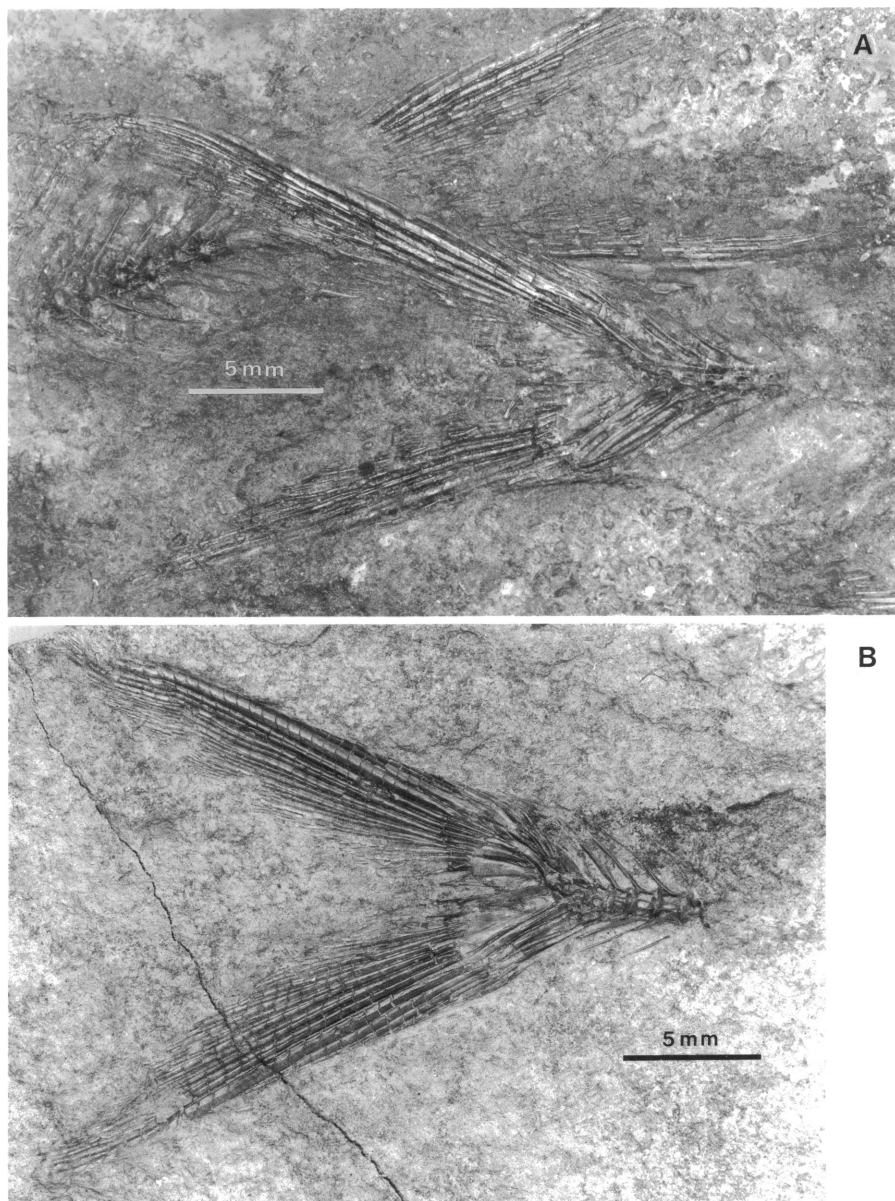
Fig. 6.   Tails of (A) AMNH 12790 and (B) DNPM DGM 1338-P (both reversed); (C) reconstruction of the caudal skeleton in *Santanaclupea*; (D) caudal skeleton in *Santanichthys diasii,* from AMNH 12780 (from Maisey, 1991a).

pterotic, ornamented in the largest specimen (AMNH 18968) by several small serrations. The preepiotic fossa (fp, fig. 5) is large, as in most living clupeoids (see Patterson, 1970, for references). Its limits are largely defined by the epioccipital, and it is floored by the pterotic.

The frontals have a lower temporal flange. In AMNH 18968 a small notch is present in the posterior margin of the orbit, perhaps for innervation of part of the supraorbital sensory canal (fig. 3C). The parietals and frontals contact each other dorsally, but farther laterally these bones are separated by a gap. A
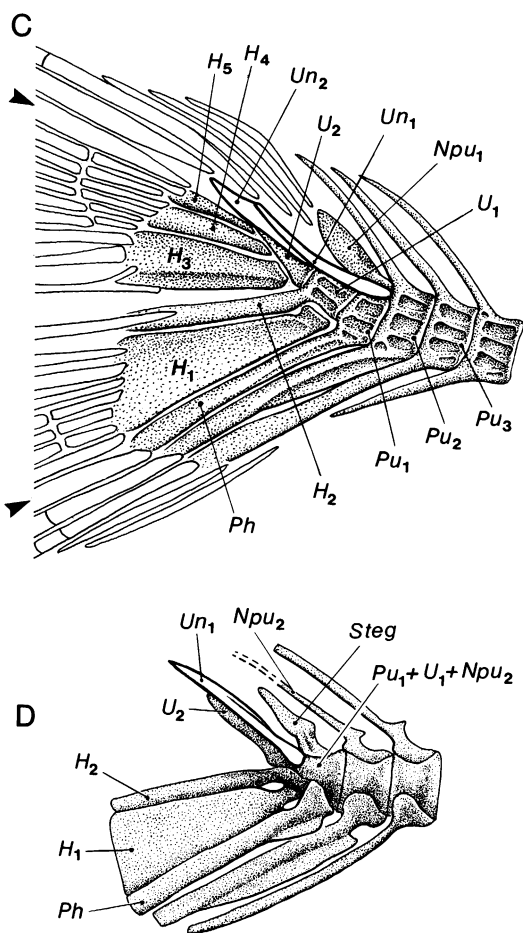
C

D

Fig. 6.   Continued.

parietal branch of the supraorbital sensory canal presumably lay below the lateral margin of the parietal, before entering the frontal via the temporal foramen. The temporal flange of the frontal is sutured to the sphenotic, and forms a small depressed area that is interpreted as the dilatator fossa. If this interpretation is correct, however, the dilatator fossa is weakly developed and is unusual in lacking any pterotic contribution.

The ventrolateral face of the sphenotic bears a circular articulatory facet for the anterior hyomandibular condyle, and meets the pterotic posteriorly (fig. 5A). The pterotic has an elongate facet (extending onto the sphenotic) for the posterior hyomandibular condyle, behind which is a short, posteroventrally directed spine. Within the pterotic are two foramina, interpreted as openings for the

recessus lateralis, although it is not clear which branches of the sensory canal network occupied each opening. A dermosphenotic has not been observed; it was either absent or else very poorly developed (as in other clupeomorphs with a well-developed recessus lateralis).

Prootic and pterotic bullae are well developed. The external surface of the prootic is pitted, with a characteristic "strawberry appearance" (fig. 4) seen in many clupeomorphs (Forey, 1975). There is a large preepiotic fossa in the epioccipital. A membranous intercalar is present (seen only in the holotype).

A canal-bearing extrascapular bone overlies part of the pterotic in AMNH 18968, but is too fragmentary for adequate description. A posttemporal bone is also present, more or less in its presumed original position behind the epioccipital, where it carries the posttemporal canal from the extrascapular.

The orbitosphenoid (Os, fig. 5A) is small but well ossified. There is a slender, almost straight edentulous parasphenoid. It is pierced by paired carotid foramina posteriorly. Within the orbit of the holotype there is a pterosphenoid, displaced from its original position. This specimen is the only one examined where the mesethmoid is preserved (fig. 4). There are traces of what may be a poorly ossified lateral ethmoid within the anterior part of the orbit in AMNH 12789. The posterior part of the vomer is visible in AMNH 12789 and 12790, but I have been unable to determine whether the mesethmoid overhung the vomer, as in engrauloids.

The jaws are long and slender, and sharp, pointed teeth are present on the premaxilla, maxilla, and dentary (fig. 5B). The predaceous habits of Santanaclupea are evidenced in the holotype by the presence of a complete skeleton of a small Tharrhias within the body cavity (fig. 8). The premaxilla is considerably shorter than the maxilla (approximately 20% of maxillary length), as in many engrauloids. A small flange of bone on the premaxilla overlaps the maxilla anteriorly. There is a low palatine articulation on the dorsal surface of the maxilla anteriorly, in front of which is a slender ethmoid articulation mesial to the premaxilla. These articulations were probably simple sliding surfaces. Two supramaxillae are present (AMNH 18968). In the lower

jaw there is a long, oblique suture between the dentary and the angular. The mandibular sensory canal lies in an open groove on the dentary for almost three-quarters of its length, but is partly enclosed in a tube anteriorly. The canal then passes through the angular to emerge on its posterior face below and behind the mandibular joint. Unfortunately the inner aspect of the lower jaw cannot be studied in this material, and it is consequently unknown whether the angular, articular, and retroarticular are fused or separate.

The anterior ceratohyal contains a large "beryciform" foramen; this primitive teleostean feature is absent in clupeiform fishes (i.e., clupeiformes sensu Grande, 1985). The hyomandibula is slender, has separate anterior and posterior articular condyles, and is inclined obliquely backward from the braincase (fig. 5B). In this last respect *Santanaclupea* resembles engrauloids.

Dermal bones of the cheek are poorly preserved, and nothing can be said about the infraorbital series. The opercular series is poorly known, mainly from AMNH 12789, 12790, and 18968.

The pectoral and pelvic girdles are preserved in these examples and also in the holotype. There are at least 15 pectoral fin-rays and at least nine pelvic fin-rays.

In AMNH 18968 the tail has been folded over itself, but the caudal endoskeleton is well preserved in DNPM 1338-P, 683-P, and AMNH 12790 (fig. 6). Five hypurals are present; among other clupeomorphs only *Denticeps* is known to have this many. Preural centrum 1 is fused to a short, expansive neural arch dorsally and to the parhypural ventrally (fig. 6).

Hypural 1 is autogenous, and articulates with ural centrum 1, which lacks a neural arch. Hypural 2 is fused to ural centrum 1. There is a distinct diastema between hypurals 2 and 3. Hypurals 3–5 are all autogenous, and all meet ural centrum 2 (which also lacks a neural arch).

Two uroneurals are present in AMNH 12790 and DNPM 683-P; the first extends anteriorly above the first preural centrum but is not fused to it. There is no evidence of any dorsal outgrowth of membrane bone on the first uroneural (this is commonly found in clupeomorphs). The second uroneural extends anteriorly as far as the articulation between ural centra 1 and 2.

There are 10 upper and 9 lower principal caudal fin-rays. The last dorsal principal ray lies on the diastema between the second and third hypural. In addition to the principal rays, there are five dorsal and four ventral procurrent rays.

The description of the caudal fin given here essentially agrees with that presented by Silva Santos (1991: 30, fig 10) of DNPM 683-P, which is regarded here as another specimen of *Santanaclupea*. The identity of that specimen will be discussed in a note at the end of this paper.

There are approximately 19–20 abdominal and 19 caudal vertebrae, although a precise count cannot be made on the basis of available specimens. Each rib is borne by a short parapophysis, and the posterior ribs do not diminish in length appreciably. The neural spines of the anterior abdominal vertebrae are unfused, as in most clupeomorphs; the condition of the neural spines on more posteriorly positioned abdominal vertebrae is uncertain. The caudal vertebrae bear single median spines.

The body is entirely covered by thin scales, although these are clearly visible only in the largest specimen, AMNH 18968 (fig. 2). Contrary to the earlier report (Maisey, 1991b) the lateral line series is completely developed, a primitive condition among clupeomorphs. A continuous series of ventral scutes is present. There is no sign of any dorsal scutes.

DISCUSSION

A. Santanaclupea as a clupeomorph. Clupeomorph fishes have been characterized (Grande, 1985) by several synapomorphies, including:

1. abdominal scutes at the ventral midline;
2. otophysic connection that penetrates the exoccipital and forms ossified bullae in prootic and usually also in the pterotic; 3. supratemporal sensory canal penetrates parietals (or parietals and supraoccipital); 4. second hypural fused with first ural centrum; first hypural autogenous; 5. well-defined preepiotic fossa; 6. dorsal scutes present.

Santanaclupea is known to possess characters 1, 3, 4, and 5, but lacks character 6. I

have not seen the otophysic connection
(character 2), but assume it was present be-
cause of the presence of well-developed
prootic and pterotic bullae, which are typi-
cally connected to a diverticulum of the swim
bladder via the otophysic connection. The
supratemporal canal passes through the pa-
rietals (character 3), but as in Recent clupeo-
morphs, the sensory canal is superficial to the
supraoccipital and not enclosed in bone. The
articulation between hypural 1 and ural cen-
trum 1 is well developed, a primitive con-
dition that is lost in more advanced clupeo-
morphs (clupeoids; Cavender, 1966). The first
ural centrum is not reduced in size, another
primitive feature (also found in *Denticeps* and
Diplomystus). This centrum is much smaller
than the first preural centrum in clupeoid clu-
peomorphs; Grande, 1985) It is concluded
that *Santanaclupea* is a clupeomorph on the
basis of characters 1–5, but that it also retains
some plesiomorphic characters in its caudal
skeleton.

Grande (1985) subdivided clupeomorphs
into two "divisions," but only a single fossil
taxon (*Erichalcis arcta*) was included in his
"Division 1" because it lacks derived char-
acters 4–6; in fact, it has not been shown to
possess an otophysic connection or prootic
and pterotic bullae, and the grounds for in-
cluding it in clupeomorphs at all are extreme-
ly weak.

B. *Comparison with Spratticeps.* Another
Lower Cretaceous (Albian) clupeomorph,
Spratticeps gaultinoides Patterson, is known
only from some isolated braincases (Patter-
son, 1970). *Spratticeps* and *Santanaclupea*
provide essentially all the information avail-
able about cranial anatomy in Early Creta-
ceous clupeomorphs, and it is instructive to
compare the braincase in these two taxa.

There is a large prootic bulla in *Spratticeps,*
but no pterotic bulla. The pterotic bulla is
well developed in *Santanaclupea,* and there
is an auditory fenestra ventrally. The su-
praoccipital separates the parietals in both
taxa; in *Spratticeps* all three bones contain
the supratemporal canal, whereas in *Santan-
aclupea* the canal lies external to the supraoc-
cipital. The preepiotic fossa is extremely small
in *Spratticeps,* and is much better developed
in *Santanaclupea.* The skull roof of *Spratti-
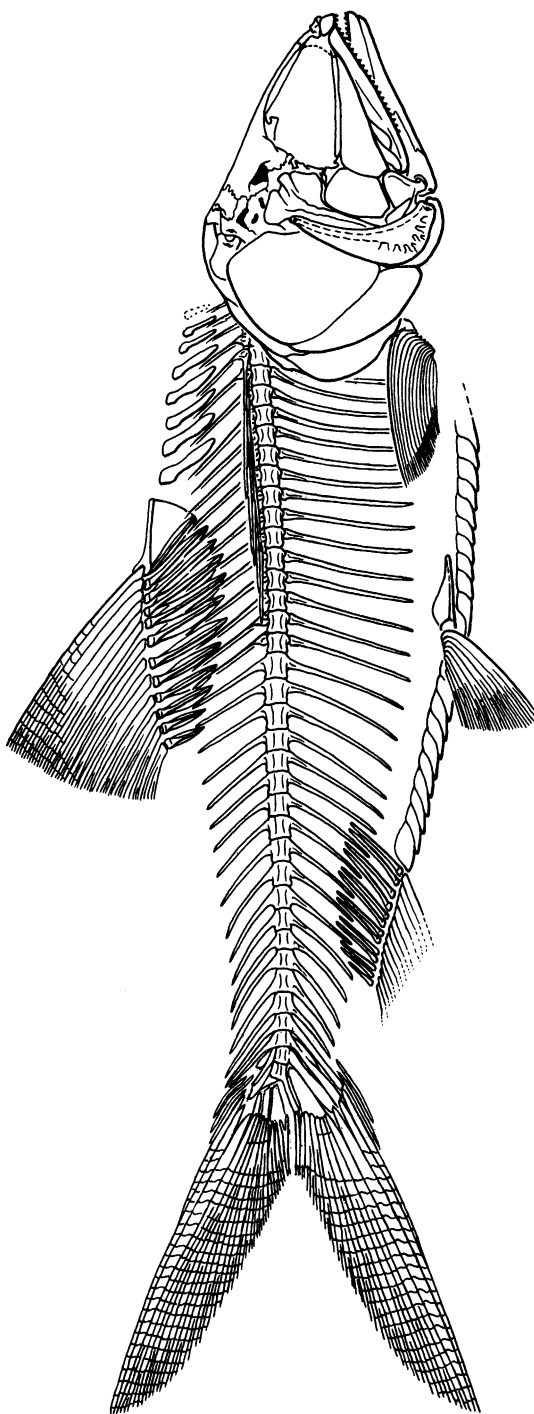ceps* is perforated by small openings for var-

Fig. 7.   Reconstruction of the skeleton in *San-
tanaclupea silvasantosi.*

ious branches of the supraorbital sensory canal, but the skull roof is more complete than in living clupeoids. In *Santanaclupea* the recessus lateralis is apparently better developed and there are large openings for sensory canals in the skull roof. The temporal foramen is exposed, as in living clupeoids, and is not covered over by the frontals and parietals as in *Spratticeps*. The overall pattern of openings for sensory canals thus is more advanced in *Santanaclupea* than in *Spratticeps*.

The hyomandibular facet in *Spratticeps* is single, and is framed by the sphenotic posteromedially, the prootic laterally, and the pterotic anteromedially (Patterson, 1970: fig. 4B). The facet is double in *Santanaclupea* and many extant clupeomorphs. In *Santanaclupea* the prootic does not help to frame the hyomandibular facets. A comparison of the hyomandibular articulations in modern clupeomorphs has not been made, but it is noted in passing that there are also two articular condyles on the hyomandibula of *Denticeps* (Greenwood, 1968: 240; the sister group of clupeiforms according to Grande, 1985). Here, the anterior facet is formed mainly in the sphenotic, but partly in the prootic, while posterior facet is formed in the pterotic. Comparison with primitive fossil and living teleosts (e.g., *Elops*, *Pholidophorus bechei*, *Leptolepis coryphaenoides*; Patterson, 1973: fig. 10; 1975: figs. 62, 89) suggests that the teleostean hyomandibular facet is primitively single and formed by three bones, the pterotic, sphenotic, and prootic. Comparison with modern *Amia* and gars is relatively uninformative, because the facet (although single) is largely formed in cartilage. A double articulation may have developed among clupeomorphs as a corollary to the pterotic bulla, although it also occurs in other fishes (notably among ostariophysans) where bullae are never developed (Arratia, 1992: 24).

It is concluded that *Santanaclupea* displays more clupeomorph synapomorphies than *Spratticeps*, and of the two is phylogenetically closer to Recent clupeomorphs. Both taxa are more convincing clupeomorphs than *Erichalcis* (cf. Forey, 1975; Grande, 1985).

C. Placement within clupeomorphs. As Grande (1985: 253) admitted, the presence of an otophysic connection of clupeomorph type in *Erichalcis*, *Armigatus*, and Ellimich-

thyiformes (his putative successive sister taxa to the clupeiformes) is speculative. *Spratticeps* may be the most primitive taxon that can be reliably considered a clupeomorph (it has a swim-bladder diverticulum entering the prootic, which houses a large bulla; Patterson, 1970: fig. 6). More parts of the skeleton of *Santanaclupea* are known, and it certainly represents a clupeomorph even in a more restricted context than that advocated by Grande (1985).

Santanaclupea possesses two of Grande's (1985) three clupeiform characters (presence of a recessus lateralis; parietals completely separated by supraoccipital), but it primitively retains the "Beryciform foramen." "Higher" clupeiforms appear to have lost this foramen independently of other teleosts. *Spratticeps* lacks the first of these characters, but shares the second and is unknown in the third. On this admittedly slender basis, both taxa are clupeiforms, but *Santanaclupea* is a more derived clupeiform than *Spratticeps*.

Within this group (= Clupeiformes of Grande) *Santanaclupea* cannot be convincingly placed within either the Denticepitoidei or the Clupeoidei without special pleading for homoplasy (for example, if *Santanaclupea* is an engrauloid lacking clupeiform characters). *Santanaclupea* fails to meet Grande's four criteria (all unknown in *Spratticeps*) for inclusion in the Clupeoidei (first uroneural fused to first preural; first ural reduced; parhypural separate from first preural centrum; lateral line scales lost). *Santanaclupea* nevertheless agrees with one higher category of clupeoid fishes (engrauloids) in its suspensorial arrangement and possibly its mesethmoid arrangement. In engrauloids, the gape of the mouth is elongate and the snout region (via the mesethmoid) projects anterior to the lower jaw (when the mouth is closed). In *Santanaclupea*, the jaws are elongate, although as preserved they seem to project slightly beyond the snout. This state of affairs invites further consideration of clupeomorph relationships and an appraisal of the characters used to defend Grande's hypothesis of clupeomorph phylogeny.

Fusion of the first preural centrum with the first uroneural occurs not only in clupeoids, but is common in ostariophysans and also occurs in some teleosts (Fink and Fink, 1981;
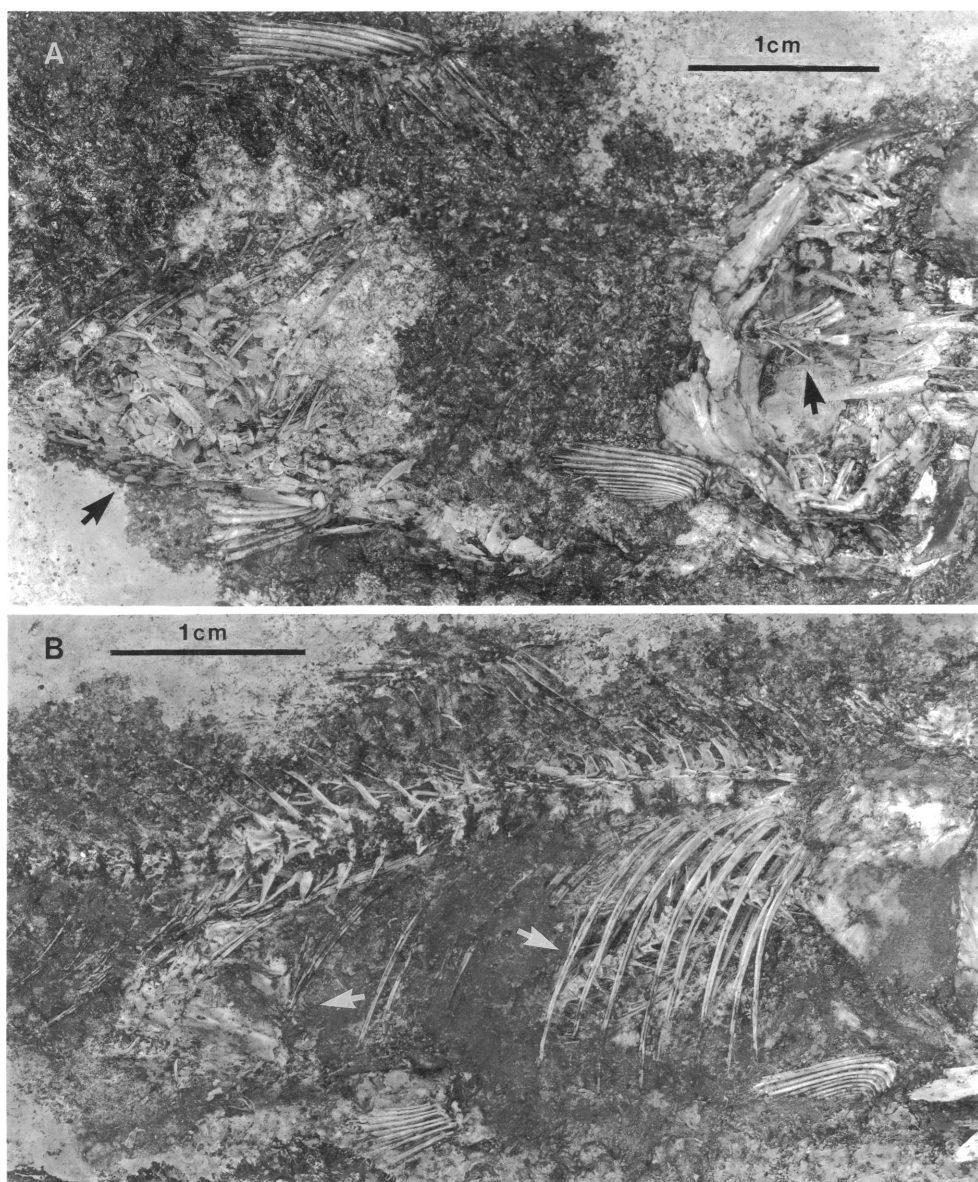
Fig. 8. Abdominal region in the holotype of *Santanaclupea silvasantosi* showing remains of prey, a small *Tharrhias* (arrowed); **(A)** caudal skeleton; **(B)** head and vertebral column (reversed).

perhaps independently of clupeoids, Schultze and Arratia, 1989). Modern clupeoids have lost all but the first one or two lateral line scales, but more primitive clupeomorphs all retain a complete series (Grande 1985: 259); the clupeoid condition could have arisen independently in different lineages, although it seems unlikely. Separation of the parhypural and first preural is also widespread among osteoglossomorphs, elopomorphs, and some euteleosts, although these bones are fused in cladistically primitive members of these taxa, e.g., *Lycoptera, Hiodon, Elops, Chanos* (Schultze and Arratia, 1988; Arratia, 1991). Moreover, these bones are not separate in two genera of dussumieriine clupeoids (Grande, 1985: 260).

Grande's (1985) characters and hypothesis

of clupeomorph relationships are founded largely on extant forms, and information on fossils is scarce. *Santanaclupea* displays a combination of characters that conflict with the interpretation of some of his characters and therefore with his hypothesis, but considerably more data from other fossil clupeomorphs are required before an alternative phylogenetic hypothesis can be presented.

D. Note on *"Leptolepis" diasii.* This small fish also occurs in concretions from the Santana Formation (Silva Santos, 1958). Its relationships were discussed briefly elsewhere (Maisey, 1991a: 273); it differs from *Leptolepis* sensu Nybelin (1974) and Patterson and Rosen (1977) in its caudal fin morphology, particularly in having a stegural of euteleostean type formed by fusion between the first preural neural arch and first uroneural (fig. 6D).

Recently, Silva Santos (1991: 30) erected a new genus (*Santanichthys*) for *"L." diasii,* and suggested it has "clupeiform" affinity. Our respective descriptions and illustrations of the caudal skeleton of this fish are profoundly different (cf. Maisey, 1991a: 273; Silva Santos, 1991: fig. 10).

The specimen on which Silva Santos based his interpretation is DNPM 683-P, which I examined in September 1992 after completing most of this study. This specimen agrees in its cranial and caudal morphology with *Santanaclupea,* not with *"L." diasii.* In particular, it has an elongate, slender, toothed maxilla and dentary, not the short edentulous jaws of *"L." diasii.* Moreover, it possesses a vertebral count consistent with that of *Santanaclupea* and higher than that of *"L." diasii* (characteristically the latter has only about 30 preural centra, of which 11 are caudal; both fishes have about 19 abdominal vertebrae). The caudal endoskeleton in DNPM 683-P agrees with that of *Santanaclupea,* and lacks several features found in the caudal fin of *"L." diasii* (e.g., fused PU1 + U1 + NPU1 articulating with the parhypural and first two hypurals; stegural present). Unfortunately it was not possible to include a photograph of DNPM 683-P in the present work. Although the holotype of *"L." diasii* (DNPM 647-P) has not been prepared in acid, its morphology clearly differs from that of *Santanaclupea* and it represents a different taxon.

I agree with Silva Santos (1991) that *"L." diasii* differs from "typical" *Leptolepis,* and its placement within another genus is justified. From well-preserved material at my disposal, I suspect that *Santanichthys* is related to *Clupavichthys* Gayet, 1989, perhaps representing a distinct species.

CONCLUSIONS

It is concluded that *Santanaclupea* is a clupeomorph, and its cranial morphology is more advanced toward the modern clupeomorph condition than in *Spratticeps.* Within clupeomorphs, *Santanaclupea* can be referred to the Clupeiformes on the basis of two of the three clupeiform characters recognized by Grande (1985). Its placement within presently recognized groups of clupeiform fishes is more problematic. One ambiguous apomorphic character (orientation of the suspensorium, especially the hyomandibula) suggests engrauloid affinity within the Clupeoidei. At this time it is impossible to determine whether its mesethmoid/vomer/premaxilla arrangement is also engraulidlike. If *Santanaclupea* is an engrauloid, it would be by far the oldest one known (the next being the Miocene *Engraulis tethensis*; Grande and Nelson, 1985).

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