Coelacanths from the Lower Cretaceous
of Brazil

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ABSTRACT

Specimens of *Mawsonia* sp. (possibly representing the type species, *M. gigas*), plus a new genus and species of fossil coelacanth, are described from the Romualdo Member of the Santana Formation, Chapada do Araripe, Ceara (Brazil). The new form, *Axelrodichthys araripensis,* is distinguished from other coelacanths on the basis of its cranial anatomy. The posterior moiety of the skull roof has a median dermal element plus three paired ossifications. Heavy rugose ornament of the dermal bones, the dermosphenotic morphology, and the number of paired posterior elements in the skull roof suggest that the new coelacanth is related to *Mawsonia.* A phylogenetic hypothesis is offered in which *Mawsonia* plus the new taxon represent the sister group of *Macropoma* and *Latimeria.* The new coelacanth is represented by several complete, articulated skeletons, among the first to be discovered in South America.

INTRODUCTION

Fossils of coelacanth fishes from South America are extremely rare and until now have consisted mostly of incomplete and fragmentary specimens. The discovery of complete examples in the Lower Cretaceous Santana Formation of Ceara (northeastern Brazil) is therefore of considerable interest to paleontologists.

The Santana Formation is exposed along the flanks of the Chapada do Araripe, a plateau extending some 180 km east-west and 40 km north-south across the Ceara-Pernambuco border and into Piaui (Lima, 1978). The principal collecting areas in Ceara are around Santana, Jardim, and Missâo Velhâo. Access is generally difficult and hazardous. The Chapada do Araripe is capped by the Exu Formation, some 200 m of current-bedded red sandstones and siltstones above the Santana Formation. The latter has much greater lithological variation, with interbedded limestones, evaporites, marls, and siltstones

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(Mabesoone and Tinoco, 1973). Fossil fishes occur in concretionary limestones at various levels in the Santana Formation, but particularly toward the base of the upper (Romualdo) Member. Slight differences of lithology allow recognition of concretions from different localities and horizons. Santana Formation coelacanths in the AMNH collection come mostly from Santana, some 50 km west of Juazeiro do Norte, but also from Jardim, slightly under 50 km to the southeast. Some specimens (e.g., AMNH 11759, from Santana) are associated with ostracods resembling *Pattersoncypris*; the low diversity of ostracods within the concretionary limestones is said to indicate a fresh or brackish environment (Bate, 1972), although this may only be true of the lower part of the Romualdo Member (Mabesoone and Tinoco, 1973). It is uncertain whether the coelacanths from Araripe were fully marine or else tolerant of brackish to fresh water.

Despite the great abundance and diversity of the fossil fishes from the Santana Formation (Silva Santos and Valenca, 1968), the fauna has still not been adequately surveyed. This is surprising when one considers the excellent state of preservation and the ease with which these fossils may be prepared in acid (e.g., Toombs and Rixon, 1950; Rixon, 1976, pl. 8). Although the Santana fishes have been known since the early 19th century (Spix and Martius, 1828; Agassiz, 1841, 1844) several rare taxa have only recently been discovered. Among the latest additions to the Santana paleofauna are coelacanths, which were first reported on the basis of incomplete cranial and postcranial remains by Campos and Wenz (1982), who reported two taxa, *Mawsonia* sp. and "Forme B." *Mawsonia* was recognized on the basis of two large skulls showing supposedly characteristic "posterior parietals" (termed postparietals here). "Forme B" was founded on a fragment of the body, preserved in part and counterpart. Without complete specimens it was not possible for Campos and Wenz (1982) to make direct comparisons between these supposedly different coelacanths.

The AMNH collection confirms the presence of two distinct coelacanth taxa in the Romualdo Member of the Santana Forma-

tion. One of these is referable to *Mawsonia,* but according to Campos and Wenz (1982, p. 1152), "Les proportions relatives de l'avant et de l'arriére-crâne, notamment la présence d'un museu étroit et allongé, indiquent que le *Mawsonia* de Ceara est spécifiquement distinct de l'espèce de Bahia et des formes Africaines, toutes datées du Néocomien à l'Albien." Unfortunately in the other coelacanth taxon from Ceara (here regarded as a new genus), the anterior skull roof is even more elongate and narrow than in Santana Formation specimens referred to *Mawsonia,* and so it is impossible to determine which of the taxa Campos and Wenz (1982) were referring to *Mawsonia.* As discussed below, the two coelacanth taxa from the Santana Formation share several peculiar features, including postparietals (also found in other *Mawsonia* spp.), suggesting that they are closely related. They are certainly separate species, but it is my view that the two are sufficiently distinct to merit generic separation.

There is some disagreement concerning coelacanth bone terminology. In the present work I have mostly followed Forey's (1981) terminology, except for features not discussed by him.

The age of the Santana fishes was set as Aptian by Silva Santos and Valenca (1968), on the basis of comparison with other ichthyofaunas. This determination was reinforced by the discovery of supposedly identical species of fossil fishes in the Riachuelo Formation of Sergipe-Alagoas, below ammonite zones representing the Albian and Upper Aptian (Silva Santos, 1981). While this may place an upper limit to their age, the Santana fish fossils could nevertheless predate the Upper Aptian by a significant amount (i.e., Neocomian or Upper Jurassic), according to available palynological and ostracod data (Maisey, in prep.).

ABBREVIATIONS

INSTITUTIONAL

AMNH, American Museum of Natural History, New York
DGM, Divisao de Geologia e Mineralogia, De-

partamento Nacional da Producao Mineral, Rio de Janeiro

ANATOMICAL

afs, anterior fossa of parietal
ang, angular
antart, antotic articulation
antpr, antotic process of basisphenoid
apa, anterior apophysis of parietal
apr, ascending process of prootic
art, articular
au, autopalatine
bsp, basisphenoid
cc, cranial cavity
col, supraorbital sensory canal
coron, coronoid
den, dentary
di, internal depression of anterior apophysis
dpr, dorsal process of ectethmoid
dsp, dermosphenotic
$faeb_1$, facet for articulation of first epibranchial
foc, fossa for otic canal
fr, frontal
g, gular
hm, hyomandibular facet
in, internasal
j, jugular canal
la, lachrymal process of lateral rostral
lj, lachrymojugal
mppa, median postparietal
mpt, metapterygoid
my, myodome
na, nasal
np, notochordal pit
op, operculum
pa, parietal
padl, descending lamina of parietal
par, parasphenoid
pls, "pleurosphenoid" suture
pop, preopercular
postcor, "posterior coronoid"
ppa, postparietal (paired)
prcon, processus connectens
preart, prearticular
pro, prootic
prof, canal for superficial ophthalmic
pt, pterygoid
qu, quadrate
so, supraorbitals
spl, splenial
sq, squamosal
st, supratemporal
tec, tectal
VII, facial nerve

SYSTEMATICS

CLASS OSTEICHTHYES

SUBCLASS SARCOPTERYGII

ORDER ACTINISTIA

FAMILY COELACANTHIDAE AGASSIZ 1844

Genus *Mawsonia* Woodward
(*in* Mawson and Woodward, 1907)

EMENDED DIAGNOSIS: Coelacanths of large size (estimated body length up to 3+ m); skull roofing bones and angular ornamented by heavy rugosities; operculum and gular ornamented by numerous radiating striae; anterior moiety of skull roof 1.5 to 2 times as long as posterior part and from 2 to 2.5 times as long as broad; posterior skull roof with three paired bones (parietals, supratemporals, and postparietals); dermosphenotic with splintlike anterior projection, and with infraorbital sensory canal located away from the anterior margin; lachrymojugal elongate, the posterior two-thirds almost straight, anteriorly extending to the tectal series; anterior margin of metapterygoid slopes obliquely forward as it rises from the pterygoid.

TYPE SPECIES: *Mawsonia gigas* Woodward (1907); Lower Cretaceous (Neocomian), Bahia Basin, Brazil.

Mawsonia cf. *gigas* Woodward

REFERRED MATERIAL

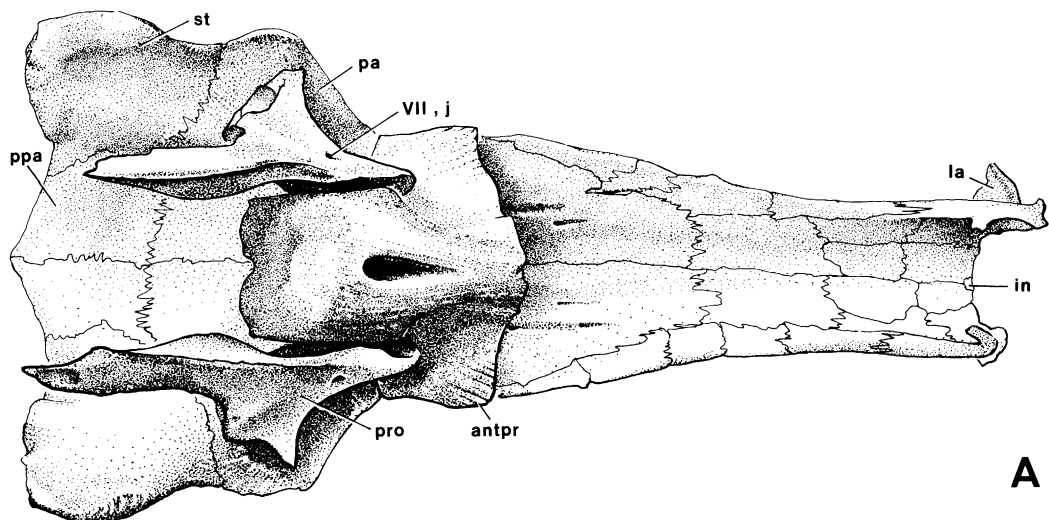|	
AMNH 11758	Nearly complete skull roof and associated elements of orobranchial skeleton.
AMNH 12216	Partial skull roof with sensory canals exposed.
AMNH 12217	Large basisphenoid with part of parasphenoid attached.
AMNH 12218	Large badly damaged basisphenoid and prootic.
?DGM 1107-P,	1109-P (mentioned in Campos and Wenz, 1982).

All the above specimens are from the Romualdo Member, Santana Formation, Chapada do Araripe, Ceara, Brazil.
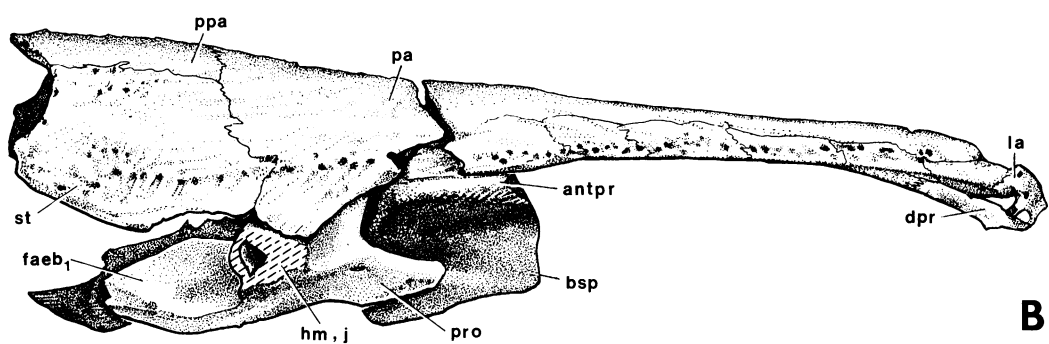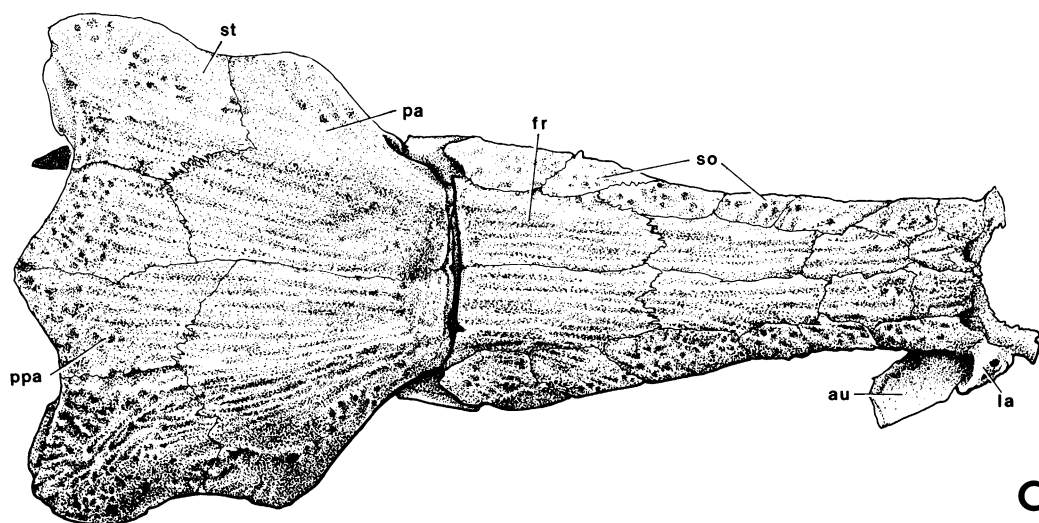
SYSTEMATIC NOTE

AMNH 11758 closely resembles the holotype of *Mawsonia gigas*, BM(NH)P 10355

Fig. 1. *Mawsonia* cf. *gigas,* AMNH 11758. Acid-prepared skull in (**A**) ventral; (**B**) lateral; and (**C**) dorsal aspects. Prior erosion has resulted in loss of parasphenoid and parts of prootics.
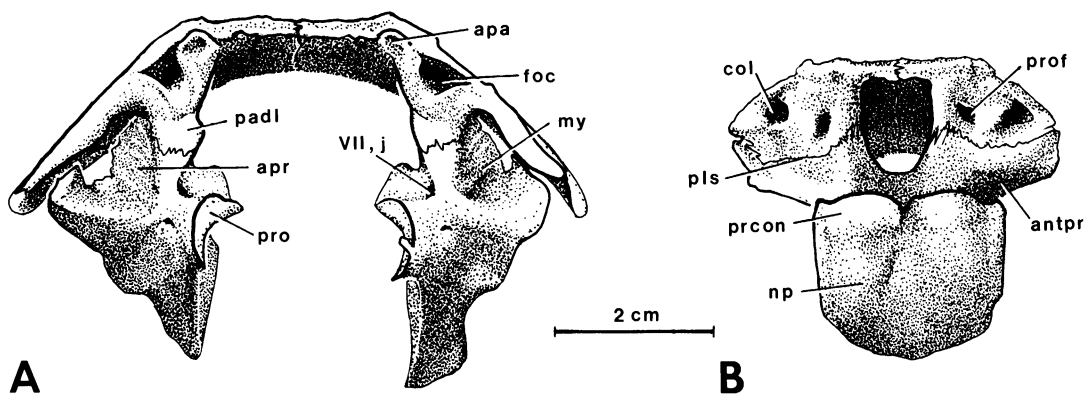
Fig. 2. *Mawsonia* cf. *gigas,* AMNH 11758. (**A**) Anterior view of otico-occipital portion. (**B**) Posterior aspect of ethmosphenoid moiety.

(Mawson and Woodward, 1907, pl. VII) in its palatoquadrate and lower jaw morphology, and in dermal bone ornamentation. Certain other features distinguish the new specimens from other *Mawsonia* spp. (e.g., proportions of skull roof, morphology of basisphenoid, parasphenoid, and otic moiety, arrangement and shape of cheek bones), but are unknown in the type species. A few additional features of the parietal in *M. gigas* have been described in detail by Casier (1961),

and close agreement is found with the new material (see below). On the basis of these descriptions, in my view the *Mawsonia* from Santana cannot be distinguished from the type species (cf. Campos and Wenz, 1982).

DESCRIPTION

Elements preserved in AMNH 11758 include both the anterior and posterior moieties of a comparatively small skull (dimen-
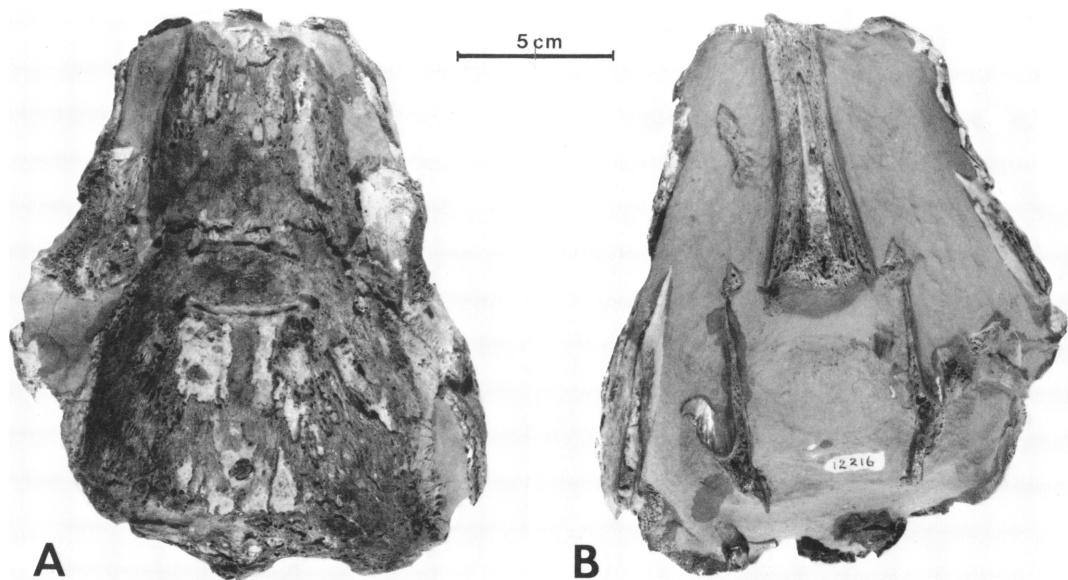

Fig. 3. *Mawsonia* cf. *gigas,* AMNH 12216. Partial skull in (**A**) dorsal and (**B**) ventral aspects. Dermal bone surfaces are worn away, revealing internal sensory canals.
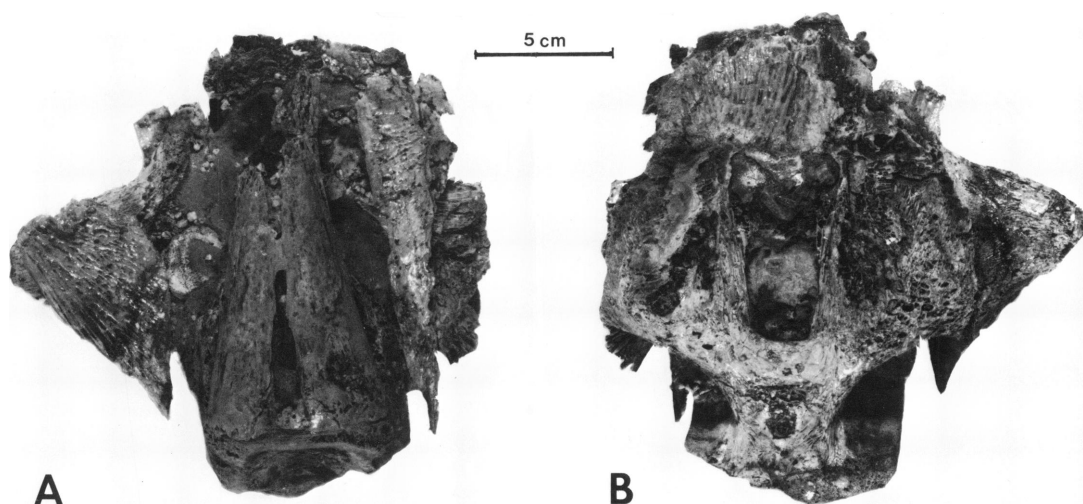
Fig. 4. *Mawsonia* cf. *gigas*, AMNH 12217. Large basisphenoid and associated dermal elements, in (A) ventral and (B) dorsal views.

sions are given below), except for the parasphenoid and ventral part of the opisthotic region (fig. 1). The right palatoquadrate and articular, both dermosphenotics, squamosals and lachrymojugals, and fragments of the operculars, ceratohyals, and other elements are also preserved. Another skull roof, together with part of the basisphenoid and prootic, is represented by AMNH 12216 (fig. 3). Much of the superficial ornamentation has been lost by erosion, exposing some parts of the sensory canal system (discussed further below). In addition, two very large but fragmentary basisphenoids are represented by AMNH 12217 (fig. 4) and 12218. Basisphenoid morphology seems to be a reliable criterion for distinguishing between the Santana coelacanths (see descriptive sections below), and the two large basisphenoids may be fairly confidently referred to *Mawsonia*. Only an outline description of the cranial anatomy will be given here.

The preserved length of the skull in AMNH 11758 is almost 170 mm, of which the oticooccipital region takes up some 54 mm. The posterior skull roof is arched like an arc of a circle, and is approx. 80 mm wide at the posterior margin. The anterior apophyses of the parietals (see fig. 5) are approx. 25 mm apart. The intracranial joint marks the widest part (40 mm) of the ethmosphenoid region, which

tapers to approx. 25 mm at the level of the nasals. The snout is consequently much narrower than in *M. tegamensis* and slightly more tapered than in *M. lavocati* (Wenz, 1975, fig. 1, pl. 1; 1981, fig. 3, pl. 2A), but the proportions in the holotype of *M. gigas* are unknown.

The antotic process of the basisphenoid is broad and winglike (figs. 1, 2). Its anterior face, consisting of unfinished cancellous bone, is shaped like a gull wing in anterior view, with the antotic process forming the "wingtip" where it forms a broad suture. The basisphenoid is not ossified as far anteriorly as the optic nerve. Sphenoid condyles are well developed, and there is a strong sliding joint between the processus connectens of the basisphenoid and a groove on the mesial surface of the prootic, but a basipterygoid process is absent. The basisphenoid is poorly preserved in *M. tegamensis*. The basisphenoid of *M. lavocati* (Wenz, 1981, fig. 1, pl. 2D–F) is shorter than that of AMNH 11758, but also has a broad, winglike antotic process. As in *M. tegamensis* (Wenz, 1975, p. 180, fig. 2) the "pleurosphenoid" merges with the ventral surface of the posterior frontal, rather than forming a separate ossification as in *Latimeria* (Millot and Anthony, 1958).

Three other incomplete *Mawsonia* skulls from Santana (AMNH 12216, 12217, 12218)

TABLE 1

Relative Dimensions—Santana *Mawsonia* (in mm)

	AMNH Catalog no.			
	11758	12216	12217	12218
Basisphenoid width (max.)	24.5	36	67.5	60.5
Gap between antotic processes	26	42.3	—	77
Length condylar surface of basisphenoid	23	—	82	—
Prootic length	63	78	—	110
Basisphenoid "wing" length	14	23	54	40+
Width between parietal articular processes	17.5	27	46	—
Length epipterygoid articulation	27	41.5	82	—
Cranial opening in eth-mosphenoid				
width	12	17.5	26	20
height	17	—	60	46

Fig. 5. *Mawsonia* cf. *gigas,* AMNH 11758. Posterior skull roof in ventral view, after removal of prootics.

include two extremely large basisphenoids, dimensions of which are given in table 1. In all these specimens the basisphenoid antotic process is shaped as in AMNH 11758, and there is no basipterygoid process.

The otico-occipital region has a pronounced prootic process jutting anteriorly over each processus connectens of the basisphenoid. Dorsolateral to this is a deep myodome, mesial to which is a large foramen, presumably for the jugular vein and facial nerve (fig. 2A). This foramen opens into a canal which emerges posteriorly in the middle of an area of unfinished cancellous bone (the hyomandibular facet), as in *Latimeria.* Another canal, presumably for the hyomandibular nerve, meets this canal mesially. The absence of perichondral bone over the hyomandibular facet suggests that the unossified epihyal either lacked a mobile articulation with the cranium, or else was separated by a layer of cartilage. The prootic ascending process is extensively sutured to a descending lamina of the parietal, below a large orifice for the otic canal. A comparable, but less extensive, descending lamina is present in *M.* aff. *tegamensis* (Wenz, 1975, fig. 4). A supratemporal descending process is absent in AMNH 11758.
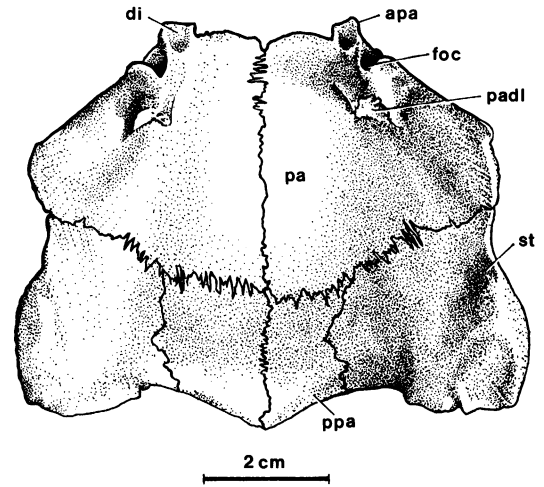
Roofing bones of the ethmosphenoid re-

gion of AMNH 11758 are arranged as in coelacanths generally (Schaeffer, 1952; Forey, 1981). The frontonasal series consists of six paired bones, although only five pairs are well developed. The left supraorbitotectal series consists of seven bones, but only six are present on the right (the anterior two apparently fused together). The anteriormost tectal is sutured to the lateral rostral as in *Latimeria* (Millot and Anthony, 1958, fig. 3c). The lachrymal process juts laterally from the skull roof and defines parts of the anterior and posterior nares. A small internasal is present, sutured anteriorly between the foremost nasals. Premaxillaries and most of the rostral elements have not been found, probably for preservational reasons.

The otico-occipital region is roofed by paired parietals (intertemporals; parietodermopterotics), supratemporals, and postparietals (seen in AMNH 11758, 12216; figs. 1, 2, 5). Postparietals were thought to be peculiar to *Mawsonia tegamensis* according to Wenz (1975), but they are evidently widespread among other (perhaps all) *Mawsonia* spp., and they also occur in the other coelacanth taxon from the Santana Formation (see below). Below these postparietals in AMNH 11758 and 12218, separate supraoccipital elements (fig. 6) and arcual bones were found; these are apparently better os-
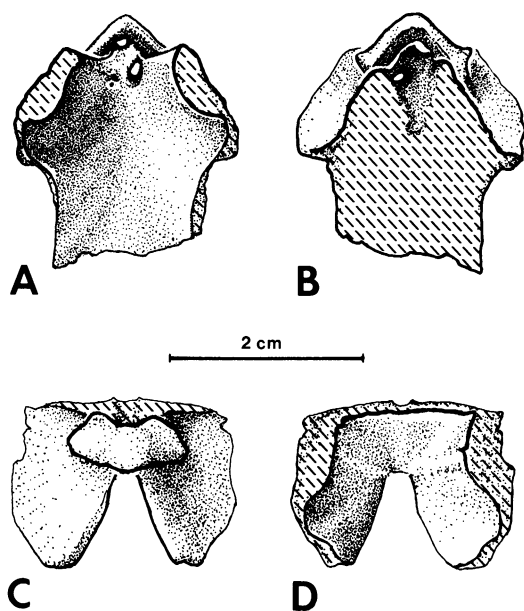
Fig. 6. Supraoccipital of *Mawsonia* cf. *gigas*, AMNH 11758, in (**A**) ventral, (**B**) dorsal, (**C**) anterior, and (**D**) posterior views.

sified in *Mawsonia* than in Recent *Latimeria* (Millot and Anthony, 1958; Jarvik, 1980).

The parietal morphology of *M. gigas* has been described in detail by Casier (1961, figs. 4A, 5A, 7, 8A, 9A) in comparison with that of *M. ubangiana* from Zaire. In AMNH 11758 and 12216, the parietal architecture matches that of *M. gigas* in virtually every respect, particularly the arrangement of the articular process (fig. 5). This close agreement perhaps offers the strongest evidence that the Santana specimens belong to the type species of *Mawsonia*.

In many coelacanths an extrascapular series either fringes (or is attached to) the skull table posteriorly, and contains the supratemporal commissure (Schaeffer, 1952). Forey (1981) regarded the presence of seven extrascapulars as a synapomorphy of *Macropoma* and *Latimeria*. It is possible that the postparietals in *Mawsonia* are the homologs of lateral extrascapulars, which otherwise seem to be absent. In AMNH 12215 the surfaces of the dermal bones have been partly stripped away, revealing the internal arrangement of sensory canals (fig. 3). The supratemporal commissure extends through the supratemporals and continues across the

postparietals. However in AMNH 11758, a much smaller skull, the commissure lies behind the supratemporals and postparietals, within a shallow groove (as in the restoration, fig. 7A). AMNH 12216 represents a much larger individual than AMNH 11758, and the observed variation between them could be accounted for by secondary enclosure of the commissure by continued postparietal growth. In neither specimen is there evidence of anteriorly directed branches of the commissure as in *Latimeria* or *Macropoma* (Forey, 1981). Unlike *Latimeria* (Millot and Anthony, 1958, fig. 10; Jarvik, 1980, figs. 222, 223) and a number of fossil coelacanths (e.g., *Whiteia, Rhabdoderma*; Lehman, 1952; Forey, 1981), in these specimens the transverse branch of the otic canal forms a continuous medial commissure across the parietals, rather than blind-ending pit lines. This commissural canal is exposed in AMNH 12216, extending across the interparietal suture (fig. 3).

Casier (1961) has compared the arrangement of sensory canals within the parietal in several coelacanths including *Mawsonia gigas, M. ubangiana, Latimeria, Whiteia*, and *Laugia*. Comparison of AMNH 12216 with his figures reveals closest similarity with *M. ubangiana* in the posterolaterally directed arrangement of the parietal branch of the otic canal. In the type specimen of *M. gigas*, the parietal branch seems somewhat straighter than in either *M. ubangiana* or AMNH 12216. However that canal was not completely traced in *M. gigas* by Casier (1961, fig. 9A), and it could therefore have curved laterally. One notable difference from both *M. gigas* and *M. ubangiana* figured by Casier (op. cit.) is the continuous transverse branch of the otic canal; in AMNH 12216 the transverse and parietal branches of the otic canal were both well developed.

The circumorbital and cheek bones of AMNH 11758 do not overlap (fig. 7A). The dermosphenotic (postorbital) is peculiar in having an elongate, narrow splint that projects anteriorly (figs. 8, 9). The dermosphenotic of *M. tegamensis* is similarly attenuated but the process is deeper (Wenz, 1975, fig. 1, pl. 1). In both cases the process of the dermosphenotic probably lay just dorsal to the lachrymojugal. The infraorbital canal in *M. tegamensis* and AMNH 11758 is located toward the posterior end of the dermosphenotic,
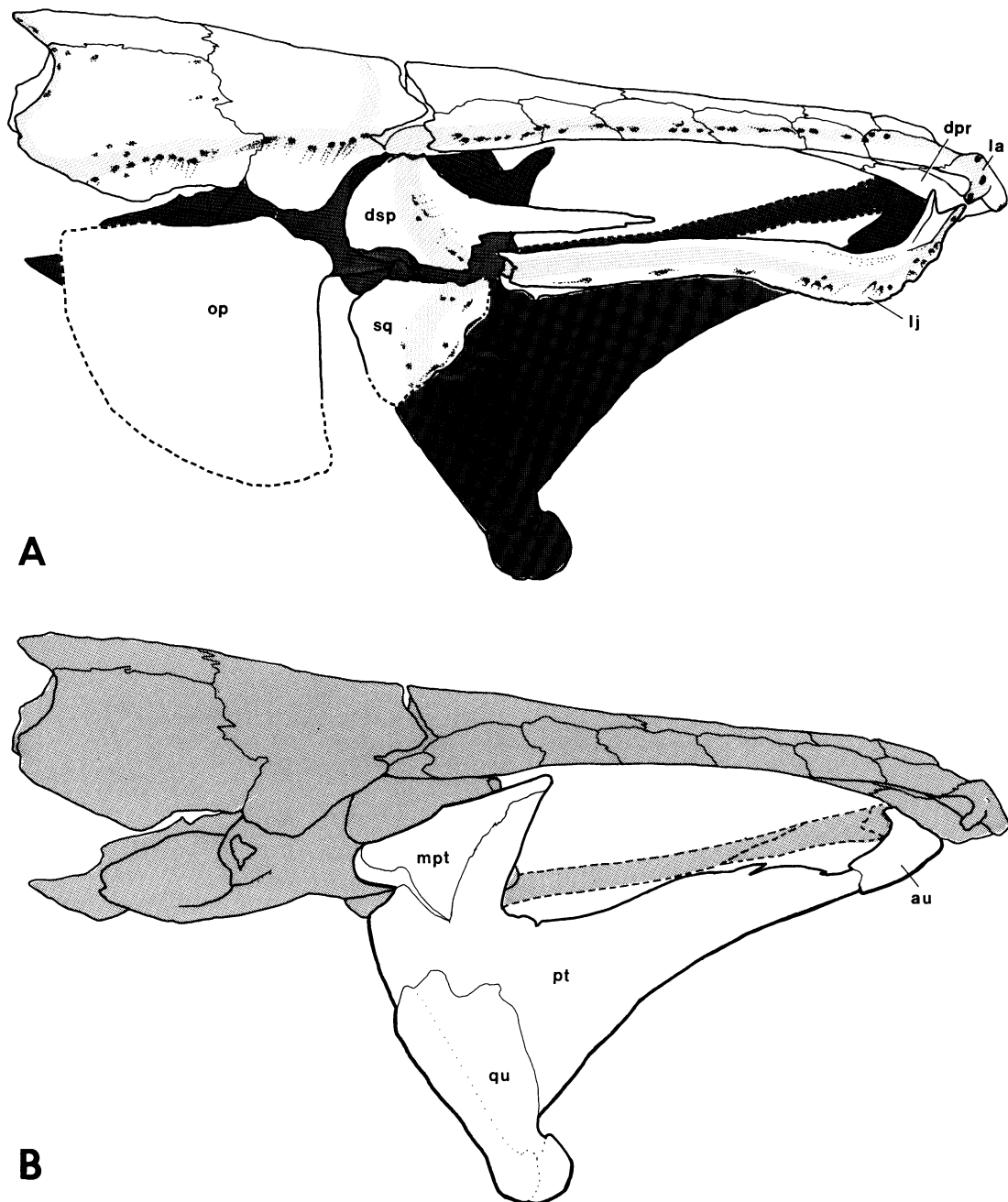
Fig. 7.   Restorations of *Mawsonia* head in lateral view; (**A**) showing dermal bones and sensory canals (light shading); palate, basisphenoid, parasphenoid (dashed), and prootic shaded darker. (**B**) Cranium and upper jaw.

rather than at its anterior margin as in many other coelacanths. Below the dermosphenotic is a small squamosal. A preopercular and subopercular have not been identified in any of the AMNH specimens referred to *Mawsonia*. Wenz (1975, fig. 1) identified a "préopercule inférieur" and "préopercule dorsale" (here = preopercular and squamosal,
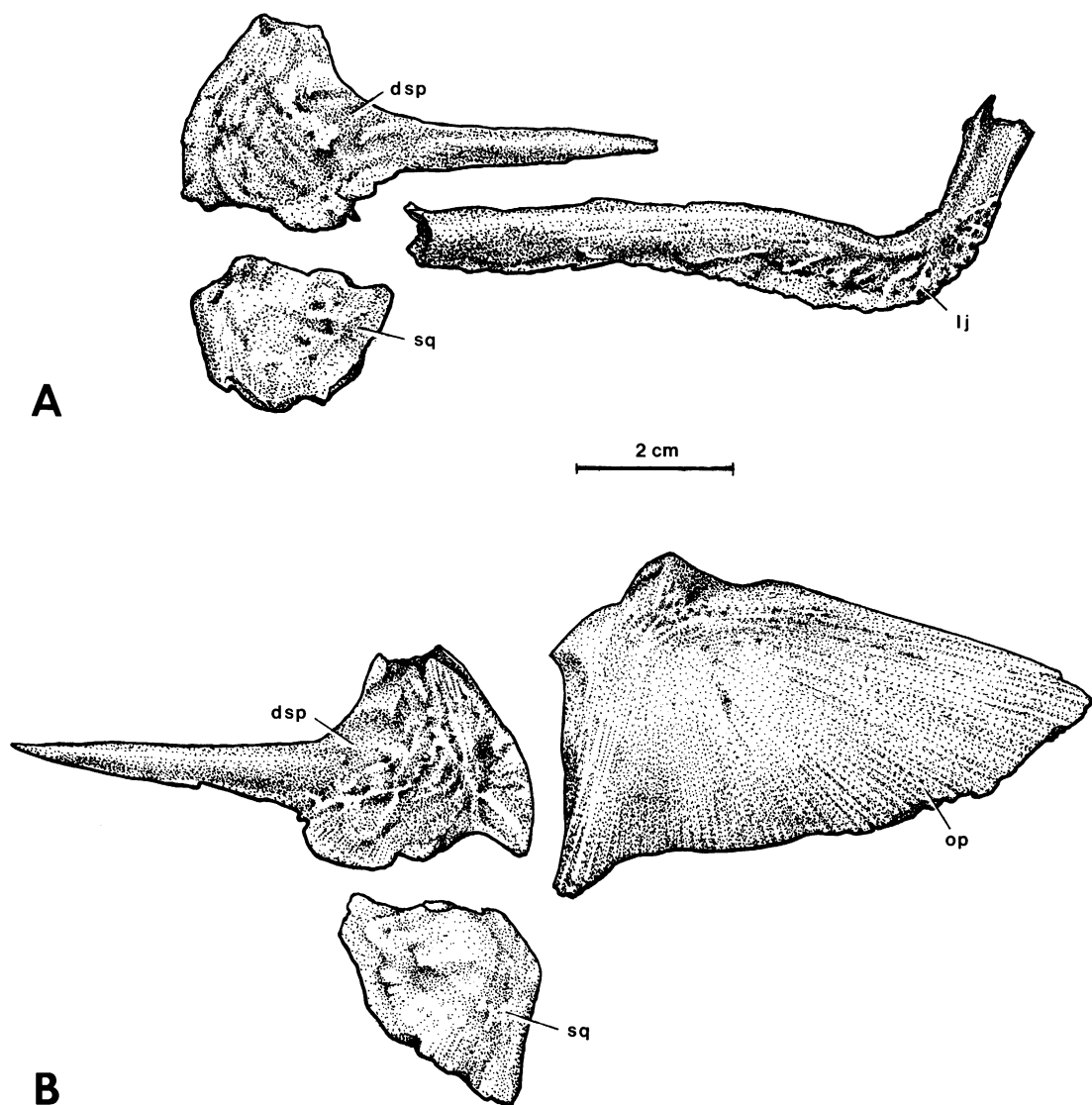
Fig. 8.   Cheek elements of AMNH 11758, lateral view; (A) right dermosphenotic, squamosal, and lachrymojugal; (B) left dermosphenotic, squamosal, and incomplete operculum.

respectively) in *M. tegamensis,* and suggested that a subopercular was absent, as in some Triassic coelacanths. The lachrymojugal of AMNH 11758 is long and slender, reaching the tectal series anteriorly. A similar elongate lachrymojugal occurs in *M. tegamensis,* and may be a characteristic of *Mawsonia* species in general.

From the overall configuration of the cheek series, and the general form of the skull in AMNH 11758 and *M. tegamensis,* the eye of *Mawsonia* probably lay farther forward than in most fossil coelacanths, where the posterior border of the eye is situated more or less level with the dermal intracranial joint (e.g., *Whitea, Chinlea, Rhabdoderma*; Lehman, 1952; Schaeffer, 1967; Forey, 1981). In *Latimeria* the eye is also somewhat anterior to the dermal intracranial joint (Millot and Anthony, 1958, fig. 1; Jarvik, 1980, figs. 205,
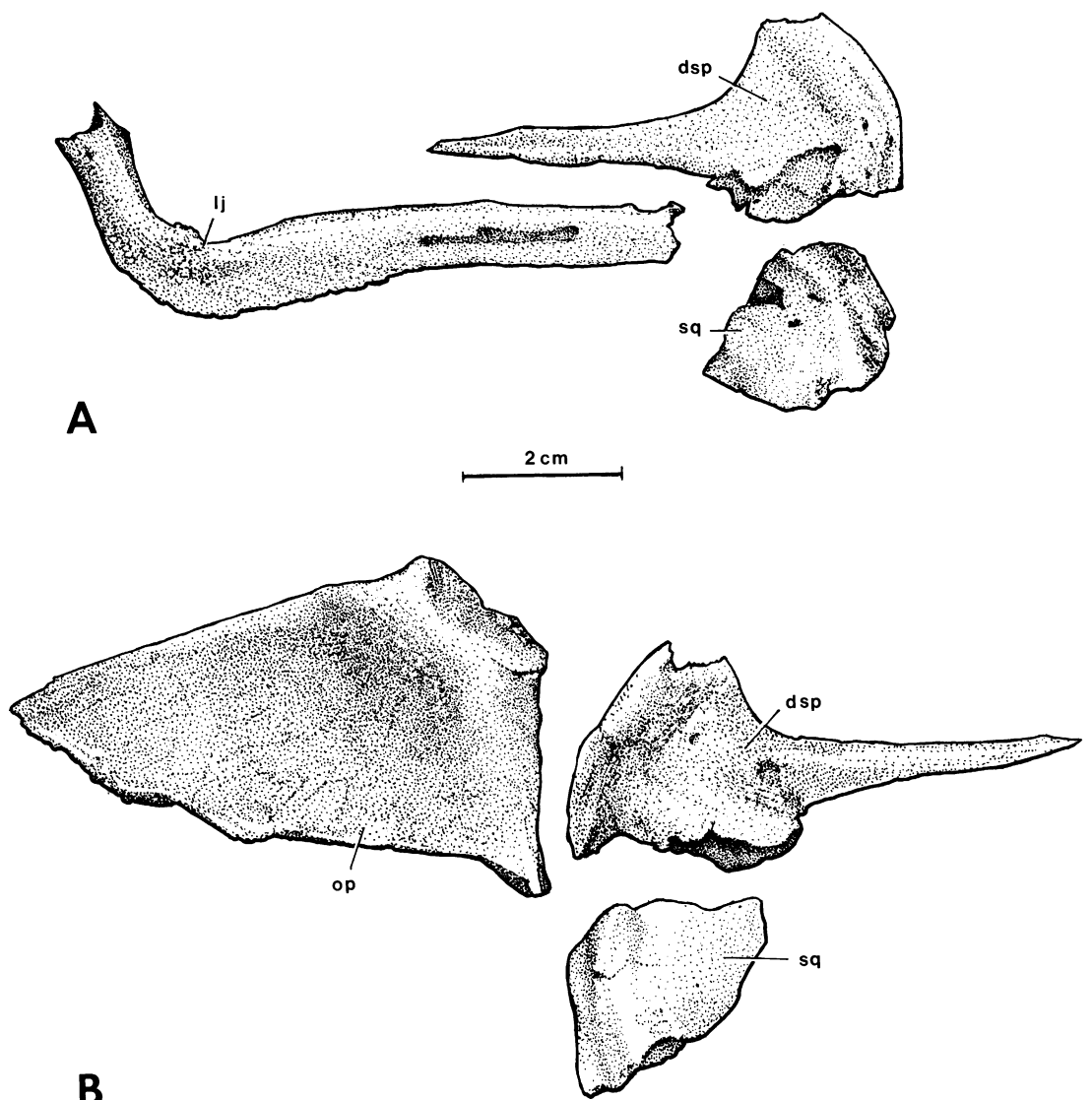
2 cm

A

B

Fig. 9.   Cheek elements of AMNH 11758, mesial view; same bones as in figure 8.

223c). This peculiarity is shared by the other coelacanth taxon from the Santana Formation (see below).

The palatoquadrate includes a pterygoid, with a single strengthening ridge on the lateral surface, and a fine covering of teeth over its visceral surface (fig. 10). To the pterygoid is sutured the quadrate, with a prominent articular facet for the lower jaw; the metapterygoid (the "hyomandibula" of Mawson and Woodward, 1907, pl. VII) with a broad ar-

ticular surface for the antotic process; and a small autopalatine anteriorly. There is no evidence for an ectopterygoid apart from some suturelike rugosities along the thin ventral margin of the pterygoid.

Fragments of the lower jaw (angular, articular, coronoid) and hyoid arch are also present in AMNH 11758 (fig. 11). As in *M. gigas,* the articular is not fused to the angular (Mawson and Woodward, 1907). The right articular of AMNH 11758 is still attached to part
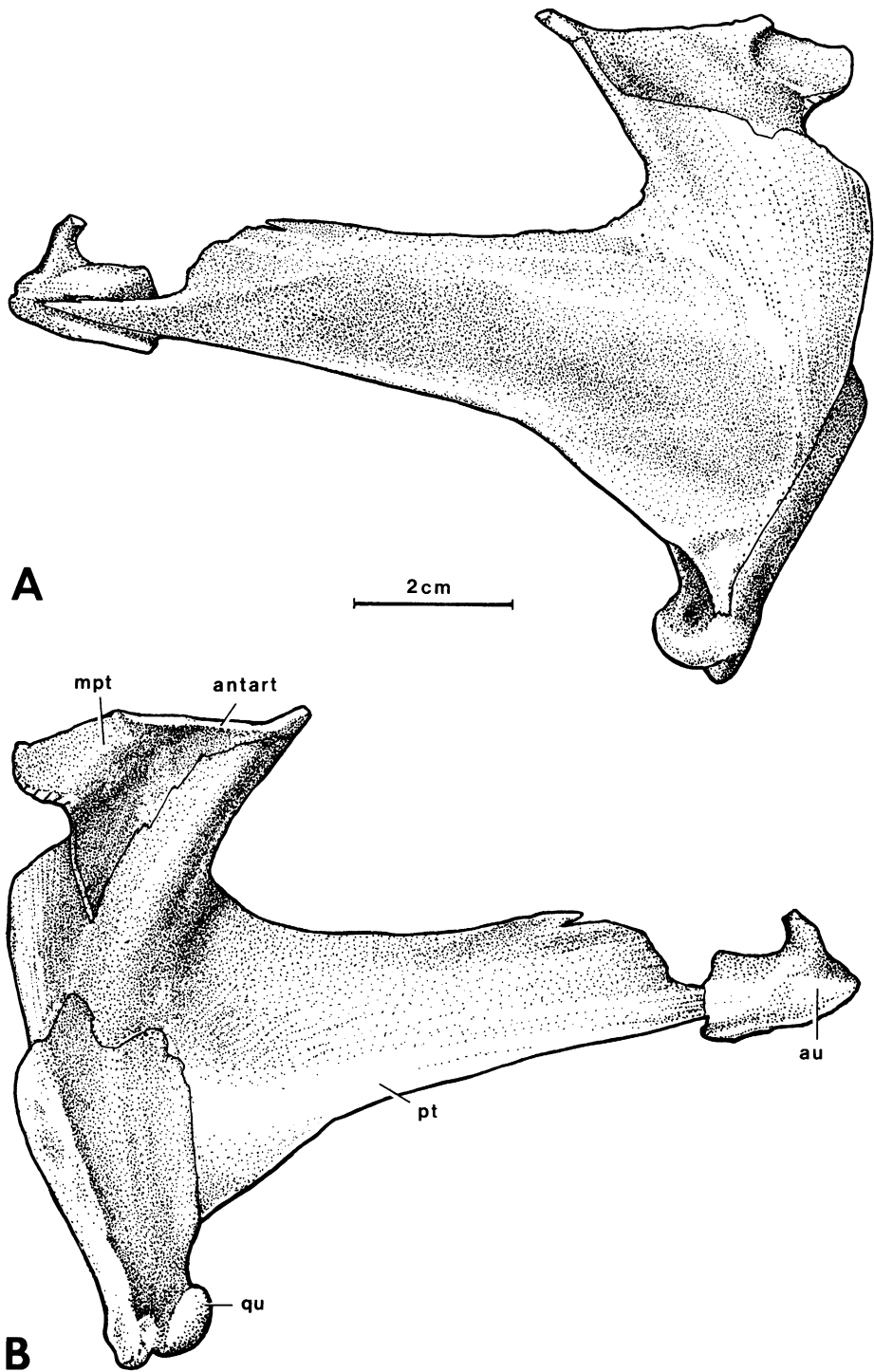
Fig. 10.   Right pterygoid, metapterygoid, quadrate, and autopalatine of AMNH 11758, in (A) mesial and (B) lateral views.
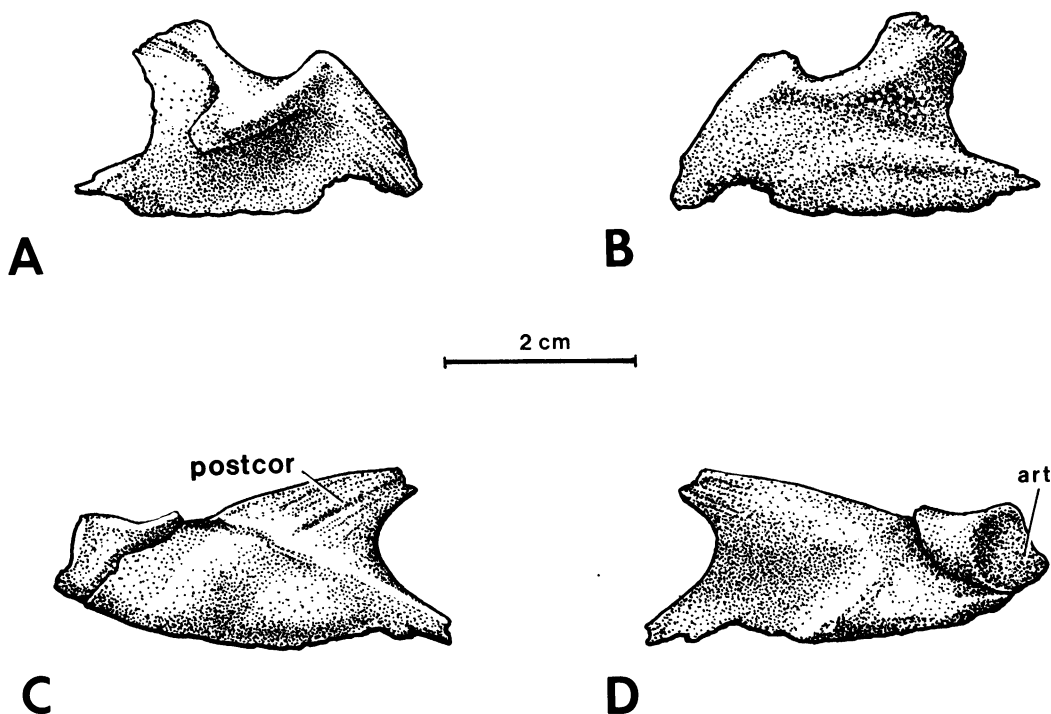
Fig. 11.   Right coronoid of AMNH 11758 in (A) lateral and (B) mesial views; right articular and fragmentary angular, in (C) lateral and (D) mesial views.

of the angular, including the coronoid eminence. The right coronoid is also preserved and can be directly compared with that of *M. gigas* (Mawson and Woodward, 1907, pls. VII, VIII), where its "triangular" shape may be an artifact of incomplete preservation. In AMNH 11758 its anterodorsal edge is thickened and indented, with a posterolaterally directed process which would have contacted the coronoid eminence of the angular. There are small tubercular teeth on only a small area of the coronoid visceral surface.

AXELRODICHTHYS, NEW GENUS

DIAGNOSIS: Coelacanths reaching estimated lengths of 1–2 m; D_1 10–11; D_2 9–10; C 17–18 in upper lobe, 15–16 in lower lobe; P 12–15; V 17–18; roofing bones of skull and angular rugose, particularly supraorbitals and tectals; operculum and gular ornamented with numerous fine radiating striae; ethmosphenoid moiety of skull roof 2.5 times longer than otico-occipital part, and at least 3 times as long as broad; posterior moiety with large parietals and supratemporals, plus a much smaller pair of postparietals separated by a median element; dermosphenotic rectangular, extends as far in front of intracranial joint as behind it; lachrymojugal semicircular, not elongated anteriorly and not reaching lateral rostral; supraorbital sensory foramina confined to snout; antotic process of basisphenoid short and robust; foramina for VII and jugular vein extremely small, jugular canal reduced or closed; scales ornamented with narrow, sometimes interrupted ridges; swim bladder wall strongly ossified. Type species: *A. araripensis* (see below).

ETYMOLOGY: Named in recognition of Dr. Herbert R. Axelrod, for his generous and valuable support of paleoichthyology at the American Museum of Natural History.

Axelrodichthys araripensis, new species

DIAGNOSIS: As for genus.
HOLOTYPE: AMNH 11759; complete fish 710 mm long (figs. 12, 13), Lower Romualdo

5 cm

Fig. 12. *Axelrodichthys araripensis*, new genus and species. Holotype, AMNH 11759, entire fish.

Member, Santana Formation, Santana, Chapada do Araripe, Ceara.

REFERRED MATERIAL (from Santana except where noted):

AMNH 11760	Large incomplete skull, acid prepared.
AMNH 11761	Badly damaged skull prepared in acid.
AMNH 12207	Large incomplete skull roof, approx. 300 mm long.
AMNH 12208	Skull, approx. 220 mm long.
AMNH 12209	Complete fish, cranium not exposed (fig. 15A); from Jardim.
AMNH 12210	Nearly complete fish lacking snout (fig. 15B).
AMNH 12211	Incomplete composite fish (fig. 15C).
AMNH 12212	Complete fish (fig. 15D).
AMNH 12213	Complete small fish with flattened skull (fig. 15E).
AMNH 12214	Flattened head with rostral bones.
AMNH 12215	Partial skull prepared in acid (fig. 25).
AMNH 12219	Large incomplete fish.
AMNH 12220	Small (370 mm long) complete fish in part and counterpart (fig. 16).

DESCRIPTION

Although several specimens have the body intact, reliable estimates of overall length are obtainable only from AMNH 11759, 12209, 12212, 12213, and 12220 (in 12209 and 12212, however, overall skull length is unavailable). Comparison of ethmosphenoid length with overall body length provides an approximate estimate of the probable maximum size. The longest ethmosphenoids (AMNH 11760, 12207, 12211) are approximately 185–190 mm long, giving an extrapolated overall length of 1.25 m (4.1 ft). Although it is possible that *Axelrodichthys* grew to even greater size, the available material suggests that it was generally smaller than *Mawsonia* (e.g., AMNH 12217, 12218) from the same formation. An outline restoration of the fish is given in figure 14.

Although the dermal skeleton can be examined in most of the specimens, the brain-

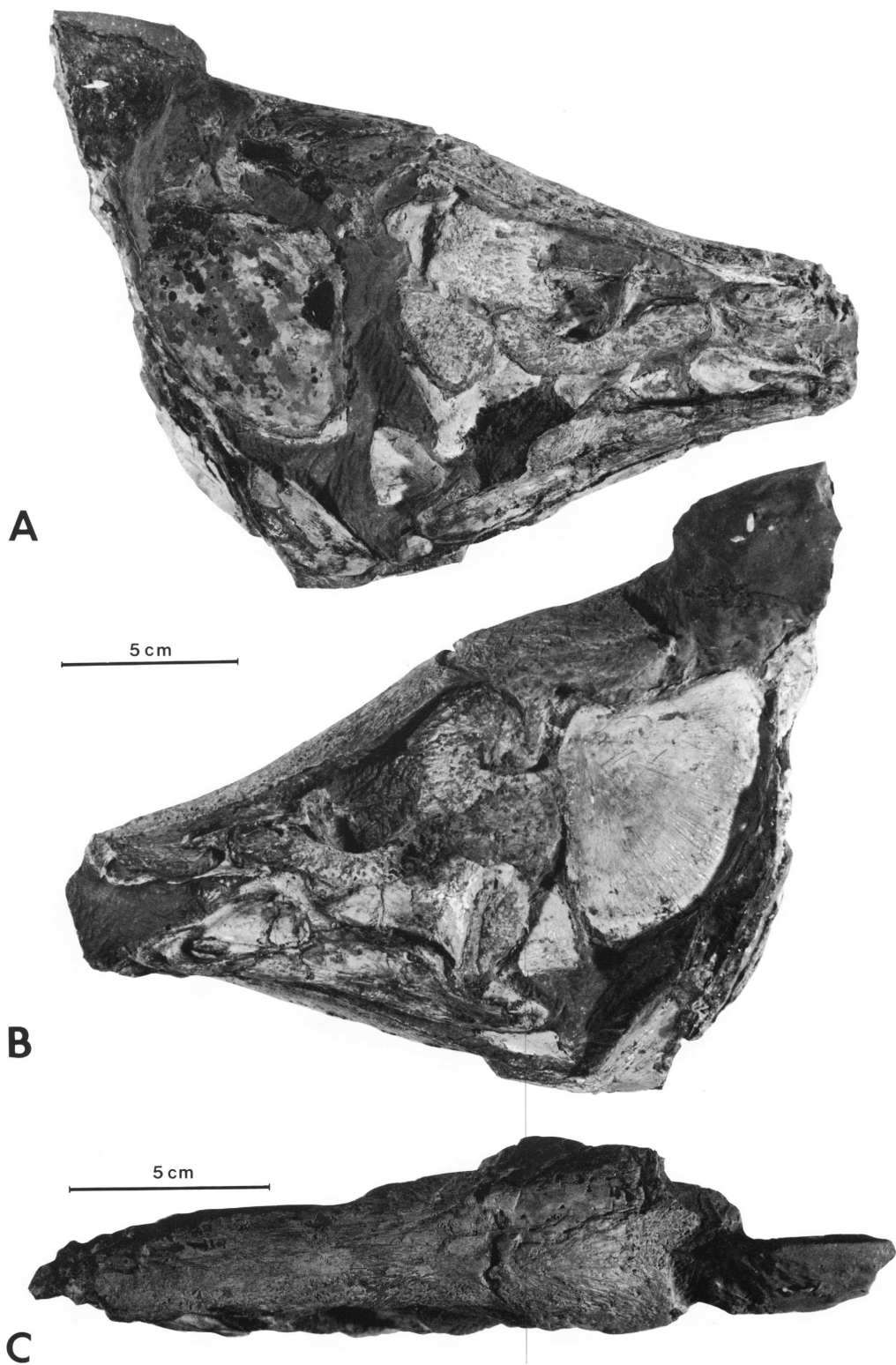Fig. 13. *Axelrodichthys araripensis,* new genus and species. Holotype, AMNH 11759, head in (**A**) right; (**B**) left; and (**C**) dorsal aspects.
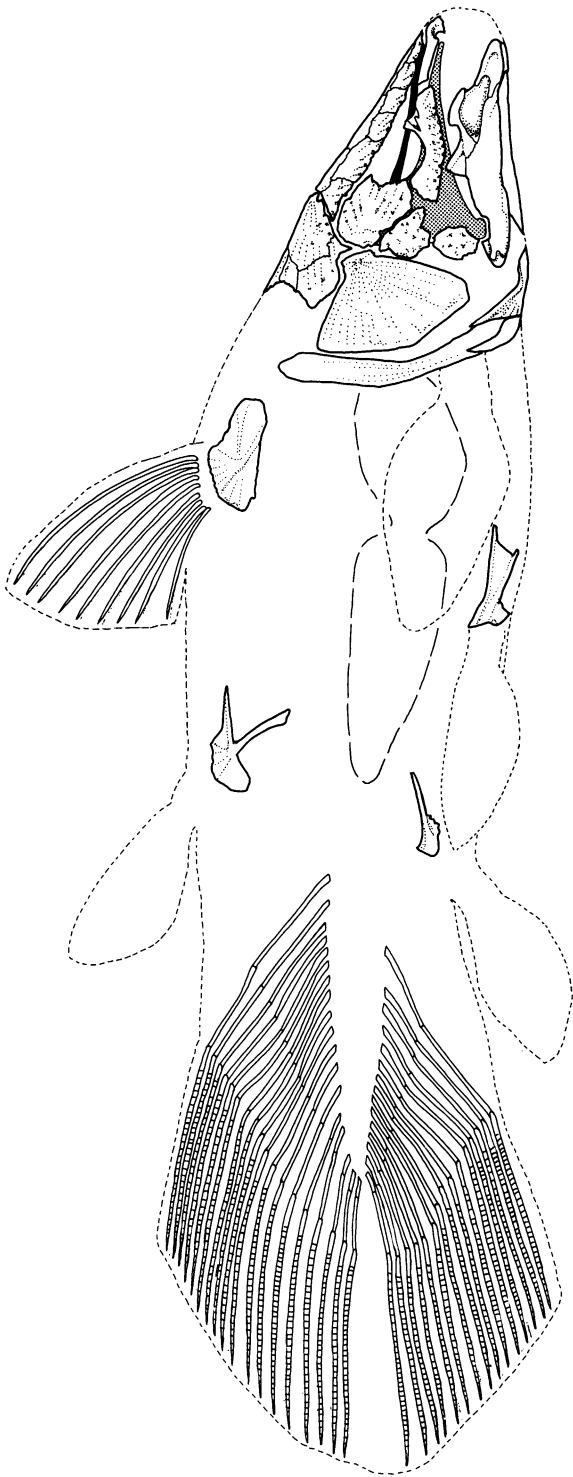
Fig. 14. *Axelrodichthys araripensis*, restoration of entire fish, except for neural arches of trunk (not shown). Body outline indicated by short dashes; swim bladder denoted by longer dashes.
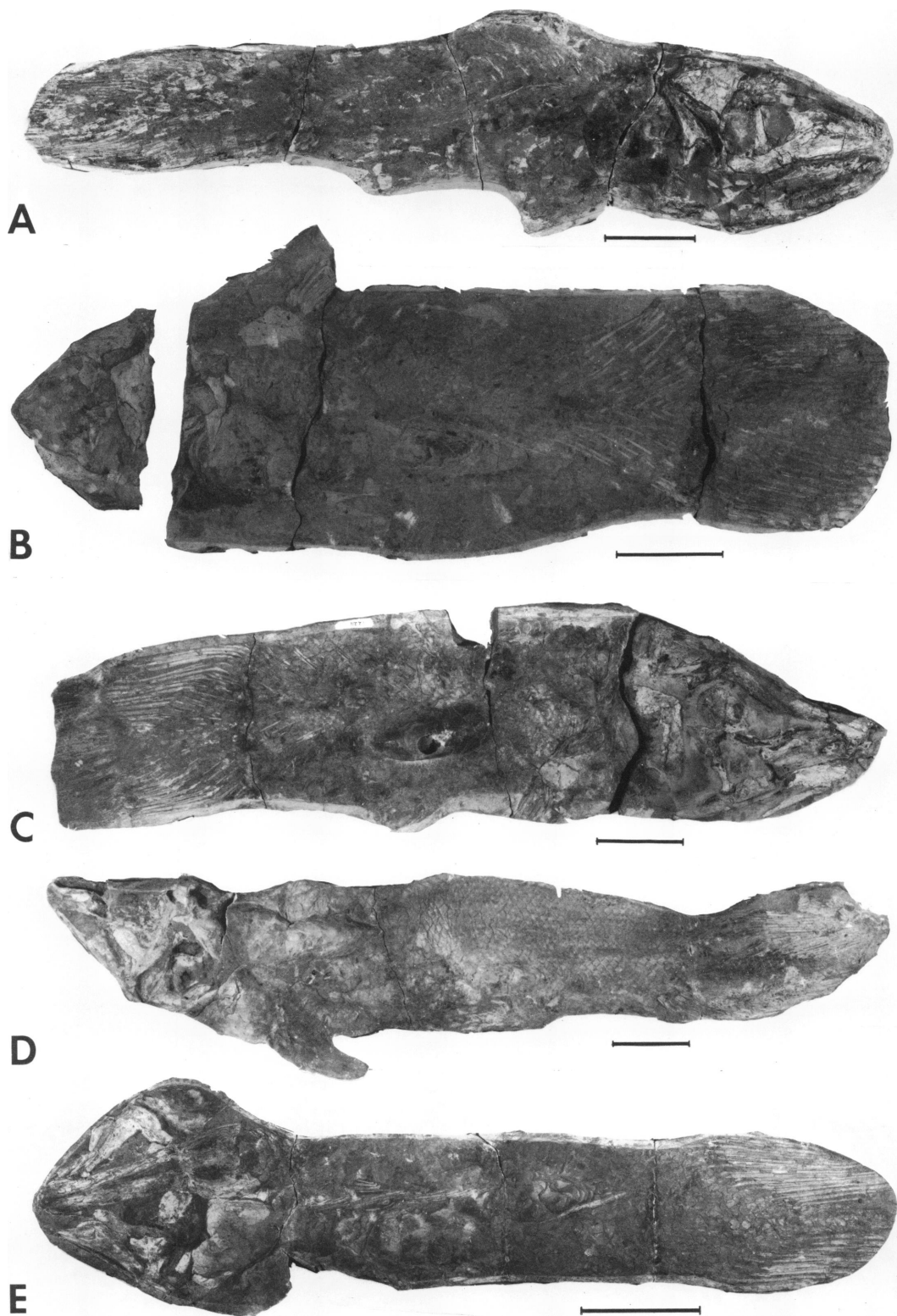
Fig. 15. Specimens referred to *Axelrodichthys araripensis*; (A) AMNH 12209; (B) AMNH 12210; (C) AMNH 12211; (D) AMNH 12212; (E) AMNH 12213. Scale bars = 10 cm.
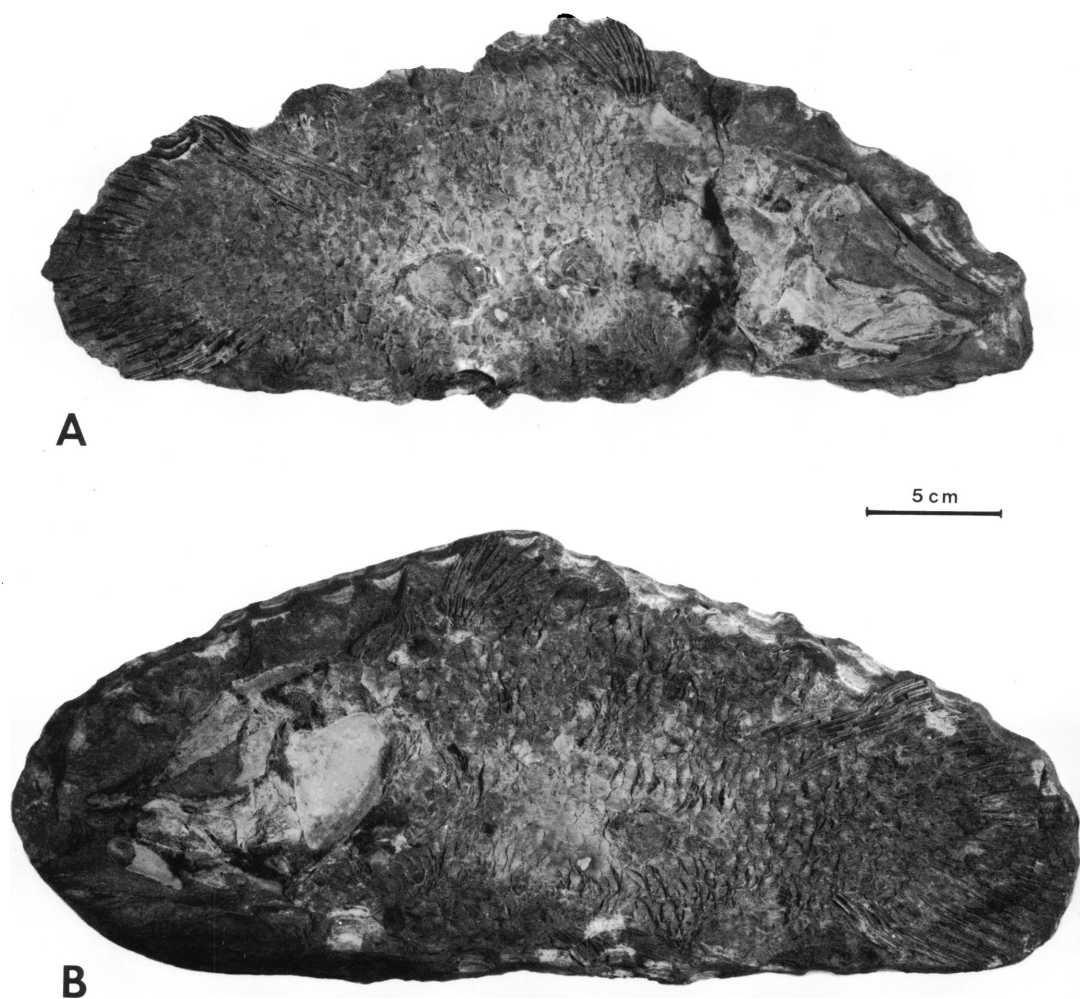
Fig. 16.   Small, complete specimen referred to *Axelrodichthys araripensis,* in part and counterpart; AMNH 12220.

case can be studied only after preparation in acid. Most of the information below concerning the braincase was obtained from AMNH 11760, 11761, and 12215 after acid preparation (figs. 17–21, 23–26).

The basisphenoid of *Axelrodichthys* differs in several respects from that of *Mawsonia* from Santana (e.g., AMNH 11758, 12217, 12218). In lateral profile, the angle between its ventral and posterior surfaces (indicated in fig. 18B) is approximately 130°, whereas in the Santana *Mawsonia* basisphenoids (and in the Moroccan *Mawsonia* sp. basisphenoid figured by Wenz, 1981, fig. 4, pl. 2D–F) this

angle is only 110°. For comparison, in *Moenkopia wellesi* this angle is approximately 125° (measured from Schaeffer and Gregory, 1961, fig. 1B); in *Rhabdoderma elegans* and *Nesides schmidti* it is approximately 140° (from Jarvik, 1980, fig. 218A; Forey, 1981, fig. 1); and in *Latimeria chalumnae* is it approximately 145° (estimated from X-ray of anterior cranium; Millot and Anthony, 1958, pl. 22).

In anterior view the unfinished cancellous bone of the basisphenoid in *Axelrodichthys* forms a deep V, rather than a gull-wing shape. The upper part of the exposed anterior margin is tilted back, forming the "floor" of the
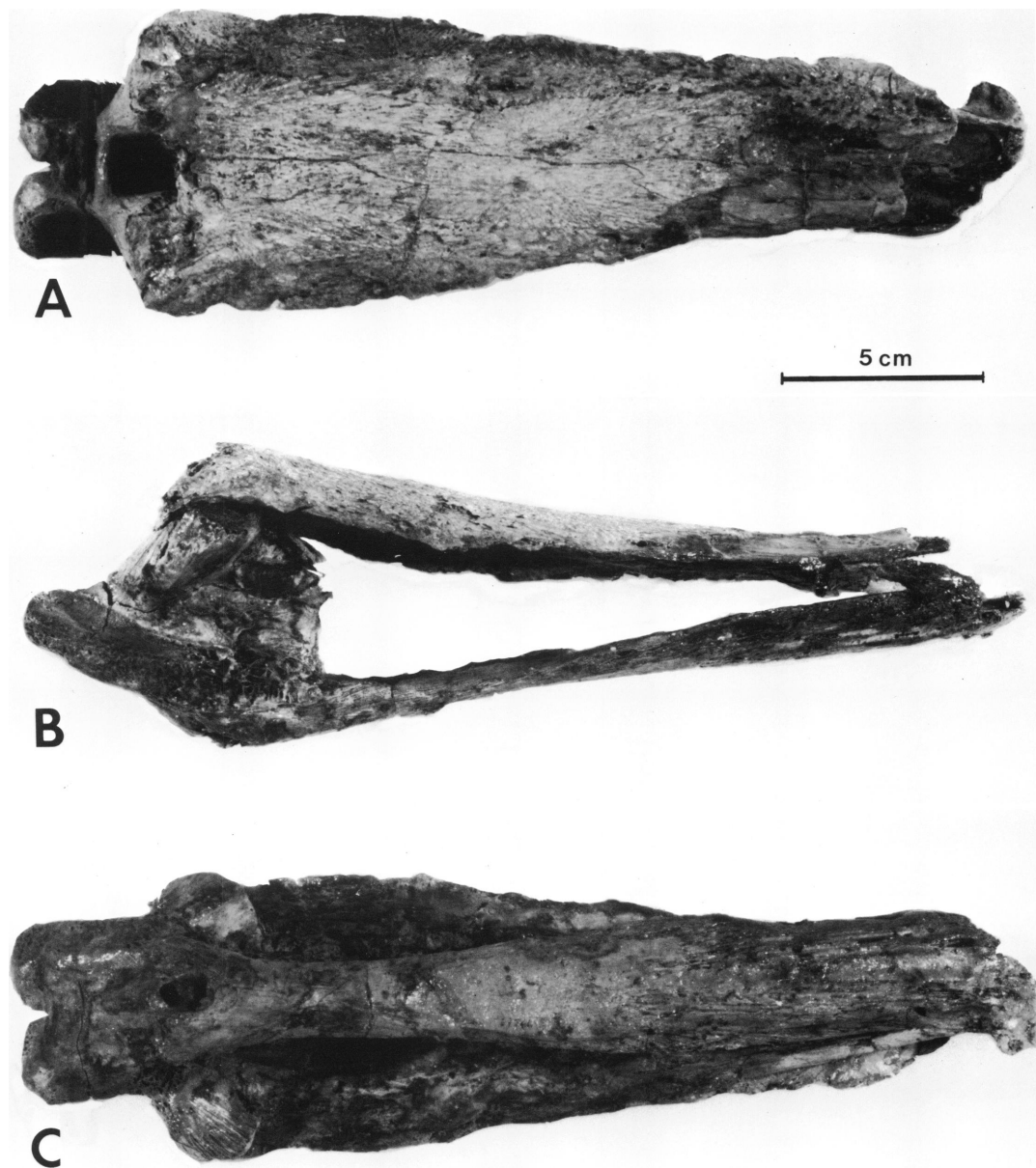
Fig. 17. Ethmosphenoid moiety of *Axelrodichthys araripensis,* AMNH 11760, in (**A**) dorsal; (**B**) lateral; and (**C**) ventral aspects.

triangular gap (presumably cartilage-filled in life) between the skull roof and basisphenoid. Sphenoid condyles are well developed, as is the sliding joint formed by the processus connectens (seen in AMNH 11760, 11761, 12215). A basipterygoid process is absent. The sphenoid condyles are separated by a somewhat deeper notch in *Axelrodichthys* (e.g., AMNH 11760) than in *Mawsonia* (e.g., AMNH 11758, 12218). In posterior view, differences are also found in the shape of the cranial cavity and in the sweep of the "pleurosphenoid" suture (compare figs. 2B, 19B). As in the Santana *Mawsonia* (e.g., AMNH
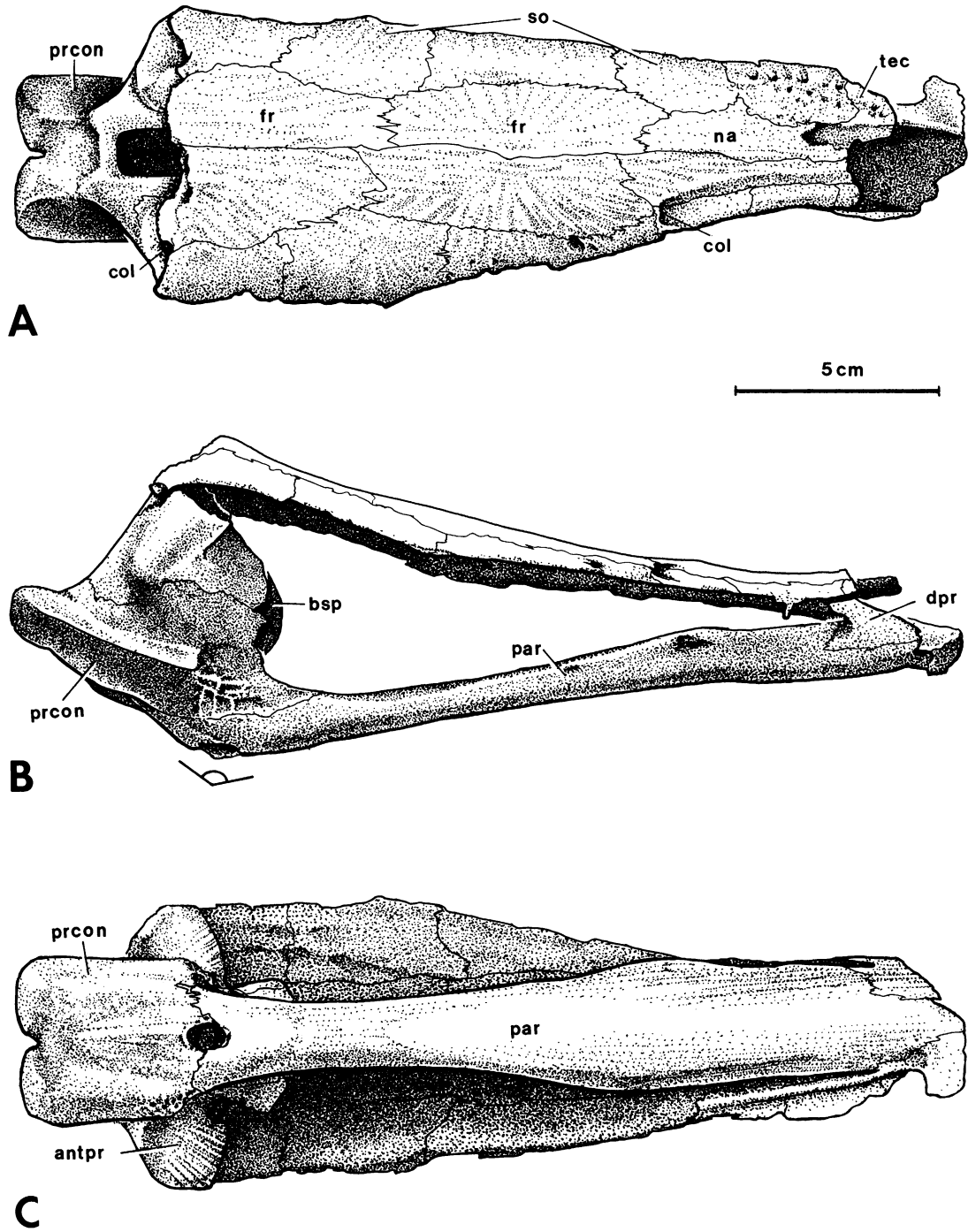
Fig. 18.   Annotated drawing of ethmosphenoid moiety in AMNH 11760.

11758, 11217, 11218) and *M. tegamensis* (Wenz, 1975), the "pleurosphenoid" of *Axelrodichthys* is continuous with the posterior frontal.

The parasphenoid and ectethmoids are long and slender (figs. 17, 18, 22B). A fine shagreen of teeth covers the anterior three-quarters of the parasphenoid. The dorsal process of the
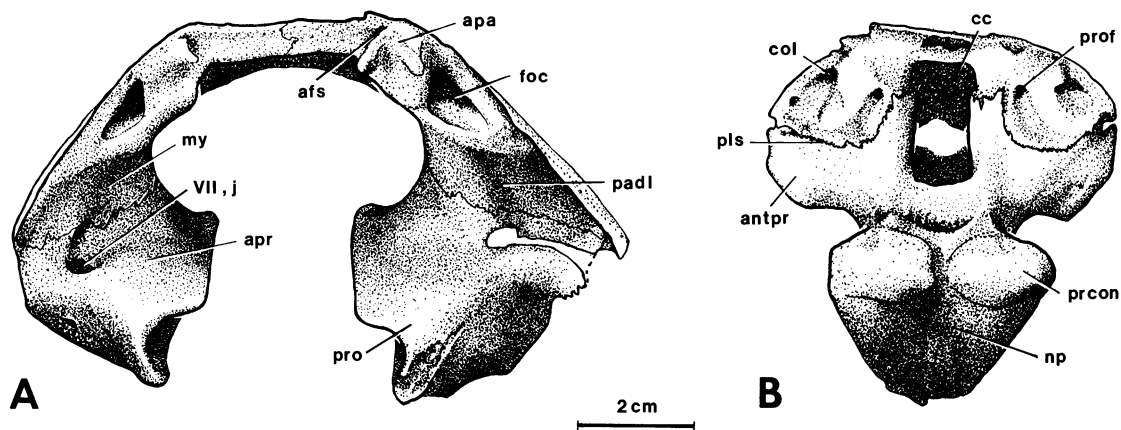
Fig. 19.   Annotated drawing of AMNH 11760; (A) anterior view of otico-occipital moiety; (B) posterior view of ethmosphenoid moiety.

ectethmoid is straighter and less steeply inclined than in either *M. lavocati* or the Santana *Mawsonia* (AMNH 11758), with a pronounced lateral protruberance anteriorly. The lateral margin of the tectal series is curved outward, unlike that in *M. lavocati* and *Mawsonia* from Santana (e.g., AMNH 11758), which curves down to flank the dorsal process laterally.

The ethmosphenoid roofing bones comprise a frontonasal series of five paired bones, flanked on either side by a supraorbitotectal series of seven bones (e.g., AMNH 11759, 12207, 12208, 12211, 12212, 12213, 12214, 12219, 12220). The superficial ophthalmic canal is enclosed for much of its length, although in the acid-prepared skull of AMNH 11760 the bone overlying the right canal has been stripped off anteriorly (fig. 18). Foramina for nerve branches supplying the supraorbital sensory canal are numerous in the snout region, but farther posteriorly (i.e., above the orbit back as far as the intracranial joint) there are virtually no sensory foramina (e.g., AMNH 11760, 11759, 11220), suggesting that the laterosensory system of *Axelrodichthys* was somewhat specialized, with its main innervation confined to the snout.

A complex pattern of small rostral bones covers the snout (e.g., AMNH 12214; fig. 22A). Elements corresponding to the medial and lateral rostrals, postrostral, and nasals 1–5 of *Latimeria* are identified. Between some of these are small round openings, presumed to be for anterior and posterior tubes of the

rostral organ, and larger openings, fore and aft of the lateral rostral, for the anterior and posterior nares. At the ventral margin of the snout is a pair of slender bones, possibly the premaxillae, but there is no sign of teeth on these elements. The lateral rostral forms a broad platform extending for some distance anteroposteriorly, lateral to the ectethmoid dorsal process (e.g., AMNH 11759, 12214; figs. 13, 14, 22A, 26).

In the otico-occipital region (figs. 19–21), the prootic process of AMNH 11760 is large. Dorsolateral to the process is a shallow myodome. Unlike the foramen in *Mawsonia* sp. from Santana (e.g., AMNH 11758), the foramen for the facial nerve and jugular canal is not separated from the myodome but instead lies laterally within its floor (fig. 19A). The ascending process of the prootic region is much broader than in AMNH 11758, and has a correspondingly broad suture with the parietal descending lamina. The supratemporal also has a low descending lamina, but this lacks a suture.

The otico-occipital region includes paired parietals, supratemporals, and postparietals (e.g., AMNH 11759, 11760, 12208), an arrangement known otherwise only in *Mawsonia* spp. (Wenz, 1975; see above). However, there is an additional median element, located at the posterior skull margin between the postparietals (fig. 14, 20A, 21A). In all specimens examined the median and paired postparietals are anamestic, and the supratemporal commissure presumably would
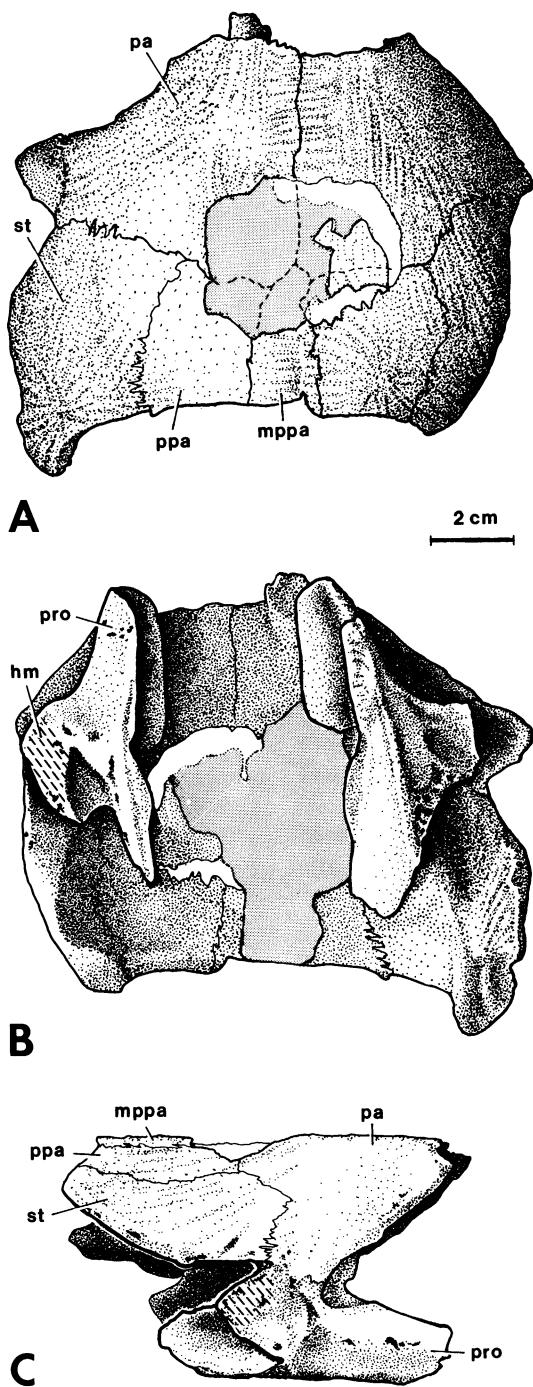
Fig. 20. Otico-occipital moiety of AMNH 11760, in (A) dorsal; (B) ventral; and (C) right lateral views. Central part of skull roof is missing, partly obscured by matrix in (B).

have lain farther posteriorly. An extrascapular series like that found in most other coelacanths seems to be absent even in complete specimens of *Axelrodichthys.*

In *Axelrodichthys* the pterygoid posterior margin is almost vertical (figs. 23, 24), with a single strengthening ridge. In lateral view, the ossified metapterygoid is shaped much as in *Mawsonia,* but the antotic articular surface is relatively narrower (e.g., AMNH 12215; fig. 25). Anteriorly the pterygoid is tapered into a thin splint, with a more downturned anterior extremity than in *Mawsonia* from Santana (fig. 14). There is no evidence of an ectopterygoid. The visceral surface of the pterygoid in AMNH 11760 is overlain by an extensive shagreen of fine teeth. A triangular autopalatine is present (AMNH 11759; figs. 13B, 26B), with an elongate, almost horizontal, sutural contact with the splintlike pterygoid.

As in *Mawsonia,* the circumorbital and cheek bones do not overlap (figs. 13–16). The dermosphenotic dorsal margin follows the anterolateral margin of the parietal and the lateral margin of the first two supraorbitals. Although the dermosphenotic extends far anteriad to the intracranial joint, as in *Mawsonia* spp., it is not splintlike. Again as in *Mawsonia,* the infraorbital canal lies posteriorly within the dermosphenotic. The squamosal and preopercular are small. A subopercular has not been found. The operculum is rounded, with fine striae radiating from its articular area over the entire lateral surface except at its very margin (figs. 13B, 16, 22A).

Instead of forming an elongate bar, as in some *Mawsonia* spp., the suborbital moiety of the lachrymojugal is semicircular, as in many other fossil coelacanths (figs. 13, 14). The eye would have been located dorsal to this curved part. In *Mawsonia* a corresponding curved region occurs at the anterior extremity (see above and Wenz, 1975, fig. 1). In both *Mawsonia* and *Axelrodichthys* the eye probably occupied a more anterior position than is usual among fossil coelacanths. In neither genus is there evidence of a preorbital bone, as occurs in some primitive coelacanths (e.g., *Rhabdoderma*; Forey, 1981). The lachrymojugal does not extend anteriorly far enough to meet the lateral rostral process
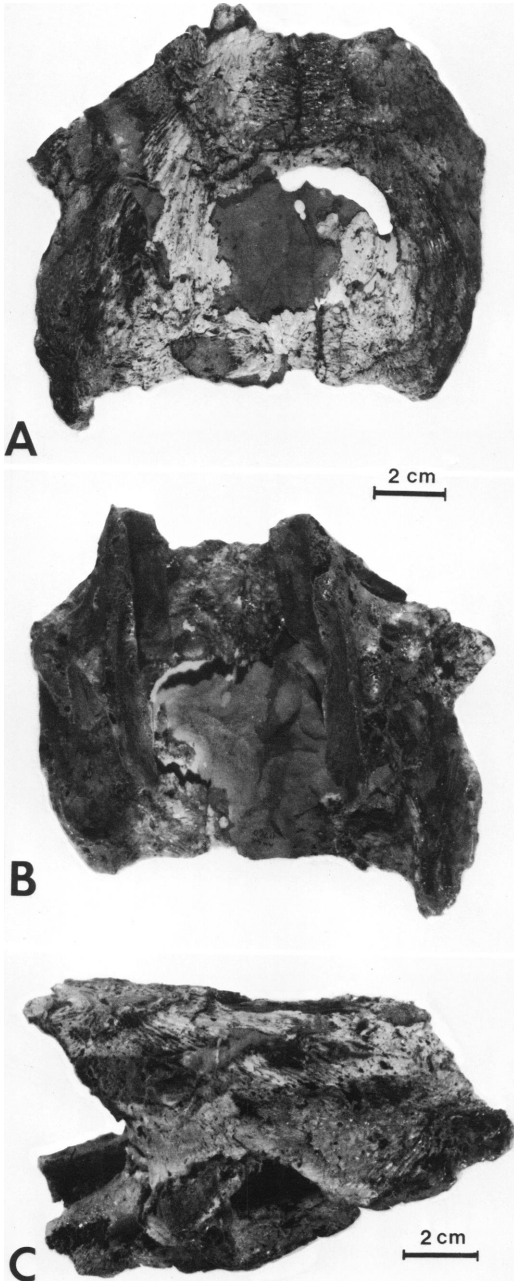
Fig. 21. Otico-occipital moiety of AMNH 11760, in (A) dorsal; (B) ventral; and (C) lateral views.

in *Axelrodichthys,* although it does so in *Mawsonia.*

The lower jaw of *Axelrodichthys* resembles that of *Macropoma,* except that there (according to Woodward, 1909, p. 176) the articular is apparently fused to the angular (not so according to Forey, personal commun.). In this respect *Axelrodichthys* is like *Mawsonia* (see Mawson and Woodward, 1907, p. 136). A bilobed coronoid is present (figs. 23, 24, 26), as in *Mawsonia.*

The postcranial skeleton is best preserved in AMNH 11759 and 12220, the two smallest specimens in the sample (figs. 12, 16). Fin-ray counts (given above in generic diagnosis) are based mainly on these specimens, and seem fairly consistent where observable in others (fig. 15). Generally the tip of the tail is not preserved, but there are traces of a median caudal lobe in AMNH 12211 and 12220 (figs. 15C, 16). Basal elements and/or girdles are ossified (see fig. 14).

The left shoulder girdle has been partially prepared in AMNH 11759, but it is damaged and incomplete. A supracleithrum (anocleithrum) has not been identified. The cleithrum is virtually unornamented, but the clavicles are ornamented by ridges ventrally. These elements appear to meet ventrally. Only a small fragment of the extracleithrum is present. The scapulocoracoid has not been observed. In none of the specimens is it possible to see whether the pectoral fin was lobed or else pedunculate, as in *Latimeria* (cf. Berg, 1940; Forey, 1981). From the positions of fin rays it is fairly certain that the pelvic, anal, and second dorsal fins were lobed as in *Latimeria.*

The swim bladder is well ossified, as in *Macropoma* and many other fossil coelacanths, and is not usually compressed, unlike the remainder of the postcranial skeleton. The swim bladder evidently resisted sedimentary compaction, which suggests that it was filled with fatty tissue in life (further suggested by the lack of sedimentary filling; the swim bladder is usually preserved hollow but with a geodelike lining of calcite). In *Axelrodichthys* the swim bladder extends posteriorly past the level of the second dorsal fin, unlike those in *Undina* and *Macropoma* (Woodward, 1891, fig. 53; 1909, fig. 49). Fur-

5 cm

Fig. 23. *Axelrodichthys araripensis,* AMNH 11760; (**A, B**) right pterygoid, metapterygoid, and quadrate in (A), lateral and (B), mesial views; (**C, D**) incomplete angular and articular in (C), lateral and (D), mesial views.

thermore, in *Axelrodichthys* the swim bladder seems to consist of two or perhaps even three chambers, separated by constrictions (e.g., AMNH 11759, 12210, 12211, 12212, 12213, 12219, 12220). In most of these specimens (AMNH 11759, 12210, 12211, 12212? and 12213) the anterior chamber lies somewhat lower in the body cavity than the remainder (see outline, fig. 14).

DISCUSSION: THE RELATIONSHIP OF MAWSONIA AND AXELRODICHTHYS

As reported by Campos and Wenz (1982), there are two distinct coelacanth taxa in the lower part of the Romualdo Member of the Santana Formation. One of these taxa is referable to *Mawsonia* and may even represent the type species, *M. gigas. Mawsonia* is relatively rarer than the other taxon, being represented in the AMNH collection only by a partial skull and cranial fragments. The other form (*Axelrodichthys,* n. gen.) differs from *Mawsonia* in several aspects of its cranial anatomy, including the proportions and general shape of the skull roof, the cheek bone arrangement, the presence of a median element in the posterior margin of the skull table, basisphenoid morphology, and associated differences in metapterygoid morphology and its articulation with the skull. This new

Fig. 22. *Axelrodichthys araripensis,* flattened head, AMNH 12214; (**A**) skull roof with rostral bones in place, plus right operculum, cheek bones, and coronoids; (**B**) parasphenoid, right pterygoid, prootics, and ?ceratohyals.
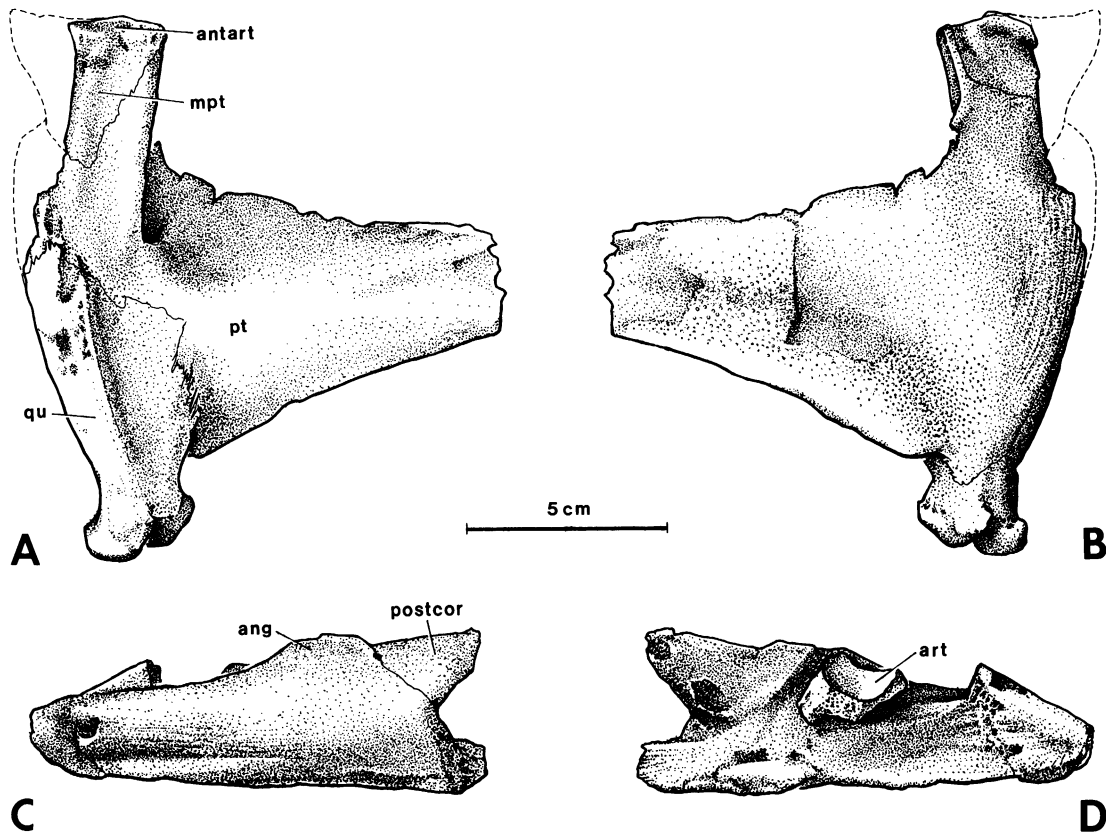
Fig. 24.   Annotated drawings of elements shown in figure 23; (A, B) pterygoid (lacking anterior ramus), metapterygoid, and quadrate; (C, D) articular and angular.
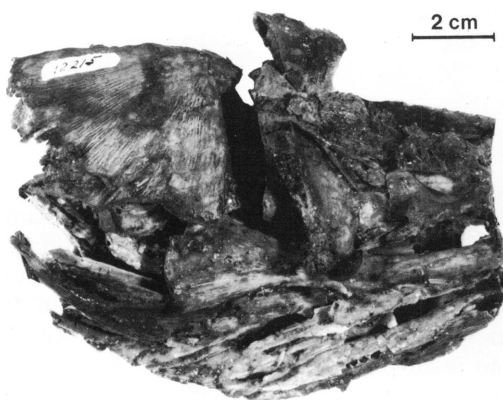

Fig. 25.   *Axelrodichthys,* AMNH 12215, incomplete skull with visceral arches, showing metapterygoid (projecting, top) attached to pterygoid, and right ceratohyal beneath quadrate.

form is considered sufficiently distinct to merit generic separation from other coelacanths.

Axelrodichthys resembles *Mawsonia* in possessing three rather than two pairs of dermal bones in the posterior skull roof, in the anterior extent of the dermosphenotic, and in the very shallow anterior limb of the pterygoid. Furthermore, in both taxa the ectopterygoid may have been unossified. *Mawsonia* (and *Axelrodichthys*) resembles *Macropoma* in its rugose dermal bone ornamentation, and on this basis it has long been suggested that *Macropoma* and *Mawsonia* are closely allied (Mawson and Woodward, 1907, p. 134; Woodward, 1909, p. 176).

In a cladistic analysis of coelacanth phylogeny, Forey (1981, fig. 14) proposed that *Macropoma* and *Latimeria* are sister taxa,
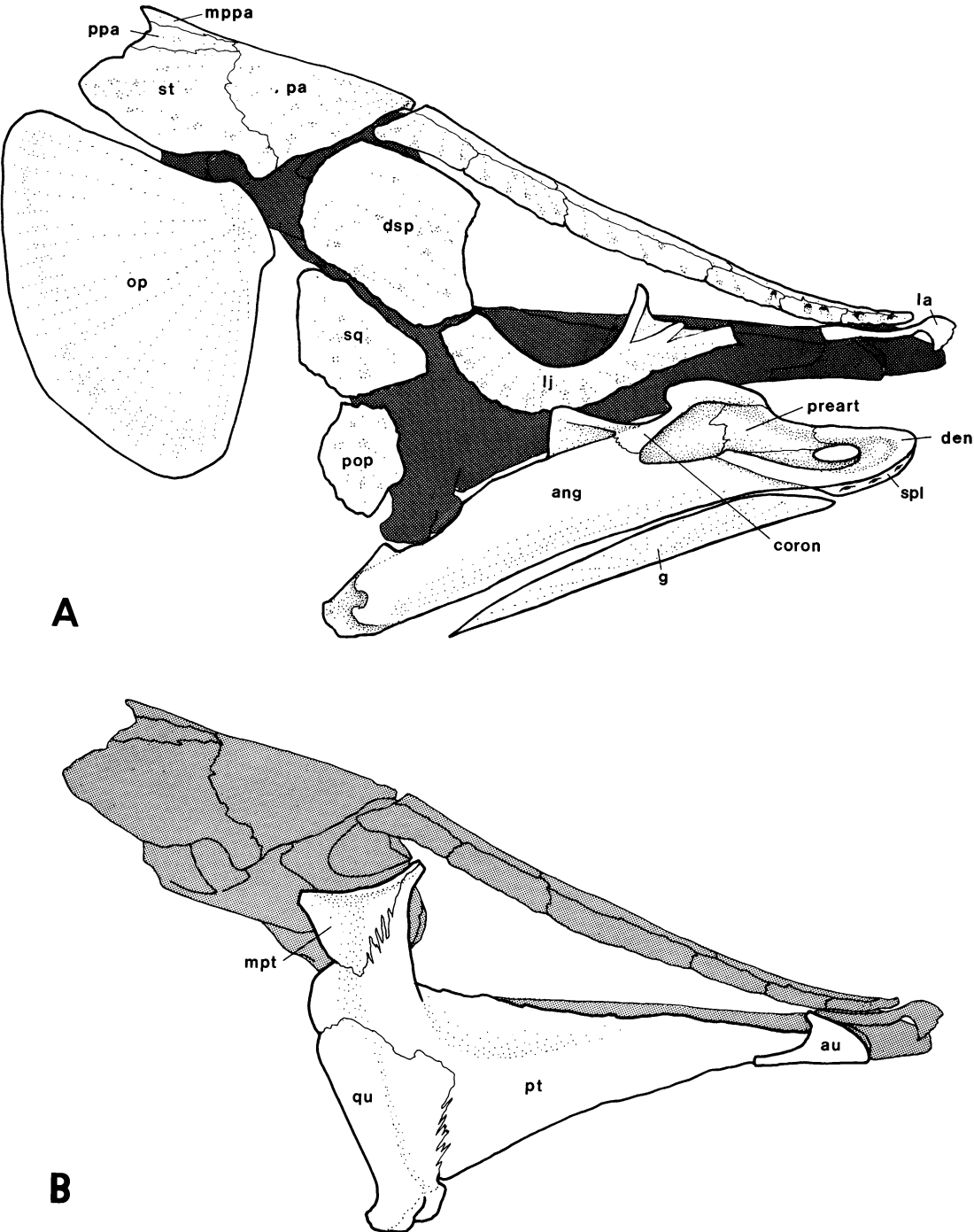
Fig. 26.　Outline restorations of the head in *Axelrodichthys,* based mainly on AMNH 11759, 11760, and 12215. (A) with cheek bones, operculum, and lower jaw in place; (B) cranium and upper jaw.

united by possession of a prootic ascending process, seven extrascapulars (subsequently omitted as a character; Forey, 1984, fig. 2), and anterior branches developed from the supratemporal commissure. *Mawsonia* was excluded from that analysis, but may now be included (along with *Axelrodichthys*).

Investigation of the present material from Brazil generally corroborates Forey's (1981) hypothesis. In particular, there is an ascending process on the prootic in both *Mawsonia* and *Axelrodichthys*. However, the descending process of the supratemporal (which meets the hyomandibular articulation in many coelacanths) is no more than a weak ridge in *Axelrodichthys* (AMNH 11760, 11761, 12215) and is absent in *Mawsonia* (AMNH 11758). According to Forey's (1981) characterization, this is probably a homoplasious condition in these taxa, since a supratemporal descending process is supposedly absent in the most primitive coelacanths, such as *Diplocercides*.

Neither *Mawsonia* nor *Axelrodichthys* possess a series of seven extrascapulars or anterior branches from the transverse commissure. Thus of the three characters which (according to Forey, 1981) unite *Macropoma* and *Latimeria*, only one (the ascending process of the prootic) is present in *Mawsonia* and *Axelrodichthys*. I conclude that *Mawsonia* and *Axelrodichthys* together form a sister group to *Macropoma* and *Latimeria*. These taxa also primitively share with *Holophagus* the presence of dorsal laminae on the parasphenoid and the ventral position of the infraorbital canal within the squamosal.

Adult *Axelrodichthys* and *Mawsonia* attained large dimensions, comparable with modern *Latimeria*. Most other Paleozoic and Mesozoic coelacanths were considerably smaller, although the Triassic genus *Moenkopia*, known only by the basisphenoid, must also have attained a similar size to *Latimeria* (Schaeffer and Gregory, 1961). In the Santana ichthyofauna, only some *Cladocyclus*, *Notelops*, and *Enneles* specimens rival the coelacanths in size (Silva Santos and Valenca, 1968).

The distribution of *Mawsonia* is thought to be of paleobiogeographical significance (Patterson, 1975; Wenz, 1980). However the discovery of *Axelrodichthys*, a genus sharing the same pattern of dermal bone ornamentation as *Mawsonia*, means that records of the latter genus require careful reinvestigation in order to determine whether some should be referred to *Axelrodichthys*. Distinguishing criteria have been noted in the dermosphenotic, lachrymojugal and parietal-postparietal complex, but basisphenoid and metapterygoid morphology may also be diagnostic. At present, *Axelrodichthys* is known only from the Santana Formation of Brazil, where it accompanies *Mawsonia*. The close similarity of *Mawsonia* from Ceara and Bahia suggests that the Lower part of the Romualdo Member (Santana Formation) may be of Neocomian rather than Aptian age.

ADDENDUM

The postcranial skeleton of *Mawsonia* is virtually unknown. According to Forey (personal commun.), the holotype of *M. minor* has closely segmented lepidotrichia in the fins, as in some Jurassic coelacanths, but the fin rays of the first dorsal and caudal fins lack denticles. These are present in many Jurassic and all other hitherto described Cretaceous coelacanths, and also occur in adult *Latimeria*. Evidence from baby *Latimeria* suggests that these denticles appear late in ontogeny. Denticles are present on the fins of the "Forme B" coelacanth described by Campos and Wenz (1982).

The fin rays of all the AMNH *Axelrodichthys* specimen are closely segmented distally, although this segmentation becomes indistinct proximally. In AMNH 11759 the posteriormost three or four rays of D_1 and the ventralmost rays of the anal fin all bear a few sparse denticles. In the small specimen, AMNH 12220, the last three rays of D_1 and the third or fourth hypocaudal fin ray also bear a few denticles. Additionally, one or two denticles have been found on the fringe of a large uncataloged caudal fin associated with an *Axelrodichthys* head. I have been unable to find denticles on the fins of any of the other specimens listed earlier.

I conclude from this that *Axelrodichthys* possessed few denticles on its first dorsal or caudal fins, even in large individuals (in fact more denticles are present on two of the smallest specimens, which seems to rule out ontogenetic variation). The apparent absence of denticles in *Mawsonia minor* may consequently be of phylogenetic importance, perhaps providing a further synapomorphy with *Axelrodichthys*.

It should be noted that in figures 2B and 19B the opening labeled "prof" probably housed the superficial ophthalmic branches of the facial and trigeminal nerve, and that the canal designated "col" is for the supraorbital sensory canal. I thank Dr. Peter Forey for pointing this out to me.

LITERATURE CITED

Agassiz, L.
1841. On the fossil fishes found by Mr. Gardner in the Province of Ceara, in the north of Brazil. Edinburgh New Phil. Jour., vol. 30, pp. 82–84.
1844. Sur quelques poissons fossiles du Brésil. Comptes Rendus Acad. Sci. Paris, vol. 18, pp. 1007–1015.

Bate, R. H.
1972. Phosphatized ostracods with appendages from the lower Cretaceous of Brazil. Palaeontology, vol. 15, no. 3, pp. 379A–393.

Berg, L. S.
1940. Classification of fishes, both Recent and Fossil. Trudy Zool. Inst. Leningrad, vol. 5, pp. 87–517.

Campos, D. A., and S. Wenz
1982. Premiére découverte de Coelacanthes dans le Crétacé inférieur de la Chapada do Araripe (Brésil). C. R. Acad. Sci., II, vol. 294, pp. 1151–1154.

Casier, E.
1961. Matériaux pour la faune ichthyologique éocrétacique du Congo. Ann. Mus. Roy. Afr. Cent., Tervuren, Sci. Géol., vol. 62, xii + 96 pp.

Forey, P. L.
1981. The Coelacanth *Rhabdoderma* in the Carboniferous of the British Isles. Paleontology, vol. 24, no. 1, pp. 203–229.
1984. The coelacanth as a living fossil. In N. Eldredge and S. M. Stanley (eds.), Living fossils. New York, Springer, pp. 166–169.

Jarvik, E.
1980. Basic structure and evolution of vertebrates, vol. 1. New York, Academic Press, 575 pp.

Lehman, J.-P.
1952. Etude complémentaire des poissons de l'Eotrias de Madagascar. K. svenska VetenskAkad. Handl., vol. 4, no. 2, pp. 1–201.

Lima, M. R. De
1978. Palinologia da Formacao Santana (Cretáceo do Nordeste do Brasil). Introducao geologica e desceicao sistematica dos esporos da Subturma Azonotriles. Ameghiniana, vol. 15, pp. 333–365.

Mabesoone, J. M., and I. M. Tinoco
1973. Palaeoecology of the Aptian Santana Formation (Northeastern Brazil). Palaeogeogr., Palaeoclimat., Palaeoecol., vol. 14, pp. 97–118.

Mawson, J., and A. S. Woodward
1907. Cretaceous formation of Bahia and its vertebrate fossils. Quart. Jour. Geol. Soc., vol. 63, pp. 128–139.

Millot, J., and J. Anthony
    1958.   Anatomie de *Latimeria chalumnae* 1.
             Squelette, muscles et formations de sou-
             tien. Paris, Cent. Natl. Rech. Sci., 118
             pp.
Patterson, C.
    1975.   The distribution of Mesozoic freshwater
             fishes. Mém. Mus. Nat. Hist. Natl., ser.
             A, Zool., vol. 88, pp. 156–174.
Rixon, A. E.
    1976.   Fossil animal remains. London, Ath-
             lone Press, vi + 304 pp.
Schaeffer, B.
    1952.   The Triassic coelacanth fish *Diplurus*
             with observations on the evolution of
             the Coelacanthini. Bull. Amer. Mus.
             Nat. Hist., vol. 99, art. 2, pp. 25–78.
    1967.   Late Triassic fishes from the western
             United States. Bull. Amer. Mus. Nat.
             Hist., vol. 135, art. 6, pp. 287–432.
Schaeffer, B., and J. T. Gregory
    1961.   Coelacanth fishes from the continental
             Triassic of the western United States.
             Amer. Mus. Novitates, no. 2036, pp. 1–
             18.
Silva Santos, R. Da
    1981.   Sobre a occurência de uma faunula de
             peixes na formacao Riachuelo, estado
             de Sergipe. An. Acad. Brasil Ciênc., vol.
             53, no. 1, p. 203 (summary).
Silva Santos, R. Da, and J. G. Valenca
    1968.   A Formacao Santana e sua Paleoictio-
             fauna. An. Acad. Brasil. Ciênc., vol. 40,
             no. 3, (3), pp. 339–360.

Spix, J. B., and C. F. P. Martius
    1828.   Reise in Brasilien, vol. 2. Munich, pp.
             770–779.
Toombs, H. A., and A. E. Rixon
    1950.   The use of plastics in the transfer meth-
             od of preparing fossils. Mus. Jour., vol.
             50, pp. 105–107.
Wenz, S.
    1975.   Un nouveau Coelacanthidé du Crétacé
             inférieur du Niger. Remarque sur la fu-
             sion des os dermiques. Colloq. Intn.
             Cent. Natl. Rech. Sci., Paris, no. 218,
             pp. 175–190.
    1980.   A propos du genre *Mawsonia,* Coel-
             acanthe géant du Crétacé inférieur d'Af-
             rique et du Brésil. Mém. Soc. Géol. Fr.,
             n. s., no. 139, pp. 187–190.
    1981.   Un Coelacanthe géant, *Mawsonia lav-
             ocati* Tabaste, de l'Albien-Base du
             Cénomanien du Sud Marocain. Ann.
             Paléont. (Vertébrés), vol. 67, no. 1, pp.
             1–20.
Woodward, A. S.
    1891.   Catalogue of the fossil fishes in the Brit-
             ish Museum (Natural History), pt. II.
             London, Brit. Mus. (Nat. Hist.), xliv +
             567 pp.
    1909.   The fossil fishes of the English Chalk,
             pt. V. Monogr. Palaeont. Soc. London,
             pp. 153–184.