

New occurrence of *Mawsonia* (Sarcopterygii: Actinistia) from the Early Cretaceous of the Sanfranciscana Basin, Minas Gerais, southeastern Brazil

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Abstract: The Cretaceous actinistian *Mawsonia* is represented by more than 360 dissociated, but well-preserved, bones obtained from the Areado Group in the Sanfranciscana Basin of Minas Gerais, Brazil. These are among the oldest records of *Mawsonia* (Berriasian, Lower Neocomian) and include previously undescribed or poorly known skeletal elements (e.g. splenial, dentary, autopalatine, zygals). The new material is referred to the type species, *M. gigas*. Morphological variation in the sample blurs some of the distinctions formerly drawn between nominal species of *Mawsonia*, and species level diversity in the genus is difficult to establish. *Mawsonia ubangiensis*, *M. libyca*, and *M. brasiliensis* are considered to be junior subjective synonyms of *M. gigas*. *Mawsonia gigas* probably appeared prior to the separation of S America and Africa and became widespread throughout much of western Gondwana (including parts of Africa), even surviving briefly on both continents following their separation. *Mawsonia tegamensis* is a morphologically distinctive Late Cretaceous African species with no evident fossil record in Brazil and which probably arose by vicariant speciation following isolation of a local *Mawsonia* population during the later stages of rifting between Northern Africa and the rest of Western Gondwana. Similarities between *Axelrodichthys*, *Lualabaea* (here regarded as Early Cretaceous in age) and recently described fossils from Morocco, Niger, and Madagascar suggest the presence of a second endemic Cretaceous mawsoniid lineage in northeastern Brazil and Africa.

Mawsonia is an extinct non-marine actinistian (coelacanth) genus that has been credited in the past with considerable biogeographical interest. It was apparently restricted to continental and estuarine palaeoenvironments of Western Gondwana (Maranhão, Ceará, Alagoas, Bahia, and Minas Gerais in Brazil; Morocco, Algeria, Egypt, Niger, and the Democratic Republic of Congo in Africa), and its first occurrences predate the late Aptian seaway between Africa and South America, while its later occurrences are on both sides of the seaway (Wenz 1980; Maisey 2000). *Mawsonia* is also the largest known actinistian, with some individuals reaching an estimated length of several meters. The most complete remains of *Mawsonia* described in the literature are from Brazil, and include articulated skulls, postcranial skeletons, and even complete skeletons, from the Neocomian of Bahia and the Albian of Ceará (Woodward 1908; Carvalho 1982; Maisey 1986; Yabumoto 2002). Unfortunately, the majority of *Mawsonia* records, on both sides of the Atlantic, consist of extremely fragmentary material. This makes it difficult to compare and evaluate it phylogenetically.

In 1995, the geologists Geraldo Norberto C. Sgarbi (Universidade Federal de Minas Gerais) and José Eloi G. Campos (Universidade de Brasília) discovered fossil bone fragments in ferruginous Early Cretaceous shales belonging to the Areado Group of the Sanfranciscana Basin, State of Minas Gerais, Brazil. Although these shales are widely exposed on low hummocks and hills, the fossil material described here came from a fairly small area covering a few hundred square meters, on the Fazenda Teresa, near Olhos d'Água do Oeste and about 40 km from the town of João Pinheiro, located in the northwestern part of the state (Fig. 1). Initially, the bones were thought to be crocodylian, but Diogenes de Almeida Campos (DNPM) subsequently recognized them as coelacanth remains, referable to the genus *Mawsonia*. Additional material (including approximately 360 disarticulated elements from the skull, cheek, jaws, hyoid arch, and pectoral fins) was collected from 1997–1999 by the authors, students and researchers of the UFRJ-DG. The coelacanth bones are associated with fin spines and cephalic spines of hybodont sharks, amiiform vertebrae, bones and teeth, semionotid scales and vertebrae,

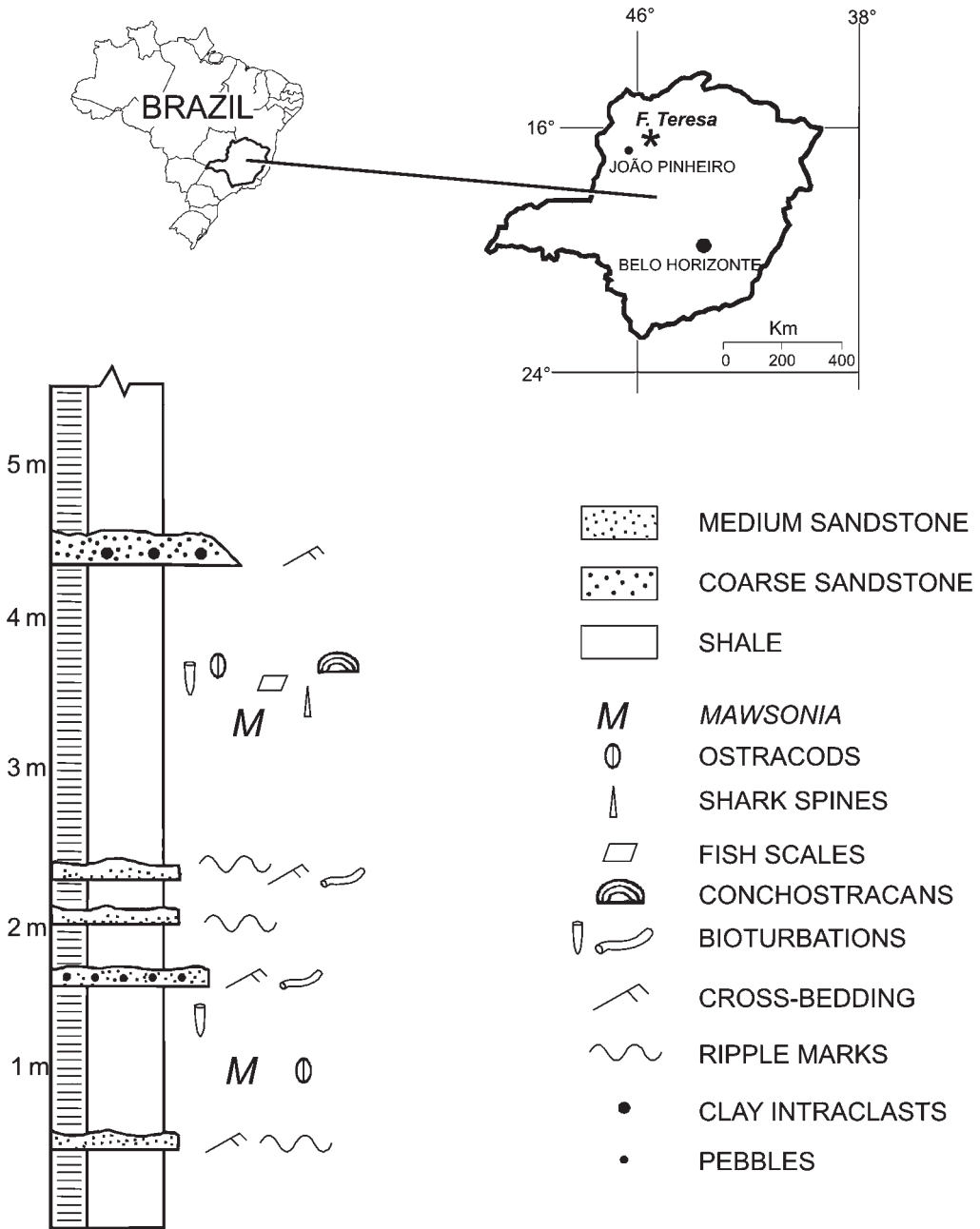


Fig. 1. Map of the collecting area and local stratigraphic sequence at Fazenda Teresa, Sanfranciscana Basin, Minas Gerais, Brazil.

conchostracans, ostracods and bioturbation structures. Although the sample is undoubtedly biased toward larger surface-picked elements, no lungfish toothplates or tetrapod bones were found.

Otherwise, the general aspect of the assemblage is fairly typical for early Cretaceous non-marine deposits in western Gondwana, particularly those from Africa (Maisey 2000). This new occurrence

is the most southerly record of *Mawsonia* known to date, and the sample represents many different individuals of varying sizes.

The material is now deposited in two different institutions; Museu de Ciências da Terra, Departamento Nacional da Produção Mineral, Rio de Janeiro (catalog prefix MCT), and the Universidade Federal do Rio de Janeiro, Departamento de Geologia (catalog prefix UFRJ-DG). All the elements are well-preserved in 3D and are essentially free of matrix, providing an opportunity to investigate morphological variation in large samples of skeletal elements from a single locality (although no meristic analyses were attempted). Almost all the specimens collected were isolated bones, apart from a partial parietonasal shield and an operculum associated with parts of a shoulder girdle. Many of the bone fragments recovered could be reunited with others, suggesting that they were freshly broken at the outcrop and that further excavation might reveal more complete remains. Besides the large number of individual specimens, the Sanfranciscana Basin material also includes skeletal elements of *Mawsonia* that have rarely been documented before, including the splenial, dentary, autopalatine and numerous zyals.

Stratigraphy of the Sanfranciscana Basin

The Sanfranciscana Basin lies within the Abaeté depression, which is separated from the Bauru depression farther west by the Alto Paranaíba Axis (Hasui & Haralyi 1991). The Abaeté depression contains an important Early Cretaceous sequence; the Areado Formation, which has customarily been divided into the Abaeté, Quiricó, and Três Barras members. From a sequence-stratigraphic viewpoint, however, these members probably represent proximal and median facies of an alluvial fan overlapping with a sedimentary complex of lacustrine origin; followed by closure of the lacustrine system and replacement by a braided alluvial plain and aeolian dune fields. Within the southern portion of the Sanfranciscana Basin, the lowest part of the sequence consists of reddish lacustrine shales and aeolian sandstones deposited in arid and warm conditions during the Late Jurassic and Early Cretaceous.

Dinosaur footprints have been recorded in sandstones near João Pinheiro (Kattah 1994; Carvalho & Kattah 1998). The middle part of the sequence consists of reddish bioturbated shales (the source of the coelacanth bones described here), plus fin spines of hyodont sharks, ganoid scales, conchostracans and ostracods are indicative of a non-marine environment including *Pattersoncypris*, *Darwinula*, *Ilyocypris* and *Cypridea*; Delicio *et al.* 1998;

Carvalho & Maisey 1998; Carvalho 2002). These shales are intercalated with siltstones and sandstones both with ripple marks, cross bedding and pebbles, all probably deposited within a flood plain at the margin of a lake. The precise stratigraphic level of the *Mawsonia*-bearing horizon is uncertain, but overlying strata contain ostracods of Barremian age (Do Carmo *et al.* 2004) as well as the Barremian–early Aptian palynomorph *Transitoripollis crisopolensis*. However, other palynological data suggest that at least part of the sequence lies close to the Barremian–Aptian boundary (notably a high *Afropollis* count and the presence of other angiosperm pollen that appear at the Barremian–Aptian boundary; Arai *et al.* 1995).

The upper part of the Areado Group consists of sandstones intercalated with shales containing freshwater fishes including *Dastilbe moraesii* and *Laeliichthys ancestralis* (Scorza & Silva Santos 1955; Silva Santos 1985), which are regarded as Aptian because *Dastilbe* is well known from Cretaceous deposits elsewhere in Brazil. Other fossils from this part of the sequence include charophytes, gymnosperms (e.g. *Araucarioxylon*, *Podozamites*, *Brachyphyllum*), angiosperms (*Paraleptaspis*, *Nymphaeites*), conchostracans and ostracods (Barbosa 1965).

Materials

Specimens from the Sanfranciscana Basin were catalogued in groups according to bone type, with the institutional prefix followed by catalog number, specimen letter (listed alphabetically), and suffix ‘P’ (Palaeontology Collection); e.g., 10 postparietals were catalogued under MCT 1384a-j-P, and another 10 under UFRJ-DG356a-j-P. This approach was adopted so that future finds could be assigned to the appropriate groups without generating additional numbers. The following list represents material catalogued as of June 2006.

MCT 1364a-P; Basisphenoid and posterior parietal
 MCT 1364b-h-P; UFRJ-DG 341a-e-P; basisphenoid
 MCT 1365a-p-P; UFRJ-DG 342a-n-P; parasphenoid
 MCT 1366a-d-P; UFRJ-DG 343a-d-P; parietal and supraorbital
 MCT 1367-P supraorbital; MCT 1368-P; lachrymojugal
 MCT 1369a-h-P; UFRJ-DG 300-P; 344a-g-P; operculum
 MCT 1370a-t-P; UFRJ-DG 345a-u-P; angular
 MCT 1371a-f-P; UFRJ-DG 346a-d-P; splenial
 MCT 1372a-f-P; UFRJ-DG 347a-e-P; dentary
 MCT 1373a-g-P; UFRJ-DG 348a-c-P; articular
 MCT 1374a-h-P; UFRJ-DG 349a-f-P; posterior coronoid
 MCT 1375-P; gular
 MCT 1376a-b-P; UFRJ-DG 350-a-b-P; autopalatine
 MCT 1377a-m-P; UFRJ-DG 351a-m-P; pterygoid
 MCT 1378a-k-P; UFRJ-DG 352a-k-P; metapterygoid

MCT 1379a-k-P; UFRJ-DG 353a-j-P; quadrate
 MCT 1380a-j-P; UFRJ-DG 354a-i-P; prootic
 MCT 1381-P; UFRJ-DG 362-P; basioccipital
 MCT 1382-P; supraoccipital
 MCT 1383a-j-P; UFRJ-DG 355a-j-P; zygale
 MCT 1384a-j-P; UFRJ-DG 356a-j-P; postparietal
 MCT 1385a-o-P; UFRJ-DG 357a-n-P; supratemporal
 MCT 1386a-e-P; UFRJ-DG 358a-d-P; extrascapular
 MCT 1387a-f-P; UFRJ-DG 359a-e-P; ceratobranchial
 MCT 1388a-h-P; UFRJ-DG 360a-f-P; cleithrum
 MCT 1389-P; UFRJ-DG 361a-b-P; scapulocoracoid

Other Brazilian mawsoniid material examined included the following:

Araripe Basin; *Axelrodichthys araripensis*: AMNH 11759, AMNH 11760, AMNH 12209–12213, MCT 1131-P; *Mawsonia* cf. *M. gigas*: AMNH 11758, AMNH 12216, 12217, 12218; *Mawsonia gigas*: UFRJ-DG 277-P; UFRJ-DG 278-P, UFRJ-DG 299-P.

Recôncavo Basin; *Mawsonia gigas*: DGM 1040-P to 1047-P.

Tucano Basin; *Mawsonia gigas*: DGM 1038-P, 1039-P, DGM 1048-P.

Grajaú Basin; *Mawsonia gigas*: MN 4532-V; *Axelrodichthys araripensis*: UFRJ-DG 220-P.

São Luís Basin; *Mawsonia gigas*: UFRJ-DG 143-P; UFRJ-DG 312-P; UFRJ-DG 313-P; UFRJ-DG 319-P; UFRJ-DG 340-P.

Anatomical abbreviations:

ant ap	anterior apophysis
ant pr	antotic process
desc pr	descending process of postparietal
Ent	entopterygoid
ext	extrascapular
gr d	groove for dentary
gr md c	groove for mandibular sensory canal
mpt	metapterygoid
ot can	otic sensory canal
pit	depression in basisphenoid for pituitary
post pa	posterior parietal
ppa	postparietal
pr con	processus connectens
q	quadrate
s ent	suture for entopterygoid
stt	supratemporal

Institutional abbreviations:

AMNH – American Museum of Natural History, New York

BMNH – The Natural History Museum, London

DGM-DNPM – Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Rio de Janeiro

MCTer/DNPM-RJ – Museu de Ciências da Terra, Departamento Nacional da Produção Mineral, Rio de Janeiro

UFRJ-DG – Universidade Federal do Rio de Janeiro, Departamento de Geologia
 MDE – Musée de Dinosaures, Espéraza, France.

Systematic palaeontology

Class Osteichthyes

Subclass Sarcopterygii

Infraclass Actinistia

Order Coelacanthiformes

Suborder Latimerioidae Schultzze, 1993

Family Mawsoniidae Schultzze, 1993

Mawsonia Woodward in Mawson & Woodward, 1907

Emended diagnosis. Mawsoniid fish of large size (including the largest known actinistians); head large and deep, with very thick dermal bones ornamented with coarse rugosities (often obscuring sensory canals) and with prominent ridges on the operculum, angular and gular; postparietal shield short and broad, parallel-sided posteriorly; two extrascapulars firmly sutured into postparietal shield and resembling an additional pair of postparietals; no median extrascapular; parietonasal shield narrow, generally more than twice as long as postparietal shield, convex dorsally in transverse and lateral view, and lacking pores; two pairs of elongate parietals present; Snout composed of a mosaic of star-shaped ossicles; lateral rostral extremely slender anteriorly, extending well in front of eye and angled dorsally at its anterior tip; Pre-orbital absent; sclerotic plates absent; tectal and supraorbital series as wide as parietonasal series, but containing comparatively few elements (usually six); posterior parietal usually meets posteriormost 3 supraorbitals; supratemporal lacks descending process; cheek bones in contact with each other; lachrymojugal elongate and slender, reaching the tectal series, with the infraorbital sensory canal located in its ventral margin; postorbital with splint-like process directed anteriorly; squamosal large, quadrangular, forming major element of cheek; lateral ethmoid of braincase with very pronounced posterodorsal process which contacts undersurface of skull roof; basisphenoid stout, with prominent, parallel-sided antotic process; palatoquadrate with very shallow anterior limb of pterygoid, bearing a single strengthening ridge on its lateral surface; autopalatine small; principal coronoid of lower jaw with a small sutural surface contacting mid-region of angular, markedly saddle-shaped in lateral view with the posterior limb considerably higher; extensive area of overlap between dentary and angular; dentary elongate and slender anteriorly; pit-lines open via small pores in the dentary and larger ones in the angular.

Type Species. *Mawsonia gigas* Woodward in Mawson & Woodward, 1907.

- 1891 'Pterosaurian' Woodward; p. 314, fig. 2.
 1896 'Pterodactyl' Woodward; p. 255, fig. A–C.
 1907 *Mawsonia gigas* Woodward in Mawson & Woodward; p. 134, Plate 7, Plate 8, fig. 1–6.
 1908 *Mawsonia minor* Woodward; 358, Plate 42, fig. 1–3.
 1935 *Mawsonia libyca* Weiler; p. 11, fig-text 1, Plate 1, fig. 5–10, 12, 17–29, 31–34, 42–46, 50–52; Plate 2, fig. 4, 9, 27, 35–36; Plate 3, fig. 1–6, 11, 13, 18.
 1961 *Mawsonia ubangiana* Casier; p. 23, fig. 4b, 5b, 6, 8b, 9b; Plate 2, Plate 3, fig. 1–2.
 1969 *Mawsonia ubangiensis* Casier; p. 16, Plate 2, fig. 2.
 1982 *Mawsonia gigas* Woodward. Carvalho; p. 522, Plate 2–8.
 1986 *Mawsonia* cf. *M. gigas* Woodward. Maisey; p. 3, fig. 1–11.
 1991 *Mawsonia* cf. *M. gigas* Woodward. Maisey; p. 317.
 1998 *Mawsonia gigas* Woodward. Forey; p. 327.
 1998 *Mawsonia ubangiensis* Casier. Forey; p. 328.
 1998 *Mawsonia libyca* Weiler. Forey; p. 328.
 1998 *Mawsonia* sp. Carvalho & Maisey; p. 32A.
 2001 *Mawsonia* cf. *M. gigas* Woodward. Dutra & Malabarba; p. 204, fig. 6C.
 2001 *Mawsonia* sp. Medeiros & Schultz; p. 216, fig. 4D.
 2002 *Mawsonia brasiliensis* Yabumoto; p. 343, fig. 1–4.

Holotype. BMNH P 10355, incomplete skull and associated bones from jaw, plus a series of isolated bones including the parietal, quadrate, articular, angular, coronoid, pterygoid and gular.

Paratypes. BMNH P 10356, right postparietal; BMNH P 10357, right operculum.

Type locality. Almeida Brandão, Salvador, Bahia, NE Brazil.

Horizon. Candeias Formation, Early Cretaceous (Neocomian).

Emended diagnosis. Large species in which the quadrate condyle can be up to 110 mm across; ornament of coarse rugosities arranged in strong longitudinal ridges on the parietals, postparietals and angular; anterior foramen for otic sensory canal of the postparietal located close to the anterior apophysis; Pre-operculum as large as or larger than squamosal, but does not meet lachrymojugal; triangular operculum ornamented with delicate ridges radiating outward from growth centre; pelvic fin located level with the first dorsal fin;

caudal fin length approximately one-third overall length.

Description. The large sample of isolated bones at our disposal provides the first opportunity to investigate morphological variation within an apparently monospecific population of *Mawsonia* from the Early Cretaceous, and to compare the sample with the type and other nominal species of the genus. Rather than presenting a tedious monographic description of all the bones, attention will be focussed on certain elements and features that seem to have bearing on the systematics of these large and spectacular non-marine coelacanths. However, numerous specimens will be illustrated in order to document the variability within the sample. *Mawsonia* specimens from the Santana Formation of Brazil, in which the head skeleton is relatively complete, were used extensively as a guide to identify isolated skull elements in the new material (including AMNH11758, originally referred to *Mawsonia* cf. *M. gigas*; Maisey 1986; *M. brasiliensis*; Yabumoto 2002; and another large undescribed specimen in the Museu Nacional).

Specimens of *M. gigas* from other Brazilian localities were also compared, including recently-discovered material from Bahia and Maranhão, but a description of that material is beyond the scope of this paper. Comparisons were also made between *Mawsonia* and *Axelrodichthys* (resolved cladistically as the sister taxon of *Mawsonia*; Forey 1998). These forms are readily distinguished by differences in the shape and proportions of the skull roof, presence (*Axelrodichthys*) or absence (*Mawsonia*) of a median extrascapular, cheek bone arrangement and differences in the articulation between the basisphenoid and metapterygoid (Maisey 1986).

Parietonasal shield. One of the most complete specimens in the sample represents the posterior part of the ethmosphenoid region from a moderately small individual (MCT 1364a-P; Fig. 2d–f). The specimen agrees in most respects with a more complete ethmosphenoid of *M. cf. M. gigas* (Fig. 2a–c), and it is also very similar to the parietonasal shield in the holotype of *M. brasiliensis* (Yabumoto 2002). Although the ornament of ridges and grooves differs in these specimens, its expression also varies within the Sanfranciscana Basin posterior parietals and does not seem to be size-related. Six isolated and incomplete parietals were identified, the largest of which is c. 60 mm long (Fig. 3), although it was not possible to distinguish between anterior and posterior parietals. In two specimens the parietal and supraorbital bones are still associated (MCT 1366d–P; Fig. 3a–b, UFRJ–DG 343d–P; Fig. 3c–d) and parietal

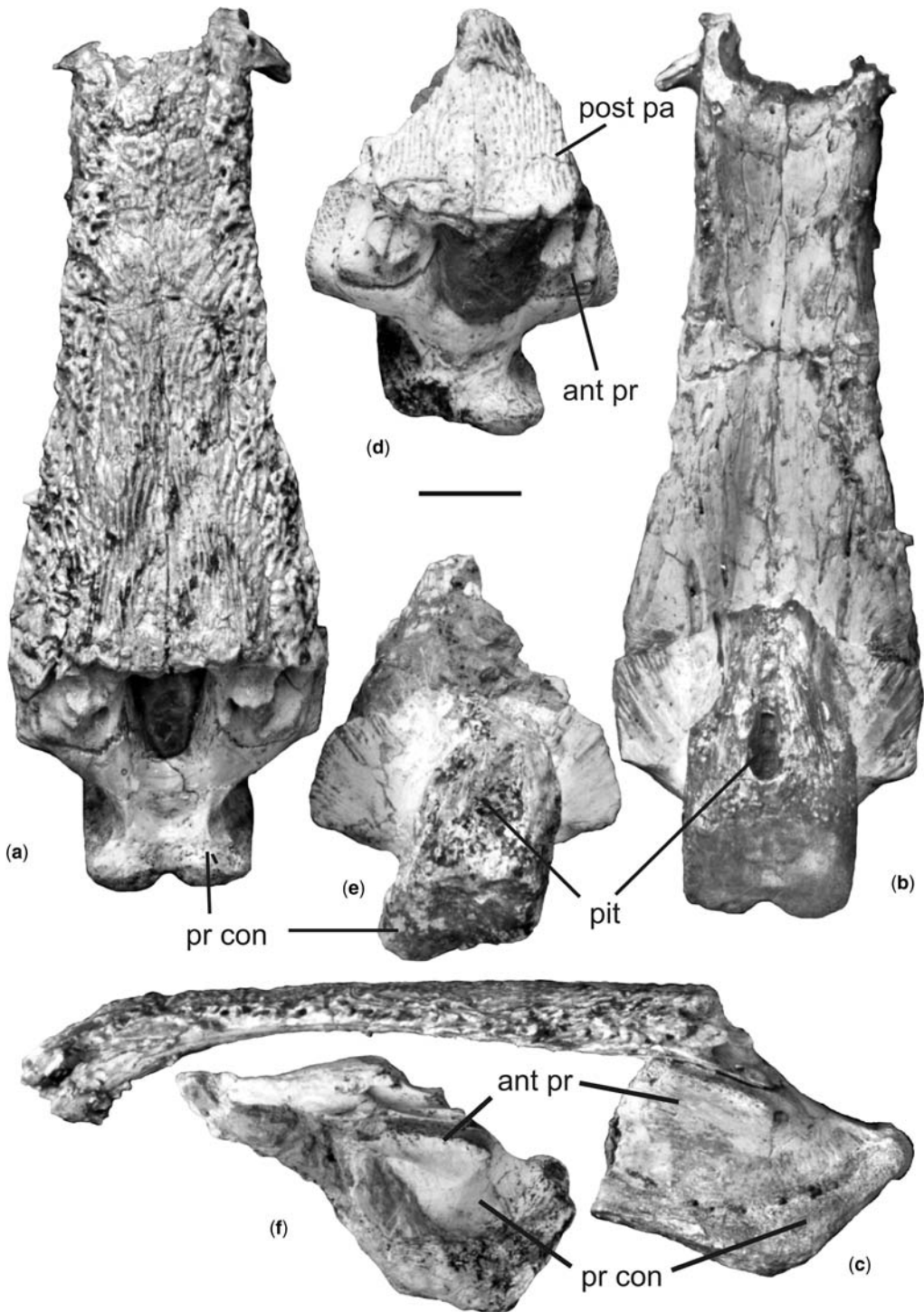


Fig. 2. (a–c), acid-prepared parietonasal shield and basisphenoid of *Mawsonia* cf. *M. gigas* Woodward (AMNH 11758, from the Santana Formation, Araripe Basin); (d–f), corresponding views of the most complete Sanfranciscana Basin specimen, referred here to *Mawsonia gigas* (MCT 1364a-P). (a–d) dorsal view; (b–e) ventral view; (c–f) left lateral view. Anterior to top in orientation (a–b, d–e) and to left (c, f). Scale bar = 10 mm.

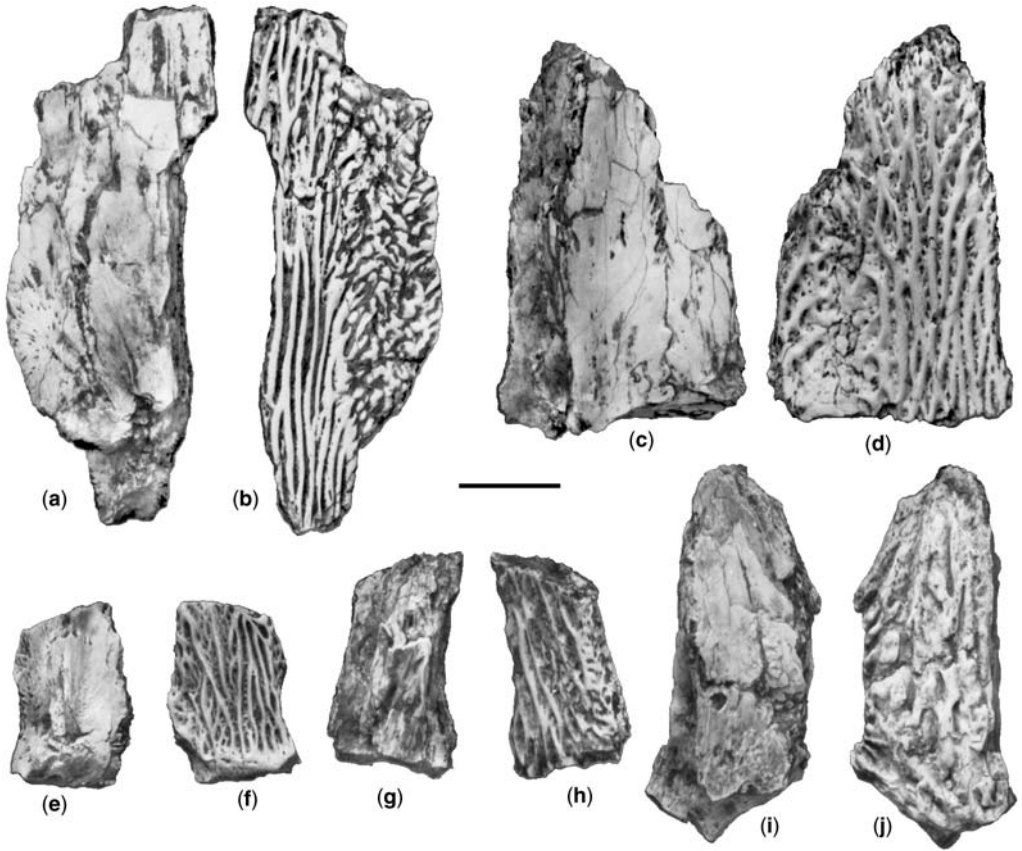


Fig. 3. *Mawsonia gigas* parietals (a–h) and supraorbitals (i–j) from the Sanfranciscana Basin. (a–b) left parietal MCT 1366c-P; (c–d) right? parietal fragment UFRJ-DG 343-d-P; (e–f) parietal fragment UFRJ-DG 343-c-P; (g–h) parietal fragment UFRJ-DG 343-b-P; (i–j) parietal fragment MCT 1367-P. Anterior to top in (a–d); orientation uncertain in other views. Scale bar = 10 mm.

fragments are still attached to some of the basisphenoids. Two associated supraorbitals were also found (MCT 1367-P; Fig. 3i–j). The posterior parietal descending process and the basisphenoid are tightly associated even in broken specimens.

The posterior parietals in MCT 1364a–P are narrow, as in *Mawsonia* cf. *M. gigas* from the Santana Formation and the holotype of *M. brasiliensis* (Maisey 1986; Yabumoto 2002). In all the Santana Formation specimens examined, the supraorbitals do not extend appreciably beyond the lateral margins of the posterior parietal, and it is thought that the Sanfranciscana *Mawsonia* is similar. In *M. tegamensis* the posterior parietals are comparatively wide and the supraorbitals do not extend behind them (Wenz 1975). However, in specimens referred to *M. lavocati*, there may be a deep notch between the posterior parietal and

supraorbital (Cavin & Forey 2004). According to Wenz (1981) *M. lavocati* and *M. tegamensis* differ in the proportion and ornamentation of bones forming the median series. All the parietals in our sample are ornamented with sub-parallel ridges that frequently branch and merge, and the supraorbital ornament is more reticulated (e.g. Fig. 3b, d, j).

Wenz (1975) noted that the lateral margins of the parietals in *Mawsonia tegamensis* are occupied by a cavity that, together with a corresponding space in the medial margin of the supraorbitals, produces a tube for the supraorbital sensory canal. The same arrangement is found in *M. cf. M. gigas* and may be characteristic of the genus.

Basisphenoid. MCT 1364a–P is an almost complete basisphenoid, still attached to the posterior parietals (Fig. 2d–f). Its antotic process is triangular in shape and is sutured dorsally to the descending

process of the posterior parietal, as in *Mawsonia* cf. *M. gigas* (Fig. 2a–c). The antotic process is strongly ridged and probably forms the insertion of the anterior adductor mandibulae muscle. The lateral surface of the antotic process is fairly smooth and straight, and the ventral surface of the basisphenoid contains a large pit (somewhat abraded in MCT 1364a–P) that probably contained the pituitary. In posterior view, the foramen of the superficial ophthalmic nerve is located near the base of the parietal descending process. The processus connectens is well-developed on either side of the basisphenoid, and passes posteriorly into the sphenoid condyles. These are large and are positioned close together. The ventral surface of the basisphenoid is strongly rounded from side to side.

Twelve other incomplete basisphenoids were also found, most of which are broken in the hypophysial region and show only the sphenoid condyles and the processus connectens (Fig. 4). The largest fragment (representing only the sphenoid condyles and processus connectens; MCT 1364f–P; Fig. 4d) is approximately 68 mm wide. Four other fragmentary basisphenoids (not illustrated here) represent parts of the antotic process, with a

sutural surface for the descending process of the posterior parietal (fragments of which are sometimes attached).

The antotic process in the Sanfranciscana Basin basisphenoids is virtually identical to that of *Mawsonia* cf. *M. gigas* (Maisey 1986), but in other Brazilian material referred to *M. gigas* the basisphenoid is poorly-preserved and the shape of the antotic process has not been determined. The basisphenoid has also not been described to *M. libyca* or *M. ubangiensis* and is poorly known in *M. tegamensis* and *M. lavocati* (Wenz 1975, 1981; Carvalho 1982). In *Mawsonia* sp. from Niger, the antotic process is slightly larger than in *M. gigas*, and its lateral margin is not as straight (Wenz 1981, fig. 4).

Parasphenoid. Although more than 30 parasphenoid fragments of various sizes were recovered, they provide little morphological information and none are illustrated here. Parasphenoid teeth seem to be confined to a small patch anteriorly, and are invariably small and closely spaced as in *Mawsonia lavocati*, *M. lybica* and *M. tegamensis*. Above the toothed area, some of the fragments show a distinct zone with strong ridges, presumably representing

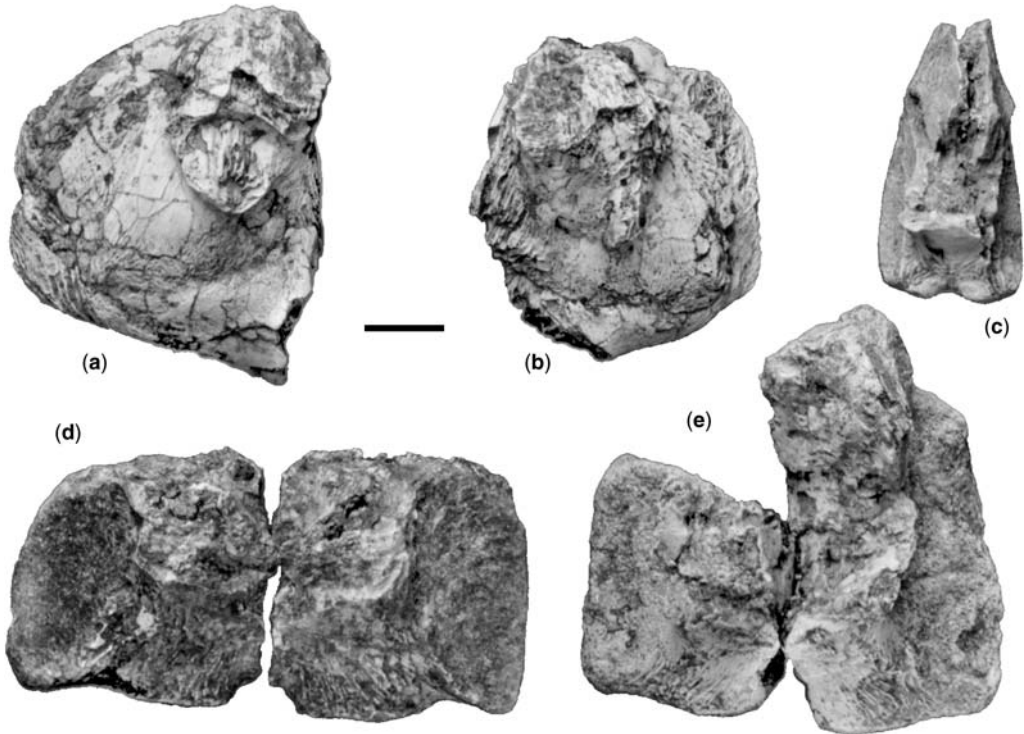


Fig. 4. *Mawsonia gigas* sphenoid condyles from broken basisphenoids, Sanfranciscana Basin. All dorsal views, anterior to top. (a) MCT 1364g-P; (b) UFRJ-DG 341-d-P; (c) UFRJ-DG 341a-P; (d) MCT 1364f-P; (e) MCT 1364e-P. Scale bar = 10 mm.

the sutural surface for the lateral ethmoids (e.g. MCT 1365e-P).

Postparietal shield. The postparietal shield is one of the better known parts of the head in *Mawsonia*, and is one of the few skeletal components that can be compared in several nominal species. The best-preserved example is an acid prepared specimen from the Santana Formation (Maisey 1986; AMNH 11758; see Fig. 5a). In the Sanfranciscana Basin sample, 20 postparietals (nine from the right side, 11 from the left), 29 supratemporals (13 right, 16 left), and nine extrascapulars have been identified. All the specimens are fragmentary but their dimensions differ greatly and they clearly represent a suite of individuals covering a wide size range.

In general, the morphology and ornament of the postparietals in our sample are typical for *Mawsonia* (Figs 5–7). The external face of the bone is entirely ornamented by ramifying ridges separated by pronounced grooves, and there is a well-developed descending process on its ventral surface. A large anterior foramen for the otic lateral line canal is present on the anterior margin of the postparietal.

In the largest Sanfranciscana Basin postparietal (UFRJ-DG 356g-P; Fig. 7), the otic canal foramen is located some distance posterolaterally from the anterior apophysis, as in the holotype of *M. gigas* (BMNH P10356), *M. lavocati* and *M. libyca*. In other Sanfranciscana Basin specimens, the canal is much closer to the anterior apophysis, as in *M. aff. tegamensis* (Wenz 1975), *M. cf. M. gigas* (Maisey 1986), and *M. brasiliensis* (Yabumoto 2002). The proximity of the otic canal foramen to the anterior apophysis therefore varies within our sample and seems unreliable as a systematic character. Also in UFRJ-DG 356g-P, the anterior apophysis is not connected by a bony bridge to the descending process arc. This bridge is also absent in several other specimens (e.g., MCT 1384-i-P; Fig. 5c, MCT 1384-b-P; Fig. 6e), but is present in some (Figs 5g; 6a, c). Forey (1998) noted comparable variation between two specimens of *M. gigas* in the BMNH collection. Presence or absence of the bridge therefore seems to be an unreliable criterion for species recognition (cf. Wenz 1981). Our sample suggests that this variation is unrelated to size and may simply reflect differences between individuals or genders.

Casier (1961) found two anterior apophyses on the anterior margin of the postparietal in *M. gigas*, but identified only one in *M. ubangiensis*. Only one is present in most Sanfranciscana Basin postparietals (e.g. UFRJ-DG356a-P; MCT.1384b-P; Fig. 6d, f), but some have two (e.g. UFRJ-DJ

356g-P; indicated by asterisks in Fig. 7). This difference probably arises as a result of differential ossification of the apophysis and is probably not a systematically useful character in *Mawsonia*.

According to Casier (1961), the postparietal in the type specimen of *M. gigas* is ornamented by parallel ridges close to the anterior process, but these were absent in his specimen of *M. ubangiensis*. However, there is considerable variation in the pattern and intensity of ornament of this region in the Sanfranciscana Basin postparietals, suggesting that it is also not a systematically useful character in *Mawsonia*.

Other variation is also observed in the Sanfranciscana Basin postparietals. In some specimens, the anterior apophysis projects in front of the bone as Casier (1961) reported in *M. ubangiensis*, but in others it is represented only by a low prominence (as he showed in *M. gigas*; Casier 1961, Fig. 4; cf. Figs 5–7 here). In many specimens, the ornamented external lamina extends up to, or even overhangs the base of the anterior apophysis, as in *M. gigas*, *M. cf. M. gigas*, *M. ubangiensis*, and *M. tegamensis*, but in some specimens the external lamina terminates some distance behind the apophysis, exposing an area of vascular bone normally covered by the external lamina (Fig. 7). Thus, there is considerable variation in the relative position of the otic canal foramen and the anterior apophysis, in the number and size of anterior processes of the postparietal, the relative forward projection of the anterior apophysis, and in the anterior extent of the dorsal lamina above the process. These features consequently do not seem to offer reliable criteria for distinguishing between species of *Mawsonia*.

The postparietals from the Sanfranciscana Basin have a continuous transverse median branch of the otic sensory canal. The opening for this branch is readily observed within the sutural surface at the midline. A similar branch is also present in *Mawsonia cf. M. gigas* (Maisey 1986, fig. 3), as well as in *M. tegamensis* (Wenz 1975, fig. 1), but Casier (1961) did not identify it in *M. ubangiensis* or in the holotype of *M. gigas*, and a median branch is apparently absent in *M. lavocati* (Wenz 1981). The arrangement of the otic sensory canal in the holotype of *Mawsonia gigas* is unknown. In *Latimeria*, a median branch is present, but it divides into anterior and posterior canals that emerge onto the surface of the bone close to the dorsal midline (Forey 1998, fig. 3.1), rather than passing entirely through the bone as in *Mawsonia*. It is therefore possible that the median branch of the otic canal passed through the postparietal in some *Mawsonia* individuals but not in others, but the systematic significance of this variation is unclear.

Nineteen incomplete prootics were collected, of which 13 are from the left side and 6 are from the right (Fig. 8). In all respects that we could

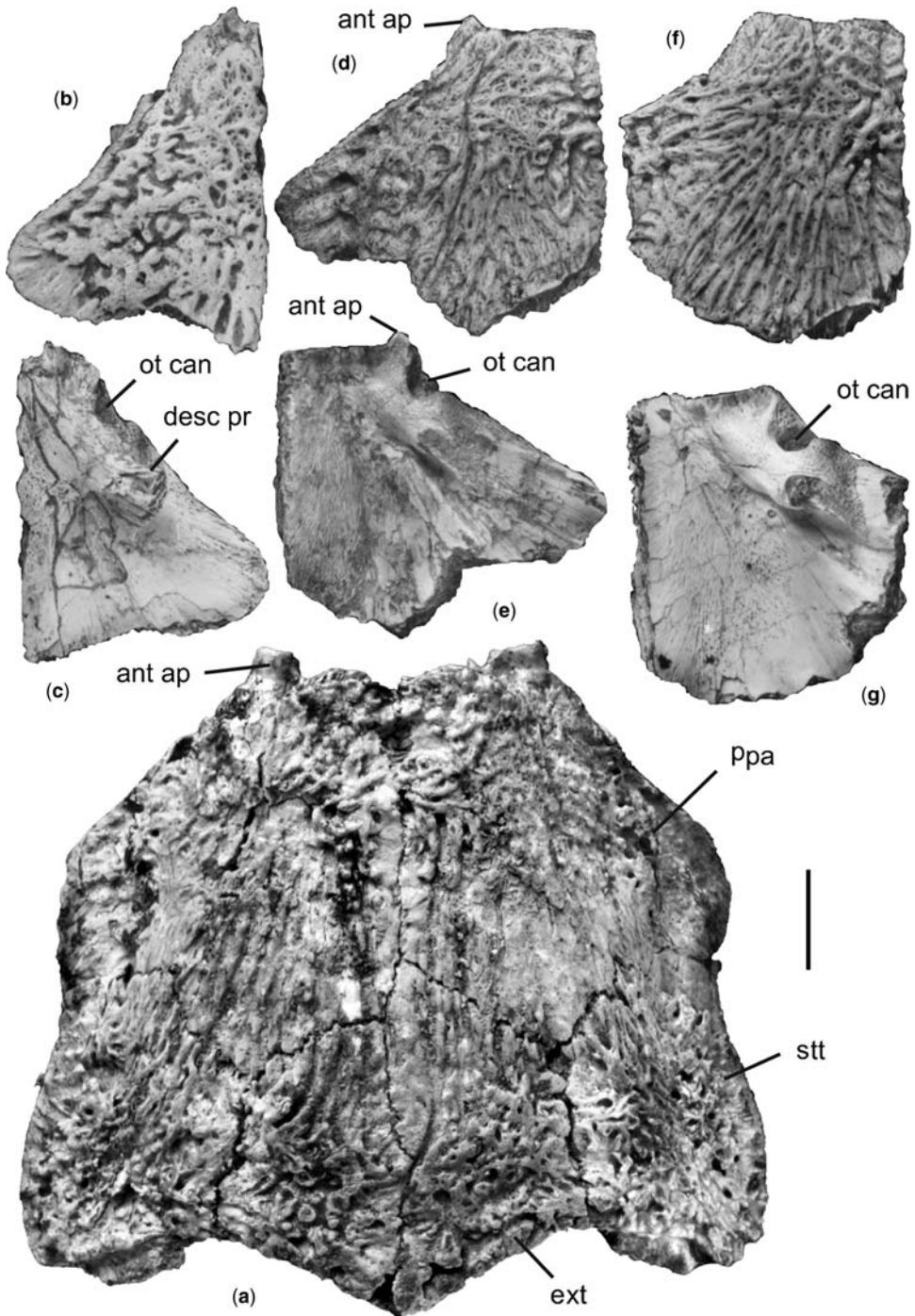


Fig. 5. (a) Complete acid-prepared postparietal shield from *Mawsonia* cf. *M. gigas* (AMNH 11758, Santana Formation, Araripe Basin), dorsal view. (b–g) *Mawsonia gigas* from the Sanfranciscana Basin, left postparietals in dorsal (b, d, f) and ventral (c, e, g) views. (b–c) MCT 1384i-P; (d–e) UFRJ 356h-P; (f–g) UFRJ-DG 356j-P. Anterior to top in all views. Scale bar = 10 mm.

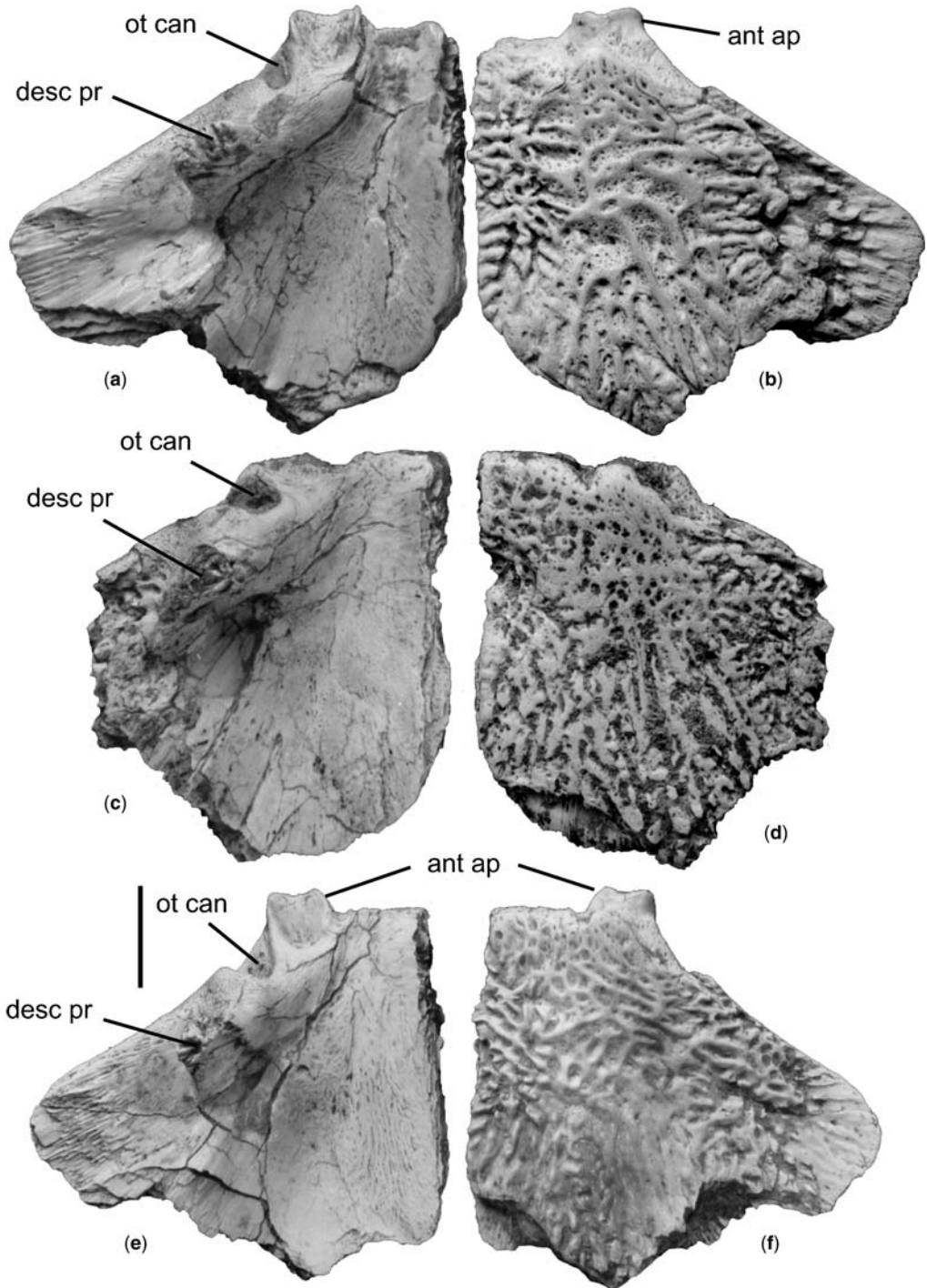


Fig. 6. *Mawsonia gigas* from the Sanfranciscana Basin, right postparietals, anterior to top, in ventral (a, c, e) and dorsal (b, d, f) views. (a–b) MCT 1384a-P; (c–d) UFRJ-DG 356a-P; (e–f) MCT 1384b-P. Scale bar = 10 mm.

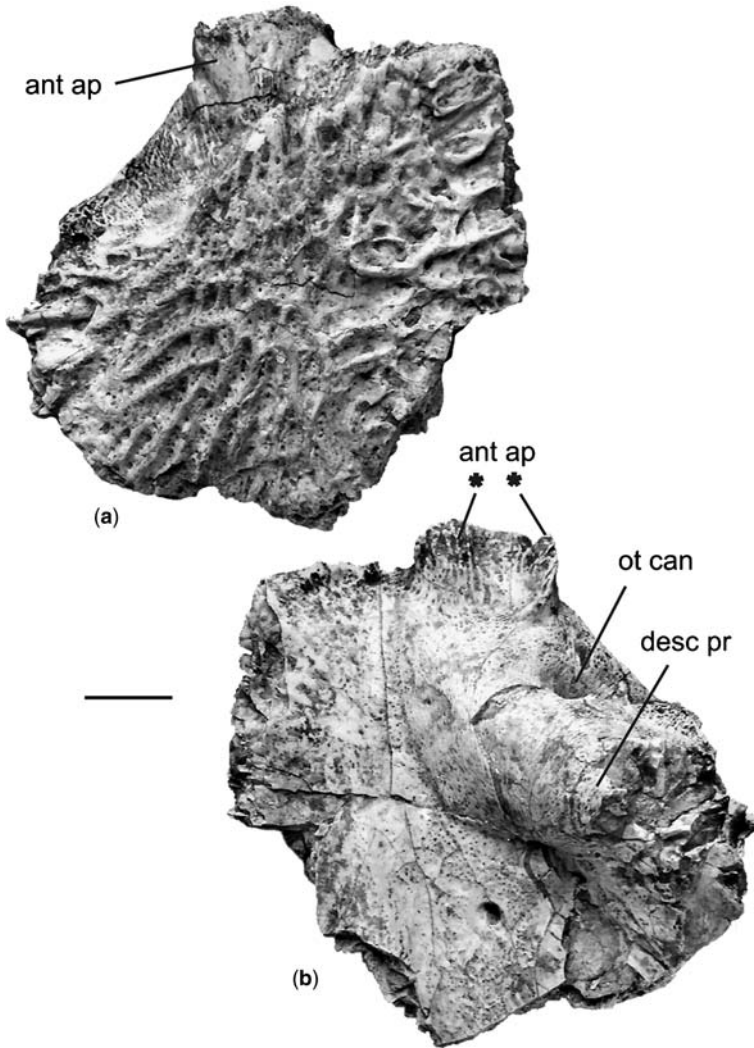


Fig. 7. *Mawsonia gigas* left postparietal from Sanfranciscana Basin, UFRJ-DG 356g-P (the largest specimen recovered), anterior to top. (a) dorsal view; (b) ventral view. Scale bar = 10 mm.

observe, the prootics are identical to those of *Mawsonia* cf. *M. gigas* from the Santana Formation (the only other form in which these have been described; Maisey 1986).

The supratemporals are distinctive bones that contribute to the rounded posterolateral margin of the postparietal shield (Fig. 9). As in other mawsoniids, the extrascapulars form an integral part of the postparietal shield and are strongly sutured to the postparietal and supratemporal (Fig. 10). All the extrascapulars in the Sanfranciscana Basin material are paired and asymmetrical and only a single pair was probably present. The largest extrascapular is approximately 40×40 mm.

Cheek bones and operculo-gular region. No postorbitals, squamosals, spiraculars, suboperculae or pre-operculae were found (perhaps for preservational reasons, since these bones tend to be rather thin and delicate) and only a single fragmentary lachrymojugal was identified. A single gular fragment was also found, 55 mm long and 25 mm wide.

Numerous thick and strongly ornamented fragments of operculae were identified in the Sanfranciscana Basin sample, some of which are shown here (Fig. 11). The operculum apparently resembles that of other *Mawsonia* species, with a thick anterior margin and a well-developed internal attachment

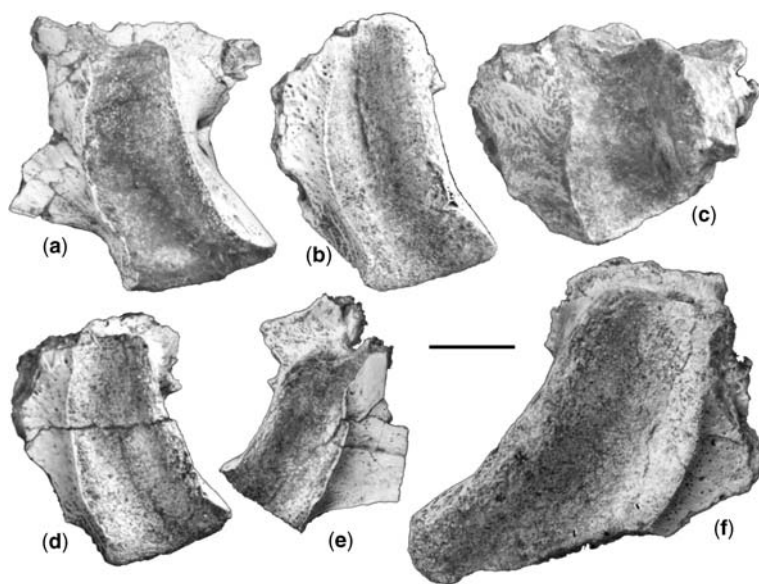


Fig. 8. *Mawsonia gigas* incomplete prootics from the Sanfranciscana Basin (mostly the articular surface for the basisphenoid), all in medial view. (a–d) left prootics; (a) MCT 1380a-P; (b) MCT 1380b-P; (c) UFRJ-DG 354c-P; (d) MCT 1380c-P. (e–f) right prootics; (e) UFRJ-DG 354g-P; (f) MCT 1380g-P. Scale bar = 10 mm.

surface for the hyomandibula. The ornament pattern in our material seems very similar to that in the paratype of *M. gigas* (Mawson & Woodward 1907), with delicate radiating ridges that become slightly coarser and reticulated on the anterodorsal region of the operculum (overlying the point of attachment to the hyomandibula).

As in other *Mawsonia* spp., the external surface of the operculum has two distinct regions, with a smooth or slightly pitted area overlying the centre of growth, and a more distal region ornamented by radiating ridges. However, the relative extent of these two areas and the emphasis of the ornament are apparently quite variable in *Mawsonia*. For example, in specimens referred to *M. gigas* from Bahia, the external surface above the growth centre is commonly smooth and comparatively small; ridges arising near here are fine but become much more coarse as they radiate across the bone (Carvalho 1982, pl. 2). Woodward (1908) described the opercular ornament in *M. minor* as very fine radiating ridges, but this may simply represent an ontogenetic difference (Carvalho 1982). The opercular ridges are also fine and weak in the holotype of *M. brasiliensis*, suggesting that this individual was not fully grown. In that specimen, about one-third of the operculum surface behind the growth centre is pitted rather than ridged (Yabumoto 2002, fig. 3). In *M. cf. M. gigas* from the Santana Formation, the pitted area is confined to the dorsal margin of the operculum, and the

remainder of the operculum is covered in fine ridges (Maisey 1986, fig. 8). In *M. tegamensis*, the opercular ornament is comparatively coarse, with an extensive network of reticulated ridges extending from the growth center over approximately half the bone surface area, and with radiating ridges more distally (sometimes interconnected transversely; Wenz 1975, pl. 5, fig. 4). In *M. libyca*, the outer surface above the growth center is unpitted and smooth, but most of the bone is covered by pronounced ridges, which extend radially from the growth center toward the margins. In *Axelrodichthys*, the operculum is ornamented by fine, radiating ridges, but the area overlying the growth centre is smooth.

Palate. No complete palates were recovered, but numerous fragmentary quadrates, pterygoids and metapterygoids were identified. All the fragments are morphologically similar to an almost complete acid-prepared palate of *Mawsonia* cf. *M. gigas* described by Maisey (1986; fig. 12a, b).

Quadrate. Isolated quadrate condyles are among the most distinctive and abundant elements in the sample, because their characteristic biconvex articular surfaces are robust and therefore more readily-preserved. At least 21 quadrate condyles are present in our sample, divided more or less equally among left and right elements (Figs 12c, d, 13). Some of the left and right elements agree

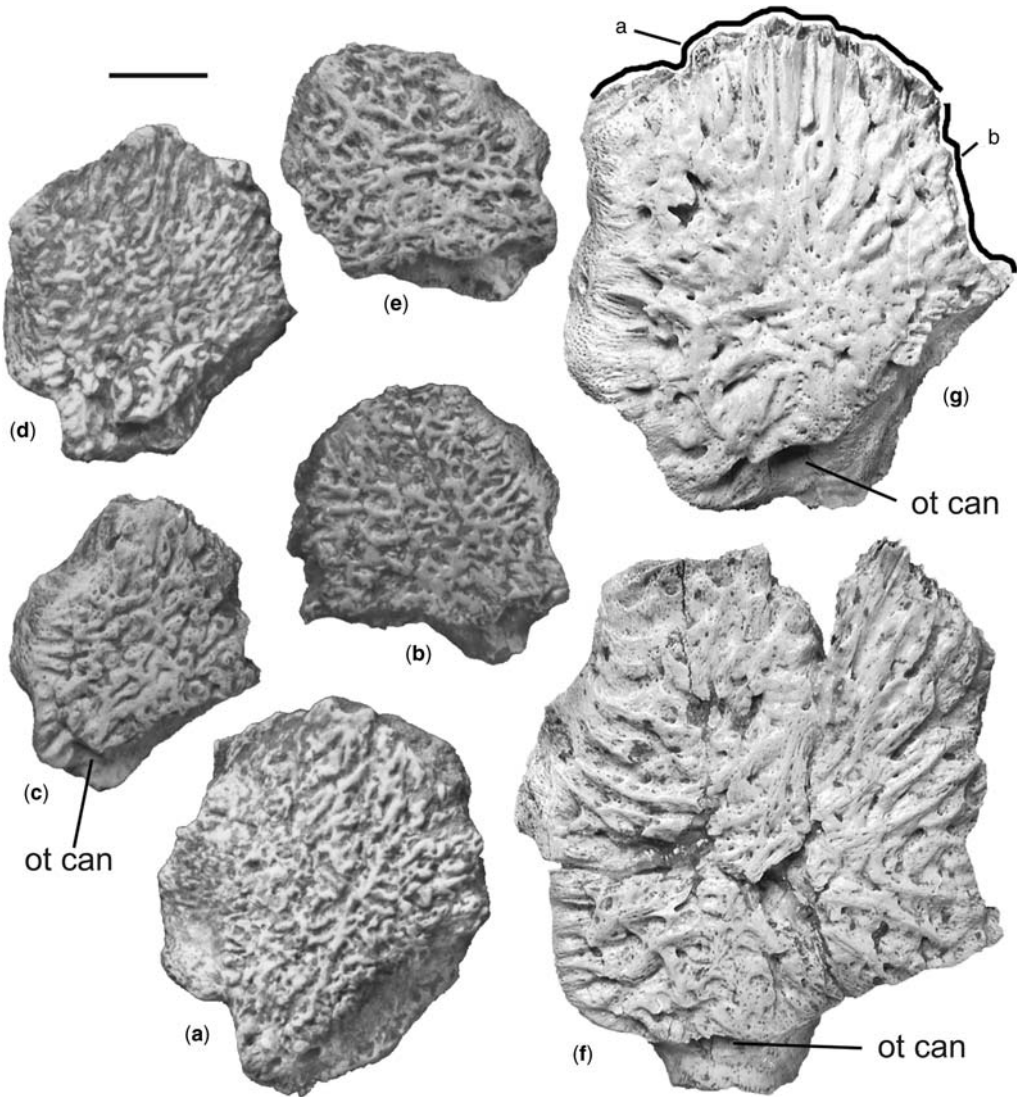


Fig. 9. *Mawsonia gigas* supratemporals from the Sanfranciscana Basin, anterior to top. (a, c–d, f–g) left supratemporals; (b, e) right supratemporal. (a) MCT 1385d-P; (b) MCT 1385h-P; (c) UFRJ-DG 357c-P; (d) MCT 1385c-P; (e) UFRJ-DG 357i-P; (f) UFRJ-DG 357a-P; (g) MCT 1385b-P. a = suture with posterior parietal; b = suture with extrascapular. Scale bar = 10 mm.

closely in size and may come from single individuals, but none could be reliably matched. The condylar heads display considerable size range, with a maximum anteroposterior length (measured from front to back across the biconvex surface) ranging from 11–31 mm. The minimum individual size represented by the Sanfranciscana Basin *Mawsonia* quadrates was estimated using the holotype of *M. brasiliensis* from the Santana Formation (an almost complete individual) as a guide. That specimen is *c.* 1435 mm overall length (Yabumoto

2002), and its quadrate condyle is *c.* 25 mm long. On that basis, our smallest specimen (MCT 1379h-P, condyle length 11 mm; Fig. 13g) represents an individual *c.* 630 mm overall length, which closely approximates the length of the type specimen of *M. minor* (said to be *c.* 600 mm long; Woodward 1908). Our largest examples (UFRJ-DG 353d-P, MCT 1379n-P; left and right elements both with a condyle length of 31 mm, possibly from a single individual; Fig. 13d, n) represent an overall body length of *c.* 1.8 m. In

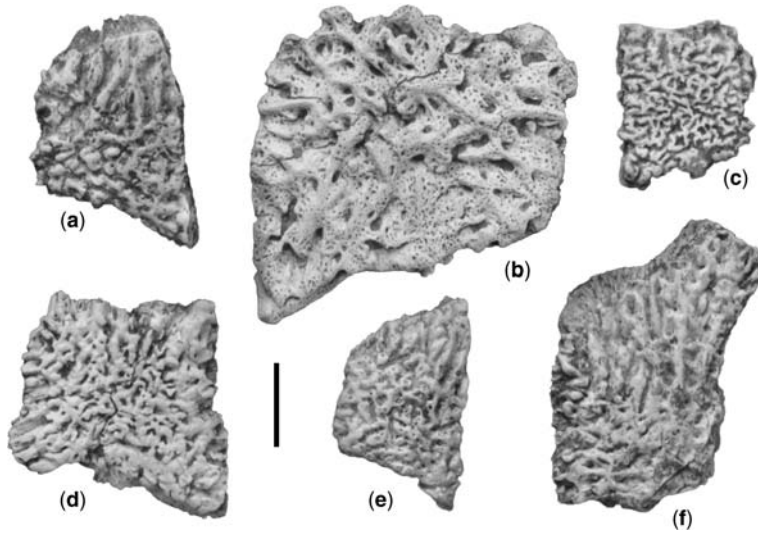


Fig. 10. *Mawsonia gigas* extrascapulars from the Sanfranciscana Basin, anterior to top. (a, d, e) left extrascapular; (b, c, f) right extrascapular. (a) MCT 1386d-P; (b) UFRJ-DG 358a-P; (c) UFRJ-DG 358b-P; (d) MCT 1386e-P; (e) MCT 1386a-P; (f) UFRJ-DG 358c-P. Scale bar = 10 mm.

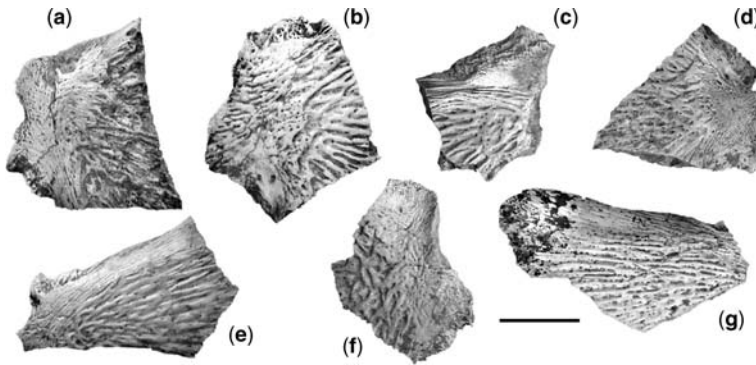


Fig. 11. *Mawsonia gigas* operculum fragments from the Sanfranciscana Basin, showing variation in the ornament pattern above the growth centre, dorsal to top. (a–b, e) left operculum, (c–d, f–g) right operculum. (a) MCT 1369b-P; (b) MCT 1369d-P; (c) UFRJ-DG344b-P; (d) MCT 1369e-P; (e) MCT 1369a-P; (f) UFRJ-DG 344a-P; (g) MCT 1369f-P. Scale bar = 10 mm.

comparison, the largest known *Mawsonia* quadrate from Brazil (DGM 1.048-P from the Neocomian of Bahia, with a condyle length of 110 mm) represents an individual with an estimated overall length of *c.* 6.3 m (20.8 ft), i.e. about ten times the length of the smallest Sanfranciscana Basin specimen and over three times the size of the largest one.

The ascending shaft of the quadrate has a deep cleft, with a rough, spongy sutural surface anteriorly, suggesting that its sutural contact with the pterygoid was very strong. The pterygoid extended

ventrally almost to the base of the quadrate, usually terminating on its mesial surface just above the anterior part of the condyle (e.g. Fig. 13j, t, u; indicated by an arrow), but occasionally extending just below the condylar margin anteriorly (e.g. Fig. 13d, n–p, s).

Metapterygoid. Twenty-two metapterygoids have been identified in our sample, although only the upper articular surface is preserved (Fig. 14). The mesial surface of the metapterygoid has a broad, strongly ridge sutural contact with the lateral face of the pterygoid below the articular

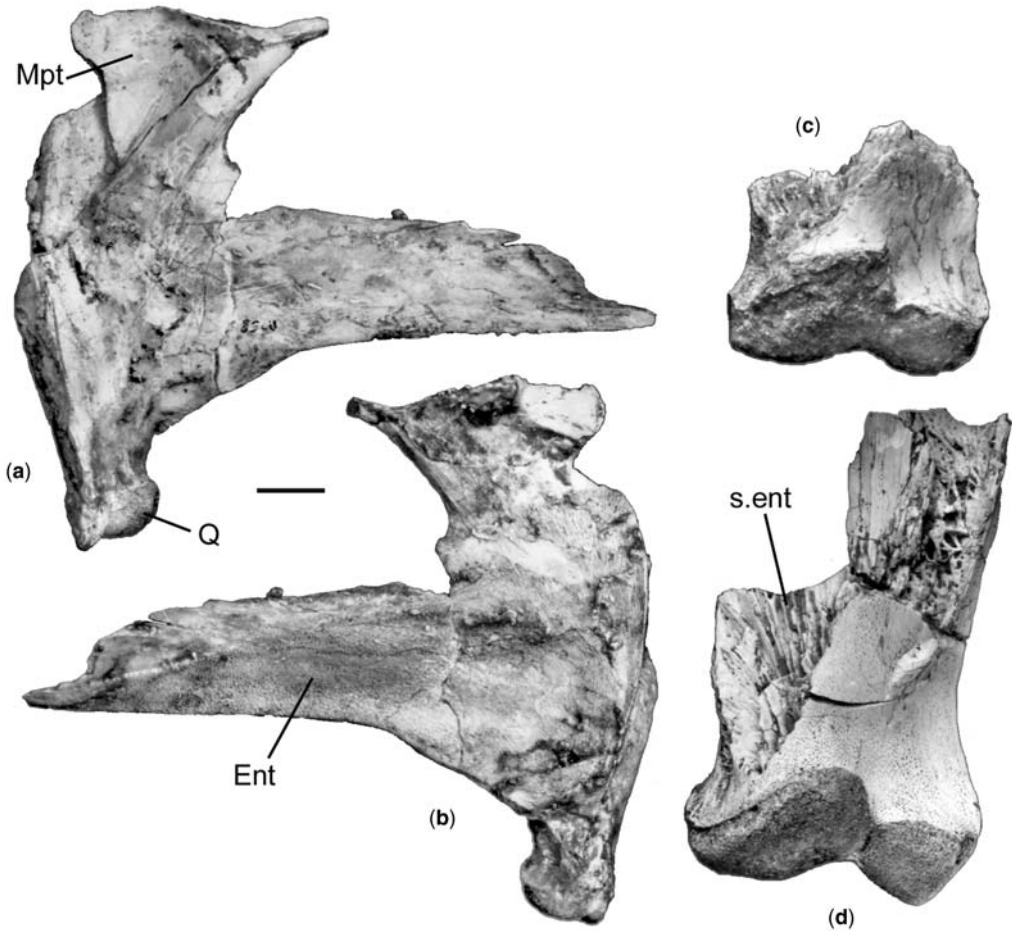


Fig. 12. (a–b) *Mawsonia* cf. *M. gigas* (AMNH 11758, Santana Formation, Araripe Basin) complete acid-prepared palatoquadrate; (a) lateral surface; (b) mesial surface. (c–d) *Mawsonia gigas* right quadrate condyles from Sanfranciscana Basin, both in mesial view. (a) MCT 1379a-P; (d) MCT 1379b-P. Scale bar = 10 mm.

region, providing a means for the left and right elements to be determined. As with the quadrates, almost equal numbers of left and right metapterygoids were collected, and the sample clearly represent a wide individual size range (although it is difficult to obtain precise dimensions because the anterior and posterior tips of the articular surfaces are frequently broken). In the smallest Sanfranciscana Basin metapterygoids (Fig. 14a, b), the preserved part of the articular surface is *c.* 11 mm long, but was probably 30% longer when complete (cf. the complete articular surface of the metapterygoid in *Mawsonia* cf. *M. gigas* from the Santana Formation is *c.* 25 mm long; Fig. 12a, b).

Pterygoid. The pterygoid elements did not reveal any characters of systematic interest and none is

illustrated here. Twenty-six tooth-covered fragments were recovered, but in most cases the margins are not preserved. However, one somewhat oval-shaped fragment resembles the posterior part of the pterygoid in *Mawsonia* cf. *M. gigas* from the Santana Formation, and other more slender pieces probably represent the pterygoid anterior process. The pterygoid teeth are small, densely spaced, and have a pebbly appearance; they are somewhat coarser than in *M. cf. M. gigas*, where the pterygoid teeth are more granular.

No ectopterygoids were identified in the sample. Four autopalatine fragments were identified but are too incomplete for illustration. The autopalatine is known only in *Mawsonia* cf. *M. gigas* (Maisey 1986, fig. 10), where it has a comparatively deep posterior part and a short, narrow dorsal process. The autopalatine in *Axelrodichthys araripensis* is

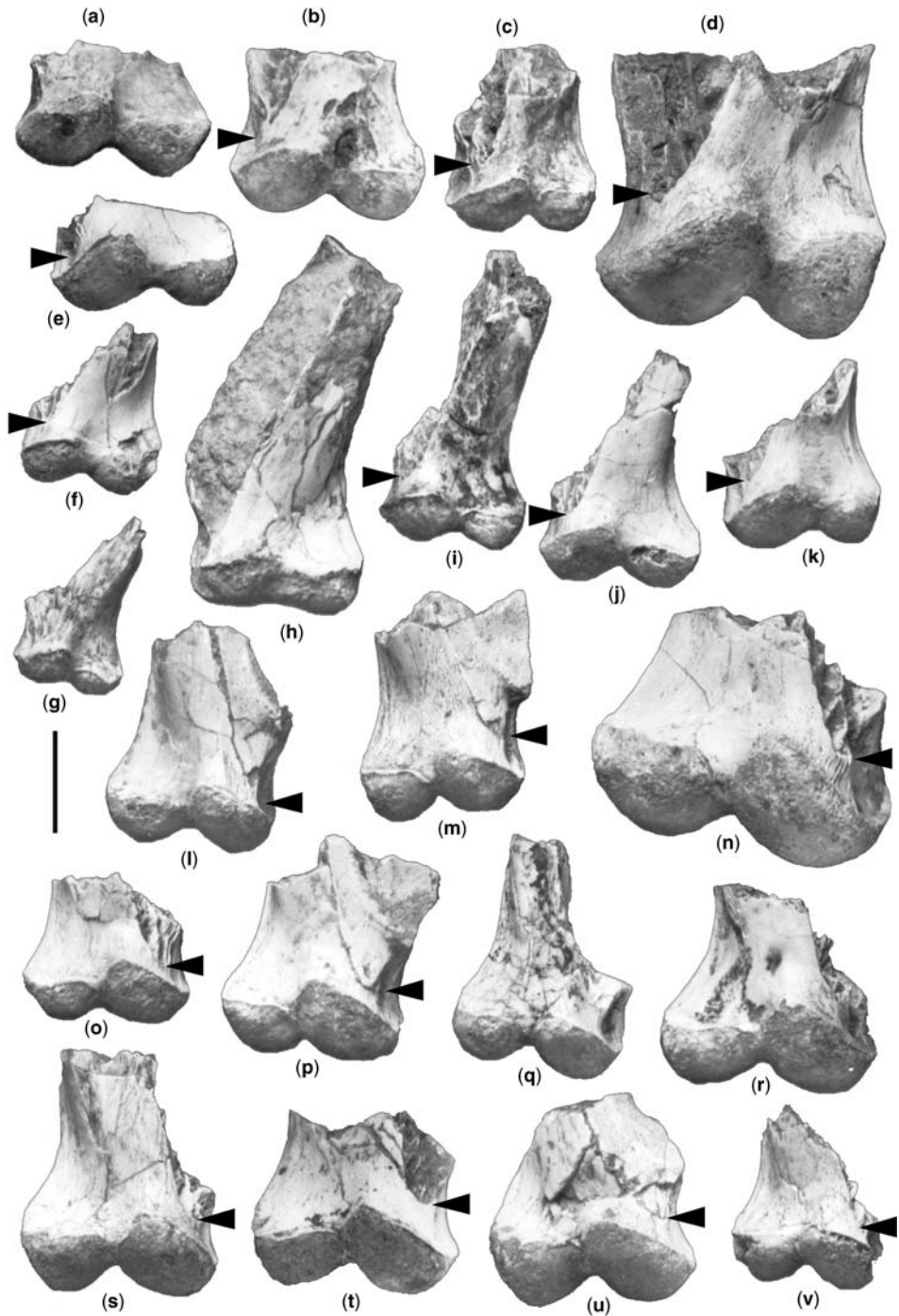


Fig. 13. *Mawsonia gigas* quadrate condyles from the Sanfranciscana Basin, all in mesial view. Arrowheads indicate lowest point of suture with entopterygoid. (a–k) right condyles; (a) UFRJ-DG 353b-P; (b) UFRJ-DG 353e-P; (c) MCT 1379e-P; (d) UFRJ-DG 353d-P; (e) UFRJ-DG 353c-P; (f) MCT 1379d-P; (g) MCT 1379h-P; (h) MCT 1379c-P; (i) MCT 1379f-P; (j) UFRJ-DG 353a-P; (k) MCT 1379g-P. (l–v) left condyles; (l) MCT 1379l-P; (m) MCT 1379k-P; (n) MCT 1379n-P; (o) UFRJ-DG 353f-P; (p) MCT 1379j-P; (q) UFRJ-DG 353j-P; (r) UFRJ-DG 353i-P; (s) MCT 1379m-P; (t) UFRJ-DG 353g-P; (u) UFRJ-DG 353k-P; (v) UFRJ-DG 353h-P. Scale bar = 10 mm.

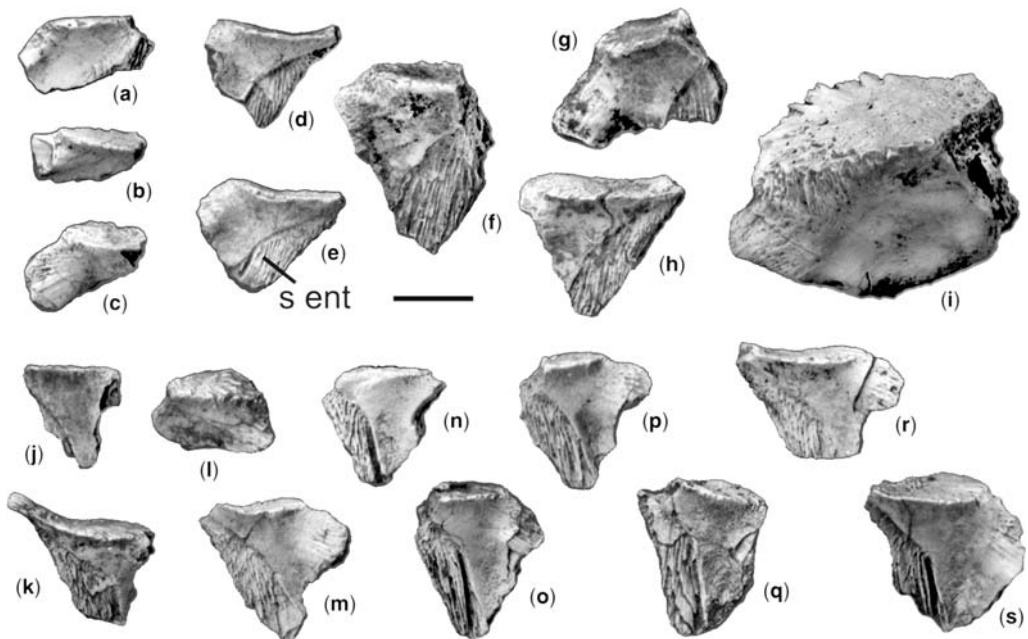


Fig. 14. *Mawsonia gigas* metapterygoids from the Sanfranciscana Basin, all in mesial view. (a–i) right metapterygoids; (a) UFRJ-DG 352a-P; (b) UFRJ-DG 352b-P; (c) UFRJ-DG 352c-P; (d) UFRJ-DG 352f-P; (e) UFRJ-DG 352d-P; (f) MCT 1378b-P; (g) UFRJ-DG 352e-P; (h) MCT 1378a-P; (i) MCT 1378c-P. (j–s) left metapterygoids; (j) UFRJ-DG 352g-P; (k) MCT 1378k-P; (l) UFRJ-DG 352h-P; (m) MCT 1378g-P; (n) UFRJ-DG 352i-P; (o) MCT 1378j-P; (p) UFRJ-DG 352j-P; (q) MCT 1378i-P; (r) MCT 1378h-P; (s) MCT 1378f-P. Scale bar = 10 mm.

more slender posteriorly, and its dorsal process is comparatively broad at the base (Maisey 1986, fig. 26).

Lower jaw. Numerous fragments of the lower jaw were recovered, including at least 42 incomplete angulars (evenly divided into left and right elements, although it was not possible to identify matched pairs) plus numerous isolated subtriangular dorsal processes. Parts of 10 splenials, 11 dentaries, 14 posterior coronoids and 10 articulars were also found.

The angulars of *Mawsonia* are easily identified by their heavy rugose ornament, with pronounced ridges arranged radially and longitudinally, sometimes forming a reticulate pattern with short connecting branches. The most complete angular is MCT 1370c-P (Fig. 15a, b). It is *c.* 95 mm long and has a maximum depth of 25 mm just anterior to its mid point (at the dorsal process). There is a distinct suture surface for the principal coronoid (a comparatively unusual feature among actinistians, possibly representing a synapomorphy of *Mawsonia* and *Axelrodichthys*; Forey 1998). A deep groove forms the overlap surface for the dentary at the anterior end of the angular. Sensory

canal pores arranged along the lateral surface separate an ornamented upper part from a smooth lower one. The gulars probably overlapped the smooth area as in *M. brasiliensis* (Yabumoto 2002, figs 3, 4). The mesial surface of the angular is concave, with a deep Meckelian fossa anteriorly and an adductor fossa farther posteriorly.

The centre of growth of the angular in *Mawsonia* is only evident on the mesial surface of the bone, within the contact surface for the pre-articular, and its position relative to the dorsal process of the angular is variable (Forey 1998, fig. 5.11). Although the angulars in our sample are fragmentary, the position of the centre of growth relative to the dorsal process was ascertained in several specimens (indicated by a dot in Fig. 15). In some specimens, the dorsal process lies far anteriorly to the centre of growth (e.g. MCT 1379h-P; Fig. 15c) as Forey (1998) showed in *M. gigas* (BMNH P.10360), but in other examples the apex is closer to the growth center (e.g. MCT 1370m-P; Fig. 15f), as in the angulars of *M. tegamensis* and *M. lavocati* (Tabaste 1963; Wenz 1981). The extent of ornament on the external surface of the angular also varies in the Sanfranciscana Basin specimens. In some, the rugose ornament extends

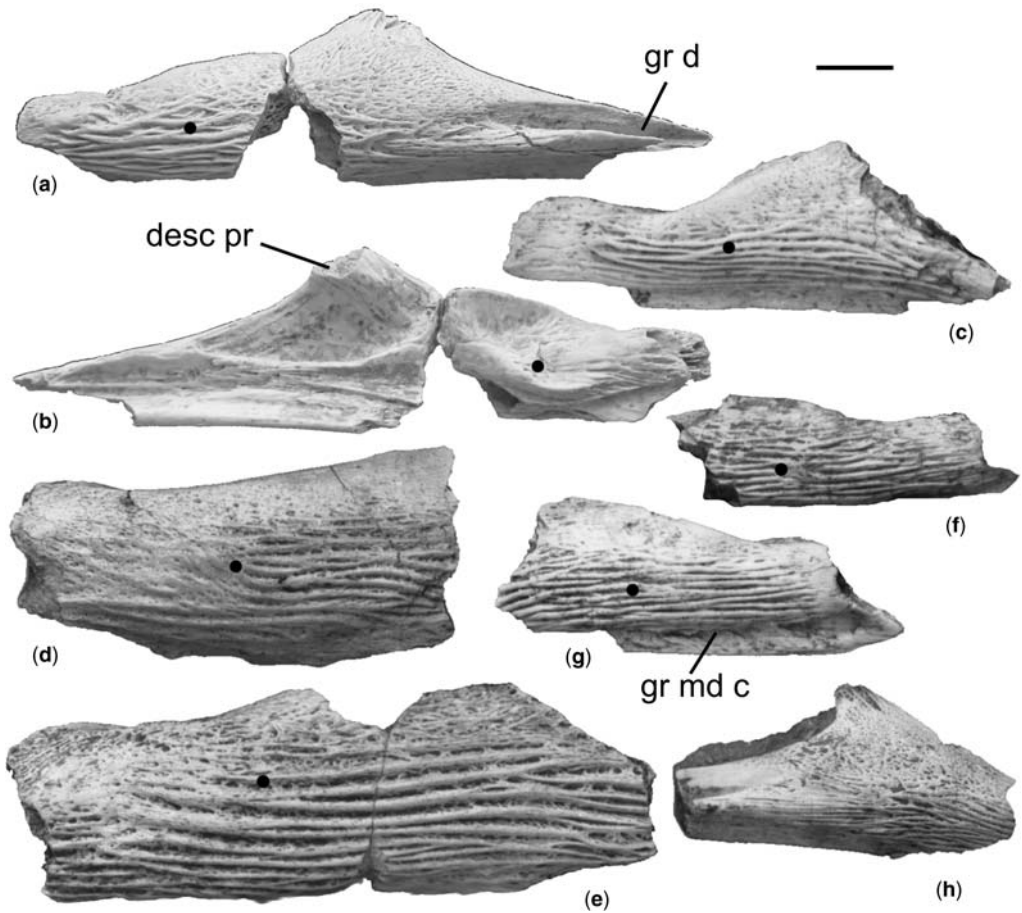


Fig. 15. *Mawsonia gigas* angulars from the Sanfranciscana Basin. (a–b) MCT 1370c-P, right angular; (a) lateral view; (b) mesial view. (c–e) fragments of right angular, anterior to right; (c) MCT 1370h-P; (d) MCT 1370a-P; (e) MCT 1370b-P. (f–h) fragments of left angular, anterior to left; (f) MCT 1370m-P; (g) UFRJ-DG 345m-P; (h) MCT 1370o-P. Position of growth centre (where determined) is indicated by a black dot. Scale bar = 10 mm.

posteriorly as far as the growth centre but rapidly fades above and behind it (e.g. Fig. 15c–e), whereas in others the ornament continues above and behind the growth centre (e.g. Fig. 15g). The dorsal margin of the angular also displays some variation in shape; in some specimens, it is gently inclined from the apex of the dorsal process to the adductor fossa, as in *M. gigas* and *M. lavocati* (e.g. Fig. 15c, f), but in others it is slightly concave and/or more steeply inclined anteriorly (e.g. Fig. 15h). The angulars included in the Sanfranciscana Basin material therefore display considerable variation in the location of the growth center, the extent and strength of the rugose ornament, and the shape of the dorsal process. Since the material is so fragmentary, however, the significance of this variation is uncertain.

Isolated principal coronoids recovered from the Sanfranciscana Basin (Fig. 16a–c) show a strong sutural surface for the dorsal process of the angular. The principal coronoid is very similar to those of *Mawsonia tegamensis* (Wenz 1975, pl. V, fig. 3) and *M. cf. M. gigas* (Fig. 16d).

Dentaries are mostly represented only by their anterior extremities and the anterior part of the adductor fossa (Fig. 16e–i). In both *Mawsonia brasiliensis* and *Axelrodichthys araripensis*, there is an anteroposteriorly elongated fenestra in the floor of the adductor fossa, formed below the suture between the dentary and pre-articular. The anterior part of this fenestra can be also seen in some of the Sanfranciscana Basin dentary fragments (e.g. UFRJ-DG 347e-P, Fig. 16h; MCT 1372f-P, Fig. 16i). In *M. brasiliensis*, the posterior

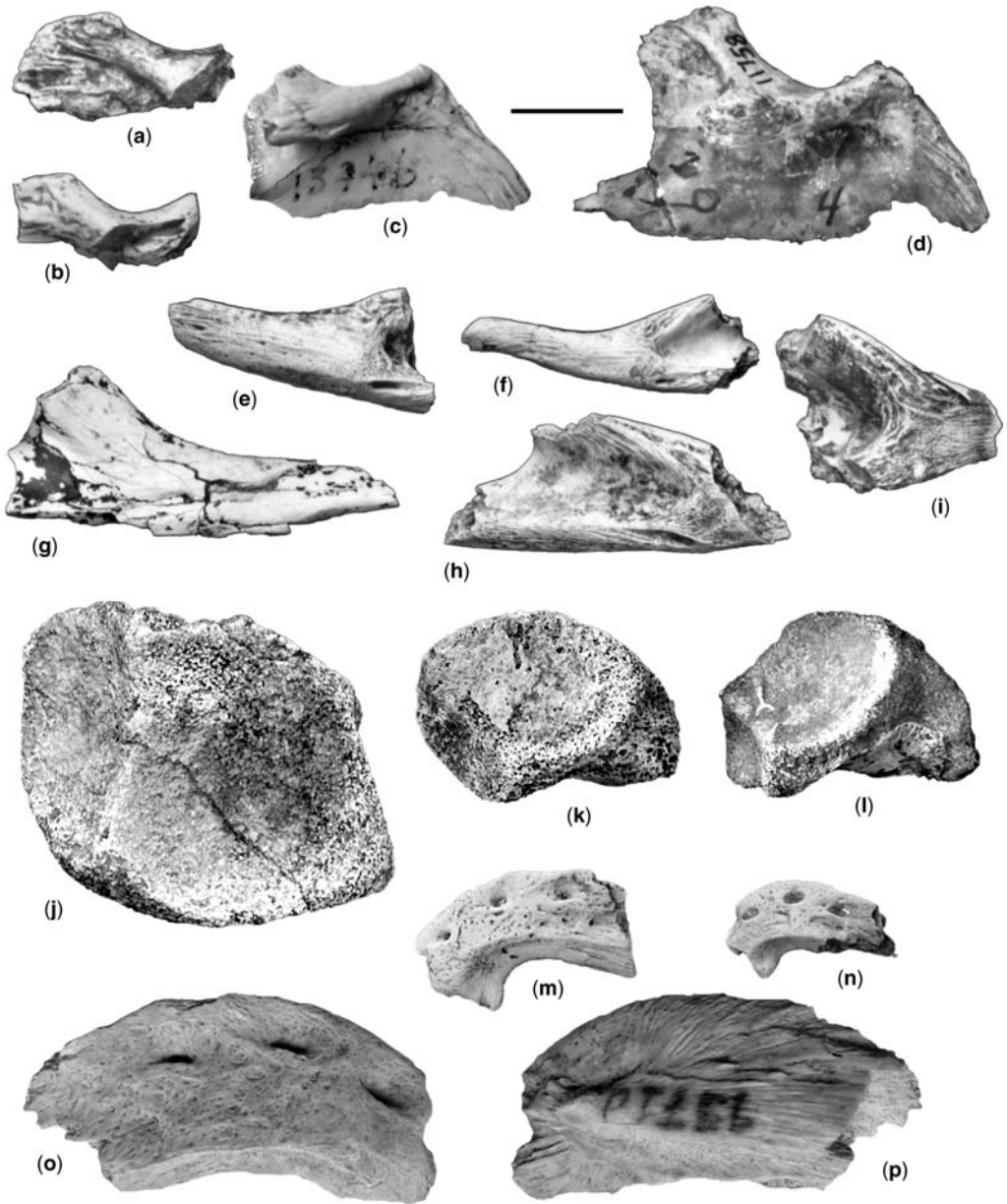


Fig. 16. (a–c) Right principal coronoids from the Sanfranciscana Basin, lateral view; (a) UFRJ-DG 349c-P; (b) MCT 1374d-P; (c) MCT 1374b-P. (d) right principal coronoid from *Mawsonia* cf. *M. gigas* (AMNH 11758, Santana Formation, Araripe Basin) for comparison, lateral view. (e–i) anterior part of dentary from the Sanfranciscana Basin, lateral view; (e–f) left dentary; (g–i) right dentary. (e) MCT 1372a-P; (f) UFRJ-DG 347b-P; (g) MCT 1372e-P; (h) UFRJ-DG 347e-P; (i) MCT 1372f-P. (j–l) isolated articulars from the Sanfranciscana Basin; (j) left articular MCT 1373b-P; (k) right articular MCT 1373a-P; (l) right articular UFRJ-DG 348a-P. (m–p) isolated splenials from the Sanfranciscana Basin; (m) left splenial MCT 1371b-P, lateral view; (n) left splenial MCT 1371c-P, lateral view; (o–p), right? splenial MCT 1371d-P (o = lateral view, p = medial view). Scale bar = 10 mm.

end of the fenestra is obscured by the angular in lateral view (Yabumoto 2002, fig. 3), whereas in *A. araripensis* it is completely exposed (Maisey 1986, fig. 26). The condition cannot be definitively determined in the Sanfranciscana Basin material, but the anterior part of the most complete angular (Fig. 15a, b) is considerably longer than in *A. araripensis* and probably overlapped the posterior part of the fenestra, as in *M. brasiliensis*. The anterior tip of the Sanfranciscana Basin dentaries are slender and elongated, again as in *M. brasiliensis* and unlike *A. araripensis*, in which the dentary is comparatively short and blunt anteriorly.

Several isolated articulars were recovered. These are large and composed of somewhat spongy cancellous bone (Fig. 16j–l). The articular has a characteristically biconcave facet for the articular surfaces of the quadrate condyle, as in actinistians generally.

The splenials have a series of sensory pores along their outer surface, but since all the examples are broken it is not possible to determine their original length or how many sensory pores they contained (only three are evident in many of the fragments; Fig. 16m–p). The splenial in other *Mawsonia* is poorly known except in the holotype of *M. brasiliensis*, where it is quite long and contains at least 5 or 6 sensory pores along its lower surface (Yabumoto 2002, fig. 4). By contrast, the splenial in *Axelrodichthys araripensis* is comparatively short and contains only 3 or 4 pores (Maisey 1986, fig. 26). The Sanfranciscana Basin splenials have a smooth narrow lower margin below the row of pores. This surface was probably not overlapped by the gulars, and in the holotype of *Mawsonia brasiliensis* the gulars only reach the posterior ends of the splenials (Yabumoto 2002, fig. 4). The gulars also just reach the splenials in *A. araripensis* (Maisey 1986, fig. 26).

Zygals and occipital bones. Zygale bones are highly distinctive lunate or semicircular chondral ossifications of the neurocranium that surround and support the unconstricted notochord in the otic region. In *Latimeria*, the zygal bones include a single anazygal dorsally, which articulates with the sphenoid condyles of the basisphenoid, and two catazygals ventrally (anterior and posterior); these occupy the basicranial fenestra and are entirely free from each other and other neurocranial bones (Millot & Anthony 1958; Forey 1998). Additional chondral bones of the otico-occipital region in *Latimeria* (largely surrounded by cartilage) include a narrow U-shaped basioccipital, small paired exoccipitals associated with the glosso-pharyngeal foramen and a small supraoccipital above the foramen magnum.

Zygal bones have rarely been described in fossil actinistians but are known in *Laugia*, *Macropoma*, *Rhabdoderma*, *Sassenia*, and *Whiteia* (Forey 1998). These bones are well developed in *Mawsonia* (they were referred to as ‘arcual bones’ in Maisey [1986, p. 7] but were not described). Zygal bones, basioccipitals and supraoccipitals are present in some acid-prepared neurocrania of *M. cf. M. gigas*; (Fig. 17a–d), which provided a basis for identifying isolated zygale and occipital bones from the Sanfranciscana Basin. Zygal bones have also been described in an undetermined mawsoniid from Morocco (Cavin & Forey 2004; MDE F36). The exoccipitals in *Mawsonia* and *Axelrodichthys* may not have ossified, and zygal bones apparently did not ossify in *Axelrodichthys*.

Anazygals from the Sanfranciscana Basin range in width from 10–16 mm (Fig. 17e–g), but no large ones were found. The bones are morphologically similar to the corresponding element in *Mawsonia cf. M. gigas* (Fig. 17c) and in MDE F36 from Morocco (Cavin & Forey 2004, figs 1, 2).

Anterior catazygals from the Sanfranciscana Basin display a far greater size range (Fig. 17i–n). Two are very large (approximately 55 mm wide and 20 mm high), and the smallest are *c.* 20 mm wide and 10 mm high. The anterior catazygal has a butterfly-shaped outline, with rounded margins showing a radial arrangement of the underlying spongy bone. They closely resemble the anterior catazygal in *Mawsonia cf. M. gigas* (Fig. 17b). Cavin & Forey (2004) did not find an anterior catazygal in MDE F36, and the bone has not been described in other mawsoniids.

The posterior catazygal is shaped like an orange segment, and complete specimens range in width between 16–25 mm, and the largest broken specimen had an estimated original width of approximately 41 mm (Fig. 17o–t). The bone is notably wider than long, resembling the posterior catazygal in *Mawsonia cf. M. gigas* (Fig. 17a). By contrast, the posterior catazygal in MDE F36 from Morocco is slightly longer than wide, with a trapezoidal outline. The posterior catazygal is unknown in other mawsoniids.

Only two incomplete basioccipitals were found, the largest of which is approximately 25 mm wide and 30 mm deep (Fig. 17h). These resemble the basioccipital in *Mawsonia cf. M. gigas* from Ararape (Fig. 17d) in having an extensive area of spongy bone that extends below the concave finished surface. The basioccipital in MDE F36 from Morocco is incompletely-preserved with no spongy bone below its concave surface (Cavin & Forey 2004, figs 1, 2).

A single broken supraoccipital fragment was also collected, but has not been illustrated here. The supraoccipital is known in *Mawsonia*

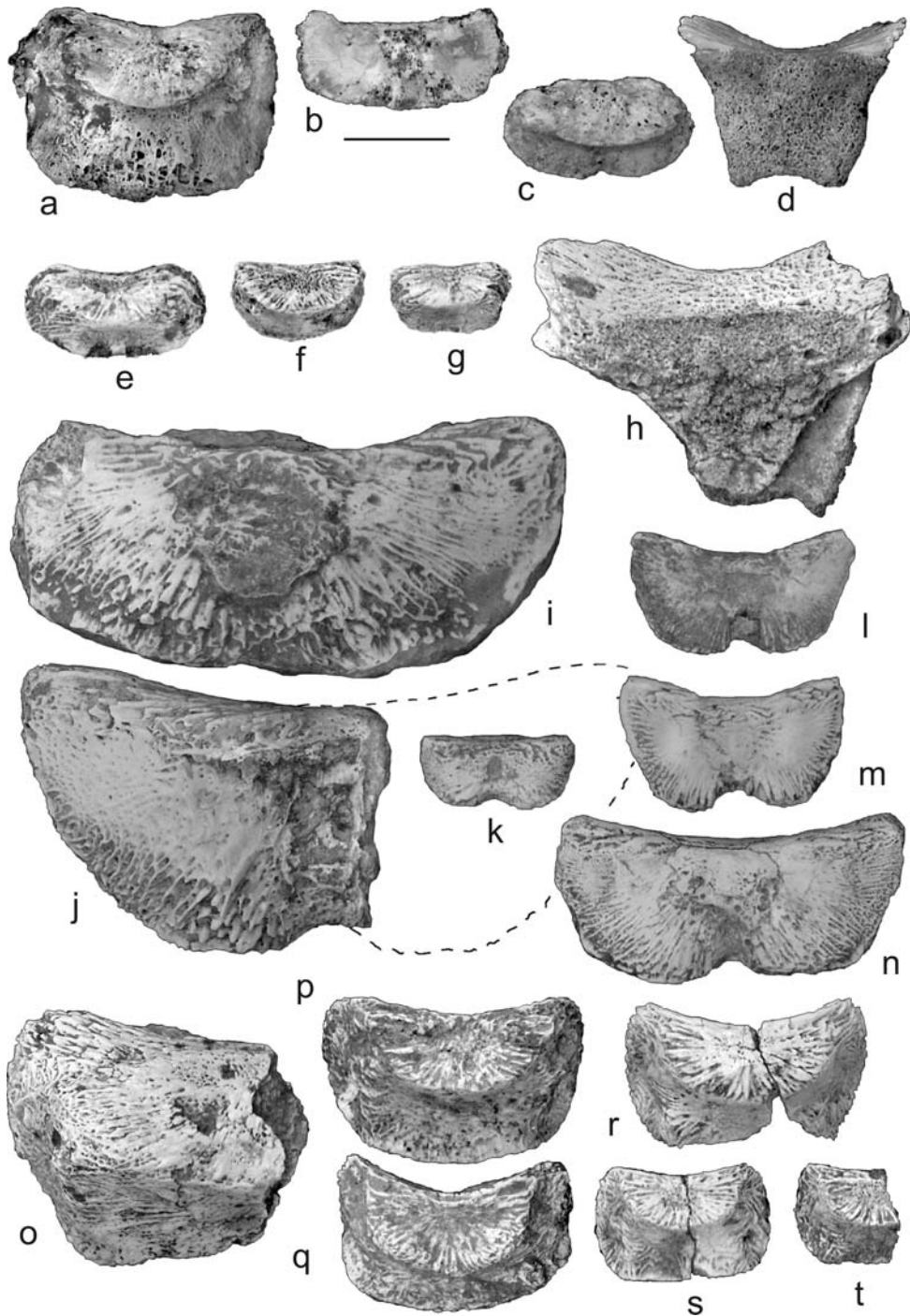


Fig. 17. *Mawsonia* zygals and occipital bones. (a–d) acid-prepared zygals and basioccipital from *Mawsonia* cf. *M. gigas* (AMNH 11758, Santana Formation, Araripe Basin); (a) posterior catazygal; (b) anterior catazygal; (c) anazygal; (d) basioccipital. (e–t) Sanfranciscana Basin specimens. (e–g) anazygals: (e) MCT 1383a-P; (f) MCT 1383b-P; (g) UFRJ-DG 355a-P. (h) basioccipital UFRJ-DG 362-P. (i–n) anterior catazygals: (i) UFRJ-DG 355c-P; (j) UFRJ-DG 355d-P; (k) UFRJ-DG 355e-P; (l) UFRJ-DG 355f-P; (m) MCT 1383d-P; (n) MCT 1383c-P. (o–t) posterior catazygals: (o) UFRJ-DG 355g-P; (p) UFRJ-DG 355h-P; (q) UFRJ-DG 355j-P; (r) UFRJ-DG 355j-P; (s) MCT 1383g-P; (t) MCT 1383h-P. Scale bar = 10 mm.

cf. *M. gigas* from Araripe (Maisey 1986, fig. 6), *M. tegamensis* (Wenz 1975, pl. 1, fig. 1b), and MDE F36 from Morocco (Cavin & Forey 2004). In *M. cf. M. gigas*, the basioccipital is not sutured to the postparietal shield; instead, the dorsal surface of the supraoccipital is flat and was separated from the overlying extrascapulars by a narrow space. The supraoccipital has a deep inverted V-shape in posterior view, with a smooth finished ventral surface. Only the dorsal part of the supraoccipital can be seen in the specimen of *M. tegamensis* figured by Wenz (1975 pl. 1), but it seems to agree with that of *M. cf. M. gigas* in shape and its position relative to the postparietal shield. The supraoccipital in the Mawsoniidae indet. from Morocco has not been illustrated, but from the description (Cavin & Forey 2004, p. 496) it seems similar to that in *M. cf. M. gigas*. The supraoccipital has not been described in

Axelrodichthys araripensis but is exposed in several acid prepared specimens, where it resembles that of *M. cf. M. gigas*.

Postcranial elements. A few postcranial bones were identified including visceral arch elements, some of which are parallel-sided and others broadly expanded, plus scapulocoracoids and fin axial mesomeres (probably from the pectoral fin). None of these bones has been described in other *Mawsonia* material, but comparison with *Mawsonia cf. M. gigas* from the Santana Formation suggests that the parallel-sided visceral arch fragments may be ceratobranchials, and the more expanded ones may be ceratohyals (Fig. 18a–e). The scapulocoracoids and fin mesomeres closely resemble those described in *Latimeria* (Fig. 18f–k).

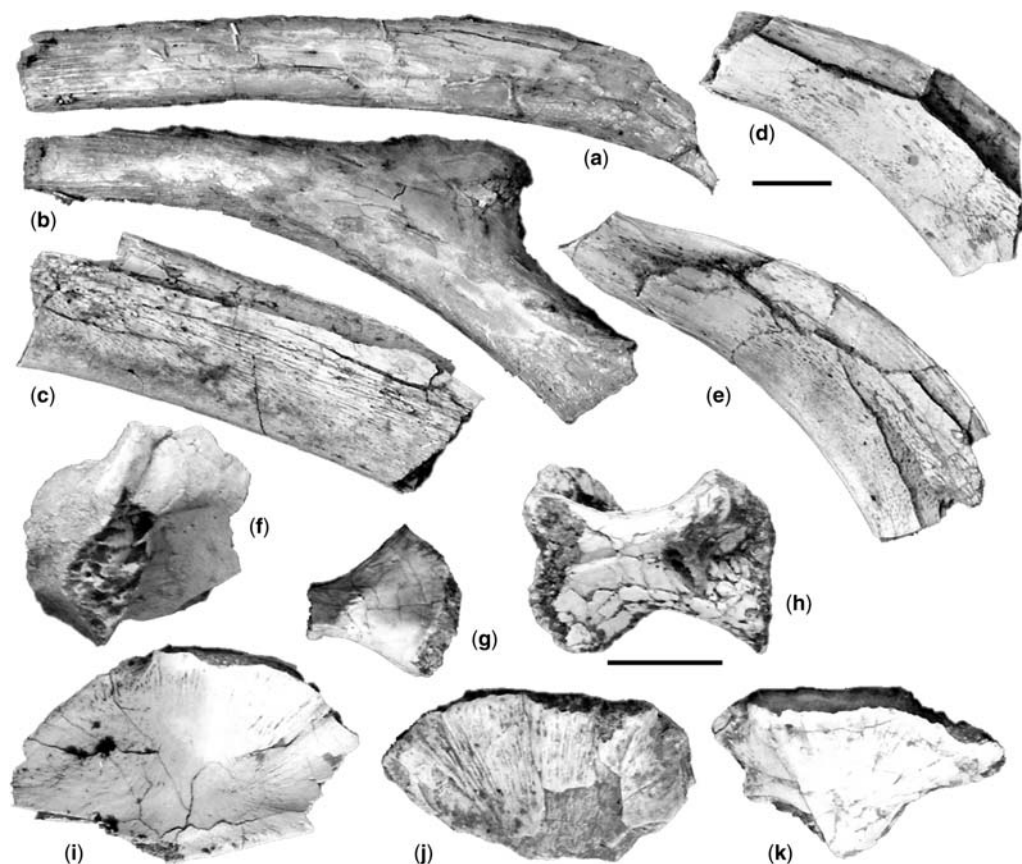


Fig. 18. (a–e) *Mawsonia* visceral arch elements; (a–b) from *Mawsonia cf. M. gigas* (AMNH 11758, Santana Formation, Araripe Basin); (a) ceratobranchial; (b) ceratohyal. (c–e) from Sanfranciscana Basin; (c) ?ceratobranchial MCT 1387a-P; (d) ?ceratohyal UFRJ-DG 359b-P; (e) ?ceratohyal UFRJ-DG 359a-P. (f–h) scapulocoracoids; (f) UFRJ-DG 361b-P; (g) UFRJ-DG 361a-P; (h) UFRJ-DG 359d-P. (i–k), axial mesomeres; (i) MCT 1392a-P; (j) MCT 1392b-P; (k) MCT 1392c-P. Scale bars = 10 mm (upper bar for a–e, lower bar for remainder).

Discussion

Occurrences of *Mawsonia*

Since *Mawsonia* was first discovered in Neocomian strata of the Recôncavo Basin, Bahia (Mawson & Woodward 1907) there have been numerous other findings in Brazil (Figs 19, 20). Several articulated specimens of *Mawsonia* (including postcranial skeletons) were collected on Itaparica Island, in the Baía de Todos Santos (W of Bahia) and were referred to the type species (Carvalho 1982). All the Recôncavo Basin material comes from the Neocomian Candeias or Maracangalha formations (Rio da Serra local Brazilian Stage; Caixeta *et al.* 1994). *Mawsonia* is also known from the Tucano Basin of Bahia (Carvalho 2002) and from the Morro do Barro Formation of the Almada Basin, near the Municipality of Ilhéus, Bahia (Carvalho 1982; Netto *et al.* 1994), including the holotype of *M. minor* (Woodward 1908). *Mawsonia* is also known from the Araripe Basin of Ceará, including articulated specimens from the Santana Formation (Albian; Campos & Wenz 1982; Maisey 1986; Yabumoto 2002) and the older and very fragmentary remains from the Brejo Santo Formation (Berriasian; Brito *et al.* 1994; Malabarba & Garcia 2000). Isolated *Mawsonia* bones are also

known from the Icó Formation, Iguatu Basin of Ceará (Neocomian), which was deposited in a continental environment (Rio da Serra local Brazilian Stage; Ponte Filho 1994); from the Itapecuru Formation (an Albian continental sequence in the Grajaú Basin of Maranhão; Dutra & Malabarba 2001); from the Alcântara Formation (a Cenomanian continental sequence on Cajual Island, in the São Luís Basin of Maranhão; Carvalho 2002); and from the Areado Group (a continental Berriasian sequence) in the Sanfranciscana Basin of Minas Gerais (described herein). In addition, a caudal fin referred to *Mawsonia* is known from the Barremian Morro do Chaves Member of the Coqueiro Seco Formation in the Alagoas Basin (Maffizzoni 1998). Thus, Brazilian records of *Mawsonia* range in age from the late Hauterivian–early Barremian to the Cenomanian, spanning all but the earliest stages of active rifting and crustal extension related to the final tectonic separation of northern South America from Africa (including the establishment of a permanent equatorial seaway between the South Atlantic and Caribbean Tethys during the Aptian; Maisey 2000).

In Africa, *Mawsonia* was first reported from the Baharija Formation (Cenomanian) of Egypt (*M. libyca*; Weiler 1935). Although the original material was destroyed during the Second World



Fig. 19. Occurrences of *Mawsonia* in the Cretaceous of Brazil. Base map modified from Schobbenhaus *et al.* 1984.

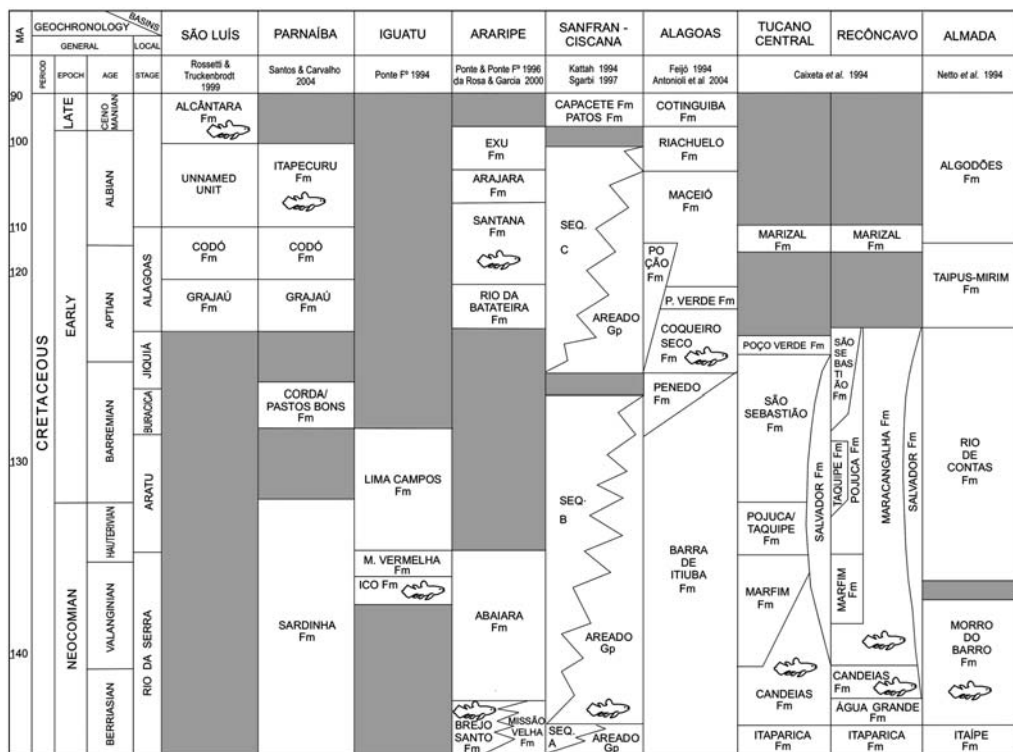


Fig. 20. Stratigraphic occurrences of *Mawsonia* in the Cretaceous of Brazil (indicated by small coelacanth outline).

War, recent excavations in Egypt have produced new material that is under study elsewhere (Grandstaff 2002). *Mawsonia* was subsequently described from the ?Neocomian of Ubangi, Democratic Republic of Congo (*M. ubangiensis* Casier 1961); from Niger, including Upper Neocomian–Barremian remains near In Gall, Aptian remains from the Tegama Series of Gadoufaoua (*M. tegamensis* Wenz 1975), and Albian remains from In Abangarit (Wenz 1981). Angular bones referred to *Mawsonia lavocati* were documented from the Albian of Gara Samani, Algeria (Wenz 1981). The holotype of *M. lavocati* is an isolated angular from the Kem Kem beds of Gara Sba, Morocco, but several partial skulls and dissociated bones have also been referred to this species (Tabaste 1963; Wenz 1981; Cavin & Forey 2004; Yabumoto & Uyeno 2005). The *Mawsonia*-bearing part of the Kem Kem sequence contains elasmobranchs that are considered to be Cenomanian in age (Serenó *et al.* 1996). New mawsoniid remains from the Kem Kem beds described by Cavin & Forey (2004) include a postparietal shield that includes paired and median extrascapulars (as in *Axelrodichthys*) and an ethmosphenoid region identified as cf. *Mawsonia lavocati*, but whose proportions

and concave profile in lateral view seem more in agreement with *Axelrodichthys* than *Mawsonia*. African records of *Mawsonia* are therefore broadly identical in age to those from Brazil, extending from the Neocomian–Barremian to the Cenomanian. The temporal range of *Mawsonia* thus encompasses much of the tectonic episode during which Brazil finally separated from NW Africa, and some of its occurrences on both sides of the Atlantic lie within regions that were tectonically active at that time (Maisey 2000).

Axelrodichthys is morphologically similar to *Mawsonia* (Maisey 1986), and these two forms are closely-related (Forey 1998). Both occur in the Santana Formation (Albian) of Brazil, and *Axelrodichthys* has also been found in the underlying Crato Formation (?Aptian; Brito & Martill 1999). We can also report a specimen of *A. araripensis* from the Albian Itapecuru Formation of the Grajau Basin (Maranhão State). Gottfried *et al.* (2004) referred an isolated median extrascapular from the late Cretaceous (?Santonian/Coniacian) of Madagascar to *Axelrodichthys*, as well as the posterior part of a mawsoniid postparietal shield (also with a median extrascapular) from the Aptian of Ingal, Niger. A late Jurassic (Kimmeridgian) age

has been suggested for the Lualaba Series in which *Lualabaea lerichei* occurs (Forey 1998), but according to Sgarbi (2000) these deposits are of early Cretaceous age. The Lualaba Series has been correlated with the Areado Group of the Sanfranciscana Basin and the sequences share important sedimentological similarities (Chaves 1991). *Axelrodichthys* and *Lualabaea* may therefore be much closer in age than was previously thought and they are very similar morphologically. Thus, Cretaceous mawsoniids with a median extrascapular occur both in Brazil and Africa, and their stratigraphic ranges are congruent but less evenly balanced than *Mawsonia*; in Brazil the occurrences are restricted to the Aptian and Albian, whereas they are much wider in Africa (possibly beginning in the late Jurassic, but at least from the Early Cretaceous to the Santonian or Coniacian). The Brazilian occurrences are more or less contemporaneous with the development of a permanent equatorial seaway between Tethys and the South Atlantic, whereas the African records begin earlier (spanning the rift/crustal extension episodes) and end later (the material from Madagascar represents the last known occurrence of mawsoniids; Gottfried *et al.* 2004).

Morphological comparisons. From Brazil, the parietonal shield is known in *Mawsonia gigas*, *M. cf. M. gigas*, *M. brasiliensis* and *Axelrodichthys araripensis* from Brazil, and from Africa it is known in *M. tegamensis*, specimens referred to *M. lavocati* (Cavin & Forey 2004; Yabumoto & Uyeno 2005) and *Lualabaea lerichei* (Saint-Seine 1955). Only the posterior parietal has been described in *M. libyca*, and the parietonal shield is unknown in *M. ubangiensis*. The holotype of *Mawsonia gigas* includes an incomplete posterior parietal that has a prominent bevelled margin and is ornamented with longitudinal ridges (Mawson & Woodward 1907).

Unfortunately, the parietals are not known in *M. gigas* from Recôncavo (Carvalho 1982), but specimens referred to *M. gigas* from the Tucano and Grajaú Basins have posterior parietals with the same ornamentation pattern as the holotype (Carvalho 2002). Parietal ornament in *Mawsonia libyca* consists of longitudinal ridges similar to those in *M. gigas* (Weiler 1935). In *M. cf. M. gigas* from the Santana Formation, the parietal situated more posteriorly is larger than the anterior one and has a wavy posterior margin (Maisey 1986). By contrast, in *M. tegamensis* the anterior and posterior parietals are more equal in length (Wenz 1975).

In *Mawsonia tegamensis* (Wenz 1975, fig. 1), the posterior parietals make contact with supraorbitals 1–3 (with 1 posteriormost), and the anterior

parietals contact supraorbitals 3–5 (the anterior-most of which contacts the posterior nasal and could be identified as a tectal, but for the purposes of this discussion the distinction is moot). In the parietonal shield of *Mawsonia cf. M. gigas* described by Maisey (1986, fig. 1C), the posterior parietals also contact supraorbitals 1–3, and the anterior parietals contact supraorbitals 3–5. In the holotype of *M. brasiliensis*, the right posterior parietal meets supraorbitals 1–4 and the anterior parietal meets supraorbitals 4–6 (the arrangement on the left side is unknown; Yabumoto 2002, fig. 2). In an incomplete parietonal shield referred to *M. lavocati* by Cavin & Forey (2004, fig. 5), each posterior parietal again contacts supraorbitals 1–3. In another specimen referred to *M. lavocati* (Yabumoto & Uyeno 2005), the right posterior parietal contacts supraorbitals 1–3, but the left one only meets supraorbitals 1 and 2. Collectively, these observations suggest that the posterior parietal in *Mawsonia* usually contacts supraorbitals 1–3, but because of individual variation, 2–4 supraorbitals may meet the posterior parietal. In *Axelrodichthys araripensis*, however, the posterior parietal typically meets only supraorbitals 1 and 2, and the anterior parietal meets supraorbitals 2–4; i.e. the number of supraorbitals arrayed along the margins of the parietals is clearly less than in *Mawsonia*. The number and arrangement of supraorbitals is unknown in *Lualabaea lerichei*.

In *Mawsonia cf. M. gigas* and the holotype of *M. brasiliensis*, the parietonal shield tapers anteriorly to a point approximately mid-way along the anterior parietal, then becomes almost parallel-sided (Maisey 1986, fig. 1C; Yabumoto 2002, fig. 2). However, in *M. tegamensis* and specimens referred to *M. lavocati*, the posterior part of the parietonal shield is parallel-sided (Wenz 1975, fig. 1; Cavin & Forey 2004, fig. 5; Yabumoto & Uyeno 2005). The parietonal shield in *Axelrodichthys araripensis* is also parallel-sided posteriorly and tapered anteriorly (Maisey 1986, figs 17, 18). In *M. lavocati*, the parietonal shield attains its maximum width at the level of the anterior parietal, where the supraorbitals are slightly expanded laterally. By contrast, in *M. cf. M. gigas* and *M. brasiliensis*, the parietonal shield is widest posteriorly. The postparietal shield in *Lualabaea lerichei* also seems to be widest posteriorly (Saint-Seine 1955, pl. III).

The posterior margins of supraorbital 1 and the posterior parietal are aligned transversely in *Mawsonia tegamensis*, *M. cf. M. gigas* and the holotype of *M. brasiliensis*, forming an almost straight posterior border to the parietonal shield. In specimens referred to *M. lavocati*, however, the posterior border of the shield is notched between the posterior parietal and supraorbital 1, and the

posterior parietals are convex posteriorly (e.g. Cavin & Forey 2004, fig. 5A). A similar notch is present between the postparietal and supraorbital 1 in *Axelrodichthys araripensis* (Maisey 1986, fig. 18A). The arrangement is uncertain in *Lualabaea lerichei*.

The profile of the parietonasal shield in lateral view displays some variation in mawsoniids, although it has rarely been observed and can be difficult or even impossible to determine in specimens that have been crushed. In *Mawsonia* cf. *M. gigas* the profile is slightly convex (Maisey 1986, fig. 1B), and the holotype of *M. brasiliensis* has an almost straight profile dorsally (Yabumoto 2002, fig. 3). By contrast, the profile in specimens referred to *M. lavocati* is markedly concave, as in *Axelrodichthys araripensis* and many other actinistians (Wenz 1975, fig. 2; Cavin & Forey 2004, fig. 6A; Yabumoto & Uyeno 2005).

In *Mawsonia gigas* from Bahia, the parasphenoid is long and slender, and the posterior portion of its dorsal face is excavated by a longitudinal canal (Mawson & Woodward 1907; Carvalho 1982), but its teeth are unknown. The dorsal surface of the parasphenoid in *M. cf. M. gigas* forms a deep V-shaped gutter posteriorly, above the posterior part of the toothed area (AMNH 12215). The anterior part of the parasphenoid has not been described in *M. cf. M. gigas* and it is unknown whether a dorsal median keel is present here or in *M. brasiliensis*. A keel extends almost to the posterior end of the toothed area in a parasphenoid attributed to *M. lavocati* (Wenz 1981, pl. 1B). A keel is also present in a parasphenoid fragment of *M. libyca* (Weiler 1935). In *M. libyca*, the parasphenoid has numerous small teeth, a dorsal median keel, and lateral expansions (Weiler 1935; Wenz 1981). In *Mawsonia lavocati* and *M. tegamensis*, the parasphenoid is slightly constricted along its length, but lacks lateral expansions on the toothed area. In *Axelrodichthys araripensis*, the parasphenoid has a median dorsal keel only anteriorly. Farther posteriorly, its dorsal surface forms a broad gutter similar to that shown by Wenz (1981, fig. 1, section d) in *M. lavocati*, rather than a deep V-shaped gutter as in *M. cf. M. gigas*.

The postparietal shield is known in several mawsoniids from Africa and Brazil. Casier (1961) provided a detailed discussion of postparietal morphology in *Mawsonia* and considered that several features were systematically important, including: the position of the anterior foramen of the otic lateral line canal relative to the anterior apophysis; the position and size of the anterior apophysis; the number and extent of anterior processes formed on the anterior margin above the apophysis; and the curvature and ornament of the entire postparietal shield. According to Casier (1961), the

foramen for the otic canal is located on the lateral margin of the postparietal in both *M. ubangiensis* and *M. gigas*, but the opening lies much farther from the anterior apophysis in *M. gigas*. Specimens referred to *M. lavocati* and *M. libyca*, the apophysis is apparently located in the middle of the anterior margin (Weiler 1935; Tabaste 1963; Wenz 1981), but it is situated laterally in the undetermined Moroccan mawsoniid described by Cavin & Forey (2004, fig. 3). Yabumoto (2002) claimed that *M. brasiliensis* and *M. gigas* differ in the position of the otic canal foramen relative to the anterior apophysis. Furthermore, according to Wenz (1975), this foramen lies much closer to the apophysis in *M. aff. tegamensis* than in either *M. gigas* or *M. ubangiensis*. Casier (1961) also distinguished *M. gigas* from *M. ubangiensis* on the basis of the number of anterior processes along the anterior margin of the postparietal (two in *M. gigas*, one in *M. ubangiensis*), and by supposed differences in the ornamentation and convexity of the postparietal shield. Wenz (1981) found a bony bridge between the anterior apophysis and descending process of the postparietal in *M. tegamensis* but not in *M. lavocati*, and suggested that this may represent a distinguishing feature.

These supposed differences are based on observations of very few specimens, whereas the Sanfranciscana Basin material represents a very large sample of individuals and reveals considerable variation, especially in postparietal morphology. Of those differences identified by Casier (1961) in *M. gigas* and *M. ubangiensis*, the position of the anterior foramen for the otic lateral line canal relative to the anterior apophysis varies within the Sanfranciscana Basin postparietals, and the location, size and number of the anterior apophyses along the anterior margin of the ornamented region is also variable (Figs 5–7). Additionally, the extent of the ornamented region on the postparietal anteriorly is highly variable, extending above the base of the anterior apophysis in some specimens but failing to reach it in others. Presence of a bony bridge (*sensu* Wenz 1981) between the anterior apophysis and descending process is variable in the Sanfranciscana Basin *Mawsonia* postparietals, as well as in *M. gigas* from Bahia (Forey 1998).

Certain features of the postparietal shield may nevertheless have systematic and phylogenetic importance. For example, the parietal shield is somewhat broad for its length in *M. tegamensis*, but is comparatively narrower in other mawsoniids. The presence and extent of the median branch of the otic lateral line canal in mawsoniids seems to be variable, although no clear distribution pattern is discernible and we suspect that Casier's (1961) reconstruction of the canal in *M. gigas* (and

perhaps in *M. ubangiensis*) is inaccurate in not depicting a median branch. The anterior apophyses are located closer to the midline in *A. araripensis* than in most fossils referred to *Mawsonia* (except for *M. libyca*, where they seem to be comparatively close together; Weiler 1935; Cavin & Forey 2004, fig. 4C). The anterior apophyses have not been observed in *Lualabaea lerichei* but, judging from the shape of its postparietal anterior border, they were probably positioned as close to the midline as in *A. araripensis*. The anterior apophyses are widely separated in the undetermined mawsoniid MDE F36 from Morocco described by Cavin & Forey (2004).

The supratemporals in MDE F36 (Cavin & Forey 2004, fig. 3) have more divergent supratemporal lateral margins than in *Axelrodichthys araripensis*, *M. gigas* and *M. tegamensis*, although the supratemporal margins are also divergent in *L. lerichei*. Isolated supratemporals from the Sanfranciscana Basin are not appreciably wider posteriorly than anteriorly, suggesting that the lateral margins of the postparietal shield were no more divergent than in *M. gigas* or *M. tegamensis*. The shape of the supratemporal in *Lualabaea lerichei* is uncertain as its margin seems to be overlain by the operculum in the holotype (Saint-Seine 1955, pl. I).

Many forms referred to *Mawsonia* possess a single large pair of extrascapulars in the postparietal shield (e.g. Wenz 1975; Maisey 1986; Yabumoto 2002). An additional median extrascapular is present in *Lualabaea lerichei*, *Axelrodichthys araripensis* and in a mawsoniid referred to *Axelrodichthys* from Niger (Saint-Seine 1955; Maisey 1986; Gottfried *et al.* 2004, fig. 2B). A large median extrascapular is also present in MDE F36 from Morocco, although the right paired extrascapular is either vestigial or absent (Cavin & Forey 2004). The median extrascapular is narrower than the paired elements posteriorly in *A. araripensis*, but is wider than them in *L. lerichei* and MDE F36. The width of the paired extrascapulars cannot be determined in the mawsoniid from Niger, and it is unknown whether the median extrascapular from Madagascar described by Gottfried *et al.* (2004, fig. 2A) was accompanied by paired extrascapulars. Both of the median extrascapulars described by Gottfried *et al.* (2004) are strongly ornamented by anteriorly radiating ridges, whereas the ornament of the median extrascapular in *A. araripensis* is comparatively subdued. Anteriorly radiating ridges also seem to be absent in MDE F36. The strongly ornamented median extrascapulars described by Gottfried *et al.* (2004) are sufficiently distinct to suggest that they may pertain to one or more new mawsoniid species. Only the anterior margin of the median extrascapular is

preserved in the holotype of *Lualabaea lerichei*, but it appears to have strong ridges that may radiate from a growth center farther posteriorly (Saint-Seine 1955, pl. I).

Opercular ornament is much finer in smaller Sanfranciscana Basin specimens than in larger ones. Two concentric ornamented fields are present on the operculum of *Mawsonia* and its sister taxon *Axelrodichthys*; a smooth or pitted proximal area, and a more distal region with radial ridges. The proximal area in *M. tegamensis* is quite extensive and covered with rugose ornament, and the radial pattern is only developed farther distally (Wenz 1975, pl. I, pl. V, fig. 4). In *Mawsonia* from Brazil, the initial radial ridges are always fine, and the ridges either remain fine or may become much heavier distally. By contrast, in both *M. tegamensis* and *M. libyca*, the radial ridges are strong over their entire length. In *Lualabaea lerichei*, the entire operculum (including the proximal area) appears to be covered by comparatively fine radial ridges (Saint-Seine 1955, pl. 1), similar to those in *A. araripensis* (Maisey 1986, figs 13B, 22A). The operculum is not known in *M. ubangiensis*.

Although the angular in *Mawsonia* is quite variable in shape and is known in several nominal species, assumptions that species can be recognized by differences in angular morphology are probably unjustified (Wenz 1975; Forey 1998). As shown earlier, the angular bones from the Sanfranciscana Basin display considerable individual variation in shape, proportions and ornament, suggesting that these features are not systematically informative.

In mawsoniids, the dentary is known only in *Mawsonia brasiliensis*, *Axelrodichthys* and *Lualabaea lerichei*. The anterior part of the Sanfranciscana Basin dentaries are elongated, as in *M. brasiliensis*. However, the dentary in *A. araripensis* lacks an anterior elongation (Maisey 1986). The anterior shape of the dentary is uncertain in *L. lerichei* (Saint-Seine 1955).

Complete postorbitals are known only in *Mawsonia tegamensis*, *M. cf. M. gigas* and *M. brasiliensis*. The postorbital in these forms is distinctive in having an anterior process extending above the dorsal margin of the lachrymojugal. In *M. tegamensis* described by Wenz (1975), the anterior process is comparatively deep and may have reached the supraorbital series. By contrast, in *M. cf. M. gigas* and *M. brasiliensis* the anterior process is splint-like and does not reach the supraorbitals (Maisey 1986; Yabumoto 2002). The postorbital lacks an anterior process in *Axelrodichthys araripensis* (Maisey 1986). The postorbital is unknown in *Lualabaea lerichei*, but Saint-Seine (1955, p. 9) noted the presence of 'les os sous orbitaires', one of which may include the postorbital.

The lachrymojugal in *Mawsonia tegamensis*, *M. cf. M. gigas*, and *M. brasiliensis* has a very distinctive morphology that may characterize the genus (Wenz 1975; Maisey 1986; Yabumoto 2002). The bone is greatly elongated anteroposteriorly, with a J-shaped upturned anterior end that may be constricted below the eye, and sensory pores are typically absent. In *M. cf. M. gigas* and *M. brasiliensis*, the anterior part of the lachrymojugal is not expanded and in *M. tegamensis* it is only slightly expanded. By contrast, in *Axelrodichthys araripensis*, the anterior part of the lachrymojugal is considerably expanded (Maisey 1986, fig. 26; Forey 1998, fig. 4.17). According to Forey (1998), the lachrymojugal is expanded anteriorly only in actinistians lacking a preorbital bone, but it is sometimes narrow even where the preorbital is absent (as in *Mawsonia*). The lachrymojugal in *L. lerichei* is elongated anteroposteriorly, but its precise shape is uncertain (Saint-Seine 1955, pls. I, III).

A pre-operculum is present in *Mawsonia tegamensis* (Wenz 1975, fig. 1, 'préopercule inferieur'), but according to Clément (2005) the bone is absent in a large undescribed *Mawsonia* skull from Morocco. The preoperculum has not been described in *M. gigas* or in *M. cf. M. gigas*, but one is present in the holotype of *M. brasiliensis* (Yabumoto 2002, fig. 3), and one has also been observed in a large undescribed head of *Mawsonia* from the Santana Formation. Although Clément (2005) coded absence/presence of a pre-operculum as uncertain in *Mawsonia*, it is undoubtedly present both in African and Brazilian specimens and its occasional absence is probably a taphonomic or preservational feature. Consequently, the pre-operculum in *Mawsonia* should be coded as present in future phylogenetic studies of actinistians. A small pre-operculum is also present in *Axelrodichthys araripensis* but apparently did not contact the squamosal, although there seems to be contact between the squamosal and postorbital (Maisey 1986, fig. 14; Forey 1998, fig. 4.17). By contrast, in *M. brasiliensis* (Yabumoto 2002) and an undescribed *Mawsonia* skull from the Santana Formation, the pre-operculum, squamosal, and postorbital form a continuous arcade. Forey (1998) suggested that the cheek bones in *Luababae* are reduced and probably did not contact each other, but it is uncertain whether a pre-operculum was present.

Ossified zygals are known in *Mawsonia cf. M. gigas* and MDE F36 from Morocco (Maisey 1986; Cavin & Forey 2004) as well as in the Sanfranciscana Basin material. Their wider distribution among mawsoniids is largely unknown, although they apparently did not ossify in *Axelrodichthys araripensis*.

Systematics of Mawsonia. There is little agreement in the literature as to how many *Mawsonia* species are valid. Cloutier & Forey (1991) recognized five species (*M. gigas* Woodward 1907; *M. libyca* Weiler 1935; *M. ubangiensis* Casier 1961; *M. lavocati* Tabaste 1963; and *M. tegamensis* Wenz 1975). Yabumoto (2002) accepted that number but added a sixth species, *M. brasiliensis*, which was distinguished on the basis of the position of the otic canal fossa (supposedly different from *M. ubangiensis*), the shape of the anterior end of the angular (less elevated than in *M. lavocati*, more concave than in *M. libyca*) and the proportions of the parietonasal and postparietal shields (different from *M. tegamensis*). Unfortunately, such differences cannot be compared across all the taxa, and many of the features (especially postparietal and angular morphology) are highly variable in the Sanfranciscana Basin material.

Ever since *Mawsonia* was first described (Mawson & Woodward 1907), all the material discovered subsequently from Brazil has either been referred to the type species or is considered close to it (Carvalho 1982; Campos & Wenz 1982; Maisey 1986; Brito *et al.* 1994; Carvalho & Maisey 1998; Maffizzoni 1998; Medeiros & Schultz 2001; Carvalho 2002). The only other nominal Brazilian species are *M. minor* Woodward, 1908 and *M. brasiliensis* Yabumoto, 2002. *M. minor* is probably a juvenile specimen of *M. gigas* (Carvalho 1982), and *M. brasiliensis* is also very similar to *M. gigas* and may be synonymous. Until now, *M. gigas* had not been formally recognized from Africa, from where four supposedly distinct nominal species have been erected (*M. libyca* Weiler 1935; *M. ubangiensis* Casier 1961; *M. lavocati* Tabaste 1963; and *M. tegamensis* Wenz 1981). Unfortunately, complete or articulated skeletal remains of *Mawsonia* are extremely rare and some of the African species are founded upon fragmentary material, placing severe constraints on the extent to which these nominal species can be compared with each other. Bones such as the angular and postparietal are known in several forms and have therefore tended to carry greater weight in systematic comparisons than they probably deserve (e.g. Weiler 1935; Casier 1961; Tabaste 1963). We do not claim to have improved this situation significantly. However, by documenting a large sample of bones from numerous individuals, we have at least established that morphological variation within a presumably single population could easily account for *some* of the differences that have been used in the past to distinguish between *some* of the nominal species.

We can find no convincing morphological features to allow recognition of more than a single species of *Mawsonia* in Brazil, the type species

M. gigas Woodward (in Mawson & Woodward 1907). Furthermore, we are not convinced that *M. ubangiensis* from Africa is morphologically distinguishable from *M. gigas*, and we therefore regard it as a subjective junior synonym of the type species. The African *M. tegamensis* differs from *M. gigas* in having a comparatively wide parietonasal and postparietal shield and perhaps also in its postorbital morphology.

The systematic status of *Mawsonia lavocati* is problematic. The holotype is an angular (Tabaste 1963), but Wenz (1981), Cavin & Forey (2004) and Yabumoto & Uyeno (2005) have all referred parts of various skulls to this species. Some of those specimens resemble *Axelrodichthys* from Brazil, although the shape of the angular described originally by Tabaste (1963) is more like that of *M. cf. M. gigas* than *Axelrodichthys araripensis*. It is possible that two different mawsoniids are present in these Moroccan deposits. Unfortunately, no reliable diagnostic features for *M. lavocati* are evident in the type specimen, and the species should be considered a *nomen vanum*. Better preserved Moroccan mawsoniid material should perhaps be referred to new taxa for which more adequate diagnoses can be formulated.

Mawsonia libyca is another problematic species, because the type and original referred specimens were unfortunately destroyed during World War II, and the species is *incertae sedis* until a lectotype is erected. Given the presence of two distinct mawsoniid taxa in the Santana Formation of Brazil and the possible existence of two taxa in Moroccan deposits, considerable care needs to be exercised in lectotype selection for *M. libyca* since the Egyptian mawsoniids may also include more than one taxon.

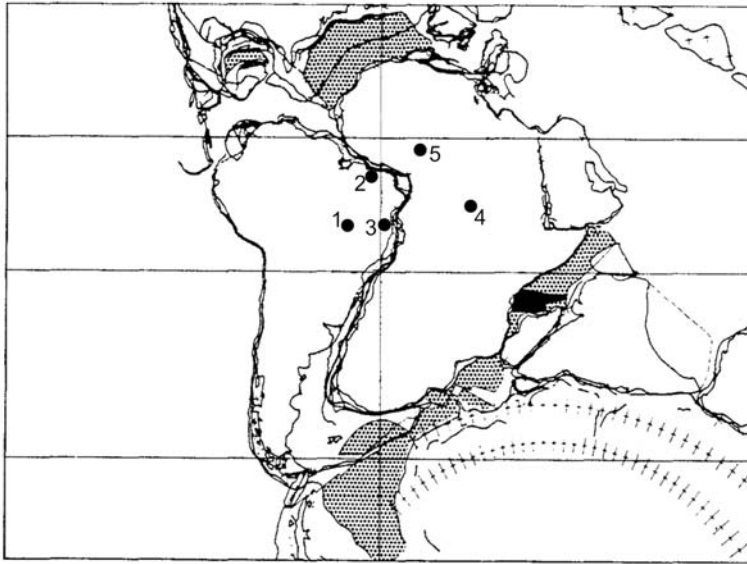
Phylogenetic relationships and biogeography. Recent discoveries of mawsoniid fossils in both Brazil and Africa have considerably improved our knowledge of these enigmatic forms, but have also raised important questions surrounding their interrelationships. The material described in the present work has blurred some of the traditional distinctions between supposedly different species of *Mawsonia*, while new fossils from Morocco suggest new character combinations among Cretaceous mawsoniids (Cavin & Forey 2004; Yabumoto & Uyeno 2005). We can only conclude that the current systematic treatment of mawsoniids is inadequate and that a thorough revision of these forms is needed.

Unfortunately, these conclusions leave little scope for biogeographical investigation of *Mawsonia*, despite its tantalizing geographic and temporal contemporaneity with tectonic events associated with the break-up of western Gondwana

(Maisey 2000). The first appearance of the genus (and of the type species, in its present broadened concept) is within Berriasian pre-rift and early syn-rift stratigraphic sequences of the Eastern Brazilian Rift System (EBRIS) in NE Brazil, and in contemporaneous syn-rift sequences of central and NW Africa (Fig. 21). Its Aptian–Albian occurrences are in syn-rift and post-rift sequences in both Africa and Brazil, and fall largely within the same geographical area as before (Fig. 22), but its latest (Cenomanian) records are mostly African, where they extend well beyond the rift basins associated with EBRIS in Africa and Brazil (Fig. 23).

Mawsonia tegamensis may represent a distinct mid-Cretaceous lineage which was apparently restricted to NW Africa, and this form was contemporary with the early and mid-Aptian tectonic events related to the separation of Africa and South America. Tectonic events within EBRIS that would eventually result in the separation of present-day Africa and South America were initiated in the late Jurassic–Berriasian (155–145 Ma), but rifting along the Equatorial Branch between NW Africa and NW Brazil and along the Benue Trough between NW and western equatorial Africa only began in the early and mid-Aptian (c. 125–115 Ma). A contemporaneous switch from active rifting to passive drifting occurred within EBRIS rift basins belonging to the Recôncavo–Tucano–Jatobá trend of NE Brazil. The most significant tectonic consequence of these events was the separation of NW Africa from NE Brazil, which remained attached to the rest of South America instead of splitting from it along with the rest of Africa (Maisey 2000).

These events provide an empirical maximum theoretical age for the isolation of a *Mawsonia* population within NW Africa. Rifting along the Benue Trough between NW and western Africa stopped during the Late Cretaceous, but the trough then became occupied by a temporary seaway between the South Atlantic and eastern (Mediterranean) Tethys (Gee 1988). Northwestern Africa was thus tectonically and/or geographically separated from both South America and the remainder of Africa throughout the mid- and Late Cretaceous (i.e. the time-frame during which *M. tegamensis* lived), and fluvial and lacustrine systems within that region may have been sufficiently isolated geographically to have provided opportunities for vicariant speciation that may have led to the appearance of *M. tegamensis*. Furthermore, the temporary epicontinental seaway also effectively separated Late Cretaceous populations of *Mawsonia* in NW Africa from those in Egypt, but it is unknown whether this had any impact on mawsoniid distribution.



			NEOCOMIAN			BARREMIAN
			BERRIASIAN	VALANGINIAN	HAUTERIVIAN	
AFRICA	NIGER	5 - <i>M. sp.</i>				
	DEM. REP. CONGO	4 - <i>M. ubangiensis</i>				
SOUTH AMERICA	BRAZIL	3 - <i>M. gigas</i> (BA)				
		2 - <i>M. cf. - M. gigas</i> (CE)				
		1 - <i>M. gigas</i> (MG)				

Fig. 21. Distribution of *Mawsonia* in the earliest Cretaceous (Neocomian–Barremian). Base map modified from Scotese *et al.* (1988).

Axelrodichthys-like mawsoniids also seem to have been distributed fairly widely across western Gondwana during the Cretaceous (although their temporal range in Brazil seems more restricted than in Africa; see earlier). At present, it is uncertain whether these forms represent a second Gondwanan mawsoniid lineage, or whether their evolutionary relationships can be correlated with tectonic events related to the separation of Africa and Brazil. *Lualabaea lerichei* is almost certainly a mawsoniid and resembles *Axelrodichthys* more than *Mawsonia*, but its phylogenetic relationships and stratigraphic age are in need of better resolution.

Cladistically, *Diplurus* and *Chinlea* are sister taxa to mawsoniids (Cloutier & Forey 1991; Forey 1998), but these forms are known only from

Triassic non-marine deposits of North America (Schaeffer 1952, 1967). The intervening history of freshwater actinistians is largely unknown, but the Gondwanan distribution of Cretaceous mawsoniids seems at odds with the known distribution of the Triassic forms unless the earlier Mesozoic tectonic histories of these regions are considered. The sedimentary basins in which *Diplurus* occurs are located along the tectonic line of separation between eastern North America and Morocco, so Triassic relatives of *Diplurus* (perhaps including ‘stem mawsoniids’) conceivably existed in NW Africa. Following the break-up of this region, freshwater actinistians have no Jurassic or Cretaceous record in North America and presumably became extinct, but they were apparently more successful in western Gondwana (where they became fairly

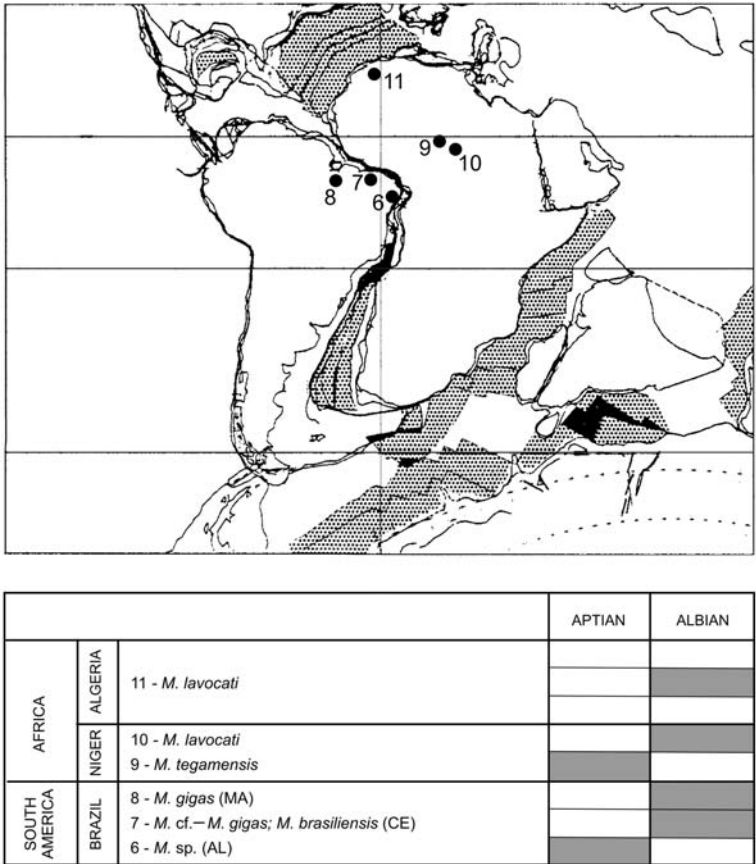


Fig. 22. Distribution of *Mawsonia* in the Aptian–Albian. Base map modified from Scotese *et al.* (1988).

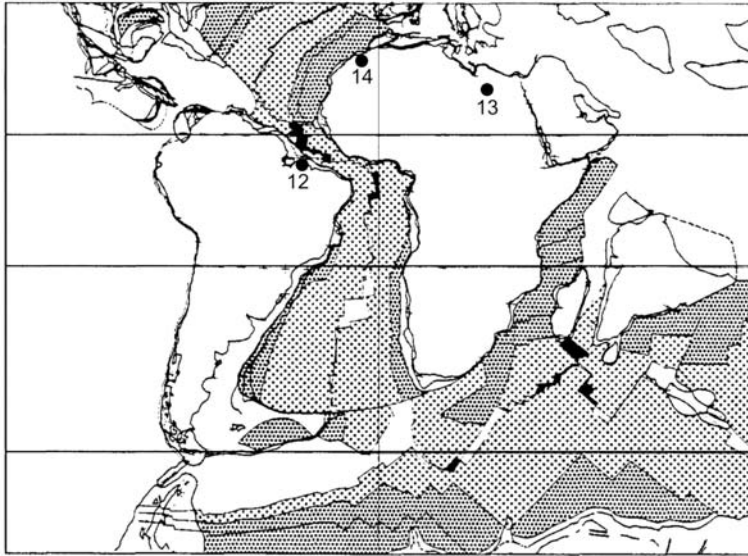
widespread and abundant). Following the Cretaceous separation of Brazil from western Africa, they survived on both sides of the South Atlantic (albeit only briefly in Brazil).

Conclusions

1. The *Mawsonia* material from the Areado Formation represents numerous individuals of various sizes. Although the remains are dominated by skull bones, other parts of the skeleton are also represented, suggesting there has been little post-mortem disturbance or taphonomic sorting. It is suggested that the sample probably represents a single population of a single species, and that morphological variations noted within the sample probably reflect individual differences among that population. The majority of individuals from the Sanfranciscana Basin represent

comparatively small individuals (2 m or less), which is considerably smaller than the largest known *Mawsonia*.

2. Morphological variations observed in the Sanfranciscana Basin material have important implications for many of the characters that were used in the past to distinguish between putative species of *Mawsonia*, particularly in the postparietal shield and lower jaw. No characters were found to distinguish the Sanfranciscana Basin material from the type species, first described from Bahia, Brazil (Mawson & Woodward 1907). Based on the present analysis, other Brazilian material (e.g. in Maisey 1986; Dutra & Malabarba 2001; Medeiros & Schultz 2001; Yabumoto 2002) cannot be distinguished confidently from the type species.
3. *Mawsonia gigas* has not been recognized previously from Africa, but it is contended here that at least two nominal African species, *Mawsonia libyca* (Weiler 1935) and *Mawsonia*



			CENOMANIAN
AFRICA	MOROCCO	14 - <i>M. lavocati</i>	■
	EGYPT	13 - <i>M. libyca</i>	■
SOUTH AMERICA	BRAZIL	12 - <i>M. gigas</i> (MA)	■

Fig. 23. Distribution of *Mawsonia* in the Cenomanian. Base map modified from Scotese *et al.* (1988).

ubangiensis (Casier 1961) are probably synonymous with the type species. Our findings expand the pre-Atlantic seaway records of *M. gigas* from NW South America into southern Brazil and parts of Africa (including *M. ubangiensis*). Post-seaway (Albian) occurrences of *M. gigas* include those from the Santana and Itapecuru Formations of Brazil and *M. libyca* from Africa. We consider the Late Cretaceous *M. tegamensis* from NW Africa may be sufficiently distinct to merit retaining it as a separate species. It may have evolved following tectonic activity that tended to isolate NW Africa from the rest of W Gondwana during the mid-Cretaceous. Some Moroccan mawsoniids share features with *Axelrodichthys* and should perhaps be removed from *Mawsonia*, and it is possible that *Axelrodichthys*-like mawsoniids formed a

distinct lineage that was endemic to the northern part of W Gondwana during the Late Cretaceous, although rifting along the equatorial seaway had by then separated NE Brazil from NW Africa.

4. *Mawsonia* systematics is still very poorly resolved and clearly is in need of major revision. At the present time only two species (*M. gigas*, *M. tegamensis*) are recognized on the basis of credible morphological evidence. Some nominal species (e.g. *M. ubangiensis*, *M. brasiliensis*) are regarded here as junior subjective synonyms of *M. gigas*, and one species (*M. lavocati*) is so poorly established that it should be considered a *nomen vanum*. Some specimens referred in the past to *M. lavocati* resemble *Axelrodichthys* and probably do not belong in *Mawsonia*. Many of the morphological differences used in the past to

distinguish between species of *Mawsonia* may have no systematic value. Moreover, some newly discovered mawsoniid fossils do not fit easily into a conventional classification scheme (Cavin & Forey 2004). Such discoveries show that improved understanding of mawsoniid phylogeny and biogeography will only emerge as more complete material becomes available and as intrapopulation variation becomes better understood.

We dedicate this paper to Peter Forey in recognition of his outstanding work on fossil fishes, especially actinistians. MSSC thanks the Companhia de Pesquisas de Recursos Minerais, Serviço Geológico do Brasil for providing funds for the senior author to visit the American Museum of Natural History in New York, and the Superintendência Regional de Belo Horizonte for field support in Minas Gerais. Funding for fieldwork by JGM in Brazil was provided by the American Museum of Natural History. We give special thanks to Dr Ismar de Souza Carvalho (Universidade Federal do Rio de Janeiro), Dr R. de Cassia Tardin Cassab and D. de Almeida Campos (Departamento Nacional de Produção Mineral), M. E. Carvalho M. Santos, Dr V. Gallo (Universidade Estadual do Rio de Janeiro), V. M. M. da Fonseca (Museu Nacional, Universidade Federal do Rio de Janeiro), Dr M. da Glória Pires de Carvalho, L. Meeker and C. Tarka (American Museum of Natural History), G. N. Sgarbi (Universidade Federal de Minas Gerais), M. S. de Carvalho for photography, and colleagues at the Companhia de Pesquisas de Recursos Minerais for supplying the diagrams and maps. We also thank G. Clément for his thorough review of the original version of this paper and for his many suggestions for improvement.

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