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A new Mesozoic coelacanth from Brazil (Sarcopterygii, Actinistia)

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Abstract. **A new genus and species of coelacanth, *Parnaibaia maranhaoensis* gen. et sp. nov. is described on the basis of four specimens from the Pastos Bons Formation in Maranhao, Brazil. This new genus and species differs from other genera of the family Mawsoniidae by having a stout median ridge on the scales, six free extrascapulars, seven elements in the supraorbital-tectal series and absence of large teeth. *P. maranhaoensis* bridges the gap between the Triassic *Chinlea* and Cretaceous *Mawsonia* and *Axelrodichthys*.**

Key words: Brazil, coelacanth, Jurassic, new species, Parnaiba Basin, Pastos Bons Formation

Introduction

Three coelacanth species were recorded from the Cretaceous of South America; *Mawsonia gigas* Woodward, 1907, *M. brasiliensis* Yabumoto, 2002 and *Axelrodichthys araripensis* Maisey, 1986 have been found in South America. Both genera form a clade with *Chinlea* Schaeffer, 1967 from the Upper Triassic of North America (Forey, 1998; Clement, 2005), but there is a gap of about 100 million years between the North American and Brazilian taxa. In the present study, a new coelacanth, *Parnaibaia maranhaoensis*, which bridges the gap both morphologically and chronologically, is described on the basis of four specimens from the Pastos Bons Formation in Maranhao, Brazil.

Terminology of coelacanth bones follows Forey (1998) and that of median fins follows Uyeno (1991).

Systematic description

Order Coelacanthiformes Huxley, 1861
Suborder Latimeroidei Schultze, 1993
Family Mawsoniidae, Schultze, 1993

Parnaibaia gen. nov.

Type species.—*Parnaibaia maranhaoensis* sp. nov.

Etymology.—*Parnaiba*, after the name of the geological basin that contains the Pastos Bons Formation.

Diagnosis.—Same as for type species.

Parnaibaia maranhaoensis sp. nov.

Diagnosis.—Mawsoniid coelacanth differing from others by the following combination of characters. Medium-sized coelacanth with a comparatively small and deep head. Standard length equal to about 4.6 times head length. Postparietal shield about half the length of the parietonasal shield. One, two or three stout median ridges on scales. Six extrascapulars. The extrascapular and the supratemporal not fused. Supraorbital-tectal series composed of seven elements. Absence of large teeth on upper and lower jaws. Caudal fin (= supplementary caudal fin of Forey, 1998) developed.

Material.—Holotype: KMNH (Kitakyushu Museum of Natural History and Human History) VP 100,257, an almost complete, articulated specimen. Total length is 580 mm. Paratypes: KMNH VP 100,258, a specimen preserved in a gray calcite geode, bones, fin rays and scales are disarticulated. Ventral surface of the head is exposed. Estimated standard length is about 260 mm. KMNH VP 100,259, a small specimen missing the caudal fin. The ventral surface of the head is exposed. Standard length is 105 mm. AMF (Aquamarine Fukushima) 9900004-64-364, an almost complete, articulated specimen, preserved in a gray calcite geode. Standard length is 242 mm.

Type locality and horizon.—Pastos Bons Formation, Maranhao, Brazil (Figure 1). The Pastos Bons Formation is a deposit of exclusively continental origin (Góes and Feijó, 1994) in the Parnaiba Basin. Bigarella (1973)

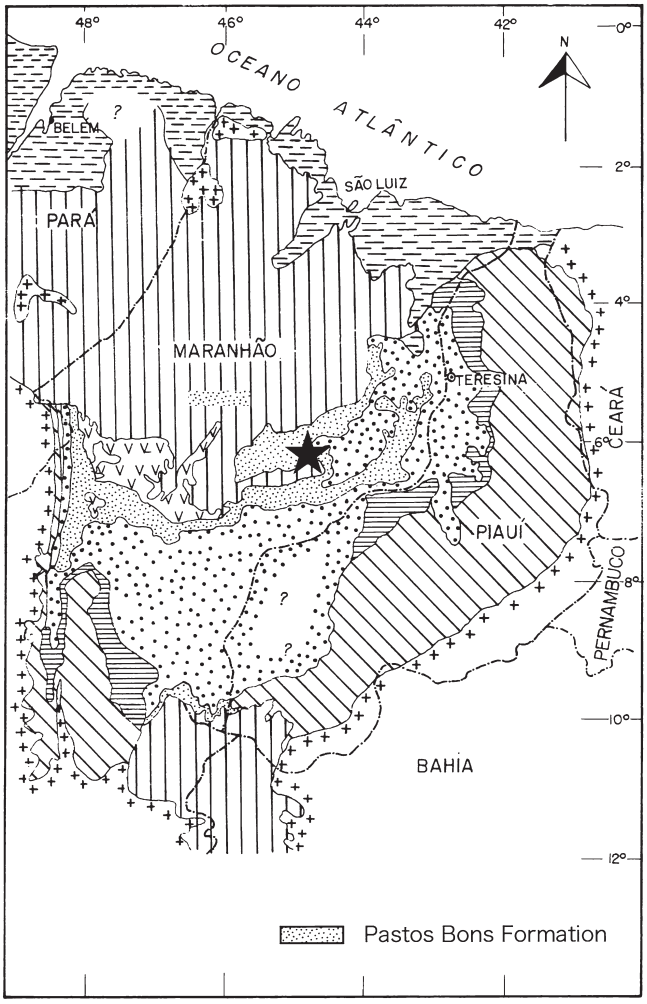

Figure 1. Geological map of the Parnaiba basin, Brazil (from Bigarella, 1973). Star indicates the locality of *Parnaibaia maranhaoensis* gen. et sp. nov.

considered the formation to be Late Triassic in age on the basis of the fossil fish fauna, which includes *Lepidotus piauhyensis* and *Semionotus* sp. in a black-shale facies. Góes and Feijó (1994) suggested that the age is Late Jurassic mainly based on ostracods and conchostracans. Several authors proposed that it probably extends into the Early Cretaceous (Pinto and Purper, 1974; Silva Santos, 1974), which is supported by the palynological analysis by Lima and Compos (1980). Gallo (2005) considered that the age is more likely to be late Jurassic than Early Cretaceous based on personal comments by R. Dino on the palynoflora.

Etymology.—The species is named for Maranhao, the state where the specimens were found.

Description of holotype.—Standard length is about 3.5 times body depth; body depth at the origin of first dorsal fin is about 125 mm; total length is about 580 mm; standard length is 435 mm; head length is 108 mm. Length of the parietonasal shield is 60 mm, the posterior end being broader, and the width of the right half is 15 mm (Figure 2). Both anterior and posterior parietals are of similar size, but the posterior one is slightly wider, each parietal is about three times as long as wide. Paired posterior and anterior nasals are more or less equidimensional. The posterior tectal, which forms a foramen with the anteriormost supraorbital, contacts both the anterior parietal and the posterior nasal. The anterior tectal is smaller than the posterior one. There are many small rostral ossicles (median rostrals) in the rostral region. The lateral rostral, situated along the ventral margins of the posterior and anterior tectals, has an oblong pore at the ventral margin of the anterior portion (Figure 3).

Six supraorbitals are present, of about 5 mm width, but with the posteriormost one slightly wider. Anterior first and second supraorbitals are sutured to the anterior parietal. The third supraorbital is longest, 12 mm, and is attached to both anterior and posterior parietals. Other posterior supraorbitals attach to the posterior parietal, the fifth being the shortest one (Figure 3).

The postparietal shield consists of a pair of postparietals and supratemporals and three pairs of extrascapulars, probably the middle extrascapular being absent. The postparietal is marked by a groove indicating the medial and the posterior pit lines. Its anterior margin is straight, without any process. The supratemporal is a smaller bone with a width equal to about two-thirds that of the postparietal. The three extrascapulars are exposed; the medial two extrascapulars are small, of equal size and are sutured to the postparietal. The largest lateral one is strongly sutured to the supratemporal and weakly to the postparietal (Figure 3).

The long lachrymojugal curves along the ventral margin of the orbit. Its anterior end is slightly expanded and is marked by a deep groove for posterior opening of the rostral organ. It is anteriorly attached to the posterior tectal and the first supraorbital. A preorbital is absent. The postorbital and the squamosal are both in contact with the posterior end of the lachrymojugal, but the exact relations of these bones are not clear due to the fact that they are broken into many pieces.

The operculum is triangular with a slightly convex dorsal margin, a rounded posterior margin and an almost straight anterior margin (Figure 3).

The dentary is almost straight with a lateral swelling and a large sensory pore located in its anterior part. The splenial resembles the dentary in shape with a slitlike sensory pore lying behind a round sensory pore. The angular is long and shallow with three oblong mandibular sensory openings at the anterior half, the most anterior

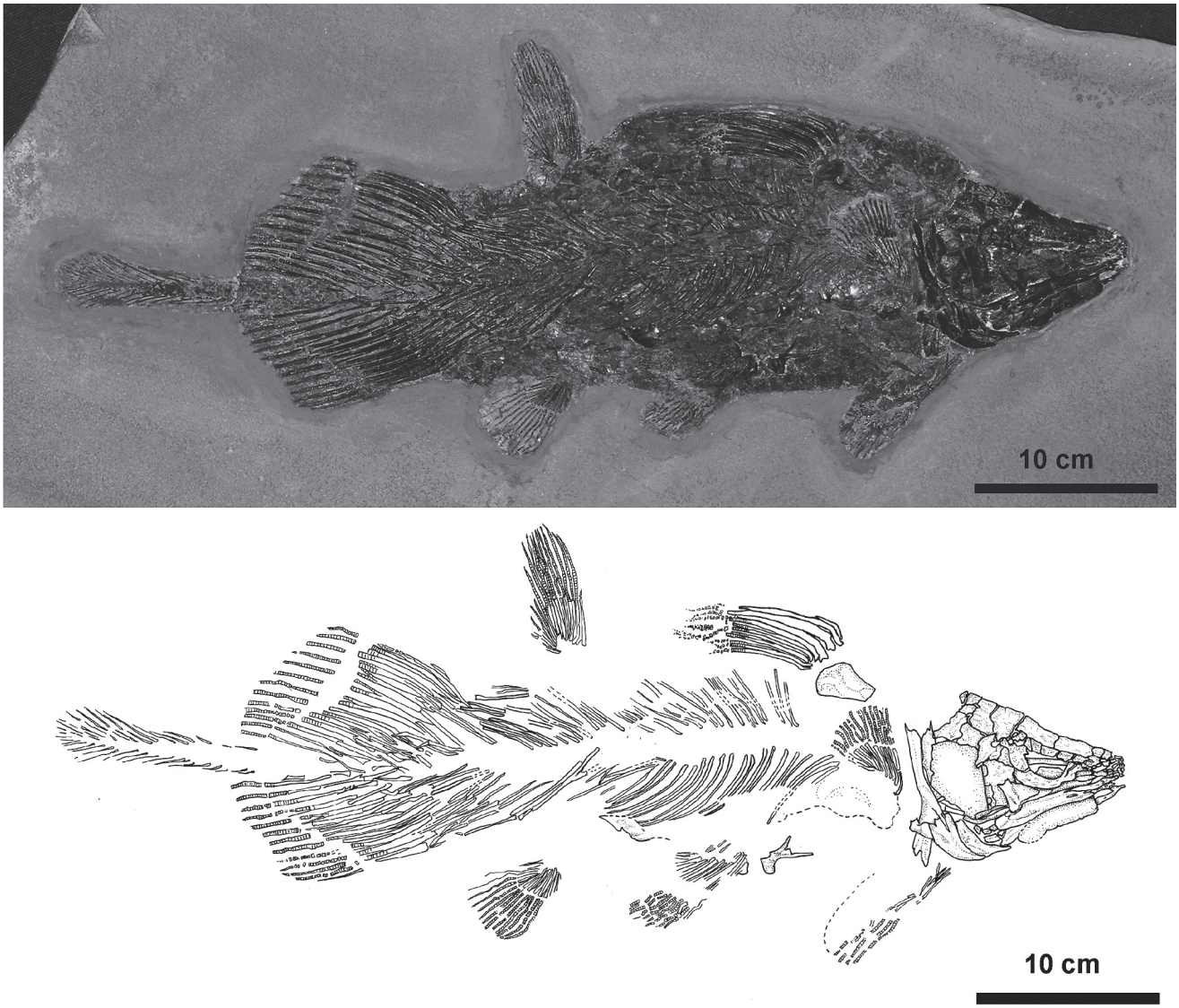

Figure 2. *Parnaibaia maranhaoensis* gen. et sp. nov., holotype (KMNH VP 100,257, 580 mm TL) from the Pastos Bons Formation in Pastos Bons, Maranhao, Brazil.

pore presents itself on the suture between the angular and the splenial. The angular contacts the dentary and the splenial at the anterior end.

The large retroarticular is in contact with the quadrate (Figure 3).

The cleithrum, extracleithrum and clavicle are well preserved. The cleithrum is long, its upper portion flat, slightly concave while the lower portion reaches near the ventral margin of the head and ends in two branches. A thick flange at the middle of the cleithrum is inserted into the inner face of the extracleithrum. The latter is thick and curving anteriorly. The clavicle is similar in shape to the extracleithrum. The left scapulocoracoid, shaped like a twisted bowtie, is preserved on the left cleithrum slightly below the middle of the broken and displaced cleithrum.

The ornamentation is rugose over most of the skull roof and cheek bones, but more weakly so over the opercle. The surface of the angular is marked by a granular ornamentation (Figure 3).

The first dorsal fin has nine long fin rays. The length of the longest ray is about 80% of the head length. The basal plate is kidney-shaped with a slightly concave antero-dorsal margin (Figure 2). The four most anterior rays have short spines on their anterior margins (Figure 2).

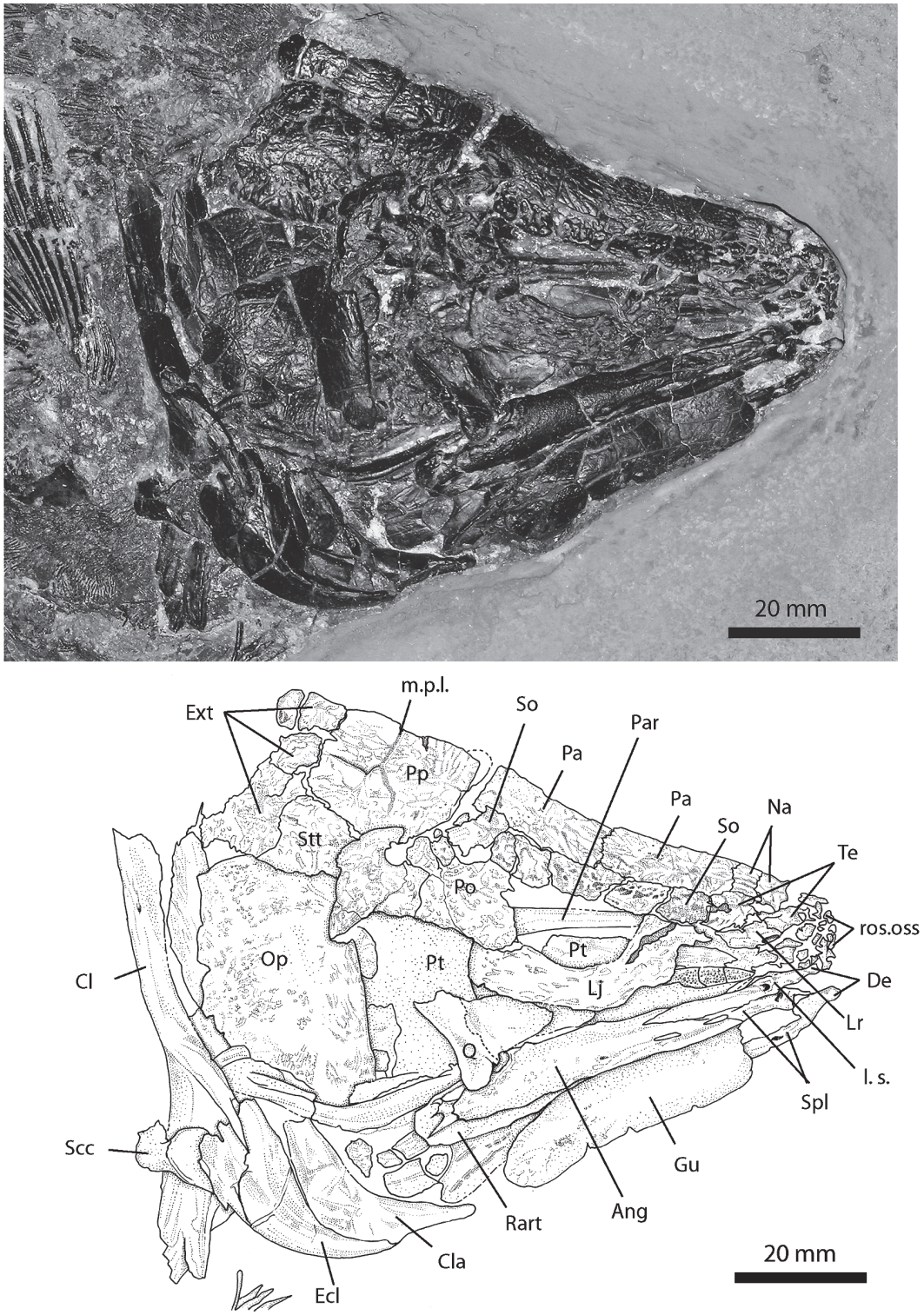

Figure 3. *Parnaibaia maranhaoensis* gen. et sp. nov., skull in lateral view, holotype (KMNH VP 100,257, 580 mm TL) from the Pastos Bons Formation in Pastos Bons, Maranhao, Brazil. Abbreviations: Ang = angular; Cl = cleithrum; Cla = clavicle; De = dentary; Ecl = extracleithrum; Ext = extrascapular; Gu = gular plate; Lj = lachrymojugal; Lr = lateral rostral; l.s. = lateral swelling of dentary; m.p.l. = middle pit line of postparietal; Na = nasal; Op = operculum; Pa = parietal; Par = parasphenoid; Po = postorbital; Pp = postparietal; Pt = pterygoid; Q = quadrate; Rart = retroarticular; ros.oss = rostral ossicles; Scc = scapulocoracoid; Spl = splenial; So = supraorbital; Stt = supratemporal; Te = tectal.

The second dorsal fin has 20 rays which are unbranched. The basal bone plate is not preserved. The third dorsal fin (= dorsal lobe of the caudal fin of Forey, 1998) is large with fifteen rays.

Both pectoral fins are preserved. The right pectoral fin with at least 21 rays is preserved behind the cleithrum. The left pectoral fin is preserved ventrally below the cleithra, but the fin rays are not well preserved. The pelvic girdle has two long and thin processes respectively dorsally and anteriorly projected. The right pelvic fin has at least 11 rays.

The first anal fin with 19 rays is located slightly behind and at the level of the second dorsal fin. The second anal fin (= ventral lobe of the caudal fin of Forey, 1998) with 14 rays is almost the same size as the third dorsal fin. The caudal fin (= supplementary caudal fin of Forey, 1998) is well developed. Its length is about 27% of the total length.

Twenty-five ribs, which are long and curved, are preserved. Long and ossified ribs are known in *Diplurus*, *Axelrodichthys*, *Chinlea* and *Changxingia* (Forey, 1998). The neural and haemal spines are long.

Scales are large and well preserved. The scales have one, two or three stout median ridges with many fine ridges on both ventral and dorsal sides (Figure 4). There are fifteen or sixteen scales by vertical rows at the middle of the body (Figure 2).

Description of paratypes.—KMNH VP 100,258: The

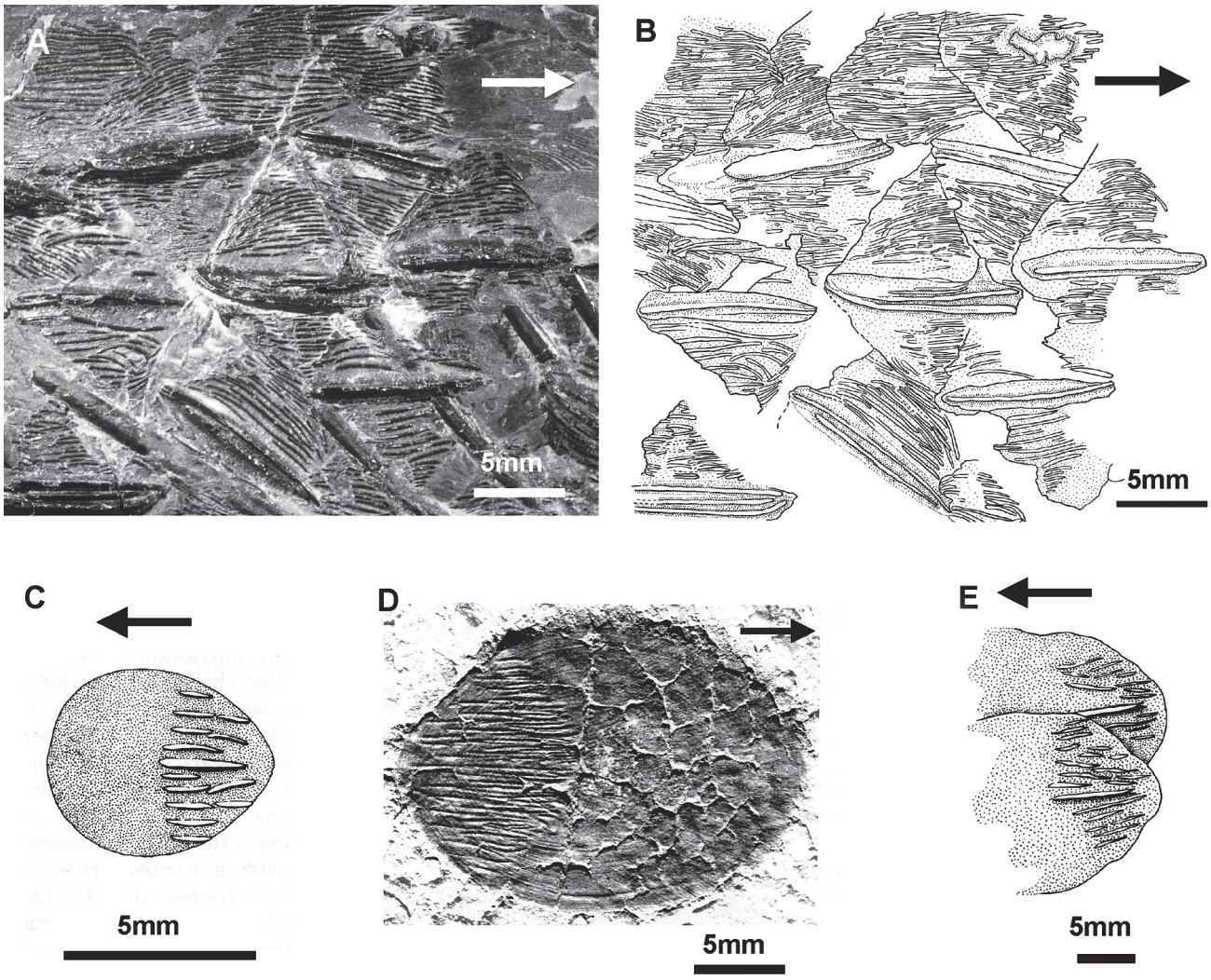

Figure 4. **A**. Photograph of scales below the first dorsal fin of *Parnaibaia maranhaoensis* gen. et sp. nov. **B**. Line drawing of scales of A. **C**. Scale of *Diplurus newarki* from Forey (1998). **D**. Scale of *Chinlea sorenseni* from Schaeffer (1967). **E**. Scales of *Axelrodichthys araripensis* from Forey (1998). Arrows indicate anterior direction.

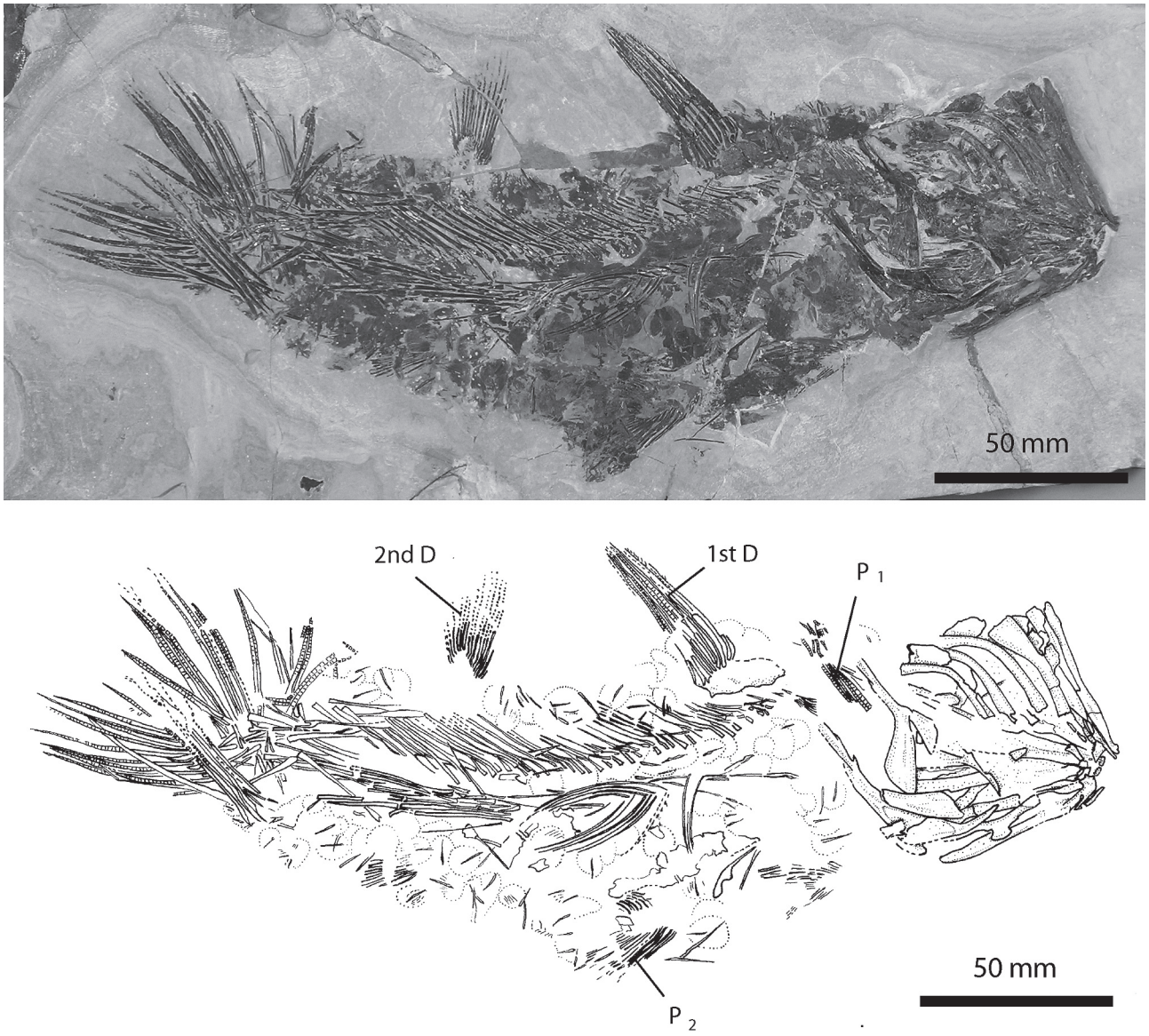

Figure 5. *Parnaibaia maranhaoensis* gen. et sp. nov., paratype (KMNH VP 100,258, 260 mm estimated SL) from the Pastos Bons Formation in Pastos Bons, Maranhao, Brazil. Abbreviations: 1st D = first dorsal fin; 2nd D = second dorsal fin; P_1 = pectoral fin; P_2 = pelvic fin.

ventral face of the head is exposed (Figures 5, 6). The right lower jaw is better preserved than the left one. The inner surface of the right dentary is exposed. The anterior portion is shallow, the posterior portion is somewhat hook-shaped and has a lower arm contacting the angular (Figure 6).

Three coronoids are observed. The equal-sized anterior two coronoids are short compared to the posterior one. Each coronoid bears small conical teeth.

The angular is long and shallow. The ceratohyal has a lateral flat protuberance at the part slightly before the middle of the bone (Figure 6). There is a similar protuberance at the middle of the ceratohyal in *Latimeria* (see Millote and Anthory, 1958) and a shallow one at the posterior part on the bone in *Macropoma* (see Forey, 1998).

The retroarticular is short, joining with the articular to form a glenoid articulation for the quadrate. The articular is relatively large and lies medial to the angular.

Most of the medial surface of the pterygoid is covered with minute teeth. Both autopalatines are preserved behind the premaxillaries. The dermopalatines have small

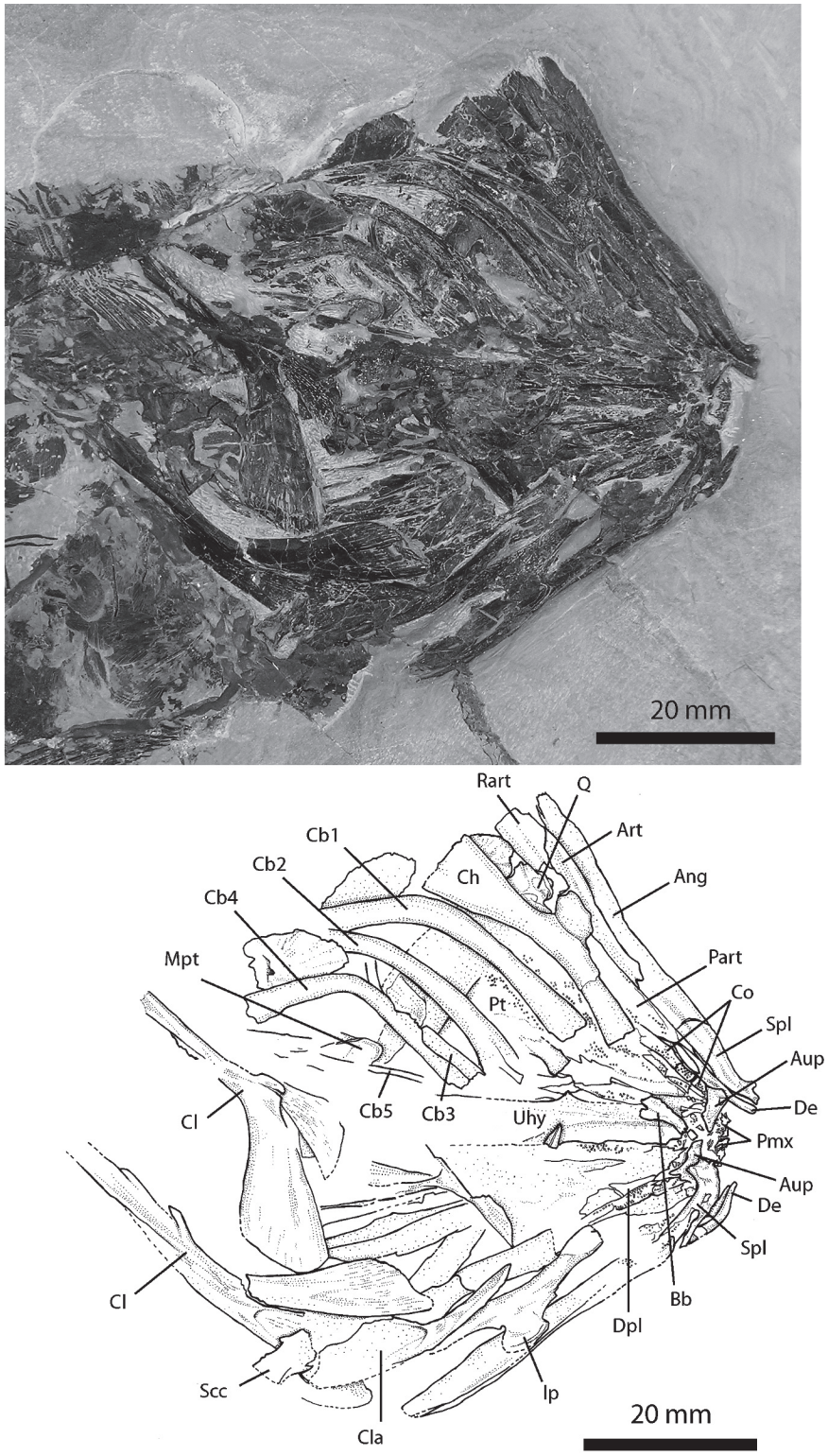

Figure 6. *Parnaibaia maranhaoensis* gen. et sp. nov., skull in ventral view, paratype (KMNH VP 100,258, 260 mm estimated SL) from the Pastos Bons Formation in Pastos Bons, Maranhao, Brazil. Abbreviations: Ang = angular; Art = articular; Aup = autopalatine; Bb = basibranchial; Cb1-5 = first to fifth ceratobranchials; Ch = ceratohyal; Cl = cleithrum; Cla = clavicle; Co = coronoid; De = dentary; Dpl = dermopalatine; lp = lateral protuberance of ceratohyal; Mpt = metapterygoid; Part = prearticular; Pmx = premaxilla; Pt = pterygoid; Q = quadrate; Rart = retroarticular; Scc = scapulocoracoid; Spl = splenial; Uhy = urohyal.

conical teeth on their ventral margins (Figure 6).

Premaxillae are preserved in the space between the anterior ends of disarticulated lower jaws (Figure 6). Each premaxilla has many minute conical teeth on the ventral surface. Specimen KMNH VP 100,258 presents a nicely preserved branchial apparatus. The basibranchial is triangular in shape with a flat ventral surface and a notch in the middle of the posterior margin. The wide urohyal has a median ridge on the ventral surface. There are five right ceratobranchials, in which the first four are curved at about mid-length (Figure 6).

Ten rays are preserved on the first dorsal fin. The second to the seventh rays have short spines on the anterior margins. The third dorsal fin and the second anal fins are disarticulated. There are nineteen rays on the second dorsal fin without spines on any ray. At least fifteen rays can be counted in the pectoral and pelvic fins. Nine rays are recognized on the first anal fin. The caudal fin is not preserved. A stout median ridge is present on most of the large scales, as in the holotype.

The wide ventral portion of the cleithrum forms a flange at the posterior and ventral margins. The cylindrical scapulocoracoid is attached slightly above the middle of the posterior flange. The anterior end of the flange articulates with the clavicle which is deep at the posterior portion and shallow at the anterior portion and which has a pointed anterior tip (Figure 6).

KMNH VP 100,259: The ventral surface of the head is exposed (Figure 7). It is difficult to recognize individual bones of the head, but a gular plate, operculum and cleithra are well preserved. The gular plate has many pits on the portion slightly behind the center of the bone and ridges radiating from there on the lateral and the posterior portions. The anterior tip of the gular plate is pointed. The inner surface of a triangular-shaped operculum is exposed. A small portion of the dorsal edge is missing, revealing an impression that shows the ridged ornamentation of the outer surface. The calcified bladder (44.5 mm long and 8.8 mm deep) is preserved as a thin layer. Seven first dorsal fin rays can be counted. Nineteen second dorsal fin rays are preserved. There are seventeen third dorsal fin rays with the third fin ray having short spines on the anterior margin. Sixteen rays of the first anal fin and fifteen rays of the second anal fin are counted. Thirteen pectoral fin rays and 20 pelvic fin rays can be counted. Some scales on the dorsal portion of the body have a stout median ridge, similar to those on the holotype.

AMF 9900004-64-364 is an almost complete specimen missing the caudal fin, the specimen is exposed on its right side (Figure 8). The head length is 71.8 mm. Its depth is 30.5 mm. The postparietal shield (24.6 mm) is slightly longer than half the length of the parietonasal shield (42.5 mm). There are ten rays on the first dorsal fin, 20 on the second dorsal fin, 16 on the third (= dorsal lobe of the caudal fin of Forey, 1998); 20 on the first anal fin, 17 on the second anal fin (= ventral lobe of the caudal fin by Forey, 1998); 13 on the right pectoral fin, 27 on the pelvic fin. The scales have a stout median ridge similar to those on the holotype.

Remarks.—This new genus has characters, (e.g., long ossified ribs, rugose ornamentation and absence of spiracular and suboperculum) corresponding to the diagnosis of the Mawsoniidae by Forey (1998). The character that most distinguishes the new genus *Parnaibaia* from other genera of the family is the stout median ridge on the scales (Figure 4). *Axelrodichthys* from the Cretaceous of South America has a median ridge on the scales (Forey, 1998), but it is not stout like that of *Parnaibaia*. This new genus differs from *Axelrodichthys* by having more rugose ornamentation on the skull roof (less rugose in *Axelrodichthys*), short spines on the fin rays of the first dorsal fin (no spine in *Axelrodichthys*), and the developed caudal fin (short caudal fin in *Axelrodichthys*). There is no tubercle or ridge ornamentation on the scales of *M. brasiliensis* (see Yabumoto, 2002). *Parnaimaia* differs from *Mawsonia* from the Cretaceous of South America and Africa (Forey, 1998) by having short spines on the fin rays of the first dorsal fin (no spine in *Mawsonia*) and the developed caudal fin (short caudal fin in *Mawsonia*) and six free extrascapulars (two in *Mawsonia*). *Chinlea* from the Upper Triassic (Carnian) Chinle Formation of Utah, Colorado and New Mexico and the Tecovas Formation of Texas (Forey, 1998) has no median ridge on the scales (Shaffer, 1967). *Parnaibaia* differs from *Chinlea* by absence of large teeth (large teeth on the premaxilla and the coronoid in *Chinlea*) and the lateral swelling of the dentary (no swelling in *Chinlea*).

Diplurus from the Lower Jurassic of North America has a median ridge on the scales (Forey, 1998), but it is not stout like that of this new genus. *Parnaibaia* differs from *Diplurus* by having the concave outline of the parietonasal shield (convex in *Diplurus*), six free extrascapulars (seven in *Diplurus*), two nasals (one in *Diplurus*), equal-sized anterior and posterior parietals (the posterior one larger than the anterior in *Diplurus*). Scales of *Libys* from the Upper Jurassic of Germany are covered with a sparse ornamentation of short ridges without a median ridge (Forey, 1998). *Parnaibaia* differs from *Libys* by having rugose ornamentation on the skull (absence of ornamentation in *Libys*), the postparietal shield being about half the length of the parietonasal shield (less than half in *Libys*), small pores of sensory canal (very large pores in *Libys*). *Garnbergia* from the Middle Triassic (Ladinian) of Germany has no median ridge on the

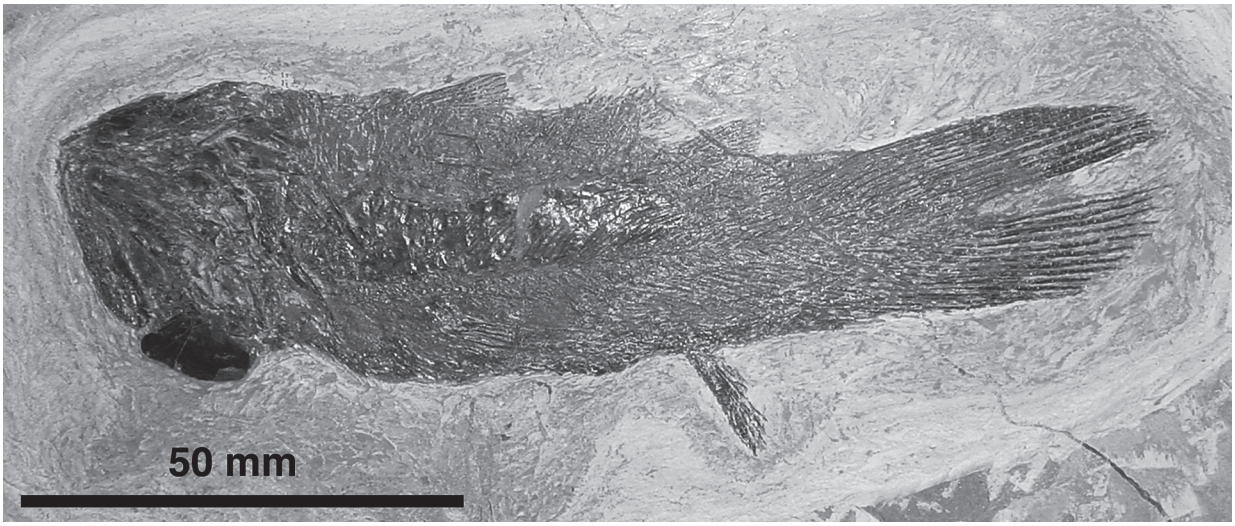

Figure 7. *Parnaibaia maranhaoensis* gen. et sp. nov., paratype (KMNH VP 100,259, 105 mm SL) from the Pastos Bons Formation in Pastos Bons, Maranhao, Brazil.

Figure 8. *Parnaibaia maranhaoensis* gen. et sp. nov., paratype (AMF 9900004-64-364, 242 mm SL) from the Pastos Bons Formation in Pastos Bons, Maranhao, Brazil.

scales (Martin and Wenz, 1984; Yabumoto and Neuman, 2005) and the elongate supraorbital has a broad contact with the lachrymojugal, whereas the lachrymojugal contacts two short supraorbitals in *Parnaibaia*.

The most recent phylogenetic analysis of relationships in the Actinistia is that of Clement (2005) with a description of *Swenzia latimerae* Clement, 2005 from the Oxfordian of Burgundy, France (Clément, 2006). His data matrix is based on the matrix of Forey (1998) with some corrections, such as of character 31, i.e., "preopercular absent (0), present (1)" (Clement, 2005).

In the present study, character 31 of the data matrix of Clement (2005) is coded state 1 instead of ? in *Mawsonia*, because the holotypes of *M. tegamensis* and *M. brasiliensis*, which are articulated specimens, have preopercular, whereas holotypes and additional specimens of other species of *Mawsonia* are isolated, disarticulated or fragmented bones. Clement (2005) coded this char-

acter as ? with the reason that *Mawsonia* cf. *M. gigas* (Maisey, 1989, 1991) and a large and complete specimen of *Mawsonia* sp. from Morocco do not display this bone. However, *Mawsonia* cf. *M. gigas* (Maisey, 1989, 1991) was regarded as *M. brasiliensis* (see Yabumoto, 2002) and most of the specimens of *Mawsonia* from Morocco are isolated, disarticulated, or fragmented bones. PAUP (v. 4.0 Beta, Swofford 2003) and MacClade (v. 4.0.5 OS X; Maddison and Maddison, 2002) analyses are performed using the modified data matrix of Clement (2005) with the present new genus. For *Parnaibaia*, 41% of the data are question marks in the matrix. PAUP analysis using porolepiforms as an outgroup resulted in 16 equally parsimonious trees (length 243, CI = 0.467, RI = 0.701, RC = 0.327). The strict consensus tree of the 16 trees resulted in this new genus forming a clade with *Chinlea*, *Parnaibaia* + *Chinlea* being the sister group of *Mawsonia* + *Axelrodichthys* and *Diplurus* is sister taxon of these two groups (Figure 9A). This new genus and *Chinlea* are very similar to each other in proportion and ornamentation of the skull bones, but the node of the two is only supported by two homoplastic characters (several median rostral 3[1]; CI = 0.333; and anterior and posterior pairs of parietals of similar size 8[0]; CI = 0.250). With the inclusion of this new genus, the strict consensus tree shows the same topology as the tree in Clement (2005, fig. 7).

Forey (1998) applied a posterior weighting procedure in his analysis of the Actinistia because the overall retention index was quite high (0.692) compared with the overall consistency index (0.465). As a further approach, the posterior weighting procedure is employed here because the overall retention index was quite high (0.701) compared with the overall consistency index (0.467). The posterior weighting procedure according to the rescaled consistency index resulted in two equally

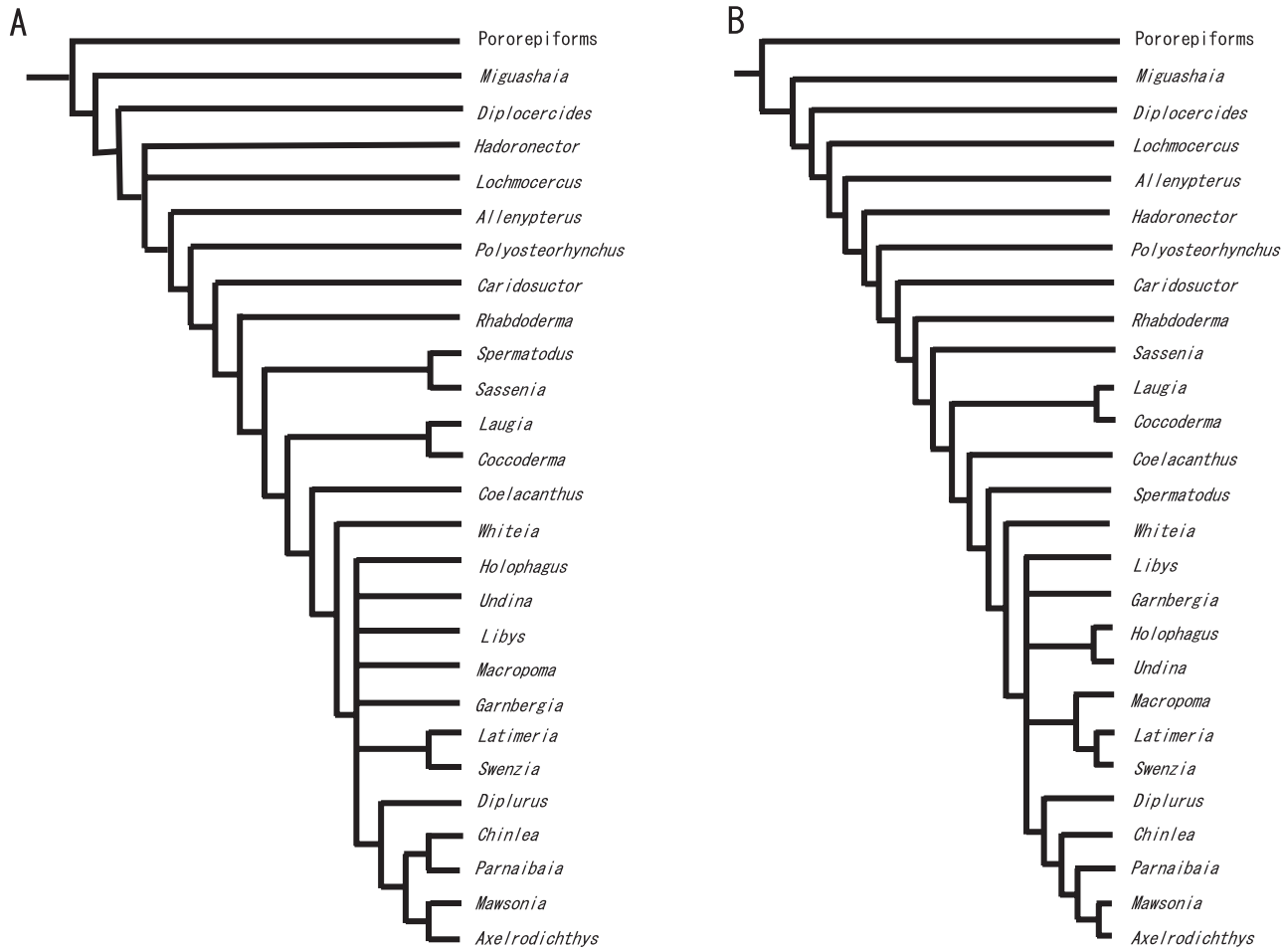

Figure 9. **A**. Strict consensus cladogram resulting from 16 equally parsimonious cladograms under the heuristic search option (TBR). **B**. Strict consensus cladogram resulting from two cladograms by a posterior weighting procedure according to a rescaled consistency index.

parsimonious trees. The strict consensus tree of the two resulted in *Parnaibaia* forming a clade with *Mawsonia* + *Axelrodichthys*, and placed them as the sister group of *Chinlea*, *Diplurus* being their sister taxon (Figure 9B). The node of *Parnaibaia* and *Mawsonia* + *Axelrodichthys* is supported by two synapomorphies (dentary with swelling 65[1] and principal coronoid sutured to angular 66[1]), but the state of character 66 is unknown in this new species; hence, this is a spurious synapomorphy. The topology of the strict consensus tree is the same as that of Forey (1998) with the coding correction of character 31. The posterior weighting procedure with the data matrices of Clement (2005) and Forey (1998) with the correction of character 31 resulted in the same two equally parsimonious trees, except *Swenzia*.

The habitat of *Parnaibaia* is freshwater, which is the same as that of *Diplurus* and *Chinlea* (Forey, 1998). *Mawsonia* and *Axelrodichthys* from the Cretaceous of South America and Africa probably were marine or could go through shallow marine water, because fossils, including *A. araripensis* and *M. brasiliensis*, from the Santana Formation have been determined to come from a shallow sea. (Martill and Wilby, 1993; Martill, 2007; Uyeno and Yabumoto, 2008).

If the age of the Pastos Bons Formation is Late Triassic (Bigarella, 1973) and *Parnaibaia maranhaoensis* is the sister taxon of *Chinlea sorenseni* Schaeffer, 1967, thus this new species possibly belongs to the genus *Chinlea*. *Chinlea* was widely distributed upon the joint continent, which was formed by North America and South America in the Late Triassic. If *P. maranhaoensis* forms a sister group with *Mawsonia* + *Axelrodichthys*, the origin of *Mawsonia* + *Axelrodichthys* dates back to the Late Triassic in South America. There is a chronological gap, the whole Jurassic period between *Mawsonia* + *Axhlrodichthys* and *Parnaibaia* or *Parnaibaia* + *Chinlea*.

If the age is Late Jurassic (Gallo, 2005; Góes and Feijó, 1994) and *P. maranhaoensis* forms a sister group with *Chinlea sorenseni*, the sister group lived in different continents and at different ages. If *P. maranhaoensis* forms a sister group with *Mawsonia* + *Axelrodichthys*, this new species, *P. maranhaoensis*, bridges the chronological gap between *Chinlea* and *Mawsonia* + *Axelrodichthys*.

The last supposition is possibly more convincing than the former one, because *P. maranhaoensis* shares a synapomorphy (the lateral swelling of the dentary) with *Mawsonia* + *Axelrodichthys* and the distribution of *Chinlea*, *Mawsonia* and *Axelrodichthys* is more congruent with the transition of the landmasses from the Late Triassic to the Early Cretaceous. The interpretation for the last supposition is that *Chinlea* probably lived in both North and South America, which formed a major part of Pangea in the Late Triassic. After the division of North and South America in the Late Jurassic, *Parnaibaia* arose in South America, which was a part of Gondwana. In the late Early Cretaceous, *Axelrodichthys araripensis*, *M. brasiliensis* and *M. gigas* appeared in South America while several species of *Mawsonia* arose in Africa (Figure 10).

Acknowledgments

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References

Bigarella, J. J., 1973: Geology of the Amazon and Parnaiba Basins. *In,* Nairn, A. E. M. and Stehli, F. G. *eds.*, *The Ocean Basins and Margins, Volume 1. The South Atlantic*, p. 25–86. Plenum Press, New York.

Clement, G., 2005: A new coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France, and the question of the closest relative fossil to *Latimeria*. *Journal of Vertebrate Paleontology*, vol. 25, p. 481–491.

Clément, G., 2006: *Swenzia*, n. nov., a replacement name for the preoccupied coelacanth genus *Wenzia* Clément. *Journal of Vertebrate Paleontology*, vol. 26, p. 461.

Forey, P. L., 1998: *History of the Coelacanth Fishes*, xiii+419p. Chapman and Hall, London.

Gallo, V., 2005: Redescription of *Lepidotes piauhyensis* Roxo and Löfgren, 1936 (Neopterygii, Semionotiformes, Semionotidae) from the ?Late Jurassic-Early Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, vol. 25, p. 757–769.

Góes, A. M. O. and Feijó, F. J., 1994: Bacia do Parnaíba. *Boletim de Geociências da Petrobras*, vol. 8, p. 57–67.

Huxley, T. H., 1861: Preliminary essay upon the systematic arrangement of the fishes of the Devonian epoch. *Memoirs of the Geological Survey of the United Kingdom*, *London*, dec. 10, p. 1–40.

Lima, M. R. and Campos, D. A., 1980: Palinologia dos folhelhos da fazenda Muzinho, Floriano, Piauí. *Boletim do Instituto de Geociências da Universidade de São Paulo*, vol. 11, p. 149–154.

Maddison, D. R. and Maddison, W. P., 2002: *MacClade 4: analysis of phylogeny and character evolution, Version 4.05*. Sinauer Associates, Sunderland, Massachussets.

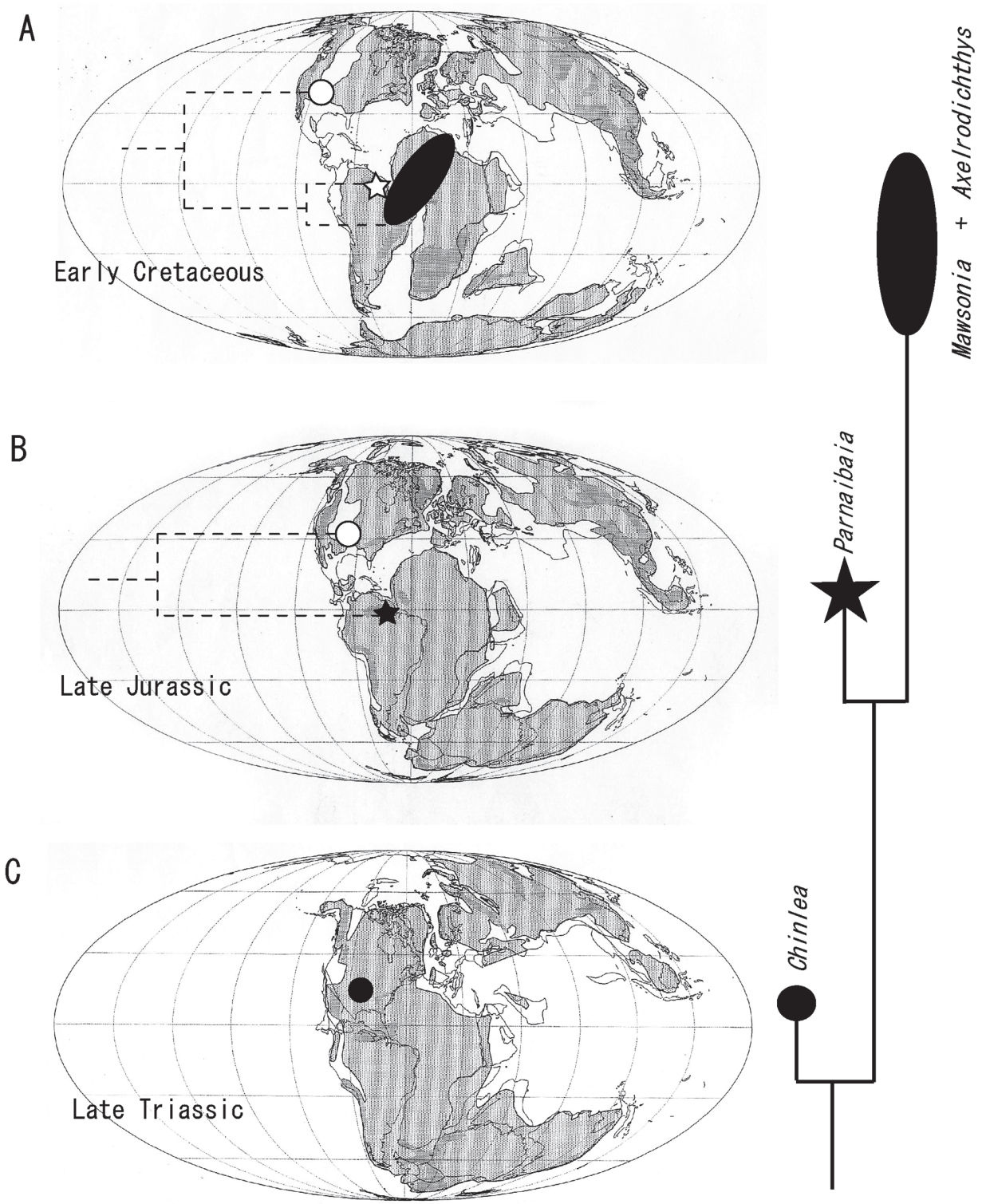

Figure 10. Paleogeographical maps from the Late Triassic to Early Cretaceous (from Smith *et al.*, 1994) and localities showing distributions of *Chinlea*, *Parnaibaia*, and *Mawsonia* + *Axelrodichthys*. Solid circle indicates the locality of *Chinlea* in the Late Triassic. Solid star indicates the locality of *Parnaibaia* in the Late Jurassic (according to the assumption developed in this paper). Solid oval indicates the distribution of *Mawsonia* spp. + *Axelrodichthys* in the Early Cretaceous. Open circles and star indicate the localities of the taxa (*Chinlea* and *Parnaibaia*) which are not recorded in each age. Solid and broken lines indicate the relationships of the three taxa according to results by the posterior weighting procedure.

Maisey, J. G., 1986: Coelacanths from the Lower Cretaceous of Brazil. *American Museum Novitates*, no. 2866, p. 1–30.

Maisey, J. G., 1991: *Santana Fossils: an Illustrated Atlas*. 459 p. IUGS-IGCP Project 242, The Cretaceous of South America. T. F. H. Publications, Neptune City, New Jersey.

Martill, D. M., 2007: The age of the Cretaceous Santana Formation fossil Konservat Lagerstätte of north-east Brazil: a historical review and an appraisal of the biochronostratigraphic utility of its palaeobiota. *Cretaceous Research*, vol. 28, p. 895–920.

Martill, D. M. and Wilby, P. R., 1993: Stratigraphy. *In*, Martill, D. M. ed., *Fossils of the Santana and Crato Formations, Brazil. Field Guides to Fossils*, 5, p. 20–50. The Palaeontological Association, London.

Millot, J. and Anthony, T., 1958: *Anatomie de Latimeria chalumnae. 1. Squellette et muscles*, 122p. CNRS, Paris.

Pinto, I. D. and Purper, Y., 1974: Observations on Mesozoic Conchostraca from the north of *Brazil. Congresso Brasileiro de Geologia*, 28, Porto Alegre. Anais, SBG 2, p. 305–316.

Schaeffer, B., 1967: Late Triassic fishes from the western United States. *Bulletin of the American Museum of Natural History*, vol. 135, p. 285–342.

Schultze, H.-P., 1993: Osteichthyes: Sarcopterygii. *In*, Benton, M. J. *ed.*, *The Fossil Record 2*, p. 657–663. Chapman and Hall, London.

Silva Santos, R., 1974: A idade geológica da Formação Pastos Bons. *Anais da Academia Brasileira de Ciências*, vol. 46, p. 589–592.

Smith, A. G., Smith, D. G. and Funnell, B. M., 1994: *Atlas of Mesozoic and Cenozoic Coastlines*, 99p. Cambridge University Press, Cambridge.

Swofford, D. L., 2003: *Phylogenetic Analysis Using Parsimony. Version 4.0 Beta*. Sinauer Associates, Sunderland, Massachusetts.

Uyeno, T., 1991: Observations on locomotion and feeding of released coelacanths, *Latimeria chalumnae*. *Environmental Biology of Fishes*, vol. 32, p. 267–273.

Uyeno, T. and Yabumoto, Y., 2008: Origin of extant coelacanths. *The Coelacanth, Fathom the Mystery 2007*, Aquamarine Fukushima, p. 24–26.

Woodward, A. S., 1907: On the Cretaceous formation of Bahia (Brazil), and on vertebrate fossils collected therein. II. The vertebrate fossils. *Quarterly Journal of the Geological Society of London*, no. 63, p. 131–139.

Yabumoto, Y., 2002: A new coelacanth from the Early Cretaceous of Brazil (Sarcopterygii, Actinistia). *Paleontological Research*, vol. 6, p. 343–350.

Yabumoto, Y. and Neuman, A., 2004: A coelacanth scale from the Upper Triassic Pardonet Formation, British Columbia, Canada. *Paleontological Research*, vol. 8, p. 337–340.

Appendix 1. Data matrix for 26 coelacanth taxa including present new genus and species, *Parnaibaia maranhaoensis* gen. et sp. nov., plus porolepiforms as the outgroup. The 108 characters are as described by Forey (1988) and Clement (2005).

	1				5					10					15					20					25					30					35					40					45					50
Diplocercides	0	0	1	?	?	?	2	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	1	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rhabdoderma	1	0	0	0	0	0	2	0	0	1	1	0	0	1	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Caridosuctor	1	0	0	0	0	0	2	1	0	1	?	0	?	?	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	1	0
Hadronector	0	0	1	0	0	0	2	1	?	1	?	0	?	?	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	?	?	0	0	0	0	0	0	0	?	1	?	0	?	1	0
Polyosteorhynchus	0	0	?	0	0	0	2	1	0	1	?	?	?	1	0	0	?	0	1	0	1	0	1	?	?	?	0	0	0	1	1	1	?	0	0	0	0	0	0	0	0	0	0	?	1	?	0	0	1	0
Allenypterus	0	?	?	?	?	?	?	2	0	0	1	?	0	?	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	?	1	1	0	0	0	0	0	0	0	0	1	0	0	1	?	?	1	0	1
Lochmocercus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	?	?	?	0	0	0	1	1	1	?	?	0	0	0	0	0	0	0	0	?	0	1	0	0	0	?	0
Coelacanthus	0	0	?	1	1	?	2	1	0	0	1	0	0	1	0	0	1	1	?	1	1	0	?	0	?	1	1	0	1	?	?	?	0	0	0	0	1	?	?	0	0	1	0	?	1	?	1	?	1	0
Spermatodus	1	0	0	0	0	0	2	1	0	1	1	0	0	1	1	0	?	1	1	1	?	0	2	0	?	1	0	0	1	?	1	1	0	1	0	0	0	0	0	0	0	0	?	?	?	?	?	0	1	0
Whiteia	0	0	?	0	0	0	2	0	0	1	1	0	0	1	1	0	1	1	1	1	1	0	0	0	1	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0
Laugia	1	1	?	0	?	?	1	?	0	1	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	?	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0
Sassenia	1	0	?	?	?	?	2	?	0	1	1	0	0	1	0	0	?	0	1	?	?	0	2	0	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Chinlea	0	0	?	0	1	?	2	0	0	0	1	0	?	?	0	0	1	1	?	1	1	0	?	?	?	?	2	0	1	1	1	0	0	?	1	1	0	0	0	0	0	0	1	?	0	?	?	?	2	0
Diplurus	0	0	0	0	1	?	2	1	1	0	1	0	1	0	1	0	2	1	1	1	1	0	0	0	?	1	1	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1
Holophagus	1	0	?	0	1	?	2	1	1	0	1	0	1	1	1	0	?	1	1	1	1	?	2	0	?	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	?	1	?	?	1	1	0
Undina	0	0	?	0	0	?	2	1	1	0	1	0	1	1	1	0	2	1	1	?	1	?	2	?	?	?	0	1	1	0	1	1	0	0	?	?	0	0	0	0	0	0	0	?	1	0	1	1	1	0
Coccoderma	1	0	?	0	1	1	2	1	0	?	1	0	0	1	0	0	1	0	1	1	0	0	2	0	1	0	1	0	1	0	1	0	0	?	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0
Libys	0	?	?	?	1	?	?	?	?	?	1	0	1	1	1	?	?	1	1	1	1	?	0	0	?	1	1	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	?	1	?	?	?	0	1
Mawsonia	1	?	?	?	?	?	2	1	0	0	1	0	1	0	0	1	1	1	?	1	1	0	2	0	?	1	2	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	?	0	0	0	1	2	0
Macropoma	0	1	?	0	?	1	2	1	1	0	1	0	1	1	1	0	2	1	1	1	1	1	2	0	?	1	0	0	1	0	1	?	0	0	1	0	0	0	1	1	0	0	0	1	1	0	1	1	1	0
Latimeria	0	0	1	1	1	1	2	1	1	0	1	0	1	1	1	0	2	1	1	1	1	1	0	0	1	0	2	1	1	1	1	1	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1
Miguashaia	0	0	?	0	0	0	1	?	0	?	0	1	?	?	0	0	0	0	0	0	0	0	2	?	0	0	0	0	0	?	1	1	0	1	?	?	0	0	0	0	0	0	0	?	0	0	0	?	1	0
Axelrodichthys	1	0	0	0	1	1	2	1	0	0	1	0	1	0	0	1	1	1	1	?	1	0	2	0	?	1	2	0	1	0	1	0	0	0	1	0	1	1	0	0	1	0	1	1	0	0	0	1	2	0
Garnbergia	?	?	?	?	?	?	?	2	1	?	0	?	0	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	?	1	0	0	0	1	1	0	0	?	0	0	0	0	?	?	?	?	?	1	?
Swenzia	0	1	?	0	?	?	2	?	?	?	?	0	1	1	?	?	?	1	?	?	1	1	?	0	1	0	1	1	1	1	1	?	0	0	1	0	0	0	1	1	0	0	0	1	1	0	1	1	1	0
Parnaibaia	0	1	1	1	?	?	2	0	0	0	?	0	?	?	0	0	1	1	?	1	?	?	2	?	?	1	2	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	1	?	?	?	?	?	2	?
Porolepiforms	0	0	1	0	0	?	1	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	?	0	0	0	1	1	1	1	1	?	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0

				55					60					65					70					75					80					85					90					100					105					110			118
0	1	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	1	?	0	1	0	0	0	0	?	?	0	0	0	1	0	1	0	0	0	0	0	?	?	0	0	0	0	?	?
0	1	0	1	4	1	0	0	0	0	1	0	0	1	0	0	1	0	1	1	1	0	1	1	0	?	0	0	0	0	?	0	0	0	1	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0
0	1	0	1	4	1	0	0	0	0	1	0	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	0	1	1	1	0	1	0	0	0	1	1	0	0	?	0	1	0
0	1	0	?	?	?	0	0	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	0	1	1	1	0	0	0	0	0	0	1	0	?	?	0	1	0
0	1	0	1	?	0	0	0	1	0	1	0	?	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	0	1	1	1	?	1	0	0	0	1	0	0	0	?	0	0	0
0	1	0	1	?	?	0	1	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
0	1	?	0	?	0	0	?	?	0	0	0	?	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?	1	0	1	0	0	0	0	0	1	0	0	?	?	0	?	0
0	1	0	1	4	1	0	?	?	0	1	?	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	1	1	1	0	1	0	0	0	0	1	0	0	?	0	1	0
0	1	0	1	4	1	?	0	0	0	?	1	?	?	?	0	1	1	1	0	1	0	1	?	?	0	1	1	0	?	?	0	0	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?
0	1	1	1	4	1	1	0	1	?	1	1	1	1	0	0	0	0	1	0	0	0	1	1	1	?	?	0	0	?	1	1	0	1	1	1	1	1	?	1	0	0	1	1	1	2	0	1	0	0	0	1	0	0	1	0	0	0
0	1	0	1	4	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	?	?	0	0	0	1	0	1	1	0	1	1	0	1	1	1	1	1	0	1	1	0	1	0	0	?	0	1	1
0	1	?	1	?	1	0	?	?	0	1	1	1	1	0	0	?	?	0	1	1	0	1	1	0	0	1	?	0	1	?	0	0	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?
1	0	?	?	?	1	1	?	?	?	1	?	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	1	1	1	1	1	?	0	0	0	?	1	0	1	?	1	?	0
1	0	1	?	?	0	0	0	0	0	1	?	1	1	0	0	0	0	1	0	0	0	1	?	1	1	?	0	0	?	?	?	0	?	1	1	1	1	0	1	1	1	1	1	1	1	0	1	0	0	0	1	0	1	?	0	0	0
1	0	1	?	?	1	1	0	0	1	1	1	1	0	0	0	1	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	?	?	1	?	?	1	?	1	1	0	1	1	1	1	?	1	1	0	0	1	1	0	?	0	1	0
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0	1	?	1	4	1	0	0	0	0	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	1	1	1	0	0	0	1	1	0	1	0	0	1	1	1	1
?	1	?	1	4	1	1	0	0	1	1	?	1	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	1	1	1	1	0	1	1	0	0	1	1	0	1	0	1	0
0	0	1	1	?	?	1	?	?	0	1	?	1	1	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1	1	?	0	1	0	0	0	1	0	1	?	1	?	0
1	0	1	1	4	?	1	0	1	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	1	1	?	0	1	?	1	1	0	?	1	1	1	1	1	1	1	0	1	1	1	2	0	1	0	0	0	1	0	1	1	0	1	0
1	0	1	1	4	1	1	0	1	1	1	?	1	1	0	0	1	0	1	0	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	1	1	1	0	1	1	0	1	1	1	2	0	1	0	0	0	1	0	0	1	0	0	0
?	1	?	0	?	?	0	0	1	?	?	0	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	0	0	0	0	?	0	0	0	?	?	0	0	0	0	?	?
1	0	1	1	4	0	1	?	?	0	1	?	1	1	1	1	0	1	1	0	0	0	1	1	1	1	?	0	?	?	1	1	0	?	1	1	1	1	?	1	1	1	1	1	1	1	0	1	0	0	0	1	0	1	?	1	1	0
1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	0	1	0	0	?	0	?	?
?	0	?	1	?	?	1	0	1	?	1	?	1	1	0	?	?	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	1	?	0	1	1	?	?	0	?	?	0	0	1	?	0	?	0	1	?
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0	1	0	0	3	0	0	0	?	0	0	?	0	0	0	0	1	0	0	1	0	1	?	0	0	0	?	1	0	1	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0