

A new Triassic coelacanth, *Whiteia uyenoteruyai* (Sarcopterygii, Actinistia) from Madagascar and paleobiogeography of the family Whiteiidae

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ABSTRACT — Three genera and four species of coelacanths, which are *Piveteauia madagascariensis* LEHMAN, *Rhabdoderma madagascariensis* (WOODWARD), *Whiteia woodwardi* MOY-THOMAS, *W. tuberculata* MOY-THOMAS have been described from the Lower Triassic of Madagascar. In the present study, we examined a coelacanth fossil from Madagascar deposited in Aquamarine Fukushima and determined it as a new species of the genus *Whiteia* of the family Whiteiidae. This new species, *W. uyenoteruyai* sp. nov. is distinguished from other species of the genus in having the combination of the following characters: 20 or more rows of fine long and short ridges separated from each other on scales, ridged ornamentation of lateral line scales on the sensory canal, eight rays on the first dorsal fin, no denticle on fin rays of the first dorsal fin and caudal fins (the third dorsal fin and the second anal fin) and ridges on the posteroventral portion of the operculum. The whiteiid coelacanths are most abundant in the Early Triassic and the origin is probably during the Early Triassic in shallow water along the northern coast of Pangea. *Guizhoucoelacanthus guanlingensis* LIU *et al.* from the Middle and Upper Triassic of China is probably derived from the Early Triassic *Whiteia*, which is most diversified among the family and survived with one species, *W. oishii* from the Late Triassic of West Timor (237–207 Ma), Indonesia. *Atacamaia solitaria* from the Late Jurassic of Chile is probably derived from *Axelia* or *Wimania*.

KEY WORDS: Actinistia, *Whiteia*, Triassic, Madagascar.

INTRODUCTION

Although known since the 19th century, coelacanths became a major center of scientific interest when a living species, *Latimeria chalumnae* SMITH, 1939 was discovered in the western part of the Indian Ocean (SMITH, 1939). This species represented the discovery of a "living fossil" after a gap of 70 million years since the youngest fossil coelacanth remains, *Megalocoelacanthus dobei* SCHWIMMER, STEWART and WILLIAMS, 1994 and *Axelrodichthys megadromos* CAVIN, VALENTIN and GARCIA, 2016, both from the Upper Cretaceous (SCHWIMMER *et al.*, 1994; CAVIN *et al.*, 2005, 2016; DUTEL *et al.*, 2012; CUPELLO *et al.*, 2015).

Coelacanths are known in the fossil record since the Early Devonian (~410 Myr), becoming highly diverse in the Late Devonian and Carboniferous (FOREY, 1988, 1998, FRIEDMAN and COATES, 2006; ZHU *et al.*, 2012). However, this clade reached the highest number of known species during the

Triassic, with more than 27 nominal species described so far (FOREY, 1998; WENDRUFF and WILSON, 2012; YABUMOTO and BRITO, 2016).

One of the richest Triassic localities for coelacanths is the Lower Triassic (Scythian) Middle Sakemena Group, in northern Madagascar from where three genera and four species had been yet described (FOREY, 1989; CLEMENT, 1999). The species are: *Piveteauia madagascariensis* LEHMAN, 1952, *Rhabdoderma madagascariensis* (WOODWARD, 1910), *Whiteia woodwardi* MOY-THOMAS, 1935, and *W. tuberculata* MOY-THOMAS, 1935. In the present study, we describe a new species of coelacanth from the Middle Sakemena Group of Madagascar and consider its affinities within the genus *Whiteia*. The holotype is permanently housed in the Aquamarine Fukushima collection, and registered under the acronym AMF 2-11-04-00-0024.

MATERIALS AND METHODS

Preparation. The specimen AMF 2-11-04-00-0024 is preserved as hard siltstone nodules in which all the bones have been leached out. Therefore, to prepare it, a latex replica was prepared using a vacuum pump, in order to remove all bubbles from the mold. This latex cast was read by a scanner and drawn on a personal computer and observed under a binocular microscope.

Counts, measurements and terminology. Meristic characters evaluations and measurements follows FOREY (1998). The terminology of coelacanth bones used here follows FOREY (1998) and ARRATIA *et al.* (2000). To avoid possible confusion of names, the terminology for the caudal region proposed by UYENO (1991) is presented in parentheses.

Additional material. The following specimens used for comparison in this study are housed respectively in the Natural History Museum of London, UK (NHM), Muséum national d' Histoire naturelle of Paris, France (MNHN), Kitakyushu Museum of Natural History and Human History, Fukuoka, Japan (KMNH), and Oishi Fossil Gallery, Josai University, Tokyo, Japan (OFG).

Whitea woodwardi: NHM P.17200-01 (Holotype); NHM P.17204-5 (Paratype); NHM P.17206-7; NHM P.17208-9; and MNHN -MAE 2509.

W. tuberculata: NHM P.17214-5 (Holotype).

W. oishii: OFG-MF0164 (Holotype) and KMNH VP 100,334a, b (Paratype).

No material of *W. nielseni* and *W. africanus* were examined here, but the character information was based on the description of FOREY (1998).

SYSTEMATIC DESCRIPTION

Order Coelacanthiformes HUXLEY, 1861

Family Whiteiidae SCHULTZE, 1993

(sensu ARRATIA and SCHULTZE, 2015)

Genus *Whitea* MOY-THOMAS, 1935

Whitea uyenoteruyai sp. nov.

(Figs. 1–5)

Material. Holotype, AMF 2-11-04-00-0024: a part and the counterpart of an almost complete specimen without the parietal shield and the supplementary lobe of the caudal fin.

Diagnosis. *Whitea uyenoteruyai* sp. nov. differs from other species of the genus by the following combination of characters: 20 or more rows of fine long and short ridges separated from each other on scales, ridged ornamentation of lateral line scales on the sensory canal, eight rays on the first

dorsal fin, no denticle on fin rays of the first dorsal fin and caudal fin (the third dorsal fin and the second anal fin) and ridges on the posteroventral portion of the operculum.

Type locality and horizon. The locality of the holotype is Ambilobe in the northern part of Madagascar and the horizon is the Lower Triassic Middle Sakamena Group.

Etymology. The species is named in honour of Dr. Teruya UYENO for his contributions to ichthyology, paleontology and studies of coelacanth.

Description of holotype. In AMF 2-11-04-00-0024, the estimated standard length (distance from snout to the base of the supplementary caudal fin lobe (FOREY, 1998)) is about 270 mm, about 2.7 times the maximum body depth, which is 100 mm at the origin of first dorsal fin and about 3 times the head length, which is about 90 mm (Figs. 1 and 2). The length of postparietal shield (distance from the anterolateral corner of the postparietal to the posterior end of lateral extrascapular) is 33 mm.

The postparietal contacts the large supratemporal, which is about half the length of the postparietal (Fig. 3). The postparietal and supratemporal have fine grooves on the surfaces. There are three extrascapulars, a pair of lateral extrascapulars and the median extrascapular. The lateral extrascapulars are round bones and the median extrascapular is a wide bone, which is almost twice the width of the lateral extrascapular. The posterior end of parietal is preserved (Fig. 3).

The right and left lachrymojugals are well preserved (Fig. 3). The anterior part, which has a relatively large oblong opening of the infraorbital canal, is directed anteriorly. The posterior part is curved with its dorsal margin forming the ventral margin of the orbit. Ornament upon the lachrymojugal consists of many tubercles, which are closely adpressed. Many small openings of the sensory canal are along the ventral margin of the lachrymojugal. The posterior end of the lachrymojugal contacts the ventral end of the postorbital.

Other cheek bones are well preserved in the left side (Fig. 3). The postorbital consists of the wide dorsal half and the narrow ventral half, which forms a sensory canal. The dorsal half and posteroventral parts of the squamosal are preserved. It is slightly larger than the postorbital. The depth of the squamosal is about 2.5 times its width. The jugal canal passes through from the middle of the anterior margin to the centre of the bone.

The posterior part of preoperculum is preserved in the left side and the anterior part is well preserved in the right side (Figs. 3 and 4). The preoperculum is a long bone and the length is more than twice the depth. The surface of the anterior part has closely adpressed tubercles. The operculum is rounded dorsally and posteriorly but pointed ventrally. There is no tubercle but ridges or grooves are on the posteroventral part of

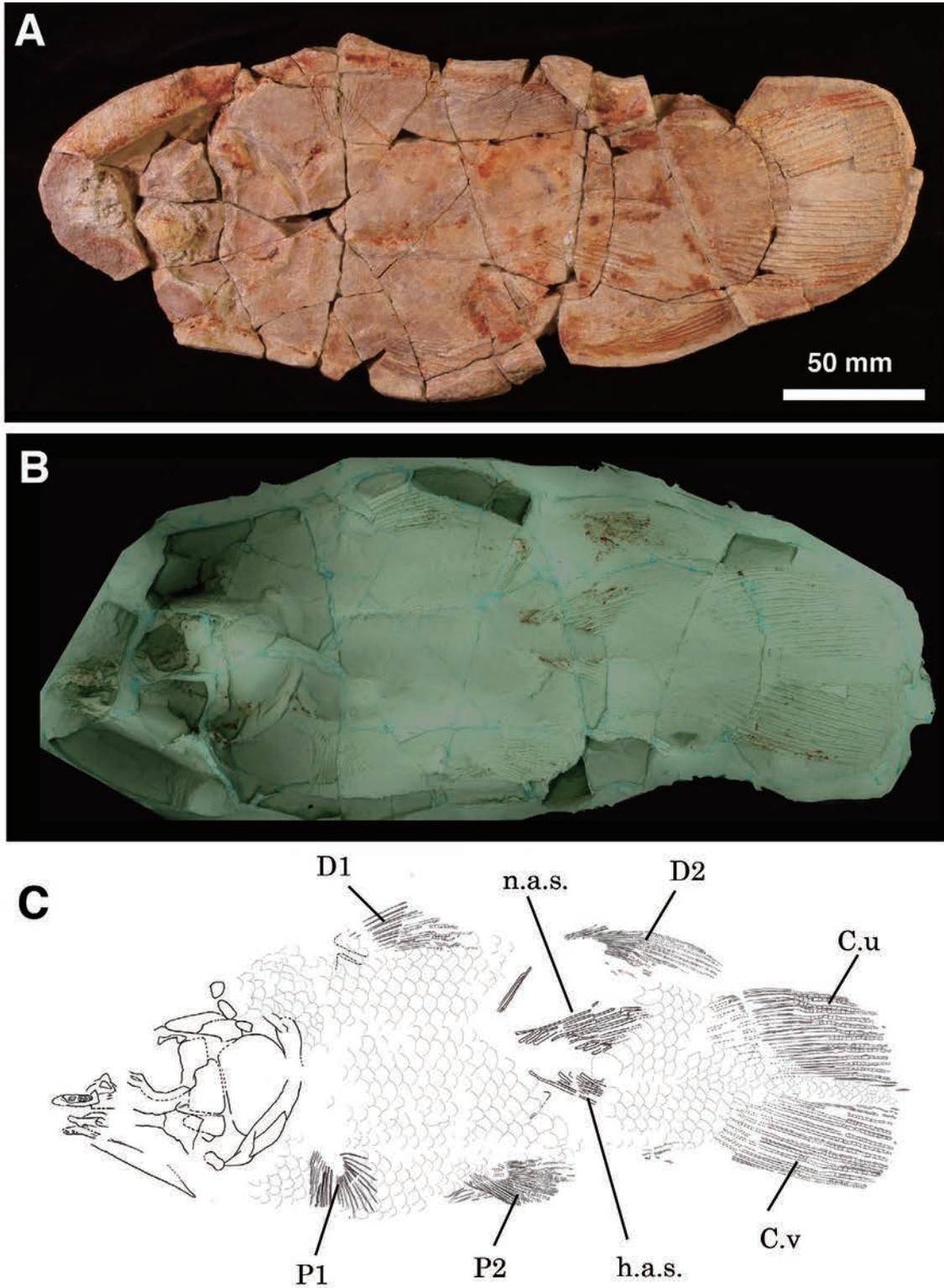


Fig. 1. *Whiteia uyenoteruyai* sp. nov., holotype AMF 2-11-04-00-0024a, A, part; B, a latex peel of A; C, drawing of B. Abbreviations: D1 := first dorsal fin, D2 = second dorsal fin, P1 = pectoral fin, P2 = pelvic fin, C. u= dorsal lobe of caudal fin; C.v = ventral lobe of caudal fin; n.a.s. = neural arch and spine; h.a.s = haemal arch and spine.

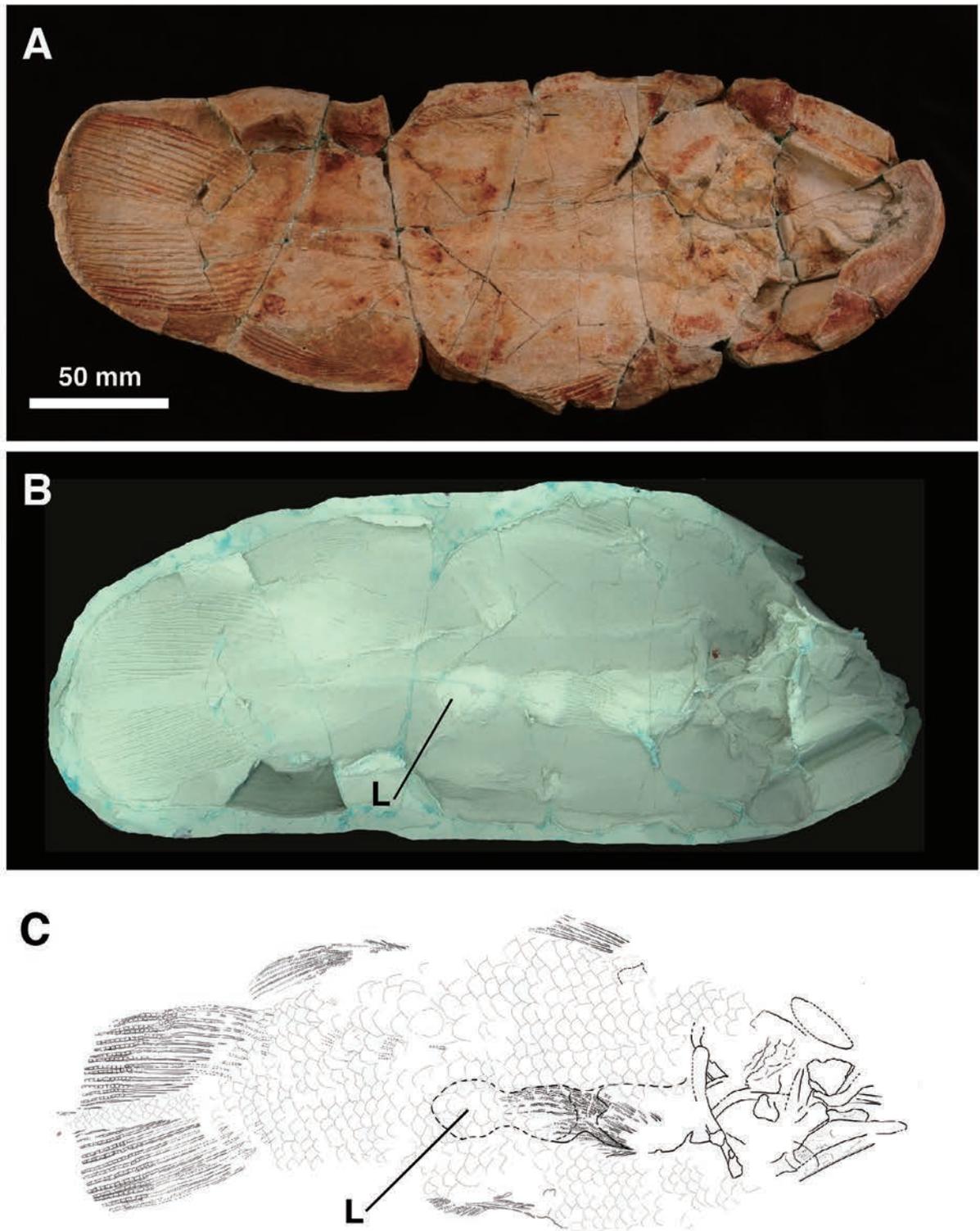


Fig. 2. *Whiteia uyenoteruyai* sp. nov., holotype AMF 2-11-04-00-0024b; A, counterpart of AMF 2-11-04-00-0024a; B, a latex peel of A; C, drawing of B. Abbreviation: L = lung.

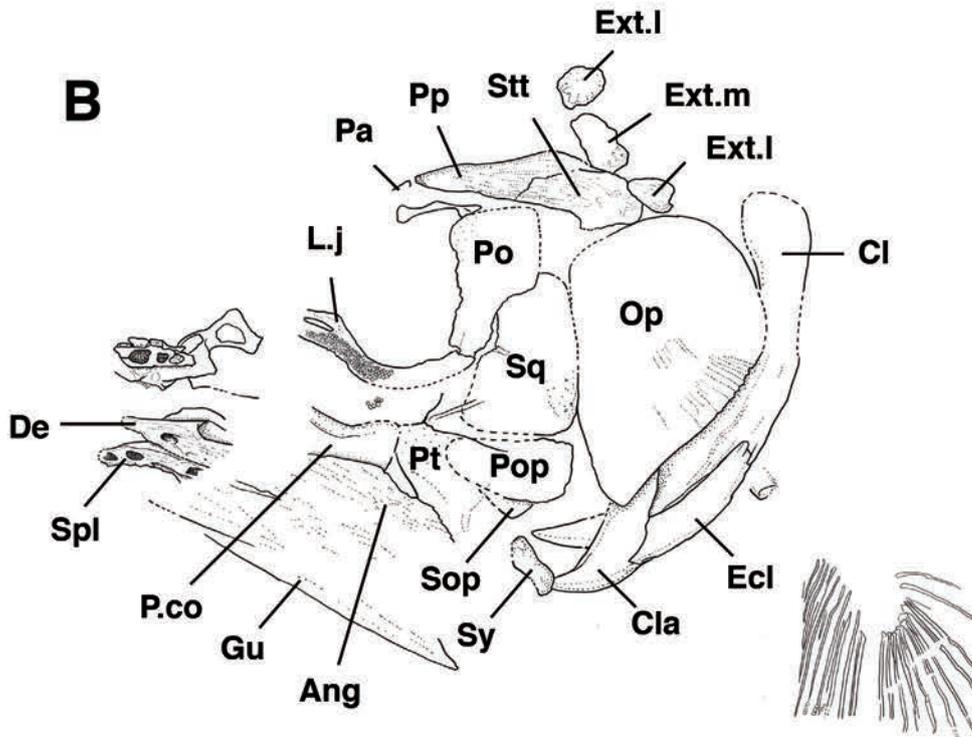
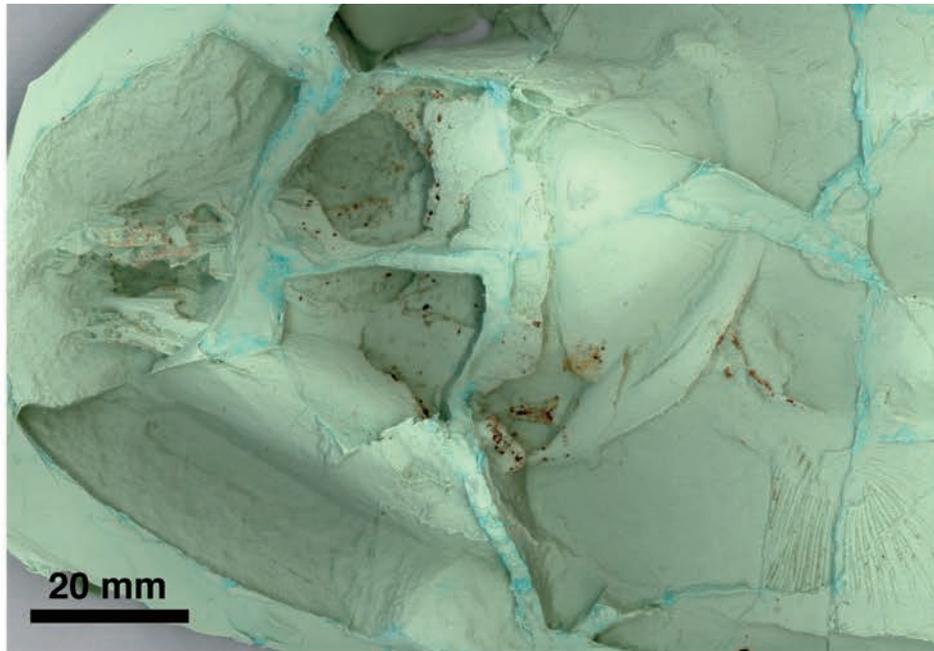


Fig. 3. A, a latex peel of the head of *Whiteia uyenoteruyai* sp. nov., holotype AMF 2-11-04-00-0024a; B, drawing of A. Abbreviations: Ang = angular; Cl = cleithrum; Cla = clavicle; De = dentary; Ecl = extracleithrum; Ext.l = lateral extrascapular; Ext.m = median extrascapular; Gu = gular plate; L.j = lachrymojugal; Op = operculum; Pa = parietal; P.co = principal coronoid; Po = postorbital; Pop = preoperculum; Pp = postparietal; Pt = pterygoid; Spl = splenial; Sop = suboperculum; Sq = Squamosal; Stt = supratemporal; Sy = symplectic.

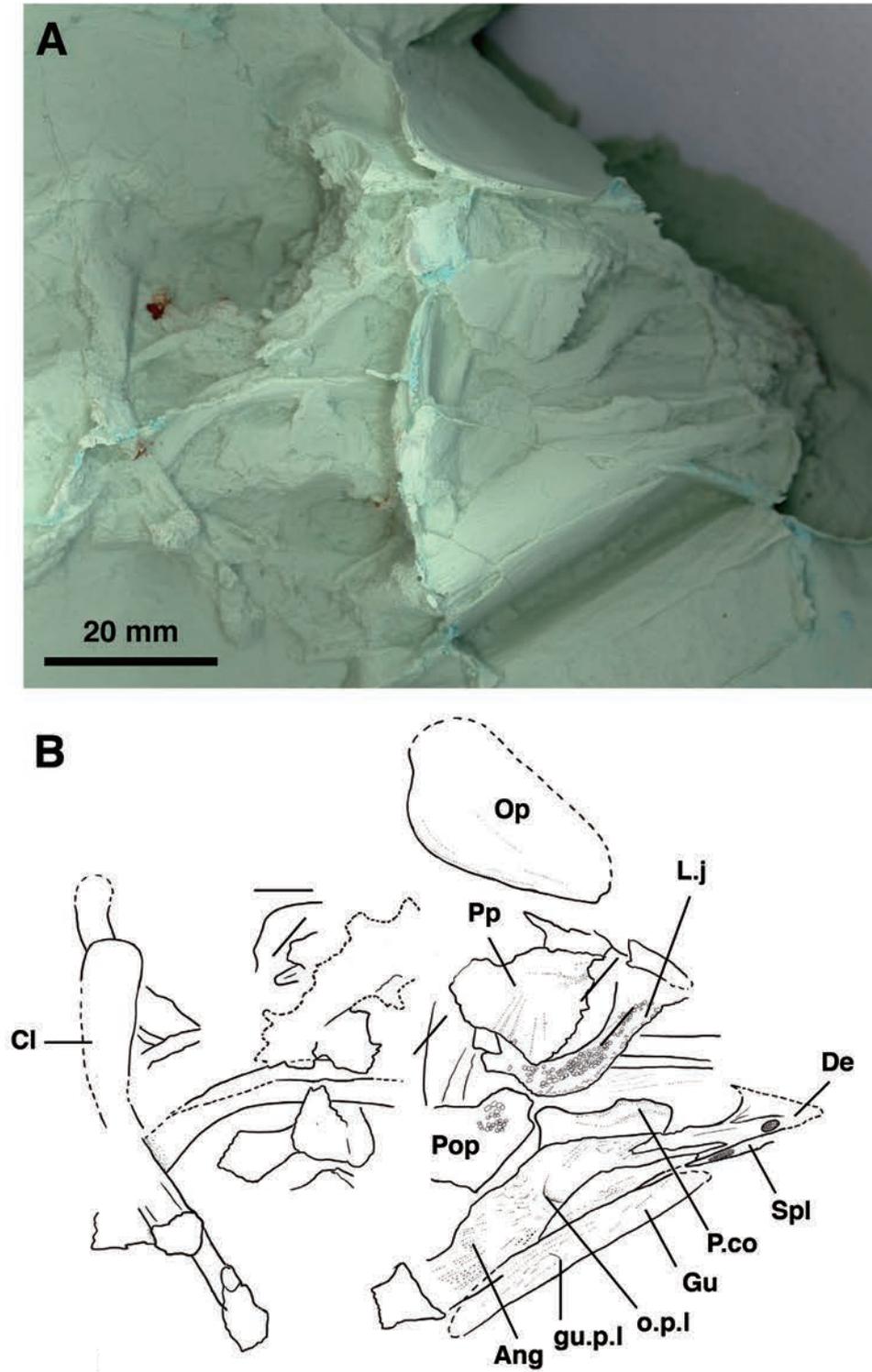


Fig. 4. A, a latex peel of the head of *Whiteia uyenoteruyai* sp. nov., holotype AMF 2-11-04-00-0024b; B, drawing of A. Abbreviations: gu.p.l.= gular pit line; o.p.l. = oral pit line; and see Fig. 3 for the other ones.

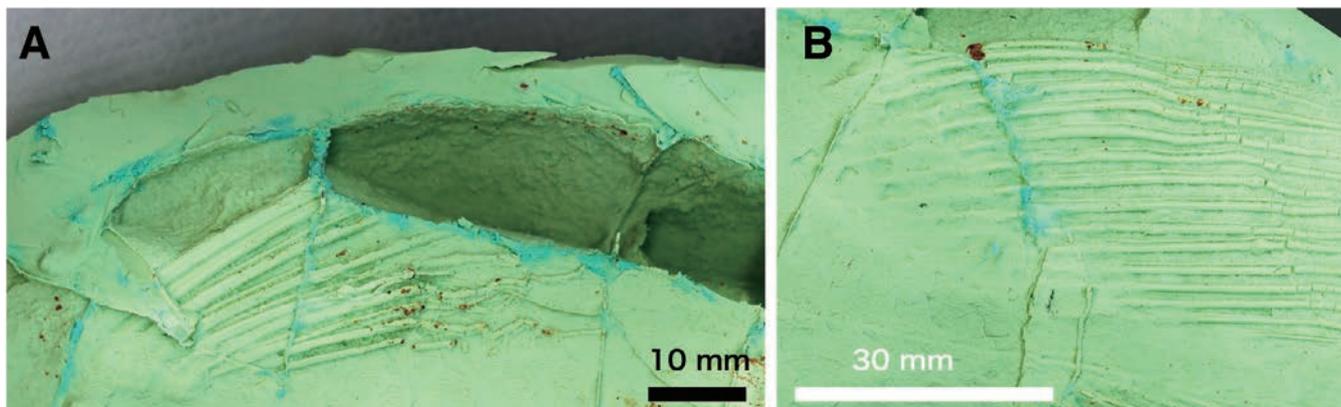


Fig. 5. Latex peel of *Whiteia uyenoteruyai* sp. nov., holotype AMF 2-11-04-00-0024a. A, first dorsal fin; B, dorsal lobe of the caudal fin. Showing no denticle on fin rays.

the bone and form a serrated margin. The posterior end of the suboperculum can be seen under the preoperculum in the left side (Fig. 3).

The angular is a shallow long bone (Fig. 4). Fine radial grooves are on the surface. The oral pit line is located at the centre of the angular and it is curved posteriorly. The anterior end contacts with the dentary and the splenial. The dentary is a hook-shaped bone and has an enlarged sensory pore on the anterior part. The dentary in this species is hook-shaped having a well separated dorsal process and it looks more like *W. nielsenii* than in *W. woodwardi* and *W. tuberculata*. The splenial is curved medially and ventrally at the anterior part (Fig. 3). Four enlarged sensory pores can be seen on the splenial. The principal coronoid is a large saddle-shaped bone, longer than deep, with the thick dorsal margin (Fig. 3).

The gular plates are preserved in both sides (Figs. 3 and 4). The posterior end is pointed and the anterior end is round. The gular pit line, which is a bow-shaped line, is located at the centre of the bone (Fig. 4). It is straight in *W. nielsenii* and *W. tuberculata*.

The symplectic is preserved between the suboperculum and the clavicle (Fig. 3). It is a short thick bone being slightly narrow in the middle. The palate is preserved in the left side, but shape cannot be seen due to covering by other bones (Fig. 3). The shoulder girdle is well preserved in the left side (Fig. 3). The clavicle covers the ventral end of the cleithrum and the extracleithrum with the pointed ventral end. The cleithrum is a long bone being slightly narrow in the part just above the middle. The extracleithrum is sutured to the posterior edges of the cleithrum and the clavicle being more closely associated with the cleithrum than the clavicle.

The first dorsal fin bears eight rays (Fig. 5). There is no denticle on the fin rays. Although scales cover the basal plate, the shape of the basal plate is recognized (Fig. 1). It is triangular with the thick anterior edge. The second dorsal fin has 15 rays and it is long and reaches to the base of the caudal

fin (the third dorsal fin).

The caudal fin (the third dorsal fin and the second anal fin) is large (Figs. 1 and 2). The dorsal lobe of the caudal fin has 16 fin rays of which the most ventral one is short and thin (Fig. 5), the ventral lobe has 16 fin rays of which the most ventral one is very short without any segment. The supplementary lobe of the caudal fin is not preserved.

The number of rays in the pectoral fin is 22 in the left side and 21 in the right side (Figs. 1 and 2). The fin is long and reaches to the point under the middle of the first and second dorsal fins, beyond the pelvic fin base.

The pelvic fins are located under the mid-length between the first and second dorsal fins (Figs. 1 and 2). The number of rays in the pelvic fin is 18 in the left side. Although scales cover the base of the pelvic fin, it is recognized that the posterior margin is thick.

Eight neural arches and spines and seven haemal arches and spines can be seen under the second dorsal fin. Two neural spines are preserved under between the first and second dorsal fins. These neural and haemal spines are long.

Scales are large and the number of lateral line scales is 38 (Figs. 1 and 2). The superficial ornamentation of scales is composed of 20 rows or more of fine long and short ridges, which remain separate from one another (Fig. 6). The surfaces of sensory canals of lateral line scales are not smooth, but ornamented by the same type of ridges on other part of scales (Fig. 6).

The lung is long about one-third of the standard length. It is marked by two constrictions (Fig. 2). The most anterior chamber is the largest and almost twice as the second one. The second and the third ones have almost the same size. Most of coelacanths have a lung covered by bony plates (BRITO *et al.*, 2010), however no bony plate could be recognized around the lung in the holotype specimen.

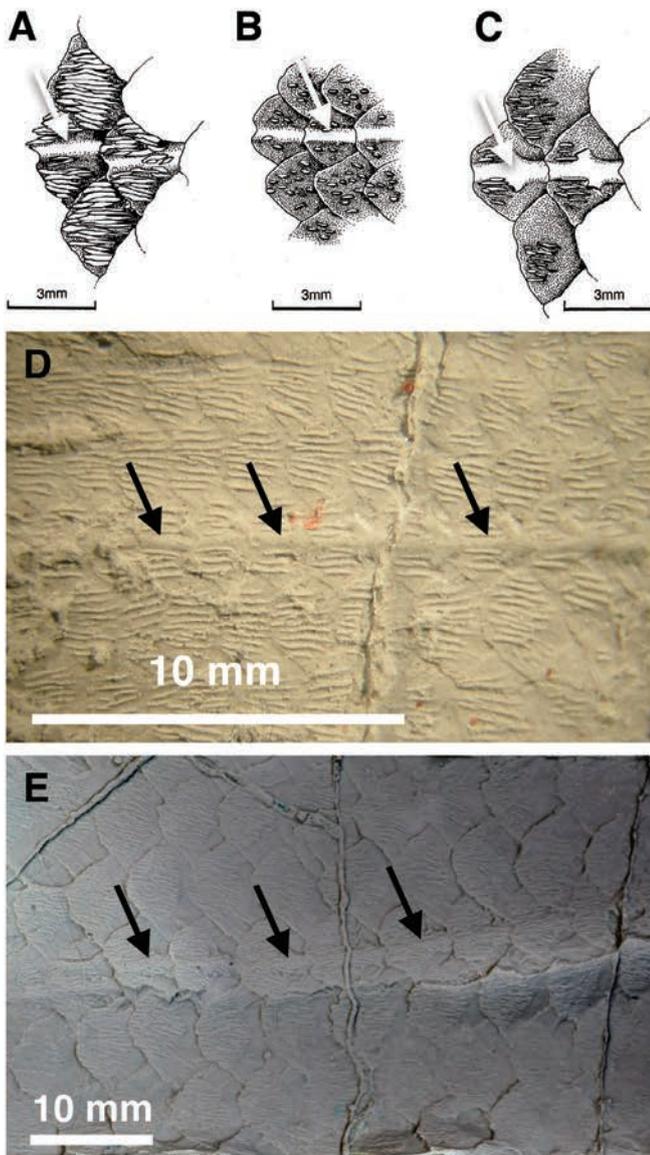


Fig. 6. Comparison of scales. A, *Whiteia nielsenii*, B, *W. tuberculata*, C, *W. woodwardii*; D, paratype (NHM P. 17204-5) of *W. woodwardii*; E, latex peel of holotype of *W. uyenoteruyai* sp. nov., AMF 2-11-04-00-0024b. Right is anterior. A, B and C are from FOREY (1998). Arrows indicate surfaces of sensory canals of lateral line scales.

DISCUSSION AND CONCLUSIONS

Five species have been described in the genus *Whiteia*, which are *W. nielsenii* FOREY, 1998 from the Lower Triassic (Scythian) Wordie Creek Formation of East Greenland; *W.*

woodwardii MOY-THOMAS, 1935 and *W. tuberculata* MOY-THOMAS, 1935 from the Lower Triassic (Scythian) Middle Sakemena Group, northern Madagascar; *W. africanus* (BROOM, 1905) from the Lower Triassic of Republic of South Africa; *W. oishii* YABUMOTO and BRITO, 2016 from West Timor, Indonesia. FOREY (1998) recognized the specimens from the Lower Triassic (Scythian) Spray River Formation, Canada, mentioned by GARDINER (1966) and SCHAEFFER and MANGUS (1976) as *Whiteia* sp.

The new taxon can be assigned to the genus *Whiteia* because of the presence of the long snout with an elongated anterior tip, the curved posterior region of lachrymojugal, operculum rounded dorsally and posteriorly but pointed ventrally and characteristics of the postorbital and the squamosal (c.f., FOREY, 1998). The identification of *W. uyenoteruyai* sp. nov. as a new species was done by a comparison to other species of the genus *Whiteia*.

Whiteia uyenoteruyai sp. nov. shares with *W. nielsenii* the presence of a hook-shaped dentary (c.f. FOREY 1998, page 149, fig. 5.9), it differs from this species in having eight first dorsal fin rays (*versus* nine in *W. nielsenii*), long and short ridges separated each other on the scales (the ridges are elongate and closed addressed to one another on scales in *W. nielsenii*), ridges on the whole surface of sensory canals of lateral line scales (these are smooth in *W. nielsenii*) (Fig. 6), and the operculum ornamented by ridges on its posteroventral portion (ornamented by tubercles without ridges in *W. nielsenii*). With *W. tuberculata*, the new species differs by the long ridges on the scales (*versus* tubercles in *W. tuberculata*) (Fig. 6).

Whiteia uyenoteruyai sp. nov. has two common characters with *W. africanus*: eight first dorsal fin rays and no denticles on fin rays of the first dorsal fin and caudal fin (Table 1). However it differs from *W. africanus* in having more numerous fine long and short ridges on the scales (20 or more rows *versus* 10 or fewer in *W. africanus*), ridges on the whole surface of sensory canals of the lateral linescales (these are smooth in *W. africanus*) (Fig. 6), and ridges on the posteroventral portion of the operculum (the operculum is ornamented by tubercles without ridges in *W. africanus*). FOREY (1998) mentioned that *W. africanus* has never been satisfactorily distinguished from other coelacanths and it may well be conspecific with *W. woodwardii*.

Whiteia uyenoteruyai sp. nov. is similar to *W. woodwardii* in having eight first dorsal fin rays and tubercles on the surfaces of the lachrymojugal. However it differs from this species in having more numerous fine long and short ridges on the scales (20 or more rows *versus* 10 or fewer in *W. woodwardii*), ridges on the whole surface of sensory canals of lateral line scales (smooth in *W. woodwardii*) (Fig. 5). It is important to emphasize that most specimens of *W. woodwardii*, including the holotype, are small individuals with less than 160 mm standard length although *W. uyenoteruyai* sp. nov. is about 270 mm. One of the largest known specimens of *W. woodwardii*, MNHN MAE 2509, which estimated standard

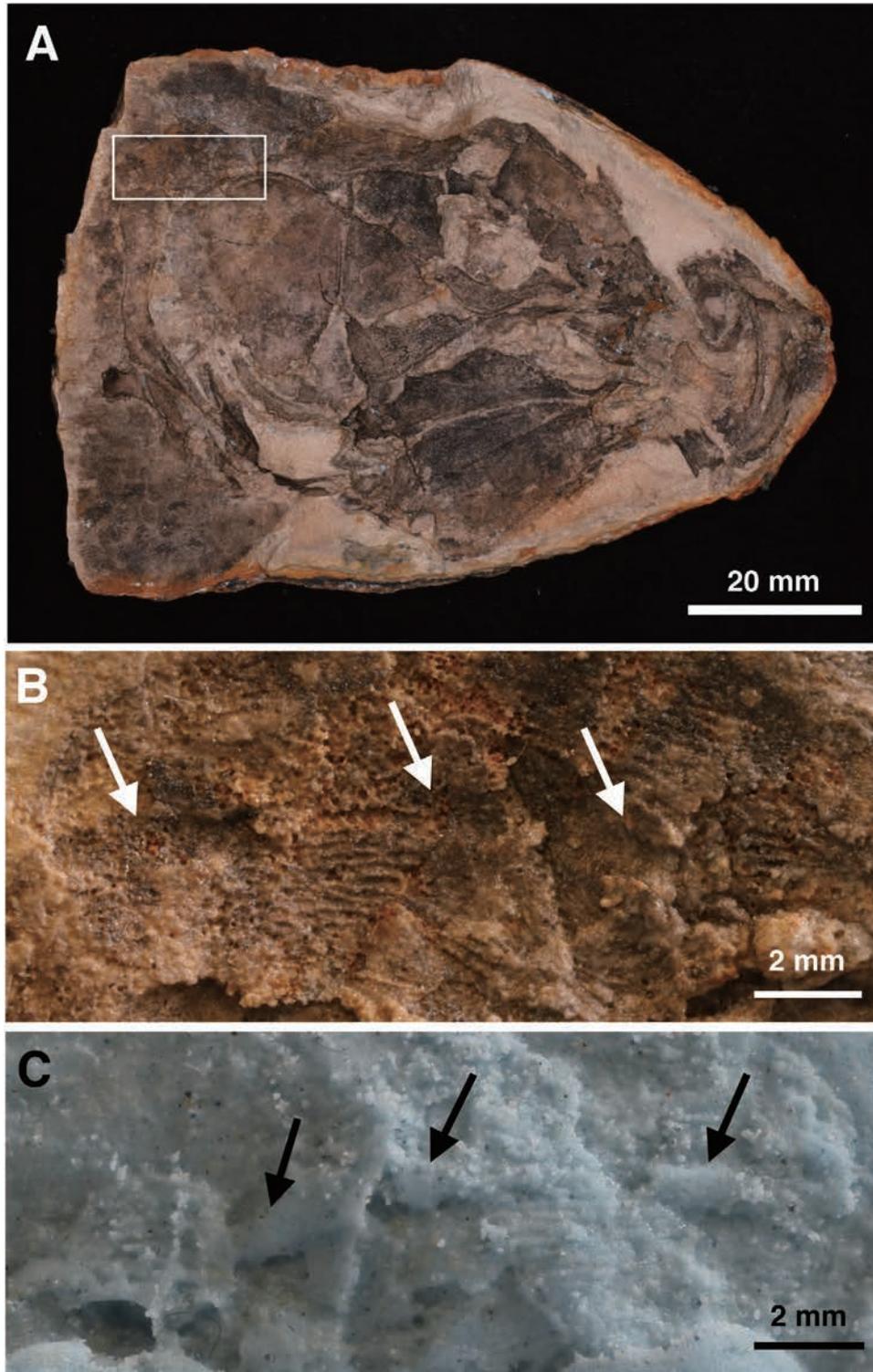


Fig. 7. Large specimen of *Whiteia woodwardi*, MNHN MAE 2509, estimated standard length 180 mm based on the head length (about 60 mm). A, head and anterior part of the body; B, rectangular part of A showing lateral line scales; C, a latex peel of B. Arrows indicate smooth surfaces of sensory canals in B and C.

Table 1. Comparison of characters in the genus *Whiteia*.

	D1	Ornamentation of scales	Sensory canal of lateral line scales	Denticle on first dorsal and caudal fins	Tubercles on operculum	Ridges on operculum
<i>W. uyenoteruyai</i>	8	20 rows or more of spares ridges	ridges	absent	absent	present
<i>W. woodwardi</i>	7–8	10 rows or less of spares ridges	smooth	present	present	absent
<i>W. tuberculata</i>	7	tubercle	smooth	present	present	absent
<i>W. nielseni</i>	9	15 to 20 rows of adpress ridges	smooth	—	present	absent
<i>W. africanus</i>	7 or 8	less than 10 rows of ridges	smooth	absent	present	absent
<i>W. oishii</i>	9	5 to 10 rows of spares ridges	smooth	present	present	absent

length is about 180 mm based on the head length (about 60 mm), smaller than the new species, presents smooth surface of the sensory canals of the lateral line scales (Fig. 7).

Other differences between these two Malagasy species are the ridges on the posteroventral portion of the operculum in *W. uyenoteruyai* sp. nov. (the operculum is ornamented by tubercles without ridges in *W. woodwardi*) and no denticle on fin rays of the first dorsal and caudal fins (there are small denticles on anterior fin rays of the first dorsal and caudal fins in NHM P. 17206-7 *W. woodwardi*). Furthermore, the ventral part of the postorbital in *W. uyenoteruyai* sp. nov. is longer than that of *W. woodwardi*. The extracleithrum is more closely associated with the cleithrum than the clavicle in this new species. FOREY (1998, page 217 and fig. 4.15) mentioned that the extracleithrum is closely associated with the clavicle in *Whiteia*. However, in the same paper, on fig. 11.18, we can note that this bone is much more associated with the cleithrum. In the specimens of KMNH VP (M09, M18, M 50) identified as *W. woodwardi* the extracleithrum is equally associated with both, the clavicle and the cleithrum.

In addition, *Whitea uyenoteruyai* sp. nov. differs from other members of the genus by: like in *W. tuberculata*, the oral pit line of the angular is curved in the new species, unlike the straight shape in *W. woodwardi*, and the long L-shaped in *W. nielseni*, and curved in *W. tuberculata* (see FOREY, 1998, fig. 5.9).

The angular has radial fine grooves in *Whitea uyenoteruyai* sp. nov., although there are few sparse tubercles in *W. woodwardi* and many closely adpressed tubercles above the oral pit line in *W. nielseni*. However, the dentary in this new species is more similar to that of *W. nielseni* than with *W. woodwardi* and *W. tuberculata*.

Finally, the gular pit line is bow-shaped in this new species, but straight in *W. nielseni* and *W. tuberculata*.

PALEOBIOGEOGRAPHY OF THE FAMILY WHITEIIDAE

The geological and chronological distributions of Whiteiidae are shown in Fig. 8. Six genera and 11 species of the family Whiteiidae have been described and five species undeterminable whiteiid coelacanths (*Whiteia* spp. from Madagascar, Africa and Canada; *Wimania* sp. from West Spitsbergen) have been recognized from Triassic and Jurassic marine deposits (ARRATIA and SCHULTZE, 2015; YABUMOTO and BRITO, 2016) (Fig. 8).

Whiteiid coelacanths are most abundant in Early Triassic and distributed in the shallow sea along the southern and northern coasts of Pangea (Fig. 8A). Five species have been found from southern deposits: *Piveteauiia madagascariensis* LEHMAN, 1952; *Whiteia tuberculata* MOY-THOMAS, 1935; *W. woodwardi* MOY-THOMAS, 1935; *W. uyenoteruyai* sp. nov., *Whiteia* sp. (NEILSEN, 1936) from the Middle Sakamena Group (252 Ma), Madagascar and *Whiteia africanus* (BROOM, 1905) from the Lower Triassic Orange Free State, South Africa (Fig. 8A, 1 and 2). Seven species have been found from the northern deposits: *Whiteia nielseni* FOREY, 1998 from the Wordie Creek Formation (252–251 Ma), East Greenland; *Axelia elegans* STENSIÖ, 1921, *A. robusta* STENSIÖ, 1921, *Wimania multirostrata* STENSIÖ, 1921, *Wimania sinuosa* STENSIÖ, 1921, and *Wimania* sp. from the Sticky Keep Formation (251–247 Ma), West Spitsbergen (STENSIÖ, 1921); and *Whiteia* sp. from the Toad-Grayling and Sulphur Mountain formations (251 Ma), British Columbia, Canada (SCHAEFFER and MAGNUS, 1976) (Figs. 8A, 3–5). Although still premature, due to the lack of a good phylogenetical resolution for the Whiteiidae, the fact that the southern coast of Pangea species are older, seems to suggest a geographical origin for the family in this part.

The late Middle Triassic and the early Late Triassic whiteiid coelacanth *Guizhoucoelacanthus guanlingensis* LIU *et al.*, 2006 has been found from Guizhou (235–228 Ma) and Yunnan (242–235 Ma) provinces, China (Figs. 8B, 6)(GENG *et*

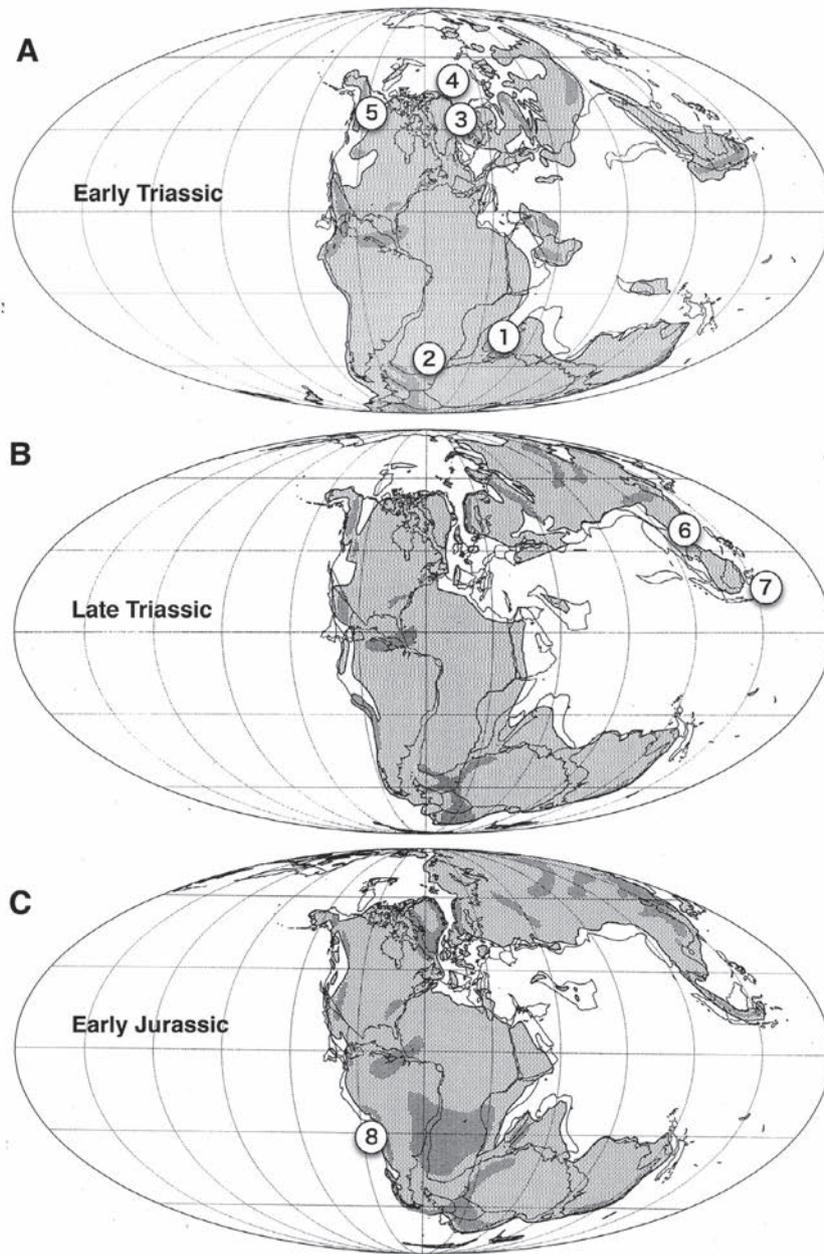


Fig. 8. Paleogeographical maps from the Early Triassic to Early Jurassic (from SMITH *et al.*, 1994) and distribution of the family Whiteiidae during Triassic and Jurassic times. A, paleogeographical map of Early Triassic; B, paleogeographical map of Late Triassic; C, paleogeographical map of Early Jurassic; 1, *Piveteaia madagascariensis* LEHMAN, 1952; *Whiteia tuberculata* MOY-THOMAS, 1935; *W. woodwardia* MOY-THOMAS, 1935; *W. uyenoteruyai* sp. nov., *W. sp.* (NEILSEN, 1936) from the Middle Sakamena Group (252 Ma), Madagascar; 2, *Whiteia africanus* (BROOM, 1905) from the Lower Triassic Orange Free State, South Africa; 3, *Whiteia neilseni* FOREY, 1998 from the Wordie Creek Formation (252–251 Ma), East Greenland; 4, *Axelia elegans* STENSIÖ, 1921, *A. robusta* STENSIÖ, 1921, *Wimania multirostrata* STENSIÖ, 1921, *Wimania sinuosa* STENSIÖ, 1921, *Wimania* sp. from the Sticky Keep Formation (251–247 Ma), West Spitsbergen (STENSIÖ, 1921); 5, *Whiteia* sp. from the Toad-Grayling and Sulphur Mountain formations (251 Ma), British Columbia, Canada (SCHAEFFER and MAGNUS, 1976); 6, *Guizhoucoelacanthus guanlingensis* LIU *et al.*, 2006 from Guizhou (235–228 Ma) and Yunnan (242–235 Ma) provinces, China; 7, *Whiteia oishii* YABUMOTO and BRITO, 2016 from West Timor (237–207 Ma); 8, *Atacamaia solitaria* ARRATIA and SCHULTZE, 2015 from Chile (199–191 Ma).

al., 2009). This species is probably derived from an ancestor in the shallow water in the western Tethys Sea, because *G. guanlingensis* is the sister of *Piveteauia* + *Whiteia* (see GENG *et al.*, 2009) and also forms a sister group of *Whiteia* with *Axelia* and *Wimania* in the phylogenetic analysis by DUTEL *et al.* (2012).

Among the family Whiteiidae, species of the genus *Whiteia* are the most abundant, five species have been described including this new species, and widely distributed around Pangea in Early Triassic and survived one species, *W. oishii* in the Late Triassic West Timor (237–207 Ma), Indonesia (Fig. 8B, 7).

Early Jurassic whiteiid, *Atacamaia solitaris* ARRATIA and SCHULTZE, 2015 from Chile (199–191 Ma) is probably derived from a group of *Axelia* or *Mimania* in Panthalassa along the western coast of Pangea (Fig. 8C), because it forms a trichotomy with *Axelia* and *Wimania* (see ARRATIA and SCHULTZE, 2015) and the species of these genera are from the shallow sea of the northern coast of Pangea.

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