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Source: *Acta Palaeontologica Polonica*, 58(1) : 175-193

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2011.0066>

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# Coelacanths from the Middle Triassic Luoping Biota, Yunnan, South China, with the earliest evidence of ovoviviparity

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Wen, W., Zhang, Q.-Y., Hu, S.-X., Benton, M.J., Zhou, C.-Y., Tao, X., Huang, J.-Y., and Chen, Z.-Q. 2013. Coelacanths from the Middle Triassic Luoping Biota, Yunnan, South China, with the earliest evidence of ovoviviparity. *Acta Palaeontologica Polonica* 58 (1): 175–193.

The fossil record of coelacanths is patchy, with very few taxa known from the Triassic of Asia. We report here two new genera and species of coelacanths from the Luoping Biota, a recently found site of exceptional fossil preservation from Yunnan, South China. The first new taxon, *Luopingcoelacanthus eurylacrimalis*, is based on four specimens, which together show most aspects of the anatomy. One specimen shows two small coelacanths inside the ventral portion of the abdominal cavity, and these are interpreted as intrauterine embryos, close to birth size, based on comparisons with previously reported embryos of the fossil coelacanths *Rhabdoderma* and *Undina*, and the extant genus *Latimeria*. Our new find extends the evidence for ovoviviparity in coelacanths back from the Late Jurassic to the Middle Triassic. The second new taxon, *Yunnancoelacanthus acrotuberculatus*, is based on one specimen, and differs from *Luopingcoelacanthus* in the dentary, lachrymojugal, number of rays of the first dorsal fin, and especially in the ornament on dermal bones and scales. A cladistic analysis shows that the new taxa are closest relatives to the derived clade Latimerioidei. The relatively high diversity of coelacanths in the Early Triassic, and adaptations of living *Latimeria* to low-oxygen conditions, suggests that the group may have included ‘disaster taxa’ that benefited from anoxic and dysoxic ocean conditions in the aftermath of the end-Permian mass extinction.

**Key words:** Actinistia, Coelacanthoidei, Latimerioidei, ovoviviparity, Luoping, Anisian, Triassic, South China.

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Received 8 May 2011, accepted 6 March 2012, available online 8 March 2012.

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## Introduction

Fossil coelacanths have been known since 1822, when Gideon Mantell described the genus *Macropoma* from the Upper Cretaceous of England (Mantell 1822), and 15 years later Louis Agassiz erected the name coelacanth (“hollow spine”) on the basis of an incomplete specimen from the Permian of England (Forey 1998). The fossil record of coelacanths now extends from the Early Devonian to the Late Cretaceous (Cloutier and Forey 1991; Forey 1998; Johanson et al. 2006). Fossil coelacanths are limited in numbers, and they show an

unusual temporal distribution, with a peak in the Early Triassic, and low numbers before and after. The Early Triassic peak consists of 13–20 species, which fell to 4–10 in the Middle Triassic, and 3–7 in the Late Triassic, according to the compilation by Cloutier and Forey (1991). These minimum numbers are based on secure taxa with good specimens, and the maxima include also incomplete specimens. The Early Triassic total, although based on a limited number of localities, represents a high point in coelacanth diversity through all geological time (Forey 1998).

The Early Triassic coelacanth taxa include two species

of *Axelia*, two of *Mylacanthus*, one of *Sassenia*, one of *Scleracanthus*, and one of *Wimania* from the Sticky Keep Formation of Spitsbergen (7 species in all), *Laugia* from the Wordie Creek Formation of Greenland, *Whiteia* from the Vega-Phroso Formation of British Columbia, Canada, *Coelacanthus*, *Piveteauia*, and two species of *Whiteia* from the Middle Sakamena Group of Madagascar, and *Whiteia* from the Beaufort Beds of South Africa (Forey 1998; López-Arbarello 2004). The four Middle Triassic genera are *Alcoveria* from the Muschelkalk of Spain, *Garnbergia* from the Muschelkalk of Germany, *Heptanema* from Italy, and *Ticinepomis* from the Grenzbitumen of Switzerland (Forey 1998). The Late Triassic taxa include two species of *Chinlea* from the Chinle Group of the southwestern United States (Schaeffer 1967; Irmis 2005; Milner et al. 2006), and one species of *Diplurus* from the Newark Supergroup of the eastern United States (possibly also *Pariostegus*; Liutkus et al. 2010; Whiteside et al. 2011). In addition are the new materials from China.

The fossil record of coelacanths from China consists of five genera from the Late Permian to the Early Triassic: the Upper Permian *Changxingia* and *Youngichthys* (Wang and Liu 1981), the Early Triassic *Sinocoelacanthus* (Liu 1964) and *Chaohuichthys* (Tong et al. 2006), and the Late Triassic *Guizhoucoelacanthus* (Liu and Yin 2006; Geng et al. 2009). Hitherto, coelacanths have not been reported from the Middle Triassic of China, and indeed, as noted, they are rare in the Middle Triassic worldwide.

Here we present a new coelacanth from the Luoping Biota, which occurs in the second Member of the Guanling Formation, of early Middle Triassic age (Zhang and Zhou 2008; Hu et al. 2011). The stratum bearing the Luoping Biota is characterized by laminated micritic limestone interbedded with muddy limestone and cherty micritic limestone (Zhang et al. 2008). This ichthyobiota is composed mostly of actinopterygian fishes, and coelacanths are relatively rare. Initial identifications indicate nine families of actinopterygian fishes (Tintori et al. 2007, 2010; Sun et al. 2009; Wu et al. 2009, 2010; Zhang et al. 2010; Wen et al. 2012), and ten new species have been named: *Macropoloichthys ani* (Tintori et al. 2007), *Luopingichthys bergi* (Sun et al. 2009), *Saurichthys dawaziensis* (Wu et al. 2009), *Saurichthys yunnanensis* (Zhang et al. 2010), *Gymnoichthys inopinatus* (Tintori et al. 2010), *Sinosaurichthys longimedialis* (Wu et al. 2010), *Sinosaurichthys minuta* (Wu et al. 2010), *Sangiorgioichthys sui* (López-Arbarello et al. 2011), *Luoxiongichthys hyperdorsalis* (Wen et al. 2012), *Perleidus sinensis* (Lombardo et al. 2011), and *Habroichthys broughi* (Lin et al. 2011). Four coelacanth specimens were recently found in the Luoping Biota, and after preparation and study, these are seen to represent two new taxa.

**Institutional abbreviations.**—LPV, Luoping County Vertebrates, a collection deposited in the Chengdu Institute of Geology and Mineral Resources, Chengdu, China.

## Material and methods

There are five coelacanth specimens from Luoping, four assigned to the new taxon *Luopingcoelacanthus*. LPV-10146 is the most complete, showing the whole body except the supplementary lobe of the caudal fin, and so is designated as holotype. Standard length is 230 mm. It is exposed on its right side with the body laterally flattened, and it is considered to be an adult because of the general proportions of the body and skull bones, as well as the presence of a short gular pit line (Clément 2005). Most of the skull roof is broken and missing, but the cheek and mandible region are relatively well preserved. LPV-10575 is a single head seen from the left side, and it best shows the skull roof, the teeth, and the pectoral girdle. LPV-5124 shows scattered head elements and a twisted body, but it preserves the characteristic parasphenoid and palate in three dimensions. The three lobes of the caudal fin are also well preserved. LPV-10872 gives some information on the basal plates of the first dorsal fin and pelvic fin. There is only one specimen of the new taxon *Yunnancoelacanthus*, LPV-12748.

Both LPV-5124 and LPV-10827 were prepared first by an engraving tool, and then by needles. All specimens were prepared by needles and dilute acetic acid under the microscope. Some bones are hollow, and it was impossible to clean them without breaking parts of their walls. We left them in their original condition.

## Systematic palaeontology

Class Osteichthyes Huxley, 1880

Subclass Sarcopterygii Romer, 1955

Infraclass Actinistia Cope, 1871

Order Coelacanthiformes Huxley, 1861

Genus *Luopingcoelacanthus* nov.

*Type species:* *Luopingcoelacanthus eurylacrimalis* sp. nov.; see below.

*Etymology:* The genus named after Luoping County.

*Diagnosis.*—As for the type species, by monotypy.

*Luopingcoelacanthus eurylacrimalis* sp. nov.

Figs. 1–6.

*Etymology:* The species name is derived from its unique feature, the triangular broad lachrymojugal.

*Holotype:* LPV-10146, a nearly complete specimen, lacking only the supplementary lobe of the caudal fin.

*Type horizon:* Member II, Guanling Formation, Middle Triassic (*Nicoraella kockeli* Zone, late Pelsonian, middle–late Anisian).

*Type locality:* Daaazi Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China (Zhang and Zhou 2008; Zhang et al. 2008; Hu et al. 2011).

*Other material.*—LPV-5124, a partial specimen; LPV-10575, a head; LPV-10827, a near-complete specimen.



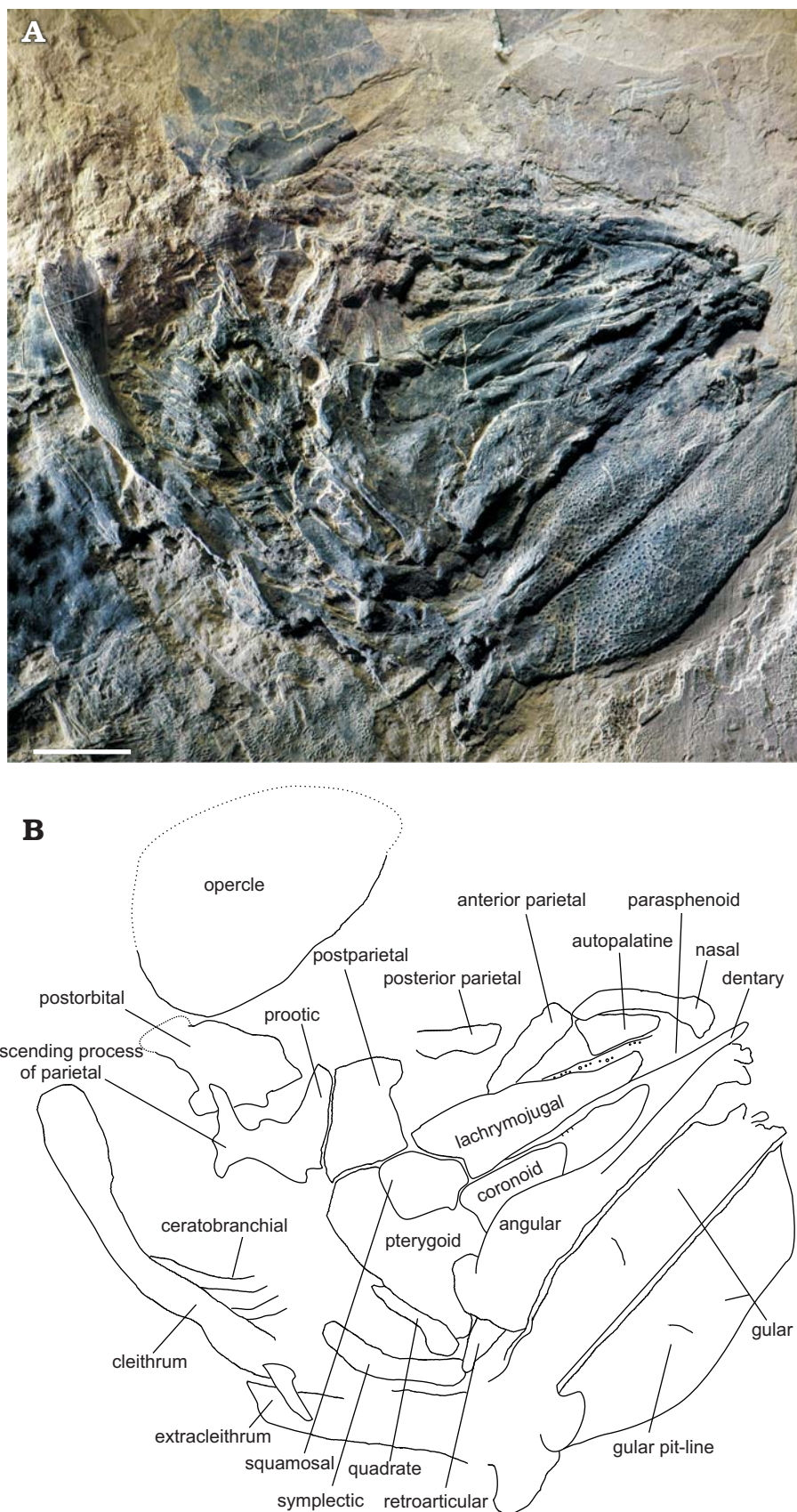


Fig. 1. Anisian (Middle Triassic) coelacanth *Luopingcoelacanthus eurylacrimalis* gen. et sp. nov. (LPV-10146) from the Middle Triassic Guanling Formation (Member II) of Daaozi Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China, holotype. Photograph of the head in lateral view (A) and interpretive drawing (B). Scale bar 10 mm.

**Diagnosis.**—Middle-sized coelacanth. Three diagnostic features are the expanded lachrymojugal, the notched dentary, the large semicircular coronoid. Skull roof has two pairs of parietals. Posterior margin of postparietals embayed. Lachrymojugal has an expanded posterior portion and a concave posteroventral margin. Squamosal has a slightly anterior expansion. Ventral surface of parasphenoid is covered by numerous granular teeth. Dentary has a deeply notched posterior border, and teeth distributed on the separated dentary plate. The first dorsal fin contains 12 robust segmented rays. The lower lobe of the caudal fin is larger than the upper lobe.

The following combination of characters, a notched dentary and an expanded lachrymojugal, is not known in any other actinistian, so the Luoping materials must represent a new taxon.

### Description

**Skull roof and dermal bones of snout.**—The skull roof is poorly preserved in all specimens, being disarticulated in LPV-10146 (Fig. 1) and LPV-10575 (Fig. 2). The latter shows the parietal shield relatively well. The postparietal is large, and its posterior margin is wider than the anterior margin. There is a depressed area in the middle, and some sensory-canal pores are distributed on its surface. The postparietal is ornamented with small rounded tubercles and striae. The anterior division of the parietonasal shield is broken. However, two pairs of parietals can be identified, as in most other coelacanths. The posterior parietal is as long as the postparietal, but the anterior one is much smaller. Both of them are covered by tiny tubercles (Fig. 2A).

There should be several extrascapulars, but only one is preserved. It is rectangular and was not sutured to the postparietal (Fig. 2). The supratemporal is triangular in shape, expanding anteriorly. It is situated at the posteroventral margin of the postparietal.

The triangular lateral rostral is seen in LPV-10575 (Fig. 2), but the ventral process is not preserved. There are three pointed grasping teeth on the premaxilla.

The supraorbital series consists of six elements (Fig. 3D).

**Cheek.**—The cheek is composed of five bones: the lachrymojugal, postorbital, squamosal, and preopercle. The outline of the lachrymojugal is conspicuous in the holotype (Fig. 1). It is elongated-triangular in shape, with the posterior portion greatly expanded and concave in the posteroventral corner. The infraorbital sensory canal also could not be made out. The postorbital is plate-like. The rectangular postorbital is large. It is broken into two pieces. The preopercular is triangular in shape, but not elongate as in *Macropoma* (Lambers 1996) and *Swenzia* (Clément 2005). As in other coelacanths, the jugal sensory canal passes through the centre of the squamosal and into the preopercular. However, the sensory canal does not run along the posterior margin as in *Macropoma* (Clément 2005); it crosses the preopercular along the median region, and runs toward its posteroventral corner (Fig. 2A). The opercular is a large subtriangular bone with rounded corners. Between the cleithrum and quadrate, a very slender symplectic is present in

the holotype (Fig. 1), articulating with the retroarticular. The ornamentation of the cheek region is not visible.

**Parasphenoid.**—The parasphenoid is well preserved in LPV-5124, in ventral view (Fig. 3A, C). It has the general spatulate appearance seen in most coelacanths, being constricted in its middle portion and widest in the anterior half. The ventral surface is concave medially. The whole ventral surface of the parasphenoid (Fig. 3C) is covered with bluntly granular teeth, as in *Diplurus* and *Axelia* (Schaeffer 1952). The posterior portion increases in height to form a slender extension supporting the basisphenoid. The large antotic process is triangular (Fig. 3B) on the basisphenoid, as in *Diplurus* and *Whiteia* (Schaeffer 1967, 1976).

**Palate.**—The palatoquadrate on each side is visible in LPV-5124. The entopterygoid has the typical triangular shape. The angle between the ventral and posterodorsal margins is about 100°, whereas it is roughly 50° in *Piveteaia* (Clément 1999) and 130° in *Diplurus* (Schaeffer 1952). The ventral border of the entopterygoid is straight, not as in *Macropoma* and *Megalocoelacanthus* where a ventral expansion is present (Lambers 1996; Schwimmer 1994). The palatal surface is covered by numerous minute teeth, as in *Diplurus* (Schaeffer 1952) (Fig. 3F).

The rectangular metapterygoid articulates with the posterodorsal surface of the entopterygoid. The quadrate is in contact with the posteroventral margin of the entopterygoid (Fig. 3F).

In the holotype (Fig. 1), the autopalatine has shifted from its original place. It is subtriangular in shape and its external surface is concave. Parts of the ectopterygoid-dermopalatine can be seen (Fig. 2). The teeth of the ectopterygoid-dermopalatine are numerous and small, but a row of larger pointed teeth is also present, as in *Swenzia latimerae* (Clément 2005, 2006).

Only the ceratohyal is visible in the hyoid arch of LPV-5124 (Fig. 3A). The ceratohyals are unusually powerful, and they are arched so that they are convex on the ventral side and concave on the dorsal. The truncated posterior end is about twice as broad as the anterior (Fig. 3E).

**Lower jaw.**—The middle part of the angular is very deep and shows the usual dorsal, rounded margin of most coelacanths. The surface of the angular is covered by numerous tubercles in the holotype (Fig. 1), as in *Sassenia* and *Holophagus*, and not by coarse ridges as in *Mawsonia* and *Axelrodichthys* (Cavin and Forey 2005). The retroarticular is well preserved. The semicircular principal coronoid is situated halfway along the length of the angular. It is much larger than is usual for coelacanths, and the dorsal margin increases in height and forms a ridge. The dentary has a forked posterior margin as in *Macropoma* (Clément 2005; Lambers 1996). Pointed teeth are distributed on the dental plate. The hook-shaped dentary and separate tooth plate were regarded as derived features by Forey (1991). The gulars are preserved on each side (Fig. 1). They are ornamented with tiny tubercles, and the gular pit-line is in the centre of the bone.



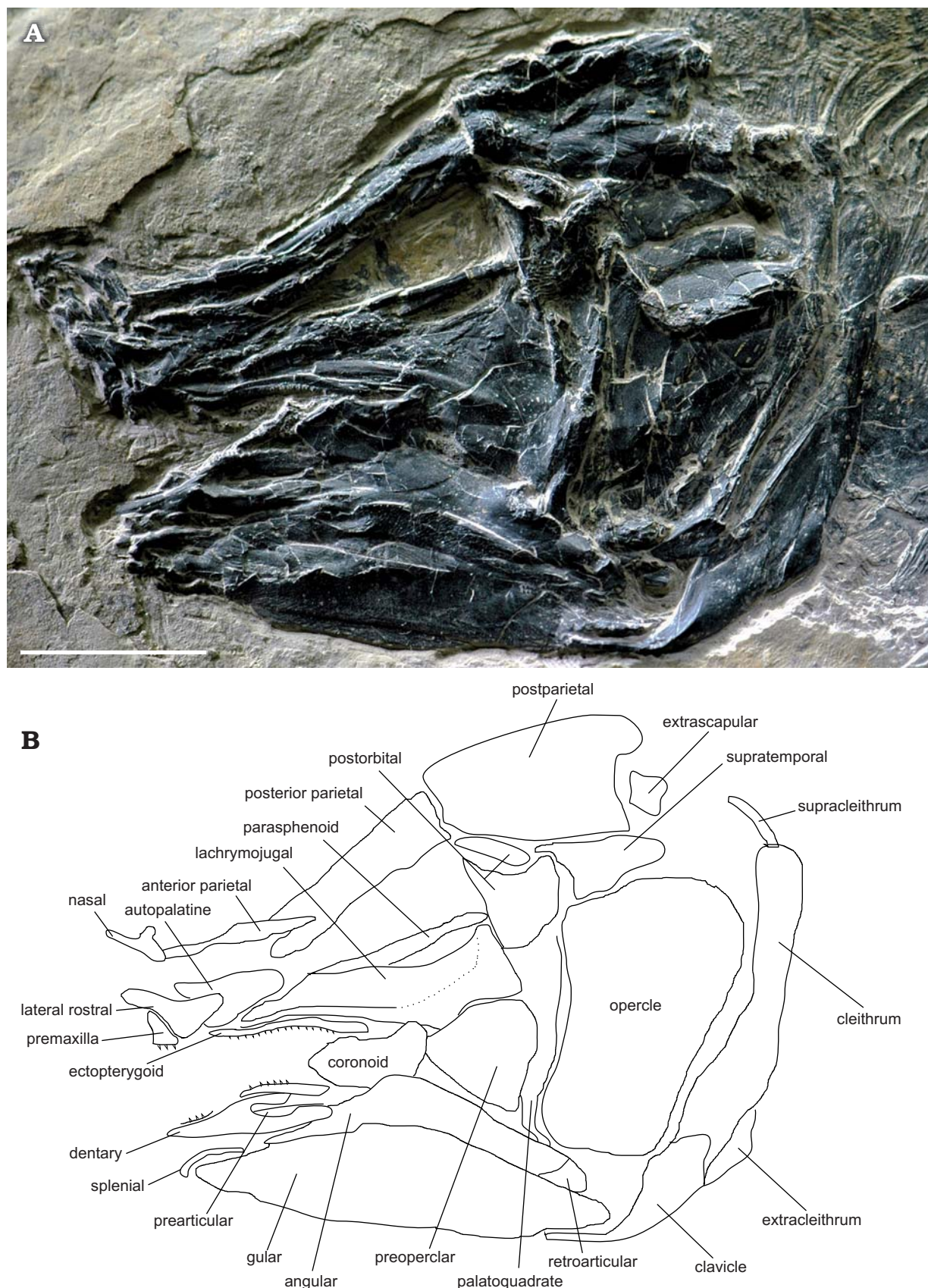


Fig. 2. Anisian (Middle Triassic) coelacanth *Luopingcoelacanthus eurylacrimalis* gen. et sp. nov. (LPV-10575) from the Middle Triassic Guanling Formation (Member II) of Daaozi Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China. Photograph of the head in lateral view (**A**) and interpretive drawing (**B**). Scale bar 10 mm.



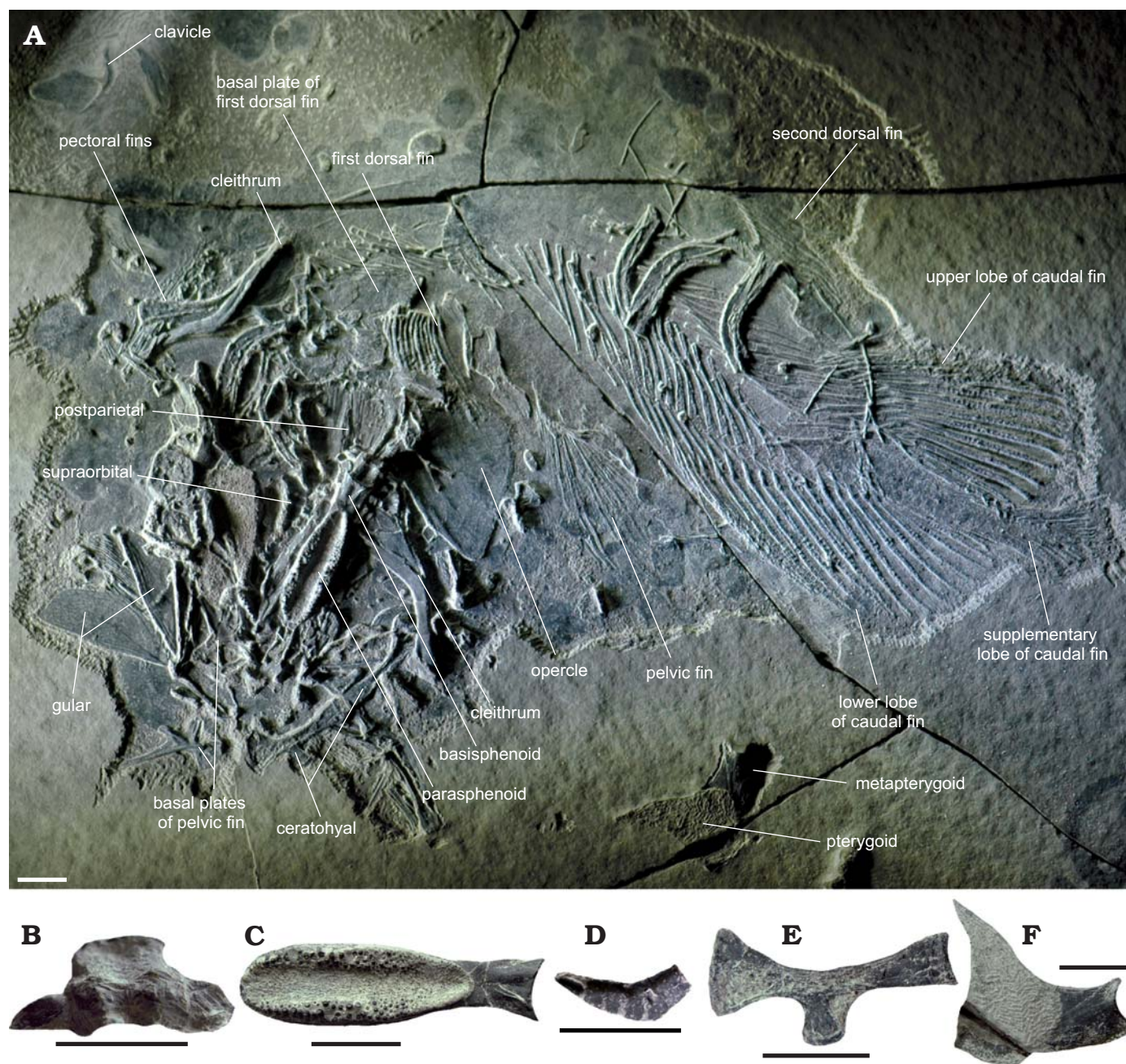


Fig. 3. Anisian (Middle Triassic) coelacanth *Luopingcoelacanthus eurylacrimalis* gen et sp. nov. A. Complete specimen (LPV-5124) from the Middle Triassic Guanling Formation (Member II) of Daaozi Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China in ventral view. B–F. Isolated cranial bones: basisphenoid (B), parasphenoid (C), supraopercle (D), ceratohyal (E), and pterygoid (F). Scale bars 10 mm.

**Shoulder girdle and pectoral fin.**—The dermal pectoral girdle is composed of the cleithrum, extracleithrum, anocleithrum, and clavicle (Fig. 2). The shoulder girdle is well preserved, except in the holotype (Fig. 1). The cleithrum is an elongate element, the middle part is very narrow and its uppermost region is oval in shape. The extracleithrum is situated at the postero-ventral corner, and the clavicle at the ventral edge. The presence of an extracleithrum is a synapomorphy of Actinistia (Forey 1998). This element is oblong and pointed at both ends. The clavicle consists of a twisted horizontal lamina, which contacted the posterior corner of the gular plate, and of a verti-

cal internally concave lamina that approached the cleithrum. The anocleithrum is a wedge-shaped bone with its ventral end overlapped by the uppermost margin of the cleithrum. The pectoral fin web contains 19–20 rays, all showing a transverse segmentation in their distal half (Fig. 3A).

**Pelvic fins.**—The pelvic fins are not complete in any specimen. The basal plates of the pelvic fins are situated far forward (Table 1), near to the level of the basal plate of the first dorsal fin. The pelvic fin is lobe-like and contains about 18 segmented fin rays. The anterior rays lengthen and the poste-



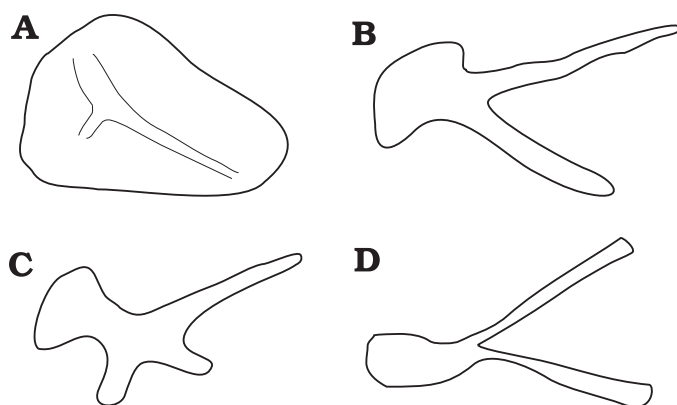


Fig. 4. Anisian (Middle Triassic) coelacanth *Luopingcoelacanthus euryla-criminalis* gen. et sp. nov. from the Middle Triassic Guanling Formation (Member II) of Daozi Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China. Outline drawings of basal plates of the fins based on LPV-10146, except A, based on LPV-5124. **A.** First dorsal fin. **B.** Second dorsal fin. **C.** Pelvic fin. **D.** Anal fin.

rior rays shorten backwards, while the middle rays are the longest. The longest pelvic fin is nearly 40 mm (Fig. 3A).

As in *Diplurus*, the basal plate (Fig. 4C) consists of a posterior division and an anterior division. The anterior division is subdivided into anterodorsal and anteroventral processes, the former being longer and extending horizontally forward, the latter being shorter and extending in an anteroventral direction to contact the anteroventral process on the other side. The posteroventral process of the posterior division is slender and its distal end contacts that of the other side. The posterodorsal process of the posterior division is broader than the posteroventral one.

**First dorsal fin.**—The first dorsal fin is supported by a triangular basal plate, with rounded corner (Fig. 4A). A strong ridge extended from the posterodorsal corner and branched towards the posteroventral and anterior corners. Its ventral margin is straight, not scalloped or irregular as in *Cari-dosuctor* and *Polyosteorhynchus* (Lund and Lund 1984). The first dorsal fin (Fig. 3A) is composed of at least 12 robust rays, segmented for the distal third of their length. On the rays, there were strong longitudinal tubercles distributed both on the unsegmented and segmented portions.

**Second dorsal fin.**—The basal plate of the second dorsal fin (Fig. 4B) is a long, deeply forked bone. It has a slender

anteroventral process extending to the 23rd neural spine, and a longer anterodorsal process. Its posterior head is plate-like which is smaller than in *Chaohuichthys* (Tong et al. 2006). About 20 segmented rays are present in the second dorsal fin of LPV-5124 (Fig. 3A). The fin rays have the same features as in the pectoral fin.

**Anal fin.**—The anal fin is lobed and it is situated slightly behind the level of the second dorsal fin (Fig. 5A). The outline is not clear because it is incomplete in all specimens. The basal plate (Fig. 4D) is similar to that of the second dorsal fin, with slender anterodorsal and anteroventral processes. The posterior division is short and broad. The two processes of the anterior division are close to the same length.

**Caudal fin.**—The caudal fin (Figs. 3A, 5A) is composed of dorsal, ventral and supplementary lobes. The supplementary lobe is missing in the holotype (Fig. 5A), but is well preserved in LPV-5124 (Fig. 3A). The ventral lobe seems to be more developed than the dorsal one, as in *Sinocoelacanthus fengshanensis* (Liu 1964). The ventral lobe contains 19–20 rays, and the dorsal one contains 15–16 rays. The rays of the dorsal lobe seem to be more inclined posteriorly than those of the ventral lobe. The rays of both the dorsal and ventral lobes are segmented for about the distal half of their length, except for the first two rays. All the lepidotrichia are ornamented with longitudinal tubercles. The supplementary lobe is well developed in LPV-5124 and contains 28 segmented rays.

**Axial skeleton.**—The axial skeleton consists of about 50 vertebrae, as in *Piveteauia* from the Triassic, but not *Coelacanthus* from the Permo-Triassic (70 vertebrae), *Coccoderma* from the Jurassic (78), or extant *Latimeria* (91–93) (Clément 1999). The neural arches are of the type usually found in actinistians. The neural spines are short between the head and the first dorsal fin and behind the second dorsal fin to the caudal fin, but they are long between the two dorsal fins. Haemal spine arches are absent in the most anterior part of the axis. The first one appears below the level of the posterior margin of the first dorsal fin. The first 11 arches are very short, thin and equal in size. Behind the second dorsal fin, the haemal arches increase in size. The pleural ribs are not ossified (Fig. 5A).

**Scalation.**—Scales may be seen behind the level of the first dorsal fin in the holotype (Fig. 5A), some of them exposed in external view. Some others are exposed showing their internal view on the left side. It is hard to identify each scale, because they overlap each other and are somewhat compacted. All scales have varying numbers of slender hollow ridges on the exposed portion, and the orientation of these ridges is highly variable: they may be parallel or arranged at slight angles to each other (Fig. 6B). In the extreme anteroventral region, the ridges are somewhat circular in shape and about 40 in number on the first 6–7 rows of scales (Fig. 6C). On the scales around the fins, the ornament also is circular tubercles. These ridges increase in length backwards. In the caudal region, the number of ridges on each scale increases to nearly 100. In the anterior portion the scales are covered with fine parallel striae.

Table 1. Main measurements (in mm) of *Luopingcoelacanthus euryla-criminalis* gen. et sp. nov. (LPV-10146).

Length from anterior tip of snout to base of supplementary caudal fin	230
Length of head	65
Depth of head	50
Length from anterior snout to base of first dorsal fin	95
Length from anterior snout to base of second dorsal fin	114
Length from anterior snout to posterior tip of pelvic girdle	106
Length from anterior snout to posterior tip of basal plate of anal fin	145



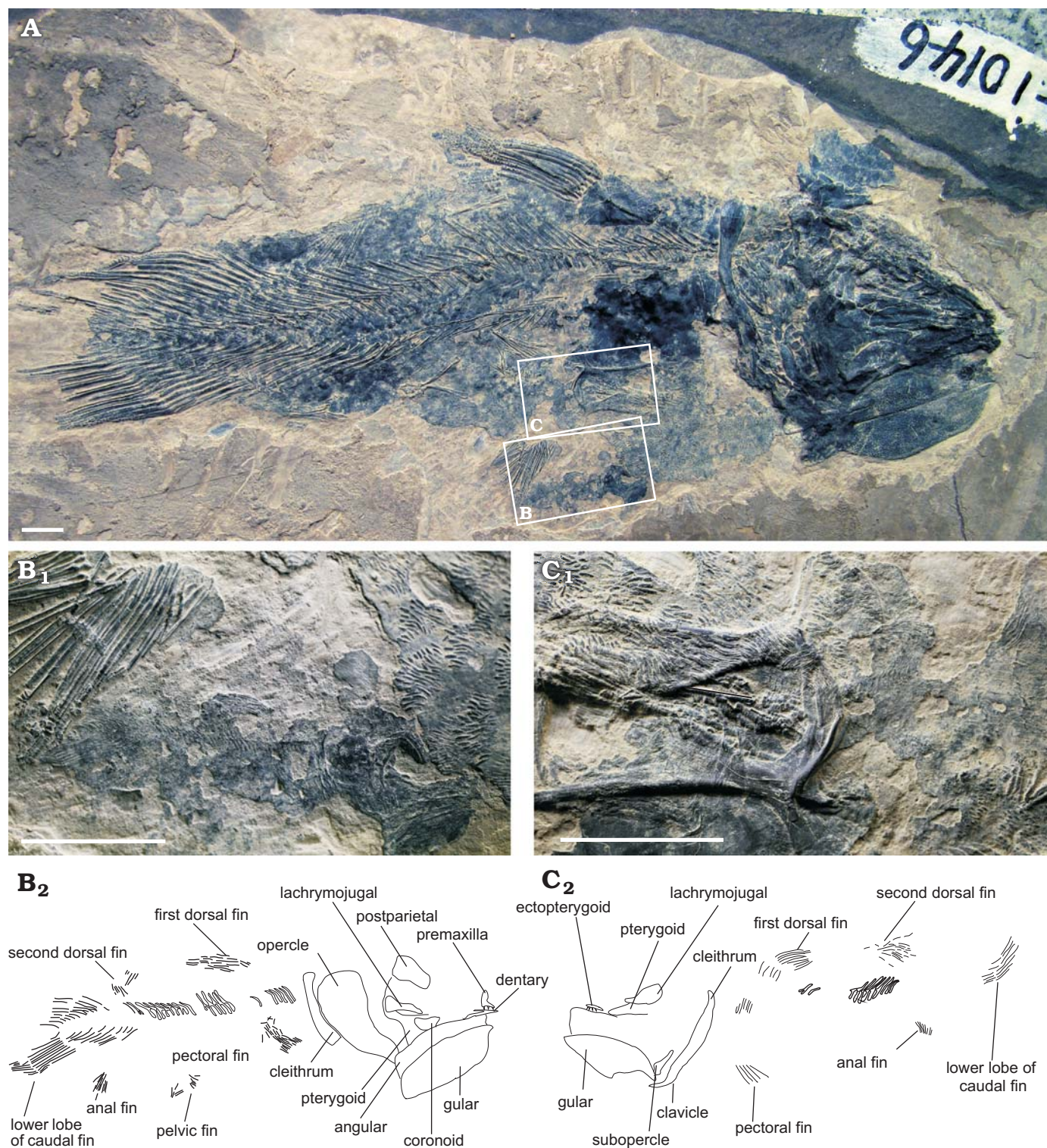


Fig. 5. Anisian (Middle Triassic) coelacanth *Luopingcoelacanthus eurylacrimalis* gen. et sp. nov. (LPV-10146) from the Middle Triassic Guanling Formation (Member II) of Daozi Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China, holotype. Complete specimen in right lateral view (A), rectangles highlight the embryos. B. Embryo from near the basal plates of pelvic fin. C. Embryo from near the pelvic fin. Photographs (B<sub>1</sub>, C<sub>1</sub>), explanatory drawings (B<sub>2</sub>, C<sub>2</sub>). Scale bars 10 mm.

**Calcified swim bladder.**—A calcified swim bladder is known in numerous actinistians, composed of superimposed bony plates. In the holotype (Fig. 5A), only the most external wall of the calcified bladder can be observed below the pectoral fin.

The internal surface was ornamented by delicate parallel striations, as in other fossil taxa.

In living *Latimeria*, the bladder is not ossified and is filled with lipids, primarily wax esters (Forey 1998), and is used



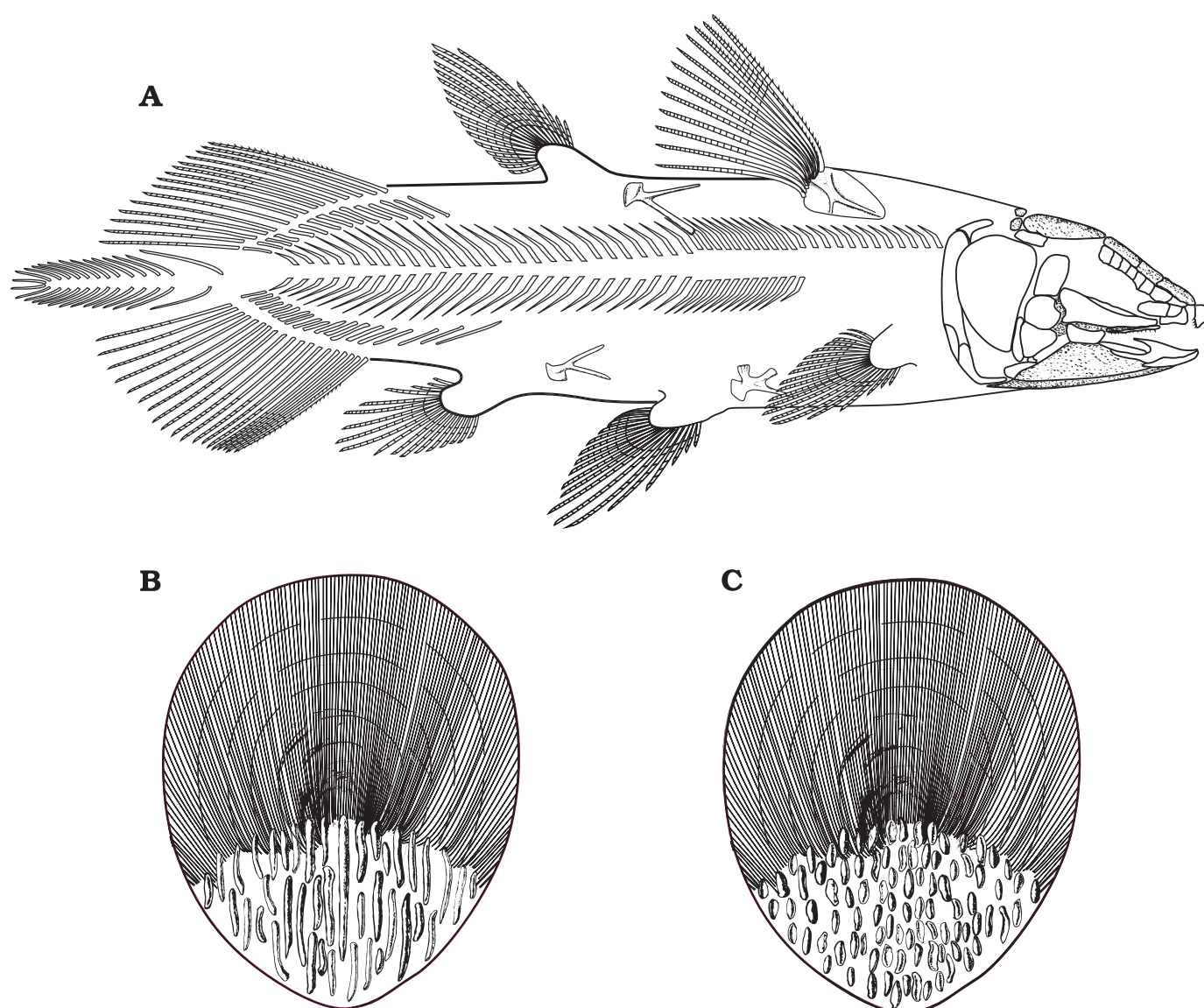


Fig. 6. Reconstruction of *Luopingcoelacanthus eurylacrimalis* gen. et sp. nov. Guanling Formation, Anisian, Middle Triassic; Daozi Quarry, Luoping, Yunnan Province, Southwest China. **A.** Whole-body reconstruction. **B.** Reconstruction of normal scale. **C.** Reconstruction of scale from the anteroventral region.

for buoyancy control. In many fossil coelacanths, on the other hand, including Palaeozoic forms (e.g., *Allenpterus*, *Caridosuctor*, *Coelacanthus*, *Hadronector*, and *Polyosteorhynchus*) and Mesozoic forms (e.g., *Axelrodichthys*, *Cocco-derma*, *Laugia*, *Libys*, *Macropoma*, *Mawsonia*, *Piveteauia*, *Swenzia*, and *Undina*), the bladder wall was covered with calcified plates (Forey 1998; Clément 1999; Brito et al. 2010). By its position, the swim bladder appears to be homologous with the lung of air-breathing vertebrates, and it may have been filled with air or fluid, as in most modern osteichthyans, not lipids as in *Latimeria*. The coelacanth swim bladder lies close behind the operculum, and is connected at the front by a single opening to the oesophagus or pharynx. The numerous overlapping bony plates linked by connective tissue seen in *Axelrodichthys* from the Early Cretaceous of Brazil may have functioned as an “ossified lung” (Bruto et al. 2010) in which the bony plates were a means to adapt to

changes in the volume of the bladder in operating like a bellows. Other putative functions include a role in maintaining hydrostatic balance, as a resonating chamber for sound production, or for hearing (Forey 1998).

**Possible embryos.**—In the ventral region of the holotype (Fig. 5A), beside the pelvic fin are two tiny coelacanth fossils. The first (Fig. 5B), near the pelvic fin, has a relatively large gular plate and trilobed coelacanth-like caudal fin. Its head length is 11 mm, and standard length is 33 mm. The second (Fig. 5C), near the basal plate of the pelvic fin, has its gular plate compressed on the swim bladder of the adult. Its head length is 8 mm, and the standard length is 25 mm. These two tiny coelacanths could be interpreted as embryos because the ratio of head length to standard length is 33%, which is higher than in the adult (28%; Table 1), a common feature of coelacanth (and many other) embryos (Cloutier



2010). Further, these two embryos show the same diagnostic generic features as the adult, for example the expanded posterior margin of the lachrymojugal (Fig. 5B<sub>2</sub>, C<sub>2</sub>) and the semicircular coronoid, confirming that the two tiny coelacanthus are examples of *Luopingcoelacanthus*. There is no evidence of a yolk sac.

These two small coelacanthus could have come to lie where they do by chance, by having been eaten, or by being unborn embryos. The first suggestion is rejected because the small specimens lie within the abdominal cavity, above some skeletal elements of the *Luopingcoelacanthus* adult individual, and below other skeletal elements. The second suggestion might seem to be reasonable because coelacanthus are predators, and modern *Latimeria* is known to feed on a range of fishes, as many as 12 species (Fricke and Hissmann 2000) that are swallowed whole; there is no evidence, however, that modern *Latimeria* is a cannibal. Further, we cannot argue that *Luopingcoelacanthus* was a cannibal because the two tiny specimens lie below the putative gut region by comparison with *Latimeria*, and they show no sign of disarticulation or acid damage. Evidence that they are indeed intrauterine embryos is that they most probably belong to the same genus as the enclosing adult, they show larval proportions, and they are in the correct, ventral region of the abdominal cavity just in front of the pelvic fins.

**Reconstruction.**—The whole-body reconstruction of *Luopingcoelacanthus* (Fig. 6A) is based primarily on the holotype, LPV-10146 (Figs. 1, 5A), with confirmation of structures and measurements from the other specimens. The head shape in particular is based on the holotype and LPV-10575.

**Geographic and stratigraphic range.**—Type locality and horizon only.

### Genus *Yunnancoelacanthus* nov.

**Type species:** *Yunnancoelacanthus acrotuberculatus* sp. nov.

**Etymology:** The genus name refers to Yunnan Province where the specimen comes from.

**Diagnosis.**—As for the type species, by monotypy.

#### *Yunnancoelacanthus acrotuberculatus* sp. nov.

Fig. 7.

**Etymology:** The species name is derived from the characteristic sharp tubercles on the dermal bones of skull.

**Holotype:** LPV-12748, a complete specimen with skull in dorsal view. Its standard length is 255 mm.

**Type horizon:** Member II, Guanling Formation, Middle Triassic (*Nicoraella kockeli* Zone, late Pelsonian, middle-late Anisian).

**Type locality:** Daaazi Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China (Zhang and Zhou 2008; Zhang et al. 2008; Hu et al. 2011).

**Diagnosis.**—A middle-sized coelacanth (Fig. 7). The posterior parietals and anterior parietals have the same length. Opercle is big with a curved posteroventral margin. Preorbital present. Coronoid is semicircular in shape. Most dermal bones on roof of skull and cheek sculptured with strong

sharp tubercles. The first dorsal fin has about 8 fin rays. Scales have fewer ridges on the exposed region.

### Description

**Skull and dermal bones of snout.**—The skull is preserved in dorsal view. The roof of the skull is composed of a pair of postparietals, posterior parietals, anterior parietals and two pairs of nasals. The posterior parietals and the anterior parietals have nearly the same size. A large supratemporal fits into wide embayments in the postparietal. The extrascapular cannot be observed.

The supraorbital series consists of five elements, as seen on both sides of the skull. The posterior two of them form the upper margin of orbit. Three tectals follow. They are excluded from the orbital margin, articulating with the lateral rostral. The triangular preorbital articulates ventrally with the first tectal.

**Cheek.**—The lachrymojugal forms the entire ventral border of the orbit. It extends forward to meet the posterior border of the lateral rostral. The posterior end meets the postorbital and squamosal at their junction. The postorbital is semicircular. Below the postorbital is the squamosal, which is roughly rectangular in shape and larger than the postorbital. The preopercle is not complete on the right side.

The opercle is subtriangular in shape with a curved posteroventral margin.

The most distinctive feature is that most of the dermal bones of the skull are decorated by not only strong oval tubercles, but also some sharp ones. This is different from any other coelacanth.

**Mandible.**—The dorsal part of angular is overlapped by the lachrymojugal. The semicircular coronoid does not lie in its original place, having been shifted post-mortem, and it overlaps the ventral side of the gular. The dentition resembles *Chinlea* (Schaeffer 1967), and is different from *Axelia*, *Maylacanthus*, and *Scleracanthus* (Schaeffer 1952; Rieppel 1980). The margin of the precoronoid supports a cluster of robust, conically pointed teeth with striated caps. The teeth on the dorsomedial surface of the dentary and prearticular have the same shape as those on the margin of the precoronoid, but they are much smaller and finer. Several small rounded teeth on the parasphenoid are observed between the two anterior parietals.

**Pectoral girdle.**—In the pectoral girdle, only a strong cleithrum and extracleithrum can be observed. The ventral region is pressed under the opercle.

**Fins.**—The pectoral fin is lobe-shaped. There are 22 fin rays, most of which are segmented for over half of their length. Pelvic fins are positioned posteriorly to the first dorsal fin, which is different from *Laugia* and *Piveteauia* (Rieppel 1980, Geng et al. 2009). They are also lobate in shape, consisting of 20 fin rays. The first dorsal fin contains about 8 fin rays, resembling *Whiteia*. The plate of the first dorsal fin is not preserved. There are 18 lepidotrichial rays in the second dorsal fin. Its plate is forked. Only 5 rays can be counted in

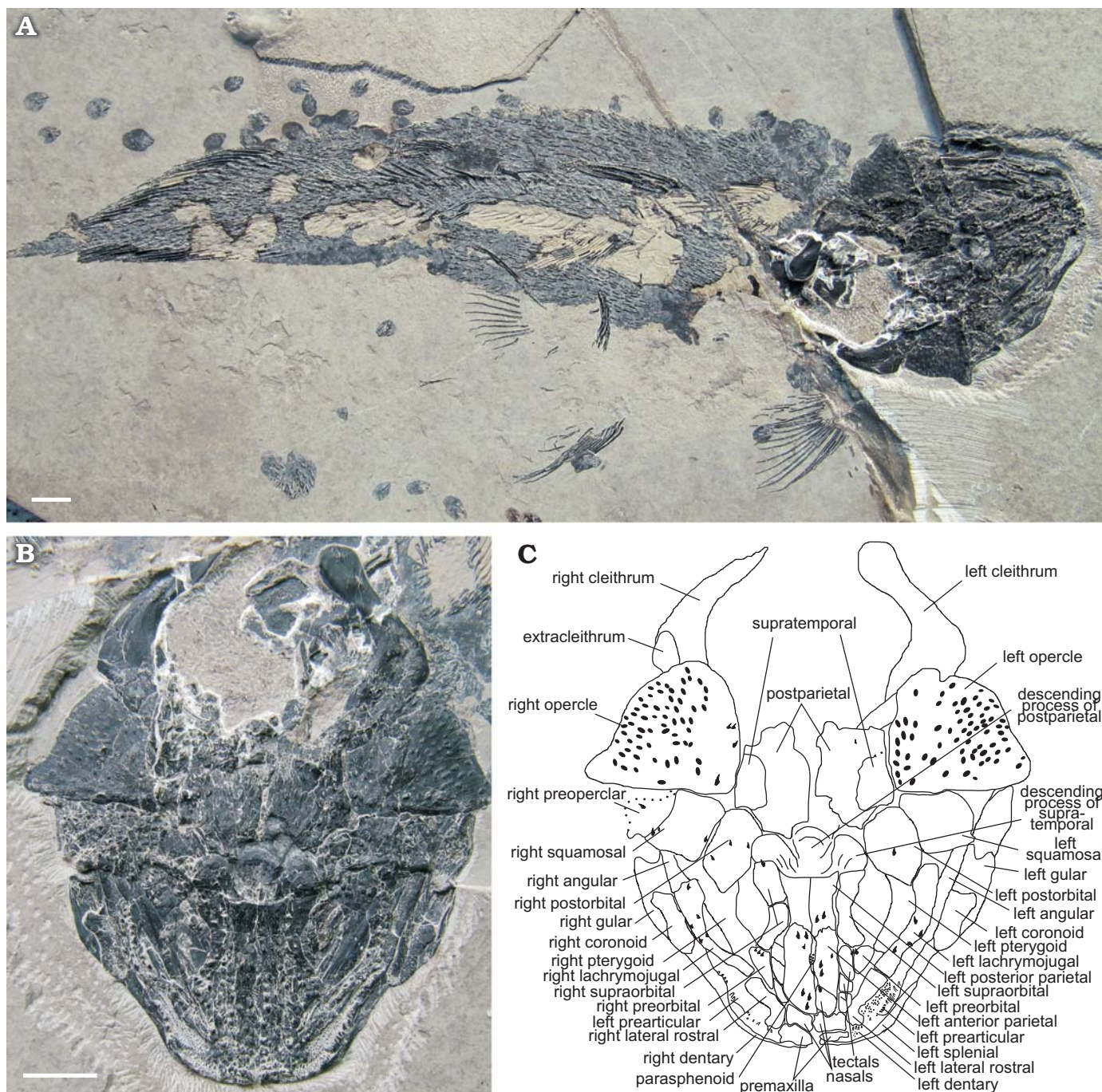


Fig. 7. Anisian (Middle Triassic) coelacanth *Yunnancoelacanthus acrotuberculatus* gen et sp. nov (LPV-12748) from the Middle Triassic Guanling Formation (Member II) of Daozi Village, Luoxiong Town, Luoping County, Qujing City, Yunnan Province, China, holotype. Complete specimen (A), photograph of the head in dorsal view (B), and interpretive drawing (C). Scale bar is 10 mm.

the anal fin. The caudal fin has 16 rays in the upper lobe, 14 rays in the lower lobe, and 26 rays in the supplementary lobe. Longitudinal tubercles decorate the lepidotrichial rays of the first dorsal fin, the upper lobe and lower lobe of the caudal fin.

**Axial skeleton.**—There are 11 neural spines between the second dorsal fin and the upper lobe of the caudal fin. In addition, 14 haemal spines are distributed between the pelvic fin and the anal fin according to the traces left.

**Scalation.**—The ligulate scales have a varying number of elongated hollow ridges in the exposed region. The number of ridges is more like *Diplurus* than *Luopingcoelacanthus* (Schaeffer 1952). In the area between the first dorsal fin and the basal plate of the second dorsal fin, and the posterior region of caudal fin, the scales only have one ridge. In the other areas, scales usually have three to seven ridges. As in other coelacanth, the scales are decorated by fine, parallel striae on the covered region.



**Discussion.**—It is clear that LPV-12748 cannot be ascribed to *Luopingcoelacanthus*, because these taxa differ in dentary, lachrymojugal, number of rays of the first dorsal fin, and decoration on dermal bones and scales. The feature which most closely resembles *Luopingcoelacanthus* is the semicircular coronoid.

We have lost some information in the extrascapular, palate, and basal plates of the unpaired fins. However, we still find that the new specimen is similar to *Guizhoucoelacanthus* in some respects. They have similar supraorbital series, post-orbital, squamosal, parietal shield, lower jaw, and number of rays of the first dorsal fin. *Guizhoucoelacanthus* has been assigned to the coelacanth family Whiteiidae by Geng et al. (2009). However, *Guizhoucoelacanthus* is a large coelacanth, with standard length about 500 mm, compared to 250 mm for our *Yunnancoelacanthus*. Because of the position of post-orbital and pelvic fins, *Yunnancoelacanthus* cannot be ascribed to either *Whiteia* or *Piveteaia*. As a result, a new genus is erected, based on the unique ornamentation on the skull.

**Geographic and stratigraphic range.**—Type locality and horizon only.

## Phylogenetic analysis

In order to find the phylogenetic positions of *Luopingcoelacanthus* and *Yunnancoelacanthus*, we added these two taxa to the data matrix of Friedman and Coates (2006), the current “standard” for cladistics of coelacanths. This data matrix had been modified from the original version compiled by Forey (1991, 1998) and by Clément (2005), including re-coding of character 31 and other changes. In addition, we added *Guizhoucoelacanthus* using the character codings given by Geng et al. (2009), listed also in Table 2 here. We add an additional state to character 68 (prearticular and / or coronoid teeth): (2) pointed and marked with fine striations. The data matrix includes 109 characters and 32 taxa. Four uninformat-

Table 2. Character codings for *Guizhoucoelacanthus*, from Geng et al. (2009), and for *Luopingcoelacanthus* and *Yunnancoelacanthus* (own data) for the 109 characters used by previous authors. Codings for the other taxa, as used in our cladistic analyses (Fig. 8), were taken from Friedman and Coates (2006).

<i>Guizhoucoelacanthus</i>			
0000??1101	?0??000111	100000101?	1010010000
00??0?0010	00????000?	1111000???	??????????
???????1?1	0011020000	010001???	
<i>Luopingcoelacanthus</i>			
???01?110?	?11?10?1??	?????1001?	1000010000
00????00110	?111?1?1??	1111000?10	0???????1?
?????1?101	0011100100	0101?0100	
<i>Yunnancoelacanthus</i>			
??00??1001	?0110101??	???001001?	10?0100000
00?????11?	0??0?0?0?	?11?0002??	??????????
????1????1	001?110100	?101?0?00	

ive characters were excluded (7, 31, 73, 83). These are coded uniformly, respectively, as parietals, two pairs (7), preoperculum present (31), antotic process covered (73), and superficial ophthalmic branch of anterodorsal lateral line nerve piercing antotic process (83).

Two phylogenetic analyses were conducted, the first in PAUP 4.0b (Swofford 2002), using a heuristic search, with all characters unordered and unweighted, and using tree-bisection-reconnection, and 5000 replicates. Consensus trees were generated, and bootstrap values (1000 replicates) calculated. The second analysis was run with equally weighted parsimony using TNT v. 1.0 (Goloboff et al. 2003, 2008). The first runs followed the settings used in PAUP, under “Traditional search”. Then, the analysis was run using the “New Technology search” option, which seeks all tree islands (sectorial search, ratchet, and tree-fusing search methods, all with default parameters). The output trees were combined in a consensus, and bootstrap analysis (1000 replicates) run.

The PAUP analysis yielded 173 trees of length 275, with consistency index of 0.40 and retention index of 0.67. The results (Fig. 8) are similar to previous analyses using earlier versions of the data set (Forey 1991, 1998; Clément 2005), showing some lack of resolution especially in the placement of the basal actinistians *Allenynpterus*, *Holopterygius*, *Diplocercides*, *Miguashaia*, *Hadronector*, and *Lochmocercus*, both with respect to each other and to the outgroups Porolepiformes and Actinopterygii. The derived clade Latimerioidei is recovered in all versions of the analysis, but relationships within the clade are not robust, as Clément (2005) noted. Both latimerioid subclades, the Latimeriidae and Mawsoniidae are well defined in the 50% majority-rule consensus tree (Fig. 8A), but are not well supported according to the bootstrap results (Fig. 8B). Despite these uncertainties, *Luopingcoelacanthus* and *Yunnancoelacanthus* are the immediate outgroups of Latimerioidei in all 173 most parsimonious trees (Fig. 8A), but these relationships are not robust, and disappear when bootstrap values over 50% are retained (Fig. 8B).

In the TNT analyses, these results were repeated under the “traditional” search. Using the “new technology” search, a much more resolved tree was obtained. There were two tree solutions, each of length 278, CI=0.410, RI=0.671, but the consensus solutions were identical to those obtained through PAUP (Fig. 8A, B), and are not illustrated.

In light of the uncertainties about the phylogeny, it is premature to explore the detailed history of the coelacanth subclades. The basal 11 taxa, from *Allenynpterus* to *Rhabdoderma* (Fig. 8A) are Devonian or Carboniferous in age, and more crownward taxa are largely Permian and Mesozoic, indicating an approximate correspondence of the phylogeny to the stratigraphic sequence. Of these more derived forms, at least four lineages crossed the Permo-Triassic boundary, namely the lineages leading to *Sassenia*, the (*Coccoderma* + *Laugia*) subclade, *Coelacanthus* (Permian and Triassic species), and everything above *Guizhoucoelacanthus*. There are too few Permian coelacanths to be able to determine whether the clade suffered through the end-Permian mass extinction,

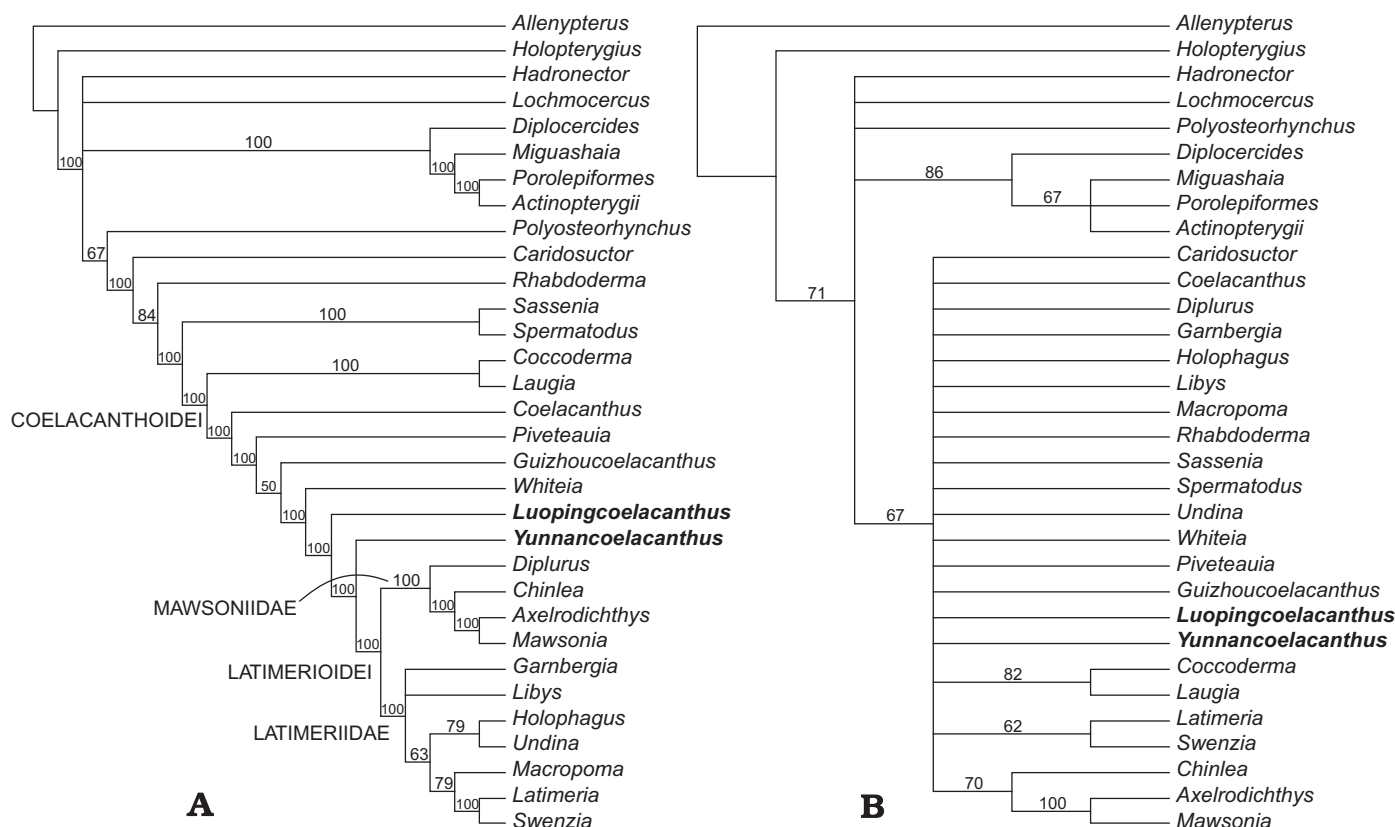


Fig. 8. Cladograms showing the phylogenetic position of coelacanth *Luopingcoelacanthus*, 50% majority-rule tree (A) and strict consensus tree with bootstrap values (B). The analysis yielded 173 trees of length 275, with consistency index of 0.40 and retention index of 0.67; bootstrap values calculated with 1000 replicates. Some major clade names are indicated in A.

but there is every suggestion that coelacanths radiated rather dramatically in the Early and Middle Triassic (Cloutier and Forey 1991), in China as in other parts of the world.

## Live-bearing reproduction in coelacanths

**Ovoviviparity in fishes.**—One of the most startling aspects of *Luopingcoelacanthus* is that the holotype carries two well-developed embryos. Among extant fishes (i.e., hagfish, lampreys, chondrichthyans, actinopterygians, sarcopterygian fishes), 54 families have species that bear live young, including the extant coelacanth *Latimeria chalumnae* (McMillan 2007). The term “viviparity” is generally used to refer broadly to live births, meaning young that are produced directly into the environment rather than hatching from an egg. The plesiomorphic condition among vertebrates is oviparity, meaning the first forms laid eggs. In evolving viviparity, the egg stage may be suppressed, and retained to a greater or lesser extent in the uterus. Coelacanths are ovoviviparous (= oviparous), meaning the embryos develop inside eggs that are retained within the mother’s body until they are ready to hatch.

Blackburn (2005) estimates that viviparity, including ovoviviparity, has originated at least 29 times among fishes

(out of a total of 140 times among vertebrates in general), as follows: teleosts, 11 origins; basal actinopterygians, 1 origin; actinistians (coelacanths), 1 origin; elasmobranchs, 15 origins; and holocephalans, 1 origin. To these can now be added placoderms, with at least one origin, represented by the oldest evidence of viviparity seen in embryos preserved in the Devonian placoderms *Austroptyctodus*, *Materpiscis*, and *Incisoscutum* (Long et al. 2008, 2009). Origins of viviparity appear to be scattered somewhat randomly through geological time, based on fossil evidence, and especially on the phylogenetic evidence assembled by Blackburn (2005), ranging sporadically through the late Palaeozoic, the Mesozoic, and the Cenozoic. Evidence for ovoviviparity, in the form of fossilized retained embryos, has been reported quite rarely (Cloutier 2010), including the Carboniferous holocephalan *Harpagofututor* (Lund 1980; Grogan and Lund 2011), and the Triassic actinopterygians *Saurichthys curionii*, *Birgeria nielsenii*, and *Peltopleurus lissocephalus* (Bürgin 1990; Renesto and Stockar 2009). Remarkably, coelacanths were the first fossil fishes for which embryos were reported (Watson 1927), in *Undina*. Compared to such intrauterine embryos, size series of relatively complete “free” larval and juvenile specimens of as many as 90 fossil fish species have been reported (Cloutier 2010).

Remarkably, the occurrence of viviparity among modern fishes is unevenly distributed, occurring in some 55% of the



900 living species of chondrichthyans, but only 1–2% of the 32,000 species of living osteichthyan fishes (Wourms and Lombardi 1992). These authors note that the evolution of viviparity from oviparity involves: (i) a shift from external to internal fertilization; (ii) retention of embryos in the female reproductive system; (iii) modification of the ovary or oviduct to become sites of gestation; (iv) structural and functional modification of the embryo and the female reproductive system; and (v) modification of extant endocrine mechanisms controlling reproduction.

Viviparity in modern fishes has been explained according to particular aspects of habitat, climate, egg size, and maternal defence ability, but no single explanation appears to cover all cases. Indeed, there are advantages and disadvantages to oviparity and viviparity. Wourms and Lombardi (1992) listed as advantages of ovoviviparity in fishes these factors: (i) enhanced survival of offspring—notoriously, fish eggs are consumed voraciously by many predators in the open water; (ii) compensation for low fecundity—ovoviparous species tend to produce fewer eggs but more offspring; (iii) improvement of reproductive niches to reduce competition, especially where many fish species share a spawning ground; (iv) exploitation of pelagic niches away from the typical sea-bed spawning grounds; (v) colonisation of new habitats, especially by ovoviparous females that can produce multiple broods from single matings; and (vi) increased energetic efficiency in viviparous females that provide nutrition in the womb, compared to the vast loss of energy through wasted embryos and yolk in egg-layers. The principal disadvantages of ovoviviparity among fishes include: (i) reduced fecundity; (ii) energetic cost to the female; and (iii) risk of brood loss through maternal death. Phylogenetic studies confirm that once ovoviviparity develops, the complex physiological changes brought about by egg retention and internal nurturing of the developing embryos mean that it is hard to reverse back to the plesiomorphic condition, namely spawning and external fertilisation of the eggs (Wourms and Lombardi 1992).

**Ovoviviparity in coelacanths.**—The reproductive mode of modern *Latimeria* was debated until the mid-1970s. Ovoviviparity had already been suggested by Watson (1927) in fossil coelacanths, based on specimens of the Late Jurassic *Undina* with two young inside. On the other hand, Schultze (1972, 1980, 1985) argued, based on finds of numerous juveniles beside eggs of the Carboniferous coelacanth *Rhabdoderma*, that all coelacanths were oviparous. On this topic, anatomical studies of modern *Latimeria* had been equivocal, until Smith et al. (1975) reported the dissection of a pregnant female *Latimeria* that retained five embryos with yolk sacs contained within the oviduct. These embryos ranged in length from 301–327 mm in a mother that was 1.6 m long, so they are 19–20% the length of the adult. This large embryonic size is a surprise, and it reflects both their starting point from relatively large eggs (up to 90 mm in diameter, the largest fish eggs known) and that these five embryos were not

close to being born, as indicated by the well-developed yolk sacs (Forey 1998). The *Latimeria* embryos feed entirely, or largely, on yolk in a massive yolk sac contained within the large egg (lecithotrophy). An earlier suggestion (Balon 1991) that additional nutrition may come from eating other eggs in the oviduct and through a yolk-sac “placenta” has been rejected by more recent work, especially by the findings in Mozambique and Tanzania of large females with for instance 26 embryos close to being born and without their yolk sacs (Bruton et al. 1992).

In the Carboniferous coelacanth *Rhabdoderma*, the eggs range up to 53 mm in diameter, and recorded juveniles are from 30–70 mm in length, with a mean adult female length of 600 mm, so giving a range of 5–12% (Schultze 1980; Balon 1991; Cloutier 2010), about half the relative size of the pre-term embryos of *Latimeria*. The eggs and juveniles of *Rhabdoderma* are found isolated, and not enclosed within their mothers, even though the juveniles retain their yolk sacs up to a body length of 50 mm. The difference in egg size and relative size of the retained young between Carboniferous *Rhabdoderma* and modern *Latimeria* suggests that at least one lineage of coelacanths may have increased the level of maternal investment in terms of extra yolk and perhaps a longer retention time for the embryos through time, presumably a way to ensure that the juveniles are ready to defend themselves as soon as they hatch (Balon 1991).

The case of the Jurassic coelacanth *Undina*, from the Solnhofen Limestone in Germany, the first reported ovoviparous actinistian (Watson 1927), has been queried. Schultze (1972) argued that the young were merely evidence for cannibalism, that the larger coelacanth had swallowed two young of the same species, and he cited as evidence the position of the reputed embryos within the body and the fact that fossil coelacanths have been found with remains of other fishes inside their bodies, evidence that they were carnivores. Others, however (e.g., Balon 1991; Forey 1998), have accepted Watson’s (1927) original view that the small coelacanths are indeed late-stage embryos. The same is true for the Cretaceous *Axelrodichthys* with three apparent embryos (Maisey 1986). Therefore, the oldest record of ovoviviparity in coelacanths hitherto has been from the Late Jurassic.

It is not particularly surprising then to be able to extend the record of ovoviviparity in coelacanths back to the Middle Triassic, by our finding of intrauterine embryos in the holotype of the new genus *Luopingcoelacanthus*. There are four lines of evidence that these are larvae of the including adult: (i) the embryos show two apomorphies of the adult taxon (expanded posterior margin of the lachrymojugal; semi-circular coronoid); (ii) they are contained in the anteroventral region of the abdominal cavity, the area where the oviduct is located in modern *Latimeria*; (iii) they show the head/body length proportions (33%) of near-hatching embryos in modern *Latimeria*; and (iv) they show similar juvenile/adult body length ratios (10–14%) seen in Carboniferous *Rhabdoderma* embryos (5–12%), but smaller than near-hatching *Latimeria* embryos (19–20% adult length).

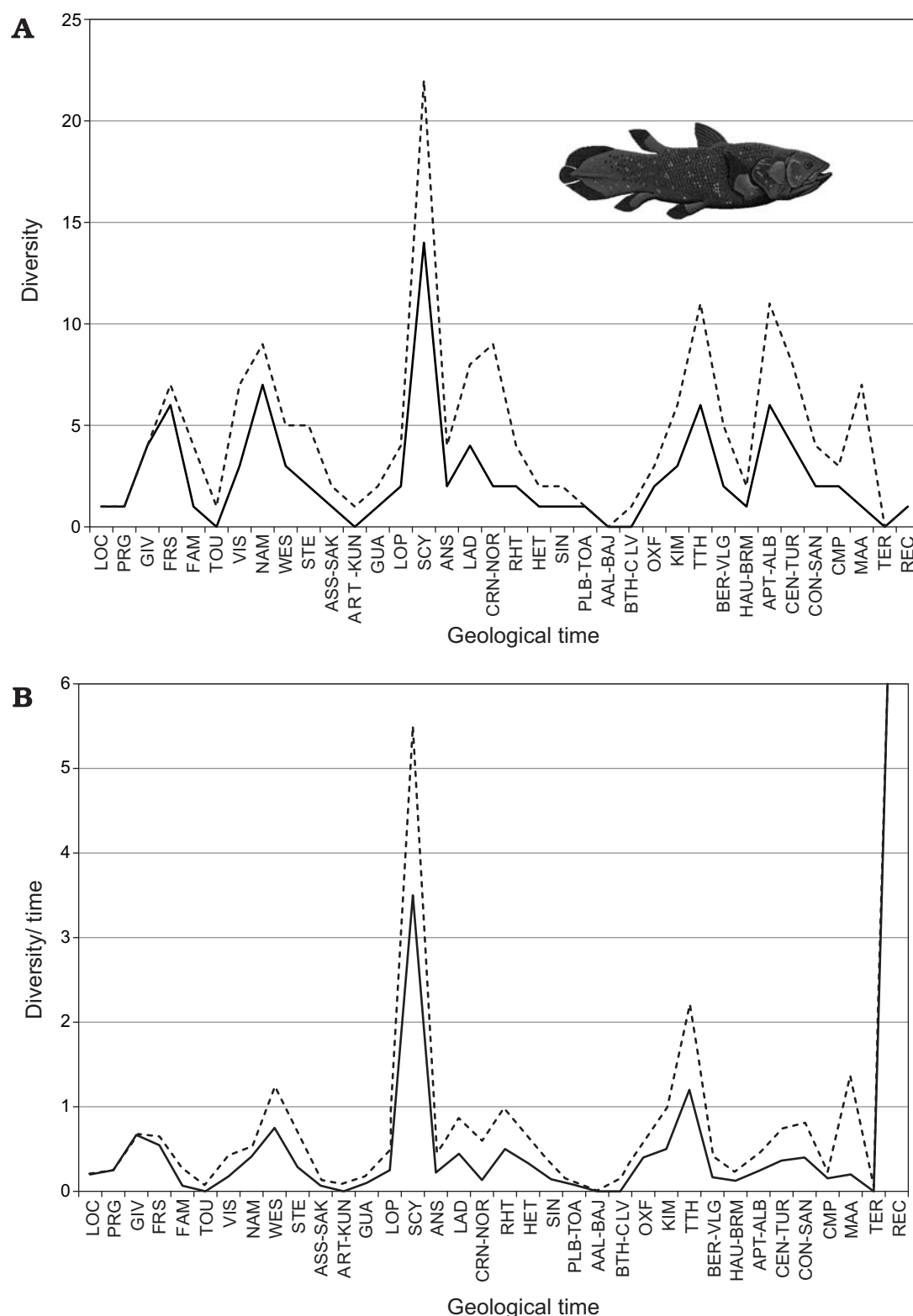


Fig. 9. Diversity of coelacanths through time, compiled from Cloutier and Forey (1991) and updated with data from the Appendix 1, showing raw data (**A**) and data standardised by duration of time bins (**B**). In each plot, the solid line shows numbers of named species, and dotted line shows additional records of unnamed coelacanth taxa. *Abbreviations of geological stages*: AAL, Aalenian; ALB, Albian; ANS, Anisian; APT, Aptian; ART, Artinskian; ASS, Asselian; BAJ, Bajocian; BER, Berriasian; BRM, Barremian; BTH, Bathonian; CEN, Cenomanian; CLV, Callovian; CMP, Campanian; CON, Coniacian; CRN, Carnian; FAM, Famennian; FRS, Frasnian; GIV, Givetian; GUA, Guadalupian; HAU, Hauterivian; HET, Hettangian; KIM, Kimmeridgian; KUN, Kungurian; LAD, Ladinian; LOC, Lochkovian; LOP, Lopingian; MAA, Maastrichtian; NAM, Namurian; NOR, Norian; OXF, Oxfordian; PLB, Pliensbachian; PRG, Pragian; REC, Recent; RHT, Rhaetian; SAK, Sakmarian; SAN, Santonian; SCY, Scythian; SIN, Sinemurian; STE, Stephanian; TER, Tertiary; TOA, Toarcian; TOU, Tournaisian; TTH, Tithonian; TUR, Turonian; VIS, Viséan; VLG, Valanginian; WES, Westphalian.



## Coelacanths and recovery from mass extinction

As noted earlier, the Early Triassic was a time of apparently high diversity of coelacanths worldwide: the total of up to 20 species exceeds the diversity found in any other time interval, in the compilation by Cloutier and Forey (1991), and in an updated version (Fig. 9). Numbers rose from 0–3 species worldwide in the Late Permian to 14–21 in the Early Triassic, and then fell to 4–9 in the Middle Triassic. These are low figures overall, and based on small numbers of specimens, and so cannot be treated as reliable in detail. The high total in the Early Triassic (Fig. 9A) is, however, not readily attributable to differing durations of time bins: at 4 Myr, the Early Triassic is the shortest of all time bins sampled by Cloutier and Forey (1991), and so when corrected for duration, the peak becomes even more strikingly high (Fig. 9B).

Perhaps the Early Triassic peak reflects the chance survival of coelacanths through the end-Permian mass extinction, and their ability to benefit from the traumatic post-extinction conditions when other fish groups were struggling to recover. Certainly, modern *Latimeria*, which live slow-moving lives, hunting at night in deep waters, show physiological characteristics of organisms that are relatively immobile, have a low metabolic rate, and live in oxygen-deficient settings (Fricke and Hissmann 2000). As these authors note (Fricke and Hissmann 2000: 385): “[*Latimeria*] survives in a present environment that is probably inaccessible to most modern fish of similar size, with their greater activity and higher rate of metabolism. Its breathing physiology and gill morphology and the unique rostral organ, a giant electroreceptor..., allow the coelacanth today—and probably also in the past—to inhabit an oxygen-poor environment of low biomass. Probably extinct coelacanthid fish were adapted to murky, oxygen-deficient, shallow-water habitats which were food limited for a piscivorous predator.”

Anoxic conditions were widespread in the aftermath of the end-Permian mass extinction (Wignall and Twitchett 1996). Perhaps the Early Triassic coelacanths were disaster taxa, and like their modern relative, were capable of occupying dysoxic and anoxic conditions, like some of the surviving brachiopods and thin-shelled bivalves of the earliest Triassic (Benton and Twitchett 2003; Chen and Benton (2012). This assumes of course that these fossil coelacanths shared aspects of their physiology with *Latimeria*: ancient coelacanths certainly show a variety of different life styles, including occasional forays into fresh waters.

Such anoxic conditions were much less widespread in the Middle Triassic, although individual horizons with abundant fish fossils at Luoping, and elsewhere, represent seasonal anoxia following algal blooms (Hu et al. 2011). But coelacanths were rare in the Luoping biota, amounting to five out of some 20 000 exceptionally preserved fossil specimens so far recovered (Zhang and Zhou 2008; Zhang et al. 2008; Hu et al. 2011). The present materials include the first reported

unborn embryos. Work on this cornucopia of new material is only just beginning and further material may emerge that can test the assumptions made here.

## Acknowledgements

We thank Chen Qing-Tao (Kunming University, Kunming, China) for his reconstruction, and Jenny Clack (Cambridge University, Cambridge, UK) and Gaël Clément (Muséum Nationale d'Histoire Naturelle, Paris, France) for many helpful comments on the manuscript. This work is supported by two projects of China Geological Survey, numbers 1212011140051 and 1212011120621.

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## Appendix 1

List of coelacanth records since 1991, as a supplement to the data given by Cloutier and Forey (1991), and forming the basis of Fig. 9. Taxa are listed stratigraphically, under three categories, A (valid species), B (named taxa, but not placed in cladogram), and C (unnamed, but definitely coelacanth). Abbreviations: Fm., Formation, Mt., Mountain.

Stratigraphic stage	Species	Geological formation	Author	Year	A	B	C
Lochkovian	<i>Styloichthys changae</i>	Xitun Fm.	Friedman	2007	1		
Pragian	<i>Eoactinistia foreyi</i>	Fairy Fm.	Johanson et al.	2006	1		
Givetian	<i>Miguashia grossi</i>	Gauja/Lode Fm.	Forey et al.	2000	1		
Givetian	<i>Gavinia syntrips</i>	Mt. Howitt	Long	1999	1		
Givetian–Frasnian	<i>Holopterygius nudus</i>	Oberer Plattenkalk	Friedman and Coates	2006	1		
Givetian–Frasnian	<i>Shoshonia arctopteryx</i>	Jefferson Fm.	Friedman et al.	2007	1		
Famennian	<i>Diplocercides</i> sp.	Kadzielnia	Szrek	2007		1	
Visean	unnamed	Rosenbeck	Witzmann et al.	2010			1
Artinskian	unnamed	Mangrullo Fm.	Piñeiro et al.	2012			1
Lopingian	unnamed	Corumbatai Fm.	Figueiredo and Carvalho	2004		1	
Lopingian	unnamed	Kupferschiefer	Diedrich et al.	2009		1	
Scythian	<i>Chaohuichthys majishanensis</i>	Helongshan Fm.	Tong et al.	2006	1		
Scythian	unnamed	Helongshan Fm.	Tong et al.	2006			1
Anisian	<i>Luopingcoelacanthus eurylacrimalis</i>	Guanling Fm.	Wen et al.	2013{?}	1		
Anisian	<i>Yunnancoelacanthus acrotuberculatus</i>	Guanling Fm.	Wen et al.	2012	1		
Carnian	<i>Guizhoucoelacanthus guanlingensis</i>	Falang Fm.	Geng et al.	2009	1		
Carnian–Norian	unnamed	Huachi	Liu et al.	1999		1	
Carnian–Norian	unnamed	Upper Triassic	Hunt	1997		1	
Carnian–Norian	unnamed	Culpepper Basin	Weems and Kimmel	1993		1	
Carnian–Norian	unnamed	Pardonet Fm.	Yabumoto and Neuman	2004			1
Norian	unnamed	Placerias Quarry	Kaye and Padian	1994		1	
Hettangian	<i>Chinlea</i> -like	Moenave Fm.	Milner et al.	2006	1		
Oxfordian	<i>Svenzia latimerae</i>	Oxfordien	Clément	2005	1		
Upper Jurassic	unnamed	Madagascar	Bürgin and Appert	1999			1
?Upper Jurassic	<i>Parnaibaia maranhaoensis</i>	Pastos Bons	Yabumoto	2008	1		
Berriasian	<i>Mawsonia</i>	Areadao Group	Carvalho and Maisey	2008	1		
Hauterivian–Barremian	mawsoniid	Cabao	Le Loeuff et al.	2010		1	
Aptian	unnamed	Crato Fm.	Brito and Martill	1999			1
Aptian–Albian	<i>Mawsonia brasiliensis</i>	Romualdo Member	Yabumoto	2002	1		
Albian	<i>Mawsonia lavocati</i>	Tegana Fm.	Yabumoto and Uyeno	2005	1		
Albian–Cenomanian	<i>Mawsonia</i> sp.	Alcântara Fm.	Candeiro et al.	2011	1		
Cenomanian	mawsoniid	Kem Kem	Cavin and Forey	2004	1		
Cenomanian	unnamed	[Brazil]	Medeiros and Villas Bôas	1999			1
Cenomanian	unnamed	[NW Germany]	Lehmann et al.	1997		1	
Turonian	<i>Palaeoctopus pelagicus</i>	Agua Nueva Fm.	Schultze et al.	2010	1		
Coniacian–Santonian	unnamed	Ankazomihaboka sandstones	Gottfried et al.	2004		1	
Campanian	<i>Megalocoelacanthus dobiei</i>	Blufftown Fm.	Schwimmer et al.	1994	1		
Campanian	<i>Megalocoelacanthus dobiei</i>	Smoky Hill Chalk	Schwimmer	2009		1	
Maastrichtian	<i>Megalocoelacanthus dobiei</i>	Navesink Fm.	Schwimmer	2009		1	
Maastrichtian	unnamed	Cruzy	Cavin et al.	2005			1