

# 贵州空棘鱼属的修订与系统发育分析<sup>1)</sup>

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**摘要:** 依据在云南富源中三叠世法郎组竹杆坡段发现的新材料, 对关岭贵州空棘鱼 (*Guizhoucoelacanthus guanlingensis*) 进行了补充描述, 并修订了鼻骨、顶骨、后顶骨、额外肩胛骨、眶后骨、偶鳍、鳞片等特征。系统发育分析表明, 贵州空棘鱼属与 *Whiteia* + *Piveteaui* 构成姐妹群, 其共有离征包括: 两对顶骨的大小相近, 第一背鳍鳍条数小于8。建议将贵州空棘鱼属归入怀特鱼科 (Whiteiidae)。

**关键词:** 云南, 中三叠世, 空棘鱼类, 系统发育

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## A REVISION AND PHYLOGENETIC ANALYSIS OF *GUIZHOUCOELACANTHUS* (SARCOPTERYGII, ACTINISTIA) FROM THE TRIASSIC OF CHINA

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**Abstract** We re-describe the coelacanth *Guizhoucoelacanthus guanlingensis* Liu et al., 2006, mainly based on a new articulated specimen from the Middle Triassic of Fuyuan, Yunnan Province, China. It is characterized by its small orbital openings, and the postorbital spanning the intracranial joint. The phylogenetic analysis suggests that *Guizhoucoelacanthus* is the sister taxon of *Whiteia* + *Piveteaui*. *Guizhoucoelacanthus* is assigned to the family Whiteiidae with derived characters including: anterior and posterior pairs of parietals of similar size; fin rays in anterior dorsal fin less than eight.

**Key words** Yunnan, Middle Triassic, coelacanths, phylogeny

### 1 Introduction

The Actinistia (coelacanths), a group of sarcopterygian fishes, is represented by fossils from the Lower Devonian (Johanson et al., 2006) to the Upper Cretaceous, and by the living genus *Latimeria* (Smith, 1939). In China, at least five coelacanth genera are known from the Upper Permian to the Upper Triassic. *Sinocoelacanthus fengshanensis* represents the first coelacanth from China (Liu, 1964), however it is poorly defined by a caudal fin from the Lower Triassic of Fengshan, Guangxi. Wang and Liu (1981) described other two Chinese coelacanths,

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*Changxingia aspratilis* and *Youngichthys xinghuaisis* from the Upper Permian Changxing Formation in Changxing, Zhejiang. Jin (1997) described the second species of *Changxingia*, *C. weii*, from the same locality as that of the type species, *C. aspratilis*. Liu et al. (1999) reported an incomplete coelacanth specimen from the Upper Triassic in Huachi, Gansu, Northwest China, and assigned it to the family Laugiidae Stensiö, 1932. Tong et al. (2006) described *Chaohuichthys majiashanensis* and some undetermined coelacanth specimens from the Lower Triassic (Olenekian) at the North Majiashan sections in Chaohu, Anhui.

*Guizhoucoelacanthus guanlingensis* was erected by Liu et al. (2006) on the basis of a single specimen from the Upper Triassic Wayao Member (Carnian) of the Falang Formation in Xinpu, Guanling County, Guizhou Province. Although the holotype is nearly complete (Liu et al., 2006, pl. I-1), the original brief description and blurry illustration of *G. guanlingensis* provided few data for the further study. Here we describe a new well-preserved specimen of *Guizhoucoelacanthus guanlingensis* from the Middle Triassic Zhuganpo Member of the Falang Formation in Fuyuan, Yunnan Province. The new examination reveals some derived character linking *Guizhoucoelacanthus* to *Whiteia* and *Piveteauia* of the family Whiteiidae (Schultze, 1993).

## 2 Systematic paleontology

### Sarcopterygii Romer, 1955

#### Actinistia Cope, 1871

#### Coelacanthiformes Huxley, 1861

#### Whiteiidae Schultze, 1993

#### *Guizhoucoelacanthus* Liu et al., 2006

**Type species** *Guizhoucoelacanthus guanlingensis* Liu et al., 2006.

**Emended diagnosis** A moderate-sized coelacanth. The head is relatively large with small orbital openings and narrow skull roof. The parietonasal shield bears three pairs of nasals, two pairs of parietals. The postparietal shield is much shorter than the parietonasal shield. The posterior margin of the postparietal shield is slightly embayed. Three extrascapulars suture closely with each other, and with postparietals and supratemporals. The cheek bones (lachrymojugal, postorbital, squamosal and preoperculum) are tightly abutted against each other. The operculum is rounded dorsally and posteriorly. Sensory canals are developed and open to the surface through a few large pores. Neural and haemal arches and spines are completely ossified. There are about 45 neural arches. The first six or seven neural arches are short. Centra and ribs are unossified. The first dorsal fin is anteriorly placed, with a large basal plate. The basal plate of the second dorsal fin is cylindrical, with slender, horizontal anterior process and anteroventral process inserted deeply between two neural spines. The basal plate of the anal fin is slender and its distal part is laterally expanded. The caudal fin consists of three lobes; dorsal and ventral lobes symmetrical; middle lobe obviously marked off from dorsal and ventral ones. All fin rays are devoid of ornament. Scales are ornamented with flattened longitudinal ridges. Lateral line scales are prominent.

**Remarks** *Guizhoucoelacanthus* was erected by Liu et al. (2006) and referred to the Coelacanthidae. The present assignment of *Guizhoucoelacanthus* to the Whiteiidae is on the basis of two pairs of parietals of similar size, and fin rays of the first dorsal fin less than eight. Schultze (1993) erected the Whiteiidae, including *Whiteia* (Moy-Thomas, 1935) and *Piveteauia* (Lehman, 1952). *Guizhoucoelacanthus* differs from *Whiteia* in having a moderate-sized individual, small orbital openings, and the postorbital spanning the intracranial joint. *Whiteia* is a small coelacanth with its standard length less than 25 cm, and bears large orbital openings and the postorbital that is entirely behind the intracranial joint. *Guizhoucoelacanthus* differs from *Piveteauia* in its unbranched jugal sensory canal, branched fin rays, and the position of the pelvic fins on the abdomen. In *Piveteauia*, the jugal sensory canal has a short dorsal branch, the

fin rays are unbranched, and the pelvic fins are anteriorly positioned.

***Guizhoucoelacanthus guanlingensis* Liu et al., 2006**

(Figs. 1–3)

*Guizhoucoelacanthus guanlingensis* Liu et al., 2006: 2–3, Plate I–1

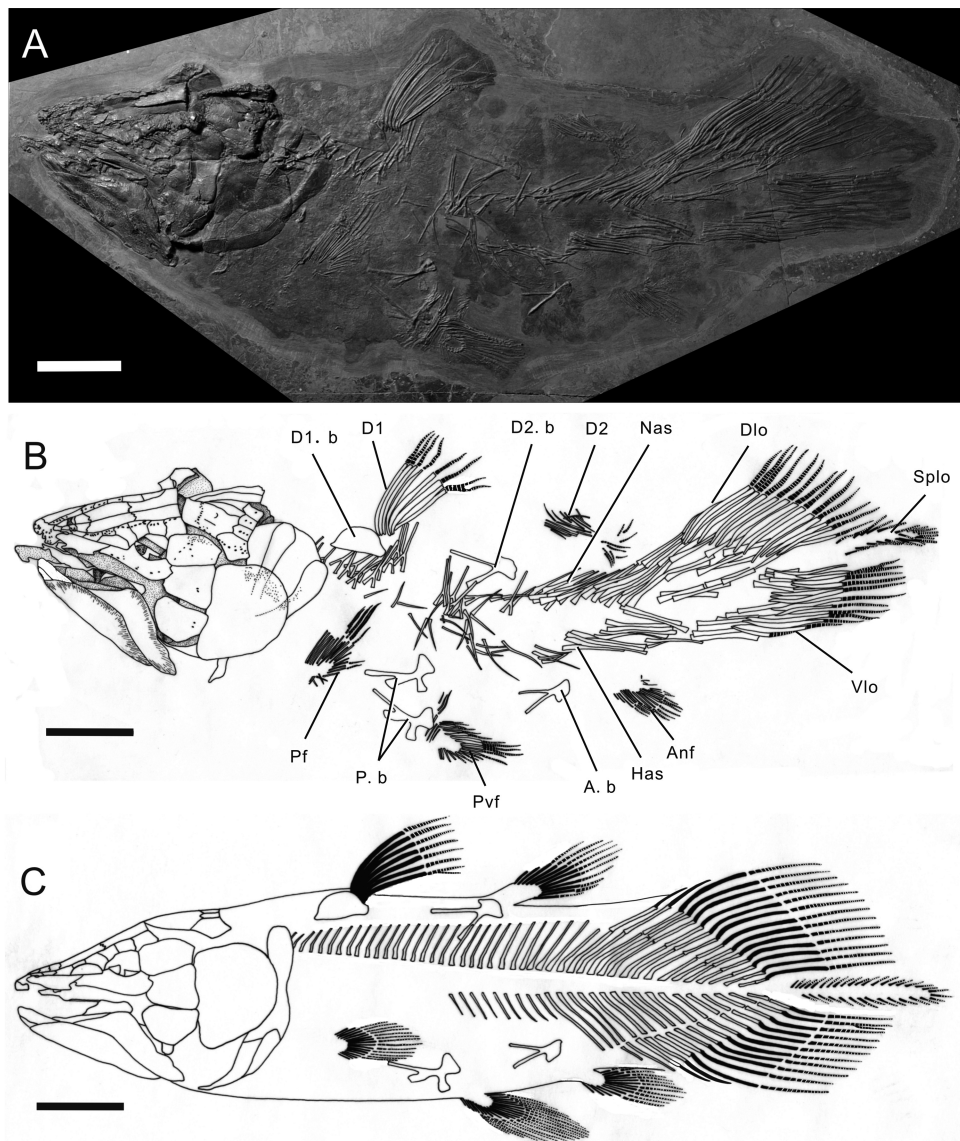


Fig. 1 *Guizhoucoelacanthus guanlingensis* Liu et al., 2006

A. Photograph of IVPP V 15153 in left lateral view; B. composite drawing based on V 15153;

C. restoration of entire fish; scale bar equals 5 cm

Abbreviations: A. b. basal plate of anal fin 臀鳍基板; Anf. anal fin 臀鳍; D1. first dorsal fin 第一背鳍; D1. b. basal plate of the first dorsal fin 第一背鳍基板; D2. second dorsal fin 第二背鳍; D2. b. basal plate of the second dorsal fin 第二背鳍基板; Dlo. dorsal lobe of caudal fin 尾鳍背叶; Has. haemal arch and spine 脉弓脉棘; Nas. neural arch and spine 髓弓髓棘; P. b. basal plate of pelvic fin 腹鳍基板; Pf. pectoral fin 胸鳍; Pvf. pelvic fin 腹鳍; Splo. supplementary lobe of caudal fin 尾鳍中叶; Vlo. ventral lobe of caudal fin 尾鳍腹叶

**Holotype** F001, a nearly complete specimen housed in the Geological Survey of Guizhou.

**Referred new specimen** A nearly complete specimen, IVPP V 15153.

**Type locality and horizon** Upper Triassic Wayao Member (Carnian) of the Falang Formation, Xinpu, Guanling County, Guizhou Province, southwestern China.

**New locality and horizon** Middle Triassic Zhuganpo Member (Ladinian) of the Falang Formation, Fuyuan, Yunnan Province, southwestern China.

**Emended diagnosis** As for genus (monotypic genus).

**Description** A moderate-sized coelacanth. The body is fusiform and the head is relatively large (Fig. 1). The body depth at the origin of the first dorsal fin is about 120 mm; total length 550 mm; standard length 438 mm; head length 155 mm (Table 1).

**Skull roof:** the anterior and posterior divisions of the skull, whose ornament is lacking, are evidently separated from each other (Fig. 2). The parietonasal shield is much longer than the postparietal shield, and its length is about 2 times the length of the postparietal shield. The intracranial joint is transversely straight. The postparietal shield is wider than the parietonasal shield, and its width is about 2.3 times the width of the parietonasal shield.

The parietonasal shield bears three pairs of nasals and two pairs of parietals (Fig. 2, Na, Pa). The three pairs of nasals were described as one pair of postrostral and two pairs of nasals by Liu et al. (2006). Liu et al (2006) were not certain of two pairs of parietals, but suggested the posterior parietal shorter and wider than the anterior parietal. Two pairs of parietals are confirmed in V 15153, with the anterior and posterior parietals of similar size, as in *Whiteia*, *Chinlea*, *Rhabdoderma*, *Allynpterus* (Moy-Thomas, 1935; Schaeffer, 1967; Forey, 1981, 1998; Lund and Lund, 1985). Four tectals (Fig. 2, Te) are followed by four supraorbitals (Fig. 2, So). They together flank the parietals and nasals. The anterior supraorbital is projected ventrally to contact the lachrymojugal and separate the preorbital from the orbital margin, as in *Whiteia* (Forey, 1998).

The anterior margin of the postparietal shield is straight and without any indentations along the intracranial joint, as in *Latimeria*, *Allynpterus*, *Hadronector*, *Diplocercides*, *Miguashaia*, *Whiteia*, *Coelacanthus*, *Diplurus*, *Undina*, *Wenzia* (Smith, 1939; Lund and Lund, 1984, 1985; Forey, 1998; Moy-Thomas, 1935; Schaeffer, 1948; Clément, 2005). The posterior margin of the postparietal shield is embayed, as in *Latimeria* and most Mesozoic coelacanths (Forey, 1998). The intertemporal is absent. The extrascapular series consists of a median and two lateral extrascapulars (Fig. 2, Ext. l, Ext. m), as in some primitive coelacanths (*Allynpterus*, *Hadronector*, *Diplocercides*, *Miguashaia*) (Lund and Lund, 1984, 1985; Forey, 1998). In Liu et al.'s (2006) description, the postparietal was described as parietal-intertemporal; the extrascapular series were uncertain.

The course of sensory canals, which were not described in Liu et al. (2006), are similar to those in *Latimeria* and *Whiteia* (Forey, 1998; Moy-Thomas, 1935). The supraorbital sensory canal (Fig. 2, so. sc) runs between the parietonasal and the supraorbito-tectal series. The tectals and supraorbitals are perforated by several large pores. The otic sensory canal (Fig. 2, ot. sc) is well developed in the postparietal, and opens to the surface along the lateral edge of the postparietal by three pores. The medial branch of the otic sensory canal (Fig. 2, ot. sc. m) opens to the surface through a series of pores. The middle and posterior pit-lines (Fig. 2, mpl, ppl) are in posterior half of the postparietal. The otic sensory canal opens to the surface in the supratemporal through about six pores.

**Cheek and opercular series:** the cheek (Fig. 2) is completely covered by a full complement of bones which fit tightly together with matching contours. There is no overlap between most of the bones. In many respects the cheek is very similar to that in *Whiteia* (Moy-Thomas, 1935; Forey, 1998).



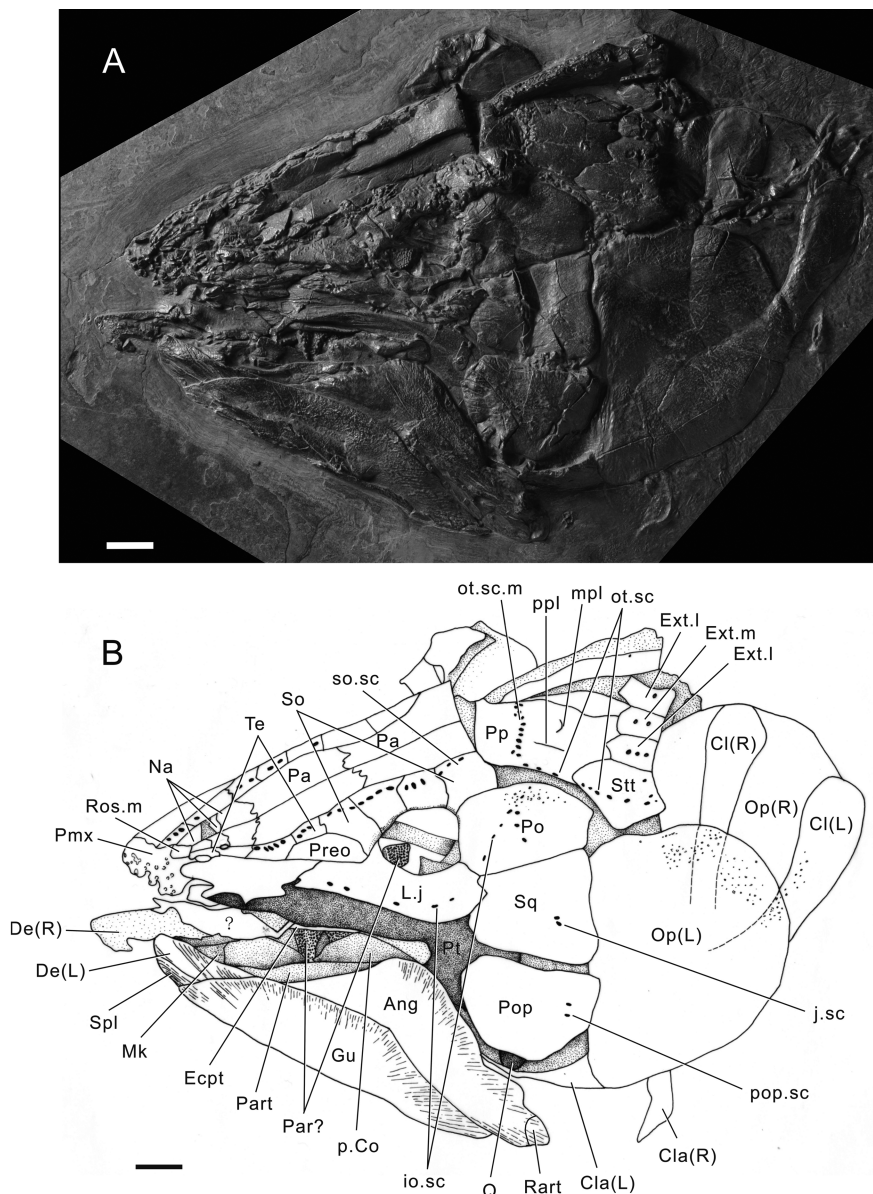


Fig. 2 Skull of *Guizhoucoelacanthus guanlingensis* (IVPP V 15153)

in right lateral view; scale bar equals 1 cm

Abbreviations: Ang. angular 隅骨; Cl(L). left cleithrum 左侧匙骨; Cl(R). right cleithrum 右侧匙骨; Cla(L). left clavicle 左侧锁骨; Cla(R). right clavicle 右侧锁骨; De(L). left dentary 左侧齿骨; De(R). right dentary 右侧齿骨; Ecpt. ectopterygoid 外翼骨; Ext.l. lateral extrascapular 侧额外肩胛骨; Ext.m. median extrascapular 中额外肩胛骨; Gu. gular 喉板骨; io. sc. infraorbital sensory canal 眶下管; j. sc. jugal sensory canal 颧骨管; L. j. lachrymojugal 泪-颧骨; Mk. mentomeckelian 麦氏软骨; mpl. middle pit-line 中凹线; Na. nasal 鼻骨; Op. operculum 鳃盖骨; ot. sc. m. medial branch of otic sensory canal 耳区管的中部分支; Pa. parietal 顶骨; Par. parasphenoid 副蝶骨; Part. prearticular 前关节骨; p. Co. principal coronoid 主冠状骨; Pmx. premaxilla 前上颌骨; Po. postorbital 眶后骨; Pop. preoperculum 前鳃盖骨; pop. sc. preoperculum sensory canal 前鳃盖管; Pp. postparietal 后顶骨; ppl. posterior pit-line 后凹线; Preo. preorbital 眶前骨; Pt. pterygoid 翼骨; Q. quadrate 方骨; Rart. retroarticular 后关节骨; Ros. m. median rostral 中吻骨; So. supraorbital 眶上骨; so. sc. supraorbital sensory canal 眶上管; Spl. splenial 夹板骨; Sq. squamosal 鳞骨; Stt. supratemporal 上颞骨; Te. tectal 案骨

The lachrymojugal (Fig. 2, L. j) is elongated in shape and strongly curved. The anterior end of the lachrymojugal reaches to beneath the preorbital, as in *Whiteia* (Moy-Thomas, 1935; Forey, 1998). The infraorbital sensory canal opens through more than five pores at the ventral part of the bone.

The postorbital (Fig. 2, Po) is nearly rectangle, unlike that in most coelacanth. Its dorsal margin is ornamented with rounded tubercles. The infraorbital sensory canal runs through the anterior portion of the postorbital and opens directly through several pores.

The squamosal (Fig. 2, Sq) is positioned below the postorbital. The squamosal is a large bone with narrow anterior and wide posterior ends. The jugal sensory canal passes through the centre of the bone, as in *Whiteia*, *Piveteauia*, *Mawsonia*, *Sassenia*, *Rhabdoderma* (Moy-Thomas, 1935; Clément, 1999; Forey, 1998). There are few pores opening from the posterior half of the bone.

Below the squamosal is a preoperculum (Fig. 2, Pop), which is also a large bone with rounded anterior margin and straight dorsal margin. This bone was termed as the quadratojugal-preoperculum in Liu et al. (2006).

The suboperculum and spiracular were described by Liu et al. (2006), however they are not preserved in V 15153. The operculum (Fig. 2, Op) is relatively big, and is rounded dorsally and posteriorly. The bone is ornamented with tubercles.

Lower jaw and gular: the lower jaw described here is same as that of the type specimen (Liu et al., 2006). The meckelian cartilage is ossified. Part of the mentomeckelian (Fig. 2, Mk) is preserved. Part of the retroarticular and the prearticular are visible in external view.

The angular (Fig. 2, Ang) is a relatively shallow bone with an obvious coronoid expansion, and bears only a narrow overlap for the gular palate. The dorsal margin is rounded. The maximum depth occurs in anterior half of the bone. The posterior part of the angular is ornamented with some small ridges.

The dentary (Fig. 2, De) is elongate, horn-like, as in most Paleozoic coelacanth, and lacks any teeth. Below the dentary is a single slender splenial with a tapering anterior end (Fig. 2, Spl).

The principal coronoid (Fig. 2, p. Co) is positioned at about the anterior part of the angular. The principal coronoid is long, low and saddle-shaped.

The gular plate (Fig. 2, Gu) is elongate, and is ornamented with many small ridges.

? Parasphenoid: two segments are present on the dorsal margin of the lachrymojugal and on the ventral margin of the pterygoid (Fig. 2, Par?). Small, rounded denticles are distributed on the palatal surface of the bones. We tentatively attribute these segments to the parasphenoid, considering the distribution of the denticles on the entopterygoid, on the prearticular and on one of the anterior coronoids.

Palate: the palate is poorly preserved. Most part of the palate is covered by the cheek bones and lower jaw. Part of the pterygoid (Fig. 2, Pt) and the quadrate (Fig. 2, Q) are visible in external view. The pterygoid is triangular, as in most of other coelacanth. The quadrate forms the articular condyle of the mandibular joint caudoventrally. The ectopterygoid (Fig. 2, Ecpt) is a slender bone beneath the pterygoid.

Postcranial skeleton: the features of the postcranial skeleton are similar to that of the holotype of *G. guanlingensis* (Fig. 1). The median and paired fins are relatively well preserved. The first dorsal fin is anteriorly placed; the second dorsal fin is situated at the middle of the body; the pelvic fin is situated slightly before the level of the second dorsal fin; the anal fin is situated at a level behind the second dorsal fin. All fin rays are unornamented, as in *Rhabdoderma*, *Laugia*, *Coelacanthus*, *Trachymetopon*, *Chinlea*, *Piveteauia*, and *Garnbegia* (Lund and Lund, 1985; Stensiö, 1932; Forey, 1998; Schaeffer, 1967; Clément, 1999; Martin and Wenz, 1984). All fin rays are not expanded and distally segmented.

**Vertebral column:** the centra and the ribs are unossified (Fig. 1). The neural and haemal spines are ossified. There are about 45 neural spines. The first six or seven neural spines are short and the posterior ones are longer. The neural spines within the anterior part of the caudal region are the longest.

**Median fins:** the basal plate of the first dorsal fin (D1) is relatively large (Fig. 1). The D1 consists of 8 distally segmented fin rays, as in many Triassic coelacanths, such as *Diplurus*, *Holophagus*, *Heptanema*, *Undina* and *Whiteia* (Schaeffer, 1948; Forey, 1998; Moy-Thomas, 1935). All the fin rays probably articulated directly on the caudodorsal border of the basal plate, again segmented for the distal third length.

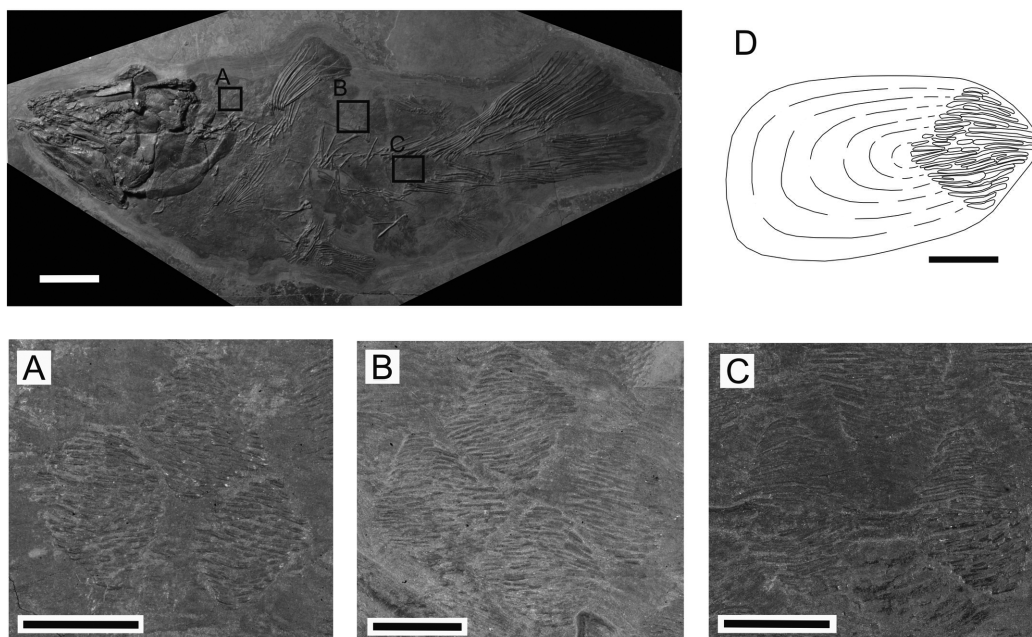


Fig. 3 Scales of *Guizhoucoelacanthus guanlingensis*, new material, IVPP V 15153

A. scales in front of the first dorsal fin; B. scales in front of the second dorsal fin; C. lateral line scales from the level of the anal fin; D. reconstruction of a scale; scale bar for the whole fish equals 5 cm; A–D scale bars equal 5 mm

The second dorsal fin (D2) is lobe-shaped (Fig. 1). The basal plate of the D2 is cylindrical, with a slender, horizontal anterior process and a stout anteriorventral process inserted deeply between two neural spines. The posterior portion of the basal plate is broad. The axial mesomeres are unossified. There are 9–12 segmented fin rays.

The anal fin is also lobe-shaped (Fig. 1). The basal plate of the anal fin is similar to that of the D2, with an anterior process and an anteriorventral process. The axial mesomeres are unossified. About 12–13 segmented fin rays are present.

As in most of other coelacanths, the caudal fin is developed as nearly equal dorsal and ventral lobes, which are structural mirror images of each other, and a separate supplementary lobe (Fig. 1). The radials of the dorsal and ventral lobes are slender and perichondrally ossified. Each fin ray is supported by one radial which in turn articulates with one neural or haemal spine. There are 15 fin rays in the dorsal lobe, and 14 fin rays in the ventral lobe. In both dorsal and ventral lobes, the first two fin rays progressively increase in length and are unsegmented. The following fin rays are segmented for about the distal half of their length. The neural and haemal spines are present in the supplementary lobe, but the radials are absent. Some

16–18 slender and segmented rays are present in the supplementary lobe.

Shoulder girdle and fin; the shoulder girdle is sickle-shaped and similar to that in other coelacanth (Figs. 1, 2). The cleithrum is well preserved. The dorsal extremity of the cleithrum is rounded. The anocleithrum is not preserved. The extracleithrum is covered by the operculum. The clavicle is preserved, but its shape is uncertain.

The pectoral fin is lobe-shaped (Fig. 1). The axial mesomeres are ossified. There are about 18 segmented fin rays.

Pelvic girdle and fin; the ossified portion of the pelvic girdle has an anterior process which is divided to two processes, and posteriorly has a medial process (Fig. 1). The posterior surface of the pelvic girdle is cartilage-capped.

The pelvic fin is also lobe-shaped (Fig. 1), like the pectoral fin. The axial mesomeres are unossified. About 22 segmented fin rays are present.

Scales; the scales are thin and well preserved (Fig. 3). There are about 80 lateral line scales from the skull to the base of the supplementary lobe of the caudal fin. The scales are ornamented with many elongate ridges, as in *Whiteia*, *Holophagus* (Moy-Thomas, 1935; Forey, 1998), about 18–20 per scale. The scale is ligulate in shape, but Liu et al. (2006) described the shape of the scale as rhombic.

**Measurement** See Table 1.

**Table 1** Measurement of *Guizhoucoelacanthus guanlingensis* new material (IVPP V 15153) (mm)

Total length	550
Distance from snout to the base of supplementary caudal fin	438
Head length	150
Depth of head	97
Distance from the snout to the base of D1	191
Distance from the snout to the base of D2	278
Distance from the snout to the posterior tip of the pelvic girdle	256

### 3 Phylogenetic analysis and results

The phylogenetic relationships of the coelacanth and their taxonomic arrangement were previously dealt with by Schaeffer (1941), Forey (1981, 1984, 1988, 1991, 1998), Cloutier (1991a,b), Maisey (1991), Clément (2005) and Friedman and Coates (2006).

In order to find the phylogenetic position of *Guizhoucoelacanthus*, we incorporated its morphological characters into the data matrix of Forey (1998) (Appendix II). Clément (2005) and Friedman and Coates (2006) corrected character 31 of Forey's (1998) matrix. A morphological character (character 109 after Friedman and Coates, 2006) and three taxa (*Wenzia* after Clément, 2005; *Holopterygius* after Friedman and Coates, 2006 and *Piveteaia* (Clément, 1999)) were added to this data matrix. The character list was after Forey (1998), Clément (2005) and Friedman and Coates (2006).

The phylogenetic analysis was conducted using PAUP 4.0b10, using the heuristic search option. All characters were set to equal weight and unordered. We obtained similar results by two different ways. The first solution (hsearch start = stepwise; addseq = simple; swap = tbr) yielded 36 equally most parsimonious (MP) trees, with a tree length = 265, consistency index (CI) = 0.4340, retention index (RI) = 0.6888. The second solution (hsearch start = stepwise; addseq = random; nreps = 1000; swap = tbr) yielded 163 equally most parsimonious (MP) trees, with a tree length = 265, consistency index (CI) = 0.4340, retention index (RI) = 0.6888. The 50% majority-rule consensus tree (MRCT) and one of most parsimony trees are

presented in Fig. 4.

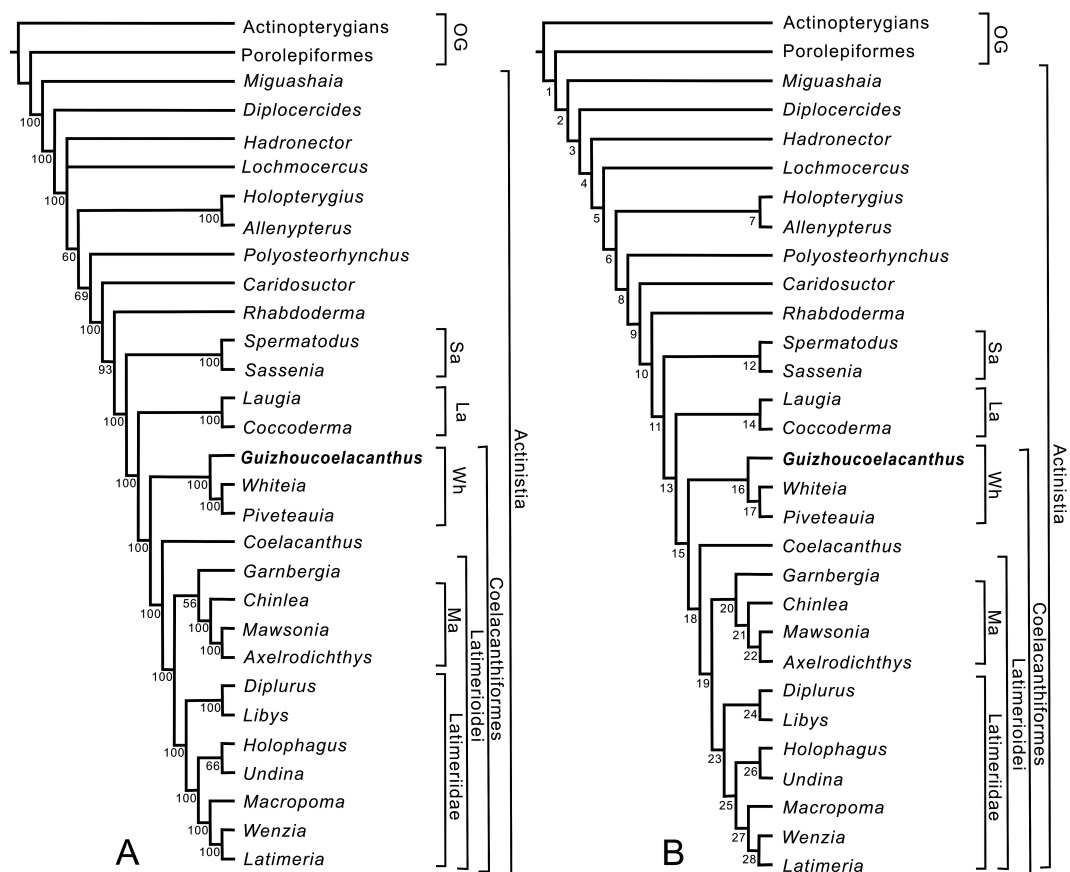


Fig. 4 50% majority-rule consensus tree of 163 most parsimony trees (A) and one of most parsimony trees (B)

Abbreviations: La. Laugiidae; Ma. Mawsoniidae; OG. outgroup; Sa. Sasseniidae; Wh. Whiteiidae; numbers on the tree correspond to the percentage of occurrence in the 50% majority-rule consensus tree (see Appendix I for the characters supporting the numbered nodes)

Among the 163 most parsimonious trees, the phylogenetic relationship of *Guizhoucoelacanthus* within coelacanth fishes remains consistent, resolved as the sister group to *Whiteia* + *Piveteauia*, supported by two synapomorphies (Node 16, Fig. 4B): the anterior and posterior pairs of parietals of similar size, and fin rays in D1 less than eight. *Whiteia* and *Piveteauia* form a sister group (Node 17, Fig. 4B), based on three synapomorphies: extrascapulars lying free from postparietals, presence of spiracular, and jugal sensory canal with prominent branches. *Guizhoucoelacanthus* was referred to the Coelacanthidae by Liu et al. (2006). In our phylogenetic result, the family Coelacanthidae in the sense of Liu et al. (2006) does not form a monophyletic group. We adopt the family Whiteiidae (Schultze, 1993), and refer *Guizhoucoelacanthus* to this family.

In our analysis, *Coelacanthus* is more derived than the Whiteiidae, and forms the sister group of the suborder Latimerioidei based on three synapomorphies (Node 18, Fig. 4B): presence of dorsal lamina of premaxilla, absence of preorbital, and pit-lines not marking postparietals. By comparison, Forey (1998) and Clément (2005) placed *Coelacanthus* as the sister



group of *Whiteia* + Latimerioidei based on three synapomorphies: dermal intracranial joint with straight margin, embayed posterior margin of the skull roof, and otic sensory canal joining supratemporal sensory canal in supratemporal.

The family Latimeriidae (including *Diplurus*, *Libys*, *Holophagus*, *Undina*, *Macropoma*, *Latimeria* and *Wenzia*), Mawsoniidae (including *Chinlea*, *Mawsonia* and *Axelrodichthys*) and the genera *Garnbergia* constitute the suborder Latimerioidei (Fig. 4A). All seven genera of the Latimeriidae constitute a monophyletic group (Node 23, Fig. 4B). All three genera of the Mawsoniidae constitute a monophyletic group (Node 21, Fig. 4B). The phylogenetic position of *Garnbergia* is unresolved because of the large number of missing data.

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#### Appendix I List of nodal character states for Fig. 4B

- Node1 → Node2: 33 (1 => 0), 80 (0→1).
- Node2 → *Miguashaia*: 12 (0→1).
- Node2 → Node3: 7 (1 => 2), 10 (0→1), 19 (0 => 1), 25 (0→1), 71 (0→1), 74 (0→1), 93 (0 => 1), 95 (0 => 1).
- Node3 → Node4: 24 (1 => 0), 34 (1 => 0), 45 (0 => 1), 90 (0 => 1).
- Node4 → Node5: 23 (2→0).
- Node5 → Node6: 63 (0→1), 97 (0 => 1).
- Node6 → Node8: 14 (0→1), 54 (0 => 1), 61 (0 => 1), 94 (0 => 1), 101 (0→1).
- Node8 → Node9: 1 (0 => 1), 3 (1 => 0), 17 (0 => 1), 20 (0 => 1), 55 (3→4), 56 (0→1), 59 (1 => 0), 61 (0→1), 67 (0→1), 102 (0 => 1), 107 (0 => 1).
- Node9 → Node10: 11 (0→1), 64 (0 => 1), 69 (0→1), 72 (0→1), 73 (0→1), 85 (0→1), 87 (0→1), 97 (1 => 0).
- Node10 → *Rhabdoderma*: 8 (1 => 0), 46 (0 => 1), 63 (1 => 0), 77 (1→0), 78 (1→0).
- Node10 → Node11: 23 (0 => 2), 29 (0 => 1), 62 (0 => 1).
- Node11 → Node12: 34 (0 => 1).
- Node12 → *Spermatodus*: 15 (0 => 1), 18 (0 => 1), 26 (0 => 1), 68 (0→1), 70 (1 => 0).
- Node12 → *Sassenia*: 69 (1 => 0), 80 (0→1), 84 (0→1).
- Node11 → Node13: 30 (1 => 0), 32 (1 => 0), 44 (0 => 1), 67 (1 => 0), 75 (0 => 1), 101 (1→0), 105 (0→1).
- Node13 → Node14: 45 (1 => 0), 47 (0→1), 48 (0→1), 91 (0 => 1), 99 (0 => 1), 100 (0 => 1), 108 (0 => 1).
- Node14 → *Laugia*: 2 (0 => 1), 7 (2 => 1), 23 (2 => 0), 26 (0 => 1), 31 (1 => 0), 56 (1 => 0), 96 (0 => 1), 97 (0 => 1).
- Node14 → *Coccoderma*: 5 (0→1), 6 (0→1), 27 (0→1), 37 (0 => 1), 38 (0 => 1), 49 (1 => 0), 89 (0 => 1), 106 (0 => 1).
- Node13 → Node15: 1 (1 => 0), 18 (0 => 1), 21 (0 => 1), 70 (1 => 0), 71 (1 => 0), 78 (1→0), 81 (0→1), 82 (0 => 1), 86 (0 => 1).
- Node15 → Node16: 8 (1 => 0), 96 (0 => 2).
- Node16 → Node17: 15 (0 => 1), 30 (0 => 1), 32 (0 => 1), 46 (0 => 1).
- Node17 → *Whiteia*: 23 (2 => 0), 36 (0 => 1), 53 (0→1), 57 (0 => 1), 59 (0→1), 84 (0→1), 98 (0 => 1), 107 (1→0).

(Continued)

- Node17 → *Piveteauia*: 7 (2 => 0), 13 (0 => 1), 29 (1 => 0), 100 (0 => 1).
- Node16 → *Guizhoucoelacanthus*: 17 (1 => 0), 25 (1 => 0), 27 (0→1), 43 (0 => 1), 45 (1 => 0), 52 (1 => 0), 61 (1 => 0), 63 (1 => 0), 64 (1 => 0), 95 (1 => 0), 105 (1 => 0), 106 (0 => 1).
- Node15 → Node18: 5 (0→1), 10 (1 => 0), 26 (0 => 1).
- Node18 → *Coelacanthus*: 4 (0 => 1), 27 (0→1), 37 (0 => 1), 42 (0 => 1), 47 (0→1), 97 (0 => 1).
- Node18 → Node19: 6 (0→1), 13 (0 => 1), 35 (0 => 1), 48 (0→1), 51 (0 => 1), 52 (1 => 0), 53 (0→1), 57 (0 => 1), 76 (0→1), 91 (0 => 1), 96 (0 => 1).
- Node20 → Node21: 27 (0→2), 43 (0 => 1), 45 (1→0), 49 (1 => 2), 92 (0→1), 104 (0 => 1), 106 (0 => 1).
- Node21 → *Chinlea*: 8 (1 => 0), 30 (0 => 1), 36 (0→1), 67 (0 => 1).
- Node21 → Node22: 1 (0 => 1), 14 (1→0), 16 (0 => 1), 38 (0 => 1), 41 (0 => 1), 65 (0 => 1), 66 (0 => 1), 68 (0→1), 98 (0 => 1).
- Node22 → *Mawsonia*: 51 (1 => 0).
- Node22 → *Axelrodichthys*: 37 (0 => 1), 56 (1→0).
- Node20 → *Garnbergia*: 36 (0→1).
- Node19 → Node23: 9 (0 => 1), 15 (0 => 1), 17 (1 => 2), 47 (0→1), 98 (0 => 1).
- Node23 → Node24: 23 (2 => 0), 27 (0→1), 49 (1 => 0), 50 (0 => 1).
- Node24 → *Diplurus*: 14 (1 => 0), 30 (0 => 1), 42 (0 => 1), 44 (1→0), 46 (0→1), 56 (1 => 0), 57 (1 => 0), 92 (0 => 1), 104 (0 => 1), 107 (1 => 0).
- Node24 → *Libys*: 39 (0 => 1), 52 (0 => 1), 60 (0→1), 68 (0 => 1), 89 (0 => 1), 99 (0 => 1), 103 (0 => 1).
- Node23 → Node25: 32 (0 => 1), 60 (0→1), 74 (1→0), 79 (0 => 1).
- Node25 → Node26: 64 (1 => 0), 67 (0→1).
- Node26 → *Holophagus*: 1 (0 => 1), 99 (0 => 1), 103 (0 => 1).
- Node26 → *Undina*: 5 (1 => 0), 28 (0 => 1), 59 (0→1), 63 (1 => 0).
- Node25 → Node27: 22 (0→1), 39 (0 => 1), 40 (0 => 1), 59 (0→1), 96 (1 => 2).
- Node27 → *Macropoma*: 2 (0→1), 89 (0 => 1), 104 (0 => 1).
- Node27 → Node28: 26 (1 => 0), 28 (0 => 1), 30 (0 => 1).
- Node28 → *Latimeria*: 3 (0→1), 4 (0 => 1), 23 (2→0), 27 (0→2), 46 (0 => 1), 50 (0 => 1), 67 (0→1), 77 (1→0), 107 (1 => 0).
- Node28 → *Wenzia*: 2 (0→1), 27 (0→1).
- Node8 → *Polyosteorhynchus*: 21 (0→1), 23 (0→1), 91 (0 => 1).
- Node6 → Node7: 109 (0 => 1).
- Node7 → *Allenhypterus*: 8 (1→0), 25 (1→0), 29 (0→1), 42 (0→1), 48 (0→1), 49 (1→0), 50 (0→1), 58 (0→1).
- Node7 → *Holopterygius*: 77 (1→0), 78 (1→0).
- Node5 → *Lochmocercus*: 21 (0→1), 101 (0→1).
- Node4 → *Hadronector*: 23 (2→1), 94 (0 => 1), 102 (0 => 1), 107 (0 => 1).
- Node3 → *Diplocercides*: 58 (0→1), 59 (1 => 0), 80 (0→1), 83 (0 => 1).

Note: The nature of the character state change is indicated by the arrows. Double stemmed arrows indicate unambiguous character state changes, meaning that the particular change will occur under any optimization (e. g. DELTRAN, as used here, or ACCTRAN). Single stemmed arrows mean ambiguous optimization (e. g. the optimization may change if different assumptions of optimization are invoked). Here we adopt DELTRAN.

Appendix II Data set with 109 characters for 29 taxa (after Forey, 1998)

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	1111111111
Actinopterygii	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Porolepiformes	0000010000	0100000000	0021000000	1111000000	0000000000	0100400000	0000000000	0100000000	0001000000	0000000000	0000000000
<i>Miguashaia</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Diploecircus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Lochmoeus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Hadronector</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Polystoeurichthys</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Allenpterus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Caridosuctor</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Rhabdosoma</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Sassania</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Spermatoodus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Cocodermia</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Laugia</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Coelacanthus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Whiteia</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Latimeria</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Macropoma</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Undina</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Holophagus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Garnbergia</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Libys</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Diplurus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Chinlea</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Mausonia</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Aetodichthys</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Wenzia</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Holopterygus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Piveteaia</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000
<i>Guizhoucoelacanthus</i>	0010001000	0000000000	0021000000	1111000000	0000000000	0100300000	0000000000	0100000000	0000000000	0000000000	0000000000

Note: new characters and taxon are in bold. 0 = plesiomorphic state; 1, 2, 3, 4 = apomorphic state; ? = unavailable characters or logical impossibility. Character 31 is corrected after Clément (2005) and Friedman and Coates (2006). The codings for *Wenzia* and *Holopterygus* are after Clément (2005) and Friedman and Coates (2006), respectively.