

## Cranial morphology of the Silurian sarcopterygian *Guiyu oneiros* (Gnathostomata: Osteichthyes)

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Cranial morphological features of the stem-group sarcopterygian *Guiyu oneiros* Zhu et al., 2009 provided here include the dermal bone pattern and anatomical details of the ethmosphenoid. Based on those features, we restored, for the first time, the skull roof bone pattern in the *Guiyu* clade that comprises *Psarolepis* and *Achoania*. Comparisons with *Onychodus*, *Achoania*, coelacanth, and actinopterygians show that the posterior nostril enclosed by the preorbital or the preorbital process is shared by actinopterygians and sarcopterygians, and the lachrymals in sarcopterygians and actinopterygians are not homologous. The endocranium closely resembles that of *Psarolepis*, *Achoania* and *Onychodus*; however, the attachment area of the vomer possesses irregular ridges and grooves as in *Youngolepis* and *Diabolepis*. The orbito-nasal canal is positioned mesial to the nasal capsule as in *Youngolepis* and porolepiforms. The position of the hypophysial canal at the same level or slightly anterior to the ethmoid articulation represents a synapomorphy of the *Guiyu* clade. The large attachment area of the basicranial muscle indicates the presence of a well-developed intracranial joint in *Guiyu*.

**Sarcopterygii, Osteichthyes, Cranial morphology, homology, Silurian, China**

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The primitive fish *Guiyu oneiros* [1] from the Silurian of China represents the oldest articulated osteichthyan, and provides unique insights into the character transformation that resulted in the standard set of sarcopterygian features [2]. Prior to the discovery of *Guiyu*, the earliest fossil record of the osteichthyans was represented only by isolated fragmentary remains, such as isolated scales and teeth [3–10]. The articulated material of *Guiyu* reinforces novel interpretations of basal sarcopterygian morphology previously based on disarticulated specimens of *Psarolepis* [11]. The mosaic of characters in some early fishes [11–14] has significantly bridged the morphological gaps between acti-

nopterygians and sarcopterygians, and between osteichthyans and non-osteichthyan gnathostomes, thus forcing a re-appraisal of the sequence of character acquisition in the early evolution of gnathostomes [15–17]. However, the early diversification of gnathostomes remains unclear due to the incompleteness of the fossil record and the lack of the detailed anatomical studies on some known taxa.

The earlier report of *Guiyu oneiros* [1] only provided a brief description of the taxon with emphasis on the mosaic of primitive gnathostome characters, and placed *Guiyu*, *Psarolepis*, and *Achoania* into a monophyletic group, the *Guiyu* clade. Here we offer a detailed description of the cranial morphology based on some newly-prepared disarticulated specimens assigned to *Guiyu oneiros*, as well as those illustrated in ref. [1], and provide a restoration of the

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skull roof bone pattern in the *Guiyu* clade [1]. All specimens were recovered from the muddy limestone of the Kuanti Formation (Late Ludlow, Silurian) in Qujing, Yunnan, China [1]. In light of new anatomical information, the homology is examined of certain cranial bones including the preorbital of basal actinopterygians and the lachrymal of sarcopterygians. The present paper follows the terminology of Westoll [18], only to align with current majority usage.

## 1 Cephalic exoskeleton

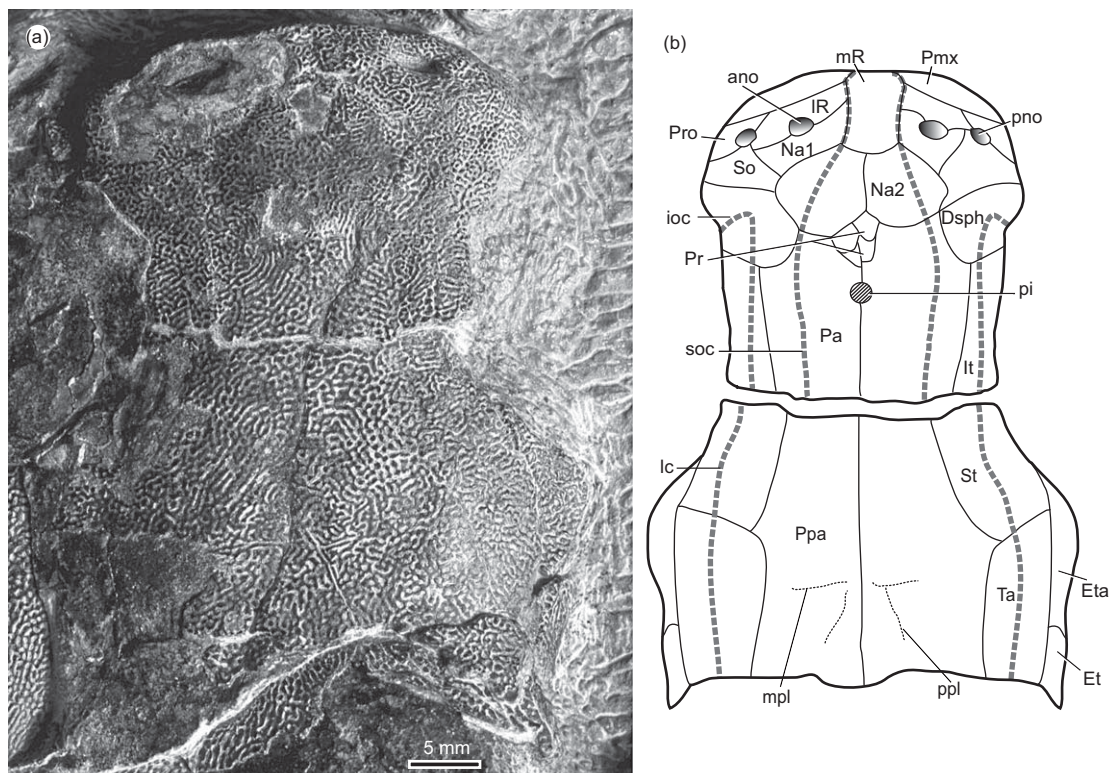
### 1.1 General features of skull roof

The holotype (IVPP V15541) has a skull roof of about 4.5 cm in length, which is divided into the parietal and postparietal shields by the dermal intracranial joint (Figure 1(a)). The parietal shield of the holotype looks broader and shorter than those disarticulated ones (Figures 2 and 3), whose length ranges from 1.9 to 2.0 cm. As evidenced by the articulated specimen, the length ratio between the anterior and posterior cranial portions in *Guiyu* is about 1.0, which is smaller than that in *Psarolepis* (1.6–1.7) [19]. In onychodonts [20, 21] and derived porolepiforms such as *Glyptolepis* and *Holoptychius* [22], the length ratio between two portions is smaller than 1.0, evidently due to the lengthening

of the posterior cranial portion. In the rest of early sarcopterygians, the anterior cranial portion is usually much longer than the posterior cranial portion as in *Psarolepis*. Considering the state in *Meemannia* [23], which is immediately basal to the *Guiyu* clade, and early actinopterygians [24], we suggest that the equal length of the two cranial portions in *Guiyu* might represent a derived feature.

The parietal shield is square shaped and has its maximum width at the level of the postorbital corners. The postparietal shield is broad posteriorly and is broadest at the level of the suture between the supratemporal (St, Figures 1, 2(f) and 3(f)) and tabular (Ta, Figures 1, 2(f) and 3(f)), and then narrows slightly. Its posterior margin is straight, with an inconspicuous medial projection.

The dermal bones on the skull roof of *Guiyu* contain relatively few discrete elements, which may represent the primitive sarcopterygian condition. They are ornamented with vermiculate ganoine ridges (Figures 1, 2, 4(a), 4(b) and 5(a)), which for the most part have fused into an irregular maze-like configuration. Ganoine comprises a glossy outer dermal coating of single or multi-layered enamel. It was once considered a characteristic feature of basal actinopterygians [14, 24, 26–29]. Richter and Smith [30] noted the presence of ganoine-like tissue in acanthodians and basal sarcopterygians, suggesting that ganoine might be plesio-



**Figure 1** *Guiyu oneiros* Zhu et al. 2009. (a) Close-up view of the head in dorsal view, holotype, V15541; (b) Reconstruction of the skull roof based on all available data. It, intertemporal; ano, anterior nostril; Dsph, dermosphenotic; Et, extratemporal; Eta, accessory extratemporal; ioc, infraorbital canal; lc, lateral-line canal; IR, lateral rostral; mpl, middle pit-line; mR, median rostral; Na1, nasal 1; Na2, nasal 2; Pmx, premaxillary; Pa, parietal; pi, pineal foramen; pno, posterior nostril; Ppa, postparietal; ppl, posterior pit-line; Pr, postrostral; Pro, preorbital; So, supraorbital; soc, supraorbital canal; St, supratemporal; Ta, tabular.

morphic for crown osteichthyans. Schultze [8] indicated the differences in surface structure between the typical ganoine in actinopterygians (with surface elevations or microtubercles) and the enamel of cosmine in sarcopterygians (with depressed hexagons marking the borders of adjacent cells); however, this distinction is not absolute since the ganoine without microtubercles is present in some actinopterygians, such as *Cheirolepis trailli* [30]. Whether the ganoine surface of *Guiyu oneiros* or the enamel surface of the dermal skeleton in other stem sarcopterygians [11, 13, 19, 23, 31] bears the microtubercles or not needs further investigation.

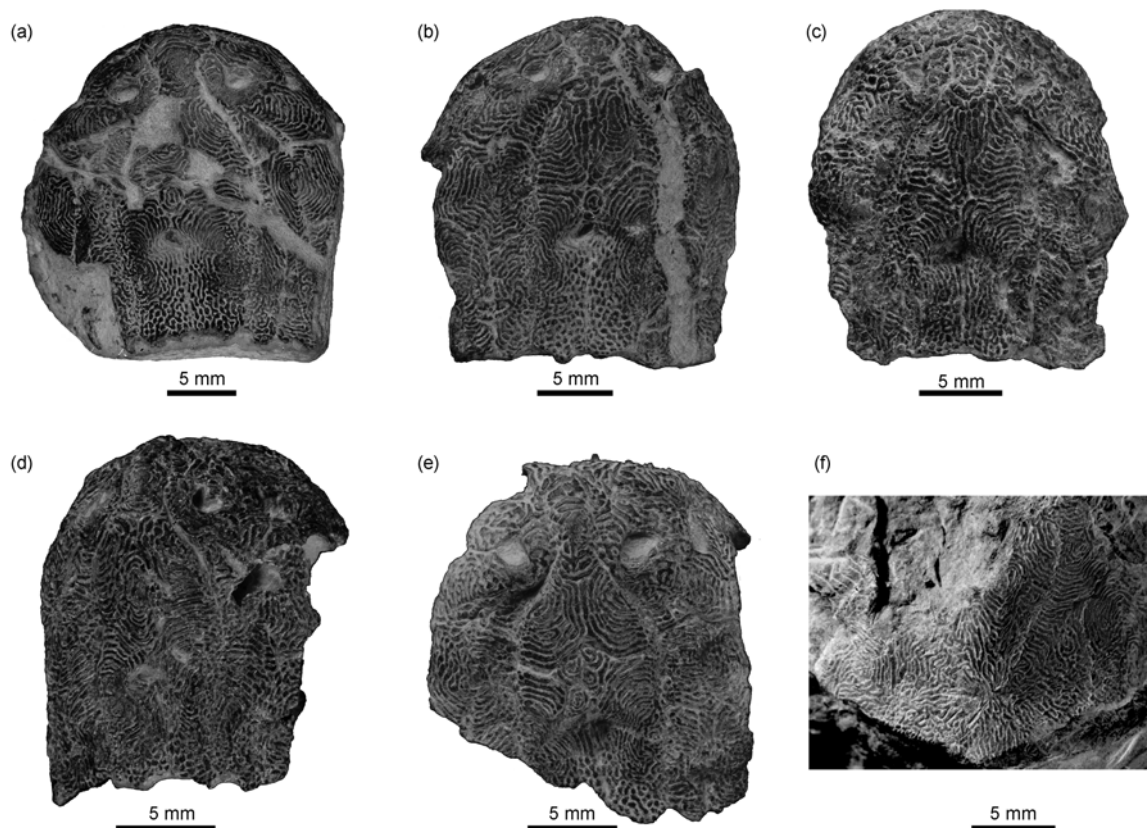
## 1.2 Parietal shield

The bone pattern is hardly discernible in the holotype (Figure 1(a)); however, some disarticulated skull specimens (Figures 2 and 3) show distinct bone sutures or patterned ridges around ossification center, based on which we outline the bone pattern of the parietal shield (Figure 1(b)).

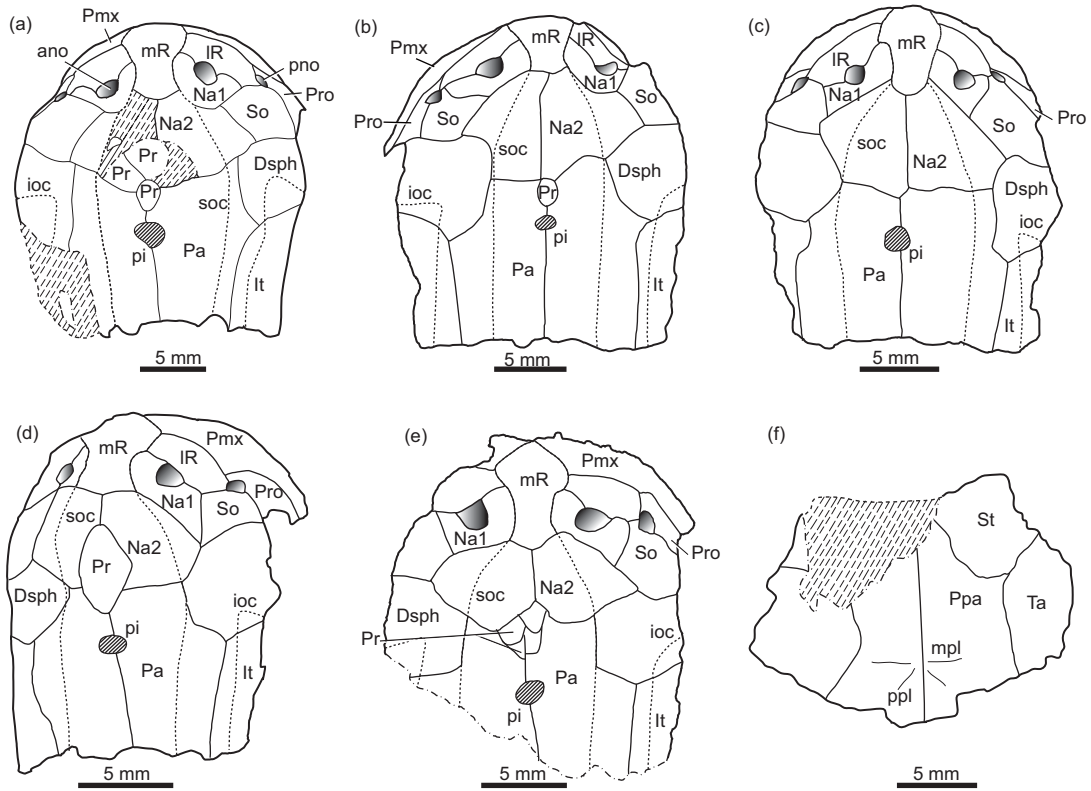
The upper jaw, in anterior view with an indistinct median projection (Figure 4(a) and 4(b)), exhibits a curvature that looks intermediate between the somewhat horizontal configuration in *Achoania* (Figure 4(c)) and the M-shaped configuration in *Psarolepis* (Figure 4(d)). The premaxillaries (Pmx, Figures 4(a), 4(b), 6 and 7(a)–(c)) contact each other at the midline ventral to the median rostral (mR, Figures 1,

2(a)–(e), 3(a)–(e), 4(b) and 5), excluding it from the occlusal margin of the jaw, as in early actinopterygians [24], *Youngolepis* [32], *Powichthys* [33, 34], and other crown sarcopterygians. The premaxillary is ribbon-shaped. It gradually increases in height posterolaterally until it meets the suture between the lateral rostral and the preorbital (Pro, Figures 1(b), 3(a)–(e), 4(b) and 5(b)), and then narrows beneath the preorbital. This marks an additional departure from *Psarolepis*, in which the premaxillary keeps increasing in height posterolaterally and forms a preorbital process (pr.Pro, Figure 4(d)) to enclose the posterior nostril (pno, Figures 1, 2(a)–(e), 3(a)–(e), 4(b) and 5). As in *Psarolepis* and *Onychodus*, the premaxillary bears two types of teeth. The ventral portion bears a row of large teeth at the mouth margin. These conical teeth are slender than those in *Psarolepis* and *Achoania*, and exhibit the regional variation. In cross section, the teeth on the posterolateral portion of the premaxillary (t.Pmx, Figure 6(d)) display a narrow ellipse shape at the base, and are longer than those close to the midline of skull roof. Dorsal to this row of larger teeth and at the margin of the dermal ornamentation of the premaxillary is a row of minute teeth.

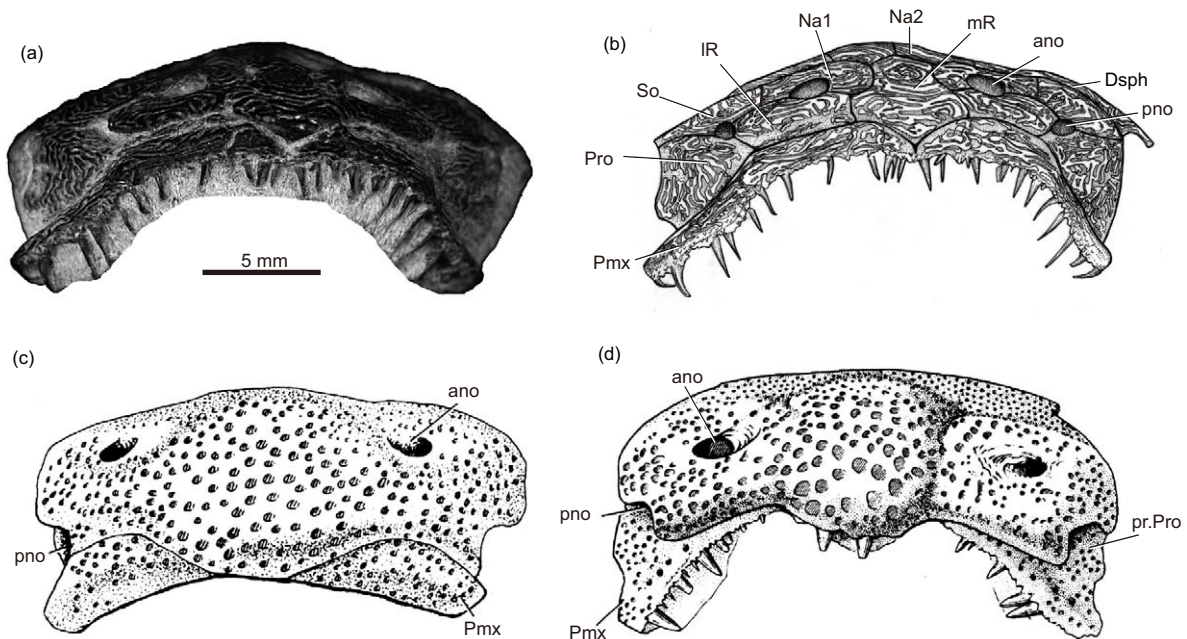
The median rostral (mR, Figures 1(b), 3(a)–(e), 4(b) and 5(b)) is lyrate in shape and occupies about 1/4 of the length of the parietal shield. Anteriorly, it inserts between the premaxillaries, but does not contribute to the occlusal margin of



**Figure 2** *Guiyu oneiros* Zhu et al. 2009, photos. (a)–(e) Parietal shields in dorsal view. (a) V15542.1; (b) V15542.17; (c) V15542.2; (d) V15542.3; (e) V15542.19. (f) Postparietal shield in dorsal view, V15542.6.



**Figure 3** *Guiyu oneiros* Zhu et al. 2009, illustrative drawings. (a)–(e) Parietal shields in dorsal view; (a) V15542.1; (b) V15542.17; (c) V15542.2; (d) V15542.3; (e) V15542.19. (f) Postparietal shield in dorsal view, V15542.6. Abbreviations see Figure 1.

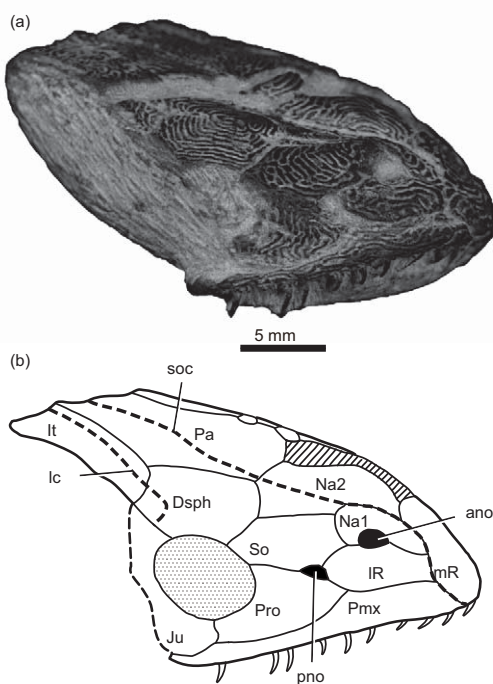


**Figure 4** Parietal shields in anterior view. (a), (b) *Guiyu oneiros* Zhu et al. 2009, photo (a) and drawing (b), V15542.1; (c) *Achoania jarviki*, drawing, after ref. [25]; (d) *Psarolepis romeri*, after ref. [19]. pr.Pro, preorbital process. Other abbreviations see Figure 1.

of the jaw. The lack of minute teeth on the median rostral is in contrast to *Psarolepis* [19] and *Achoania* [13], in which

the median rostral bears some conical teeth and contributes to the occlusal margin of the jaw. Laterally, the median ros-





**Figure 5** *Guiyu oneiros* Zhu et al. 2009. Parietal shields in lateral view, V15542.1, photo (a) and drawing (b). Ju, jugal. Other abbreviations see Figure 1.

tral contacts the lateral rostral and the nasal 1 with an embayed border. Its posterior margin is posteriorly arched.

The lateral rostral (IR, Figures 1(b), 3(a)–(e), 4(b) and 5(b)) has a long contact with the premaxillary, and ventrally encloses the relatively large anterior nostril (ano, Figures 1(b), 3(a)–(e), 4(b) and 5(b)), which is situated on the dorsal side of the skull roof as in *Psarolepis* and *Achoania*. The anterior nostril is oval-shaped, with its long axis running antero-medially and postero-laterally. Like *Onychodus* [20], *Styloichthys* [35], porolepiforms [22, 36] and actinopterygians [24], *Guiyu* lacks the dermintermedial process, which is present in the Tetrapodomorpha [37, 38] and some primitive sarcopterygians such as *Psarolepis* [19], *Achoania* [13], *Youngolepis* [32], *Diabolepis* [39–41], and *Powichthys* [33, 34, 42].

Two pairs of nasals (Na1 and Na2, Figures 1(b), 3(a)–(e), 4(b) and 5(b)) are situated posteromedial to the anterior nostril. The nasal 1, similar in size to the lateral rostral, is much smaller than the nasal 2, and delimits the dorsal margin of the anterior nostril. A posterolaterally-running groove, which serves for the supraorbital canal (soc, Figures 1(b), 3(a)–(e) and 5(b)), passes through the surface of nasal 2. The median contact between the nasals in *Guiyu* is extraordinary for primitive sarcopterygians, where the nasals of both sides are usually separated by the postrostral(s). The same condition can be seen elsewhere only in tetrapods, such as *Ichthyostega* [43] and *Acanthostega* [44]. This resemblance possibly reflects a parallel evolution.

The supraorbital (So, Figures 1(b), 3(a)–(e), 4(b) and

5(b)) is situated lateral to the nasals, and has a variable size. It contributes to the dorsal margin of the posterior nostril, which faces anterodorsally. The posterior nostrils are not well preserved in the holotype (Figure 1(a)); however, in our isolated specimens (Figures 2 and 3), the posterior nostrils are visible in dorsal view, indicating that they are more dorsally positioned than in other early sarcopterygians such as *Psarolepis* and *Achoania*.

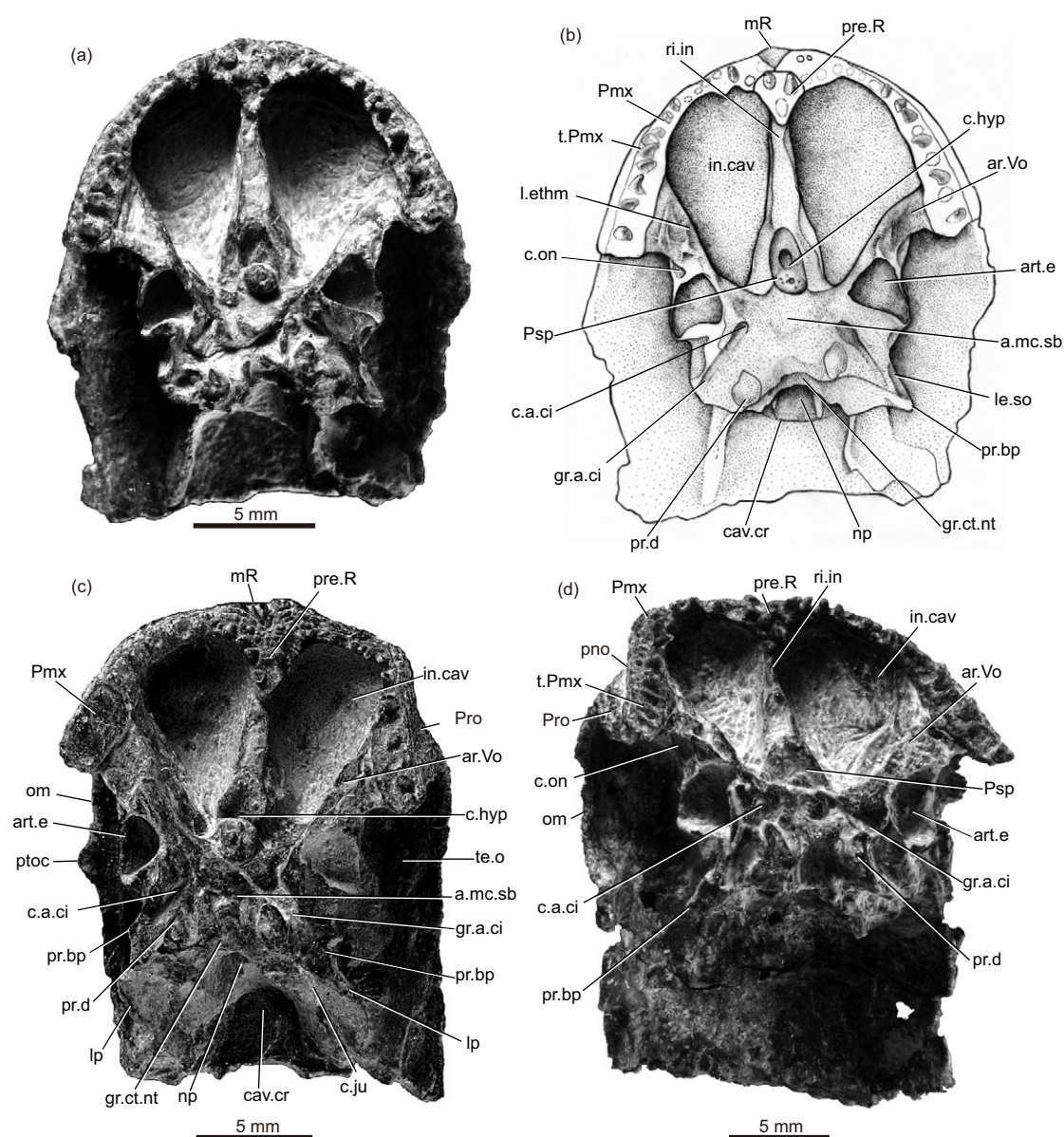
On the lateral face of the snout, dorsal to the premaxillary is a triangular bone, which we label the preorbital. Dorsally, this bone contacts the lateral rostral and supraorbital, and encloses the posterior nostril. Posteriorly, it forms part of the orbital margin. The homology of this bone as a component part of the parietal shield will be discussed below.

Posterior to the nasals are a group of polygonal bones recognized as the postrostrals (Pr, Figures 1(b), 3(a)–(e) and 5(b)). The size and number of the postrostrals are variable in different specimens (Figures 2 and 3). In V15542.1 (Figures 2(a) and 3(a)), at least three postrostrals lie posterior to the nasal 2; in V15542.17 (Figures 2(b) and 3(b)), only a small postrostral is visible between the nasal 2 and the parietal (Pa, Figures 1(b), 3(a)–(e) and 5(b)); in V15542.2 (Figures 2(c) and 3(c)), no postrostral can be seen and the nasal 2 is in total contact with the parietal; in V15542.3 (Figures 2(d) and 3(d)), a relatively large postrostral inserts forwards between the nasal 2 bones, and reaches the level at the midway of orbital margin (om, Figure 6); in V15542.19 (Figures 2(e) and 3(e)), four small mosaic bones are identified as the postrostrals.

The large, paired parietals lie posterior to the postrostrals and nasals. Anteriorly, this bone can reach the level of the postorbital corner (Ptoc, Figure 6(c)) of the skull roof. A small round pineal foramen (pi, Figures 1(b) and 3(a)–(e)) is situated well posterior to the orbits, and completely enclosed by the parietals of both sides.

The parietal is flanked laterally by the dermosphenotic (Dsph, Figures 1(b), 3(a)–(e), 4(b) and 5(b)) and intertemporal (It, Figures 1(b), 3(a)–(e) and 5(b)). The dermosphenotic is a relatively large bone and contributes to the dorsal margin of the orbit. The intertemporal is an elongate, irregular bone, which sutures anteriorly with the dermosphenotic, and tapers slightly towards the front.

The sensory canal system of the parietal shield is well displayed in the holotype and isolated specimens. In general, the courses of the supraorbital canals constitute a shape resembling a bowling pin in outline. Anteriorly, they run along the sutures between the median rostral and the neighboring bones (Pmx, IR and Na1), and are very close to the midline. They are situated medial to the anterior nostrils, resembling *Psarolepis*, *Achoania* and other sarcopterygians, but in contrast to actinopterygians, in which the supraorbital canals diverge anteriorly and run between the anterior and posterior nostrils. The infraorbital canal (ioc, Figures 1(b) and 3(a)–(e)) joining the supraorbital canal in the snout



**Figure 6** *Guiyu oneiros* Zhu et al. 2009. Anterior cranial portion in ventral view. (a), (b) V15542.2; photo (a) and drawing (b). (c) V15542.3, photo. (d) V15542.18, photo. a.mc.sb, attachment area for the basicranial muscle; ar.Vo, vomeral area; art.e, ethmoid articulation; c.a.ci, canal for the internal carotid artery; c.on, orbito-nasal canal; c.hyp, hypophysial canal; c.ju, canal for the jugal vein; cav.cr, cranial cavity; in.cav, internasal cavity; gr.a.ci, groove for the internal carotid artery; gr.ct.nt, groove for insertion of connective tissue sheath surrounding notochord; l.ethm, lateral ethmoid; le.so, suborbital ledge; lp, postorbital pillar; np, notochordal pit; om, orbital margin; pr.bp, basiptyergoid process; pr.d, descending process; pre.R, prerostral; Psp, parasphenoid; Ptoc, postorbital corner; ri.in, internasal ridge; t.Pmx, teeth on premaxillary; te.o, tectum orbitale. Other abbreviations see Figure 1.

might have a sutural course as in *Youngolepis*; however, this identification, as well as the trajectory of the ethmoidal commissural canal, needs additional evidence, for instance, CT scan data. At the level of the posterior limit of the median rostral, the supraorbital canals diverge posteriorly and run through the nasal 2 bones. Unlike those in *Styloichthys* and *Youngolepis*, they do not form lyre-shaped courses. Further backwards, the supraorbital canals traverse longitudinally the parietals, and terminate at the posterior edge of the parietal shield. No parietal pit-line is discernable in the available specimens. Close to the ossification center of the

dermosphenotic, the infraorbital canal joins the main lateral-line canal (lc, Figures 1(b) and 5(b)), which runs posteriorly through the intertemporal and extends to the postparietal shield.

### 1.3 Postparietal shield

Isolated specimens (V15542.4–6, 21) of the posterior cranial portion (Figures 1, 2(f) and 3(f)) show three pairs of dermal bones: postparietal, supratemporal, and tabular bones. The postparietal (Ppa, Figures 1, 2(f) and 3(f)) is

long and narrow, with its posterior edge wider than the anterior edge. A lateral expansion is present at the level of the suture between the supratemporal and tabular. Close to its medial margin, the postparietal carries a middle pit-line (mpl, Figures 1, 2(f) and 3(f)) and a posterior pit-line (ppl, Figures 1, 2(f) and 3(f)), resembling the condition in *Mee-mannia* [23], *Dialipina* [14], and *Ligulelepis* [12, 45]. In other basal sarcopterygians, these two pit-lines are situated more laterally. The middle and posterior pit-lines are posteriorly located as in *Psarolepis*, *Youngolepis*, *Powichthys*, and *Diabolepis* [39], in contrast to the anterior position in porolepiforms [22] and onychodonts [20, 21]. There is no indication of the supraorbital canal or anterior pit-line on the postparietals. In actinopterygians, the anterior pit-line is situated on the postparietal [24].

The postparietal is flanked by the supratemporal and tabular, which together carry the main lateral-line canal longitudinally. The suture between the supratemporal and postparietal extends posterolaterally. The tabular is bordered anteriorly by the supratemporal and medially by the postparietal. In accordance with *Psarolepis* [19] and *Achoania* [13], but in contrast to *Youngolepis* [32], *Powichthys* [33, 34] and Porolepiforms [22], no pit-line is visible on the tabular.

On the holotype, lateral to the tabular and the anterior half of the lateral extrascapular, there is a small bone which is referred to the extratemporal (Et, Figure 1). The extratemporal is also present in *Kenichthys* [46, 47], *Powichthys* [33, 34], *Youngolepis* [32], *Onychodus* [20], rhizodonts [48–50] and some osteolepiforms, and might represent a primitive condition in sarcopterygians. The loss of extratemporal in coelacanth and some advanced osteolepiforms is probably secondary [51]. Unlike the condition in *Onychodus* and rhizodonts, the extratemporal does not contact the supratemporal anteriorly. An elongate crescent-shaped bone in front of the extratemporal and flanking part of the supratemporal and tabular is termed as the accessory extratemporal (Eta, Figure 1). The extratemporal and accessory extratemporal missing from the disarticulated specimens may reflect their loose connection to the supratemporal and tabular.

The spiracular notch lies anterior to the accessory extratemporal and lateral to the supratemporal. It is more anteriorly positioned than the spiracular notch in *Youngolepis* [32], *Onychodus* [20], and rhizodonts [48–50].

#### 1.4 Dermal bones on the mouth roof

Dermal bones on the mouth roof (Figures 5 and 6) include the parasphenoid (Psp, Figures 6 and 7(a)–(c)) and the pre-rostral (pre.R, Figures 6 and 7(a)–(c)). Like *Psarolepis* and *Onychodus*, *Guiyu* has a small, oval or lozenge-shaped parasphenoid. By comparison, the parasphenoid of *Achoania* is relatively large and teardrop-shaped [13]. The parasphenoid is situated posteriorly to the internasal ridge

(ri.in, Figures 6 and 7(a)–(c)) and pierced by the hypophysial canal (c.hyp, Figures 6 and 7(a)–(c)). The opening is relatively larger than that of *Psarolepis* and *Achoania*. On specimen V15542.19 (Figure 7(c)), the parasphenoid is broken just across the hypophysial opening and the hypophysial canal is clearly visible along the depth of the basisphenoid. The surface posterior to the hypophysial opening is covered with a small denticulate layer, while in *Onychodus*, this surface is anterior to the hypophysial opening. The hypophysial opening is slightly anterior to the ethmoid articulation in *Guiyu*, as in *Psarolepis* and *Achoania*, in which the opening is almost at the same level of the ethmoid articulation (art.e, Figures 6, 7(a) and 7(b)). In other sarcopterygians such as *Onychodus*, *Youngolepis*, and porolepiforms, the hypophysial opening is much more posterior to the ethmoid articulation. The relative position of the hypophysial opening might indicate the variation of the brain cavity in these sarcopterygians.

Antero-lateral to the parasphenoid, the internasal cavity (in.cav, Figures 6 and 7(a)–(c)) is enclosed by a flattened rectangular region posterior to the premaxillary. This area forms a rugged surface composed of ridges and grooves of unequal size and different shape and represents the area for the attachment of the vomer (ar.Vo, Figures 6 and 7(a)–(c)). Chang and Smith [52] considered the irregular raised areas and grooves on the attachment area as a shared character by *Youngolepis*, *Powichthys* and *Diabolepis*. In *Psarolepis* and *Achoania*, the corresponding attachment area lacks similar ridges and grooves.

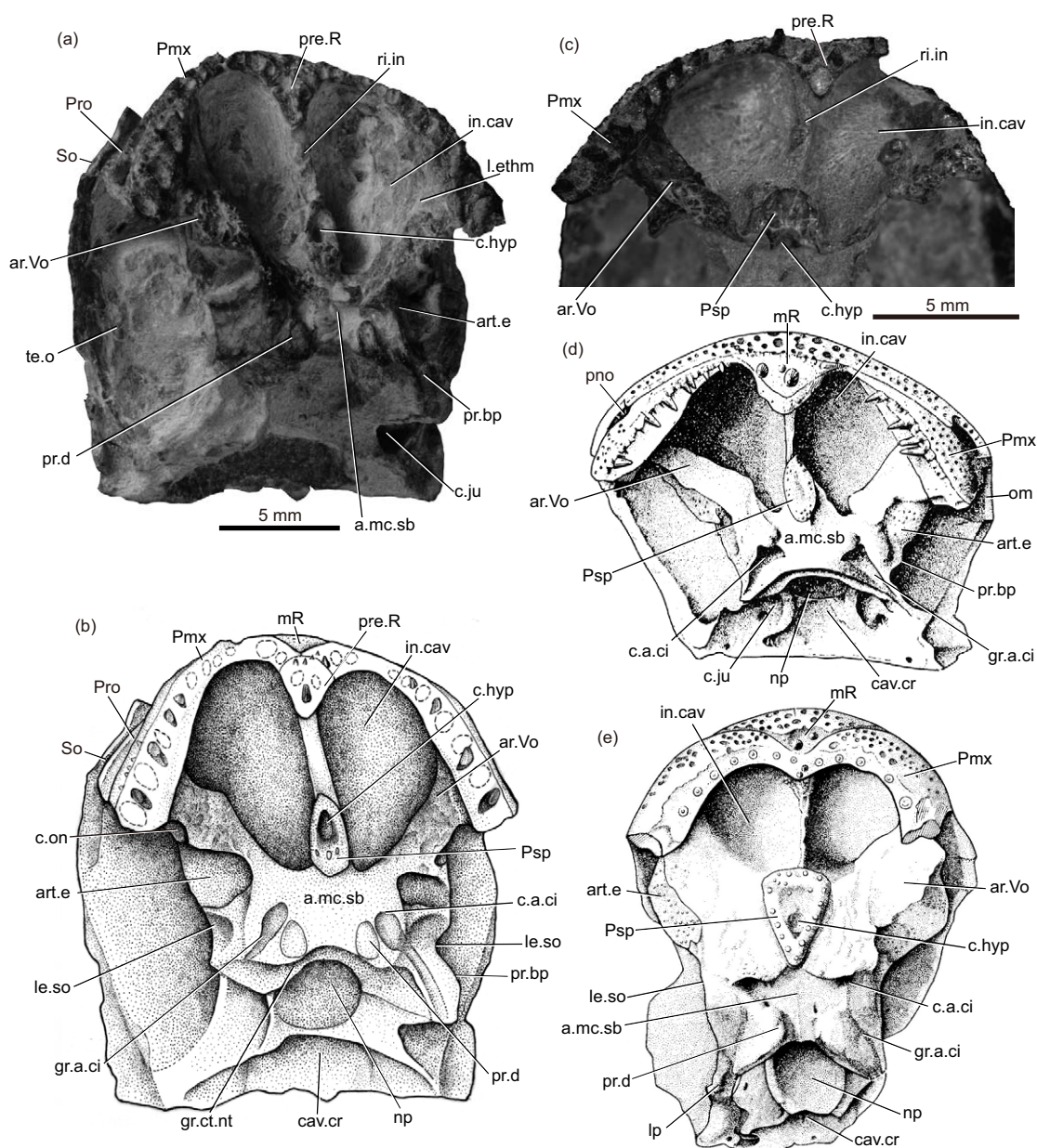
Remarkable is a small, drop-shaped, and unpaired tooth-bearing bone covering the anterior portion of the median ethmoid. Anteriorly, it contacts the premaxillae of both sides, and contributes to the occlusal margin of the jaw. This bone has never been found in other known osteichthyans, but topologically corresponds to the pre-rostral plate of placoderms. It is likely that the presence of a pre-rostral plate is a shared feature of osteichthyans and placoderms, and was independently lost in actinopterygians and other sarcopterygians.

## 2 Endocranium

### 2.1 General features

The endocranium of *Guiyu*, comprising the ethmosphenoid and otoccipital portions, is much less ossified than that of *Psarolepis* and *Achoania*, raising difficulties in unveiling anatomical details on lateral sides of its ethmosphenoid portion and in the otoccipital portion. The ventral side of the ethmosphenoid endocranium shows a striking resemblance to that of *Psarolepis* [19], *Achoania* [13] and *Onychodus* [20, 53] in the large pear-shaped internasal cavities, a long and narrow internasal ridge in front of a small triangular parasphenoid, and the same position of ethmoid articulation on the postnasal wall and the large attachment area for the





**Figure 7** Anterior cranial portion in ventral view. (a), (b) *Guiyu oneiros*, V15542.17, photo (a) and drawing (b). (c) *Guiyu oneiros*, V15542.19, photo. (d) *Psarolepis romeri*, drawing, after ref. [19]. (e) *Achoania jarviki*, drawing, after ref. [13]. Abbreviations see Figures 1 and 6.

basicranial muscle.

### 2.2 Ventral surface of ethmosphenoid

The ethmosphenoid is represented by five specimens (V15542.2, 3, 17–19). Similar to *Psarolepis*, *Achoania* and *Onychodus*, *Guiyu* bears a pair of large pear-shaped internasal cavities. Anteriorly and antero-laterally, the internasal cavity is bordered by the premaxillary, and posterolaterally by the attachment area for the vomer, which is somewhat rectangular in shape. Medially, the cavity is separated from its counterpart by the prerostral, the long and narrow inter-

nasal ridge and the parasphenoid from anterior to the posterior. Posteriorly, it terminates at the level of the posterior limit of the parasphenoid. As in *Psarolepis* and *Onychodus* but not in *Achoania*, the cavity is very deep, especially in its anterior portion, suggesting its function to accommodate the large parasymphysial tooth whorl of lower jaw [19, 53].

The internasal ridge as the main part of the median ethmoid indicates the long ethmoid division, relative to the short sphenoid division of the ethmosphenoid. Anteriorly, it is covered by an unpaired, small triangular prerostral. It becomes broader posteriorly, and forms the support for the short lozenge-shaped parasphenoid.



The lateral ethmoid (l.ethm, Figures 6(b) and 7(a)) forms the dorso-lateral wall of the internasal cavity, as well as the medial and ventral walls of the nasal capsule of either side. It also forms the support for the vomer, as in other sarcopterygians except onychodonts, in which the vomer is absent [20]. Posteroventrally, the lateral ethmoid merges into the postnasal wall (w.pn, Figure 8) which is directed anterolaterally to posteromedially. The poor ossification makes it difficult to locate the profundus canal on the wall. However, a laterally-facing opening, here identified as the orbito-nasal canal (c.on, Figures 6, 7(a) and 7(b)), is visible immediately behind the attachment area for the vomer. This canal has a mesial position relative to the nasal capsule as in *Youngolepis* [32, 54] and porolepiforms [36], rather than the lateral position in *Eusthenopteron* [54, 55].

Specimen V15542.17 reveals a thickened ridge along the ventral surface of the orbital margin (Figure 7(a) and 7(b)). This ridge is formed by the extensive orbital tectum (te.o, Figure 7(a)), and fused with the lateral margin of dermosphenotic and intertemporal. The orbital tectum is also extensive in *Psarolepis*, *Youngolepis*, *Powichthys*, *Kenichthys* dipnoans, and porolepiforms [19, 52].

At the level of the orbital notches, the ethmosphenoid exhibits a pair of large, posteroventrally faced fossae, which represent the ethmoid articulations for the palatoquadrate. This articulation facet is oval or pear-shaped, with the long axis running anteromedially and posterolaterally. As in *Onychodus*, it straddles the lateral ethmoid and sphenoid ossification. However, the ethmoid articulation in *Guiyu* has a more medial position than that of *Onychodus*.

Posterior to the ethmoidal articular area, the suborbital ledge (le.so, Figures 6, 7(a) and 7(b)) passes into the lateral knob structure representing the basiptyergoid process (pr.bp, Figures 6, 7(a) and 7(b)). The basiptyergoid process is broad in *Youngolepis*, *Powichthys*, porolepiforms, and *Diabolepis* [52], whereas in *Guiyu*, *Psarolepis*, and *Achoania*, this process is represented by a slightly lateral bulging, which indicates the weak ligament connecting the basal process of the pars palatoquadrate. In V15542.3, the basiptyergoid process is connected with the interorbital wall by the postorbital pillar (lp, Figure 6(c)), as in *Psarolepis*, *Achoania*, and *Styloichthys* [35].

Anteromesial to the basiptyergoid processes, a pair of round knobs (pr.d, Figures 6, 7(a) and 7(b)) are comparable to the descending processes in *Achoania*, *Youngolepis* and *Powichthys* [34].

Anterolateral to the descending process reveals a posterolaterally directed foramen (c.a.ci, Figures 6, 7(a) and 7(b)), which may represent the opening for the internal carotid artery. Behind the opening, a groove extends posterolaterally to the position medial to the basiptyergoid process. This groove is referred herein as the groove for the internal carotid artery (gr.a.ci, Figures 6, 7(a) and 7(b)) through which the artery passes the opening into the cranial cavity, as in *Psarolepis* and *Achoania*.

The basisphenoid on ventral aspect also shows a large,

rugose space for the attachment of basicranial muscle (a.mc.sb, Figures 6, 7(a) and 7(b)), which is delimited by the parasphenoid, the grooves for internal carotid arteries, and the descending processes. The similar large attachment area is also found in *Psarolepis*, *Achoania*, and *Onychodus*, indicating their enhanced capacity for intracranial joint movement [21].

Specimen V15542.17 reveals an opening lateral to the lateral wall of the notochordal pit that may correspond to the jugal canal (c.ju, Figure 7(a)). The canal is laterally bridged by the postorbital pillar, as shown in V15542.3 (Figure 6(c)).

### 2.3 Posterior face of ethmosphenoid

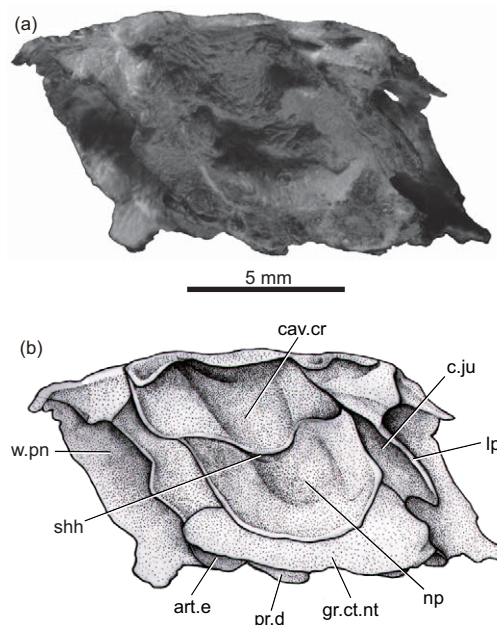
The posterior face of the ethmosphenoid is well exhibited by specimens V15542.2, V15542.3, and V15542.17. As in *Psarolepis*, the notochord pit (np, Figure 8) is enclosed ventrally by a groove, which may have served for the insertion of the connective tissue sheath surrounding the notochord (gr.ct.nt, Figures 6, 7 and 8) [19, 22].

The notochord pit is dorsally separated from the cranial cavity by a horizontal shelf (shh, Figure 8). The cranial cavity (cav.cr, Figure 8) is narrow ventrally and wide dorsally.

## 3 Discussion

### 3.1 Homologization of some dermal cranial bones in osteichthyans

There are many competing arguments regarding the ho-

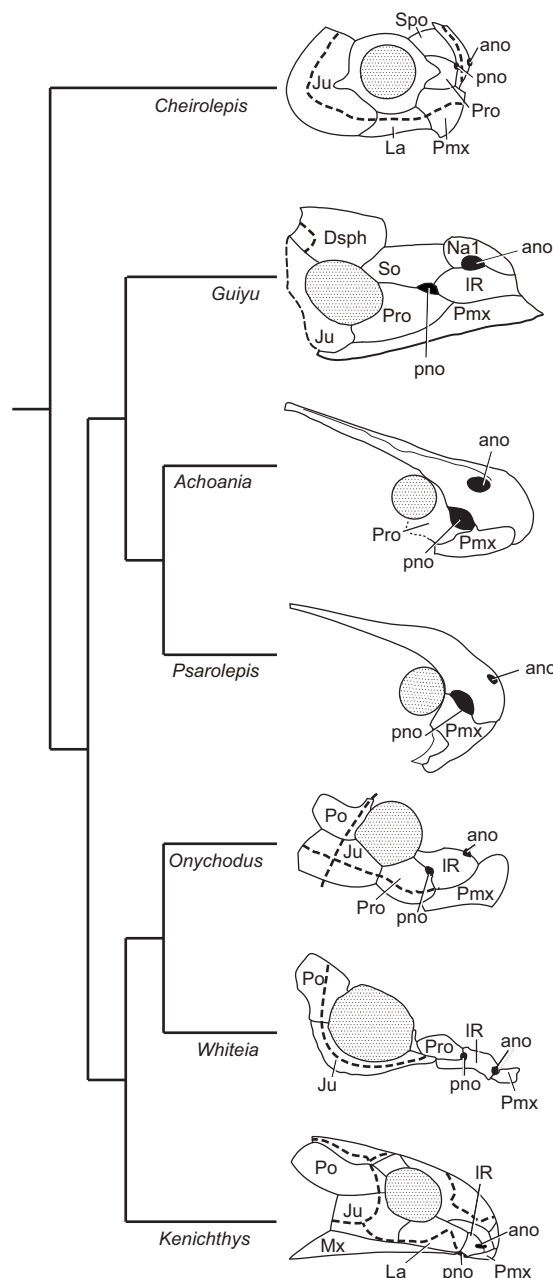


**Figure 8** *Guiyu oneiros* Zhu et al. 2009. Anterior cranial portion in posterior view, V15542.3, photo (a) and drawing (b). shh, horizontal shelf between cranial cavity and notochord pit; w.pn, postnasal wall. Other abbreviations see Figures 1 and 6.

mologization of dermal bones in osteichthyans (e.g. [18, 56–62]). Westoll [18] adopted the terminology of tetrapod skull bones for fishes, whereas Jarvik used the neural structures to justify the orthodox nomenclature of skull bones in bony fishes [43, 61–63]. Jollie [59] followed Westoll's theory and tried to use a common terminology for different major lineages of osteichthyans. Recently, Schultze [62] discussed the nomenclature and homologization of cranial bones in actinopterygians and refuted Jarvik's scheme. However, most of these discussions dealing with the homologization of dermal bones were focused on the middle series bones or the lateral sensory canal bones, such as frontal and parietal between piscine osteichthyans and tetrapods (e.g., [58, 59, 61]), parietal and postparietal between actinopterygians and sarcopterygians (e.g., [57, 58, 62]), and dermopterotic and supratemporal in actinopterygians and sarcopterygians [62]. Up to now, there is no doubt on the homology of lachrymal between actinopterygians and sarcopterygians. For instance, Schultze [62] noted that the infraorbital bone 1 of actinopterygians is homologous with the lachrymal of sarcopterygians. In accordance with this homology, he further restored a lachrymal for *Psarolepis*; however, this restoration lacks any fossil evidence from *Psarolepis*. The cheek bone pattern of *Guiyu* will compensate this deficiency and provide an alternative story.

The posterior nostril of *Guiyu* is enclosed posteriorly by a small triangular bone of skull roof, topologically resembling the preorbital (or antorbital) in actinopterygians [14, 28, 63], which encloses the posterior nostril and lies dorsally to the premaxillary (Figure 9). In *Onychodus* [20], the bone delimited the posterior nostril is termed 'lachrymal', which lies dorsally to the maxillary and premaxillary. It is much more anteriorly positioned than the lachrymal in other sarcopterygians [63, 65], where the lachrymal is always situated posterior to the premaxillary. We suggest that the 'lachrymal' of *Onychodus* corresponds to the preorbital of *Guiyu* and actinopterygians and should be the component of the skull roof rather than the cheek. *Achoania* [13] also seems to have a preorbital enclosing the posterior margin of the posterior nostril by comparison to the condition of *Guiyu*. In *Psarolepis*, the posterior nostril is enclosed by a process of the premaxillary (pr.Pro, Figure 4(d)) which might be formed by the fusion of the preorbital and the premaxillary. By comparison to *Guiyu*, the premaxillary of *Psarolepis* is more likely to be in contact with the jugal posteriorly and an assumed lachrymal in the restoration of *Psarolepis* of Schultze (ref. [62], Fig. 7E) is not present. The presence of the preorbital in some primitive sarcopterygians suggests that the posterior nostril enclosed by the preorbital or the preorbital process is plesiomorphic rather than apomorphic [66] in actinopterygians. In some actinopterygians, the preorbital is either lost or fused to the premaxillary as in *Psarolepis* and this should be a parallelism between these two groups.

Coelacanth bears a "lachrymojugal" that makes a long



**Figure 9** Comparison of some dermal cranial bones in osteichthyans. The posterior nostrils of *Guiyu* and actinopterygians are enclosed posteriorly by the preorbitals. The so-called "lachrymal" in *Onychodus* should correspond to the preorbital of *Guiyu*. The "lachrymojugal" in coelacanth is interpreted as a single bone (jugal). The lachrymal is likely to be absent in the *Guiyu* clade, onychodonts, and coelacanth, indicating that the lachrymals in sarcopterygians and actinopterygians are independently derived. *Cheirolepis* after ref. [27], Fig. 20; *Achoania* after ref. [13], Fig. 1; *Psarolepis* after ref. [13], Fig. 2; *Onychodus* after ref. [20], Fig. 4; *Whiteia* after ref. [64], Fig. 4.15; *Kenichthys* after [47], Fig. 1. La, lachrymal; Mx, maxillary. Other abbreviations see Figures 1, 5 and 6.

posteroventral contribution to the orbital margin, and the absence of the lachrymal used to be considered as the fusion to the jugal [64]. By comparison to *Guiyu* and *Onychodus*, we propose that this bone is better interpreted as a single bone (jugal) without inclusion of additional *ad hoc* element.

As discussed above, the lachrymal is absent in stem-group sarcopterygians including *Guiyu*, onychodonts and coelacanth, and this absence can hardly be interpreted as the multiple loss. We suggest that the absence of lachrymal is a primitive sarcopterygian feature, and the Rhipidistia (Dipnomorpha and Tetrapodomorpha) would be derived in the innovation of a lachrymal. In this case, the lachrymal of actinopterygians should be independently derived, and the lachrymals in sarcopterygians and actinopterygians are not homologous.

### 3.2 Endocranial features relating to the intracranial joint in *Guiyu*

The intracranial joint separates the endocranium of some sarcopterygians into two distinct parts and has been the subject of many functional interpretations. Features relating to the intracranial joint include the basicranial muscles, the adductor muscles, the descending process, etc. The basicranial muscle is recently discussed by Lu and Zhu [21] who proposed that *Qingmenodus* and coelacanth shared well-developed intracranial joint according to their lengthened basicranial muscle. Here we describe the large attachment area of basicranial muscle and strong descending processes that may indicate the well-developed intracranial joint in *Guiyu*.

The basisphenoid of *Guiyu* shows a large, rugose space for the attachment of basicranial muscle, which is delimited by the parasphenoid, the grooves for internal carotid arteries, and the descending processes. The similar large attachment area is also found in *Psarolepis* and *Achoania*. In *Onychodus*, the corresponding area which is posterior to the parasphenoid should also be the attachment of basicranial muscle. The large attachment area of basicranial muscle indicates their enhanced capacity for intracranial joint movement [21] and should be a primitive condition in sarcopterygians. However, the condition of the basicranial muscle in the otoccipital region of *Guiyu* remains unknown, because the otoccipital is not extensively ossified.

Another character relating to the intracranial joint is the descending process, which was first reported in *Powichthys* [34], and presumed to be articulated with a subchordal plate. When this process was found in *Youngolepis* [32], it is directed towards a stout paired basicranial process extending anteroventrally from the otoccipital and suggested to be connected through synarthrosis to the basicranial process in the otoccipital region. This process has also been found in *Achoania* and *Styloichthys* [34]. In *Psarolepis*, Yu [19] compared two round knobs in the sphenoidal portion (knob m. sc., ref. [19], Fig. 3) to the descending processes, and this identification was followed by Friedman [67]. However, this round knob topologically differs from the descending process which is posteromedial to the basipterygoid process and posterior to the groove for the internal carotid artery in *Youngolepis*, *Powichthys*, *Achoania*, and *Styloichthys*. In

*Psarolepis*, the knob is positioned anterior to the groove for the internal carotid artery and anteromedial to the basipterygoid process. So, we suggest the absence of a descending process in *Psarolepis*. The strong descending process suggests a tight connection to the otoccipital and might contribute to the intracranial joint movement.

### 3.3 The position of hypophysial opening relative to the ethmoid articulation

The hypophysial opening of *Guiyu* is slightly anterior to the ethmoid articulation, which is well revealed by specimen V15542.19 (Figure 7(c)). This is in accordance with *Psarolepis* and *Achoania*, in which the opening is almost at the same level of the ethmoid articulation. In actinopterygians and other sarcopterygians such as *Onychodus*, coelacanth, rhipidistians including *Youngolepis* and *Powichthys*, the hypophysial opening is much more posterior to the ethmoid articulation. Therefore, the hypophysial canal at the same level or slightly anterior to the ethmoid articulation is a synapomorphy of the *Guiyu* clade.

The relative position of the hypophysial opening might indicate the variation of the brain cavity in these sarcopterygians, as the hypothalamus is part of the diencephalon [68]. The ethmoid articulation is always situated along the lateral side of the lateral ethmoids, which form the mesial walls of nasal capsules [20]. So, the anterior position of the hypophysial canal may suggest a relatively short telencephalon or a short olfactory tract. However, this assumption needs more evidence, for instance, CT scan data.

## 4 Conclusions

(1) The skull roof bone pattern is restored in the *Guiyu* clade for the first time: parietal shield almost as long as the postparietal shield; the median rostral deficient of minute teeth and not contributing to the occlusal margin of the jaw; nasals meeting in the midline; postrostrals variable in size and number; middle pit-lines and posterior pit-lines situated close the midline.

(2) The posterior nostril of *Guiyu* is enclosed posteriorly by the preorbital as in actinopterygians. The comparison with *Guiyu* and actinopterygians suggests that the posterior nostril of *Onychodus* and *Achoania* is also enclosed by the preorbital rather than by the lachrymal, and the presence of the preorbital might be a derived feature for the common ancestor of actinopterygians and sarcopterygians.

(3) The lachrymal is absent in the *Guiyu* clade, onychodonts, and coelacanth, and the lachrymals in sarcopterygians and actinopterygians are independently derived.

(4) The ethmosphenoid of *Guiyu* shows a striking resemblance to that of *Psarolepis*, *Achoania*, and *Onychodus* in large pear-shaped internasal cavities, a long and narrow internasal ridge in front of a small triangular parasphenoid,



the same position of ethmoid articulation on the postnasal wall, and the large attachment area for the basicranial muscle. *Guiyu* bears a preorostral plate in the mouth roof, which is a shared feature of osteichthyans and placoderms. The attachment area of vomer with irregular ridges and grooves is suggestive of *Youngolepis* and *Diabolepis*.

(5) The *Guiyu* clade bears the hypophysial canal at the same level or slightly anterior to the ethmoid articulation, whereas in actinopterygians and other sarcopterygians the hypophysial canal is obviously behind the ethmoid articulation.

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