

A Devonian predatory fish provides insights into the early evolution of modern sarcopterygians

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Crown or modern sarcopterygians (coelacanths, lungfishes, and tetrapods) differ substantially from stem sarcopterygians, such as *Guiyu* and *Psarolepis*, and a lack of transitional fossil taxa limits our understanding of the origin of the crown group. The Onychodontiformes, an enigmatic Devonian predatory fish group, seems to have characteristics of both stem and crown sarcopterygians but is difficult to place because of insufficient anatomical information. We describe the new skull material of *Qingmenodus*, a Pragian (~409-million-year-old) onychodont from China, using high-resolution computed tomography to image internal structures of the braincase. In addition to its remarkable similarities with stem sarcopterygians in the ethmosphenoid portion, *Qingmenodus* exhibits coelacanth-like neurocranial features in the otic region. A phylogenetic analysis based on a revised data set unambiguously assigns onychodonts to crown sarcopterygians as stem coelacanths. *Qingmenodus* thus bridges the morphological gap between stem sarcopterygians and coelacanths and helps to illuminate the early evolution and diversification of crown sarcopterygians.

INTRODUCTION

Living sarcopterygians fall into three major groups: coelacanths, lungfishes, and tetrapods (limbed vertebrates). Most of the recent molecular and morphological phylogenetic analyses place the lungfishes and tetrapods as extant sister groups—forming a clade that is sometimes termed “Rhipidistia”—and the coelacanths as the sister group to that clade (1–4). The subclass Sarcopterygii forms the sister group to the subclass Actinopterygii, which together constitute the class Osteichthyes. With the exception of the tetrapods, sarcopterygians have a long evolutionary history of diversity decline and are nowhere near as diverse today as they were at the beginning of their history. As a consequence, their early fossil record contains a number of groups that have proved more or less difficult to place in relation to the extant members, such as the onychodonts (1, 2, 5, 6).

Until recently, the onychodonts, which are an exclusively Devonian group of mostly marine sarcopterygians, were represented by only six named genera. The recently described *Qingmenodus* from the Early Devonian of China (7) is now the best known early representative. Of the other five genera, two are known from single specimens (*Grossius* and *Luckeus*) (8, 9) and one from dermal bone fragments (*Bukkanodus*) (10). The *Strunius* material from the Late Devonian (Frasnian) of Bergisch Gladbach in Germany is articulated but strongly flattened (11); near-contemporary *Onychodus* material from Gogo in Western Australia is perfectly three-dimensional and includes braincase components, but large parts of the braincase appear to have been unossified, and the preserved components are often more tantalizing than informative (12). Fragmentary jaw materials from the Lochkovian fauna of South China and northern Vietnam (13, 14) suggest that the fossil record of onychodonts may extend back to the earliest Devonian, almost coeval with the earliest rhipidistians (*Youngolepis*, *Diabolepis*, and *Powichthys*).

Onychodonts are characterized by a distinctive head morphology that includes large parasymphysial tooth whorls with sigmoid teeth on their lower jaws and commensurately large internasal pits on

the ethmoid floor to accommodate the whorls (6, 12). In *Onychodus*, the ethmosphenoid region of the braincase has a series of distinctive features that all appear to form a functional complex with the strongly developed parasymphysial tooth whorls and internasal pits: notably, the vomers are absent, the parasphenoid is short, and the notochordal facet is extremely large (12).

This onychodont character complex has always been regarded as autapomorphic (12). Tooth whorls and internasal pits are also present in porolepiforms (for example, *Porolepis* and *Holoptychius*), *Powichthys*, and *Youngolepis*, which are Devonian members of the lungfish stem group (15–18), but these parts are smaller than those of onychodonts, and the associated cranial architecture is less extreme. However, the hypothesis that the onychodont character complex is specialized has recently been challenged by the discovery of three very early osteichthyans—*Guiyu*, *Psarolepis*, and *Achoania*—from the Late Silurian to Early Devonian (Ludlow to Lochkovian) of Yunnan, China (19–21). These genera combine onychodont-like ethmosphenoids, as well as lower jaws equipped with large parasymphysial tooth whorls, with primitive characteristics that suggest a placement in the sarcopterygian stem group or possibly the osteichthyan stem group (19, 22, 23). Some researchers have interpreted this character distribution as evidence that these early Chinese osteichthyans form a clade with onychodonts (6), but this conflicts with other characters such as the presence of a single humerus in *Onychodus* (and crown sarcopterygians) (12) but a multibasal pectoral fin in *Psarolepis* and *Achoania* (24). An alternative possibility is that the distinctive and seemingly specialized onychodont gestalt is, at least in part, primitive for the Sarcopterygii. Resolution of this problem requires a well-supported phylogenetic placement for the onychodonts.

Poor ossification of the character-rich neurocranium, along with conflicting character states, has until now resulted in disagreement about the placement of onychodonts in a sarcopterygian phylogeny (1–3, 5, 6, 25). The recent discovery of *Qingmenodus*, an Early Devonian (Pragian, ~409 million years ago) onychodont from China with a well-ossified braincase (7), has begun to remedy this deficiency in the data; notably, the otoccipital region of *Qingmenodus* shows a posteriorly large positioned attachment for the basicranial muscle

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reminiscent of the condition in coelacanths (7). However, until now, the cranial cavity and associated spaces of onychodonts have remained largely unknown, except for a few structures (the external semicircular canal tract, the mesial wall of the nasal cavity, and parts of the ethmosphenoid cranial cavity) visible in acid-prepared specimens of *Onychodus* from Gogo (12).

We describe here a newly discovered anterior cranial portion, permitting a completely reconstructed virtual cranial endocast of *Qingmenodus*. It provides the first detailed interpretation of internal neurocranial anatomy in onychodonts, allowing extensive comparisons with other sarcopterygians, in particular those that have been studied by serial grinding or computed tomography (CT) scanning (15–17, 26–33). This study sheds light on the relationships of onychodonts and helps us to understand the sequence of character acquisition in the early evolution of sarcopterygians. We show that onychodonts form a plesion in the coelacanth stem group, casting light on the earliest steps in the evolution of this morphologically distinctive and still extant sarcopterygian group.

RESULTS

General morphology of *Qingmenodus* skull

The anterior or ethmosphenoid cranial portion (Fig. 1, A and C, and figs. S1 and S2), IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V16003.5, has suffered a moderate amount of lateral compression, as shown by the upright-oval shape of the notochordal facet and the strong transverse curvature of the skull roof. The dermal

surface is covered with closely spaced tiny pores (fig. S1A). Few sutures can be observed in the skull roof of the anterior cranial portion, except those bounding the premaxillae and median rostral, and the short midline suture between the parietals posterior to the pineal plate (fig. S1A). The premaxillae meet in the midline, but the median rostral is more deeply inserted between them than in *Onychodus* (12). The posterior midline contact between the parietals is a general sarcopterygian feature (15), contrasting with the condition in *Onychodus* where the parietals are wholly separated by the pineal plate (12).

The ethmosphenoid braincase (Fig. 1, A and C, and figs. S1 and S2) of *Qingmenodus*, in most respects, resembles a more completely ossified version of *Onychodus* (12). Noteworthy similarities include the short parasphenoid, large and very elongate internasal cavities, a long and narrow internasal ridge, and knob-like basiptyergoid processes. However, there are also some important differences. The notochordal facet, which is extremely large in *Onychodus*, is of a more normal size in *Qingmenodus* (fig. S2, C and D); as a corollary to this, the processus connectens is located dorsal to the notochordal facet rather than on the side of it as in *Onychodus*, and the posterior part of the cranial cavity is deeper. High-resolution CT (HRCT) scanning revealed that the posterior part of the braincase was concealed by a posteriorly extended triangular-shaped matrix block (fig. S2). When this block is removed digitally, the posterior margin of the anterior cranial portion exhibits a strong posteroventral slope in profile from the skull roof to the processus connectens (fig. S2, B and D), as in coelacanths, porolepiforms, and (to a lesser degree) osteolepiforms (15, 16); this margin also slopes posteroventrally in *Onychodus*, but because it is much shorter than in *Qingmenodus*, the overall

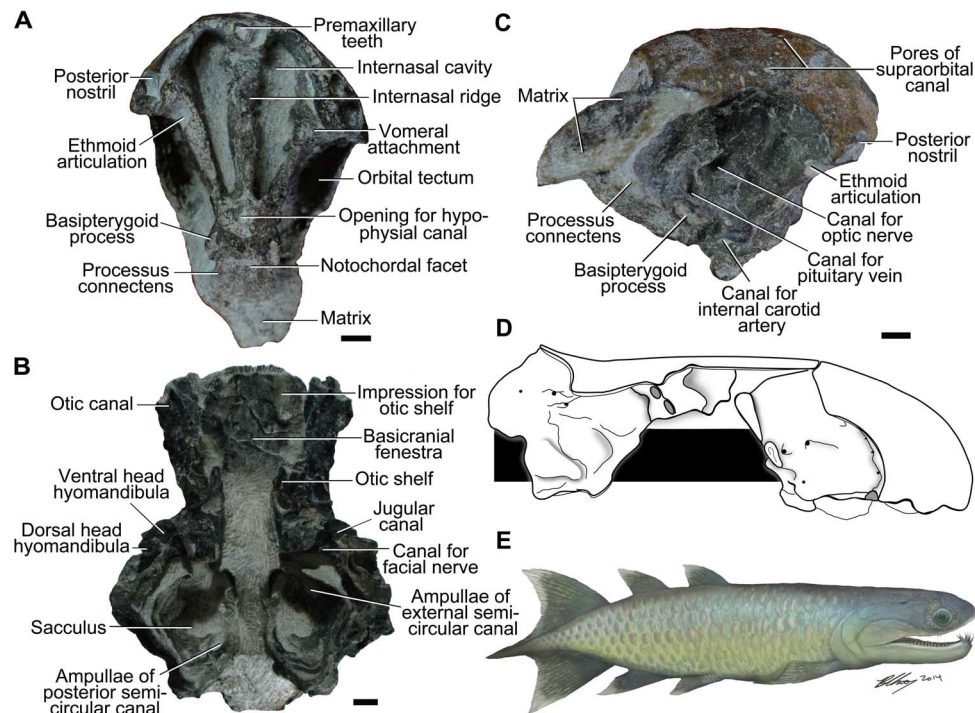


Fig. 1. *Qingmenodus yui*, an early onychodont from Pragian, South China. (A) Anterior cranial portion (IVPP V16003.5) in ventral view. (B) Posterior cranial portion (IVPP V16003.6) in ventral view. (C) Anterior cranial portion (IVPP V16003.5) in right lateral view. (D) Tentative restoration of the natural shape of the neurocranium in right lateral view. (E) Life restoration drawn by B. Choo (Flinders University, Australia). Scale bars, 2 mm. (D and E) Not drawn to scale.

profile of the posterior margin of the ethmosphenoid is rather different (12). In *Psarolepis*, *Guiyu*, and *Achoania*, the entire posterior margin slopes anteroventrally (19–21). No pineal opening is present in *Qingmenodus*.

The new posterior cranial portion of *Qingmenodus* (Fig. 1B and fig. S3, A to D), IVPP V16003.6, is slightly smaller than the holotype (fig. S3, E and F) (7), about 3.1 cm in length and 2.4 cm in width. It preserves three pairs of dermal bones: postparietals, supratemporals, and tabulars (fig. S3A), revealing that *Qingmenodus* has a large spiracular notch like *Strunius* (11), rather than a small and inconspicuous notch like *Onychodus* (12) and *Grossius* (8), as previously thought. The lateral commissure on the right side of the skull preserves two obvious hyomandibular facets (Fig. 1B and fig. S3, C and D), indicating that *Qingmenodus* has a double-headed hyomandibula, as in crown sarcopterygians. *Onychodus* was interpreted as having a single-headed hyomandibula (12), but this was inferred from an incompletely ossified hyomandibula without corroborating evidence from the lateral commissure. A partially preserved double-headed hyomandibula is present in articulation in the holotype of *Qingmenodus* (fig. S4) (see below).

Cranial endocast of *Qingmenodus*

The well-ossified neurocranium of *Qingmenodus* allows us to investigate brain structures in early onychodonts (which is the first time that the internal morphology of the neurocranium of the group can be accessed in detail) and adds to our knowledge of brain evolution in early sarcopterygians. The modeled cranial endocast of *Qingmenodus* (Fig. 2) includes anterior and posterior parts separated by the intracranial joint. These two parts are fitted together by using the perimeter of notochordal facet as reference (Fig. 1D and fig. S5). Furthermore, using the shape of the notochordal facet as a guide, the natural shape of the laterally compressed anterior part of the anterior cranial part has been restored as well (Fig. 2 and fig. S6).

The inner ear region of the cranial endocast resembles that of the Devonian coelacanth *Diplocercides* (29) in that the labyrinth cavity is posteriorly positioned (raising the level of the posterior margin of the otocipital), the top of the labyrinth cavity rises no higher than the flat-topped brain cavity, and the sacculus bulges laterally to almost fill the space encompassed by the horizontal semicircular canal (Fig. 2, A and B, and fig. S7, B and C). *Qingmenodus* and *Diplocercides* also exhibit similarity in the openings for the oculomotor and trochlear nerves, which are placed in the diencephalic portion of the cranial cavity rather than in the mesencephalic portion, as in other Devonian sarcopterygians (fig. S7). By contrast, the general morphology of the ethmosphenoid part of the cranial cavity, as well as most of its details, differs fundamentally from that of coelacanth. *Qingmenodus* resembles porolepiforms (for example, *Porolepis* and *Glyptolepis*) (16) in bearing adjacent pineal and parapineal organs (Fig. 2, A and B). The general shape of the hypophysial fossa in *Qingmenodus* agrees with that of *Eusthenopteron* (15), which is ventrally extended and without a posterior lobe. The hypophysial fossa in *Glyptolepis* and *Powichthys* is elongated, with distinct vertical and horizontal limbs (16, 31). Unlike that of coelacanth, the exit for the profundus branch (Fig. 2B) in *Qingmenodus* lies in the intracranial joint, and the maxillary and mandibular branches of the trigeminal nerve (Fig. 2, A and B) are in the anterior part of the otocipital, as in most rhipidistians (1, 34). The lateral line canals embedded in the dermal bones are clearly visible in the HRCT scan (fig. S8, A to C). Like in most early sarcopterygians (15), but unlike in *Onychodus* (12), the course of the

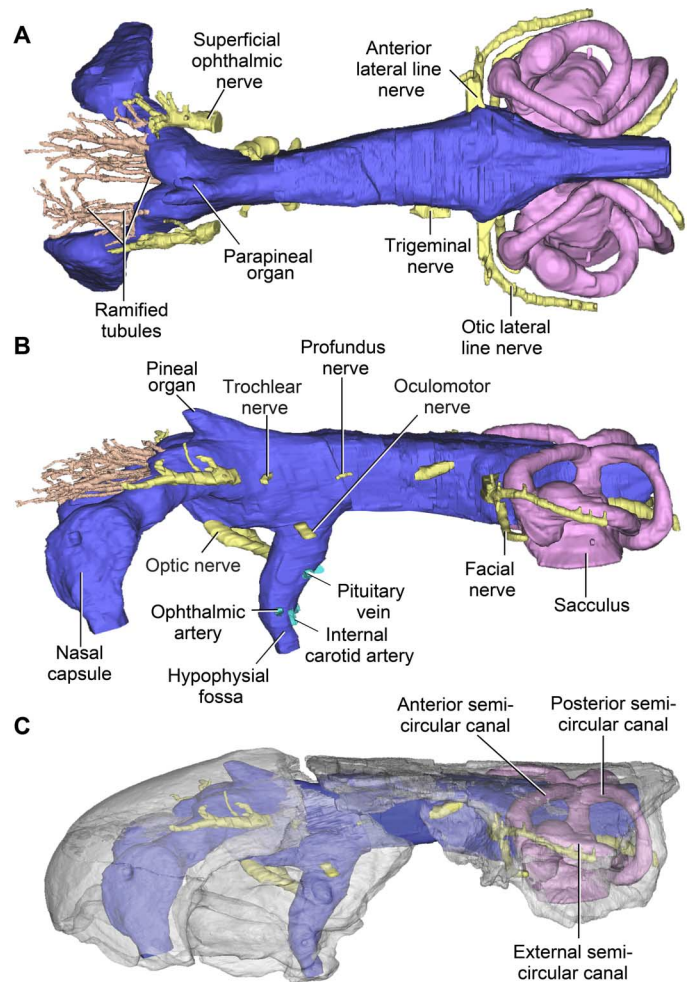


Fig. 2. Digital neurocranial endocast restorations of *Q. yui*. (A to C) In dorsal view (A), lateral view (B), and left lateral view with transparent braincase (C). Main color key: blue, cranial cavity; yellow, cranial nerves; orange, tubule system; pink, inner ear cavity. Not drawn to scale.

supraorbital canal is lyre-shaped. The proportions of the canal system suggest that the parietals are relatively short.

Despite those similarities with a range of early sarcopterygians, *Qingmenodus* differs from them in many aspects. The laterodorsally positioned nasal capsules are large, elongate, and oblong (Fig. 2), similar to the condition in *Onychodus* (12). The nasal capsules are triangular-shaped in Devonian Dipnomorpha (17, 29–33) and Tetrapodomorpha (15, 28, 29), but broader and more rounded in *Psarolepis* (35). The mesencephalic portion is longer than that in other Devonian sarcopterygians, occupying ~20% of the whole length of the cranial cavity (fig. S7). This might be connected with the elongate otocipital portion in onychodonts. A possible glossopharyngeal nerve (IX) lies medial to the ampulla of the posterior semicircular canal, as in coelacanth and rhipidistians (15, 29).

The most unexpected neurocranial feature of *Qingmenodus* is the presence of a ramified tubule system in the snout region, which originates from the branches of the superficial ophthalmic nerve (Fig. 2, A and B, and figs. S8 and S9). These tubules extend antero dorsally, and some of them enter into the supraorbital canal, highlighting the close

relation between the ramified tubule system in *Qingmenodus* and the lateral line sensory system (fig. S8). Laterally, the superficial ophthalmic nerve also sends many branches into the supraorbital canal (fig. S8B). Such a tubule system recalls the rostral tubuli in the basal dipnomorph *Youngolepis* and Devonian lungfishes (fig. S9, B and D) (36–40), which was regarded as one of the diagnostic features for lungfishes (2, 38). Recently, a similar tubule system has been found in the Devonian tetrapodomorph *Gogonassus* (41). The discovery of such tubule systems in many sarcopterygian groups casts new light on what was previously regarded as a “lungfish character” and provides an opportunity to obtain a better understanding of their homology and function.

Hyomandibula of *Qingmenodus*

A very small incomplete hyomandibula preserved in approximately life position has been reconstructed by HRCT of the holotype (Fig. 3). Its distal part is broken off, and the proximal part occupies about 7% of the whole length of the otoccipital region (fig. S4). The restored hyomandibula (Fig. 3, C to F) is comparable to that of *Onychodus* (12), with regard to overall shape and the absence of a hyomandibular canal. However, in contrast to the condition described for *Onychodus*, the hyomandibula in *Qingmenodus* has double articulation facets (Fig. 3E) on its proximal end, as in coelacanth and rhipidistians (15). A single-headed hyomandibula is regarded as a primitive gnathostome character, and its presence in both *Onychodus* and *Psarolepis* was thought to be a feature that could place these taxa outside of the crown sarcopterygian clade (6). However, the interpretation of *Onychodus* was based on hyomandibula with incompletely ossified proximal ends (12); unlike in *Qingmenodus*, the articular facets for the hyomandibula on the braincase are not preserved. We believe that it is unlikely that two so closely related and, in other respects, anatomically similar fishes such as *Qingmenodus* and *Onychodus* would differ with regard to this character, which is otherwise stable across crown Sarcopterygii, so we suggest that *Onychodus* was misinterpreted in the original description (12).

DISCUSSION

Phylogenetic implications

The phylogenetic relationship of onychodonts has long been debated (fig. S10) (1–3, 5–7, 19, 25, 42, 43), partly for lack of sufficient neurocranial data. In previous phylogenetic analyses involving onychodonts, either the characters of onychodonts were mainly based on skull roof,

dermal bones, and postcranial skeleton (5, 25) or the data matrix was limited by a small number of taxa and characters (7). The fully ossified neurocranium of *Qingmenodus* remedies this deficiency and provides crucial data to investigate the phylogenetic position of onychodonts among sarcopterygians.

We conducted a new analysis by assembling an enlarged and revised data matrix based on those from several recent publications (2, 3, 5, 7, 19, 44, 45). The new data matrix includes 37 taxa and 242 characters, of which 13 characters (11 of them based on CT data) are new (see the Supplementary Materials for a complete character list and coding for all included taxa). The analysis gave 845 equally most parsimonious trees of 544 steps each [consistency index (CI), 0.5092; retention index, 0.7488]. There is a high degree of consensus between the trees, with areas of instability being limited to the in-group relationships of coelacanth and actinopterygians; the former probably reflects phylogenetic loss, the latter possibly the absence of a non-osteichthyan outgroup. Relationships within and between the lungfish and tetrapod total groups (Dipnomorpha and Tetrapodomorpha) are fully resolved. All trees recover lungfishes as the extant sister group of tetrapods, with coelacanth as the sister group of the lungfish-tetrapod clade, and are thus compatible with recent molecular analyses (4) (fig. S11).

On the basis of the new analysis, the onychodonts, excluding *Bukkanodus*, are monophyletic and form the sister group of coelacanth (figs. S11, S12, and S13). The node uniting onychodonts and coelacanth is supported by five unambiguous characters (character 72, posteriorly positioned attachment for basicranial muscle; character 88, absence of the quadratojugal bone; character 162, absence of the branchiostegal rays; character 239, laterally bulging sacculus of the inner ear; and character 241, the oculomotor and trochlear nerves issue from the diencephalic cavity). In the new analysis, *Bukkanodus* is placed as the sister clade of onychodonts plus coelacanth. This taxon is only known by a few dermal bone fragments with ~90% missing data and does not offer sufficient information for a reliable assignment. The cranial data revealed by *Qingmenodus*, such as a well-developed processus connectens (character 66), posteriorly situated attachment for the basicranial muscle on the otoccipital (character 72), and similar arrangements of brain cavity features (characters 239, 241, and 242), strongly support the close affinity between onychodonts and coelacanth.

In the new analysis, the *Guiyu* clade is positioned unambiguously in the sarcopterygian stem group. The clade of crown sarcopterygians is supported by 26 characters, 15 of them uniquely shared (CI, 1). *Styloichthys* is assigned as the sister taxon of rhipidistians (dipnomorphs plus tetrapodomorphs). Although there are only two homoplasious

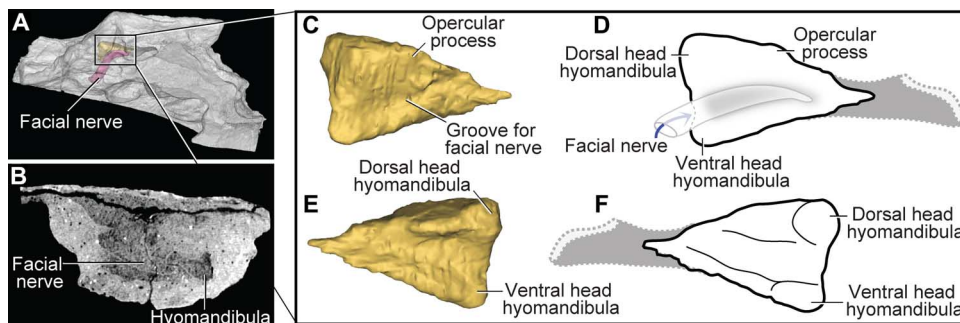


Fig. 3. Hyomandibula of *Qingmenodus*. (A) Digital restoration of hyomandibula (in yellow) and facial nerve (in pink) in the holotype (IVPP V16003.1) of *Q. yui*, in left lateroventral view with transparent braincase. (B) Transverse slice through the hyomandibular and facial nerve canal. (C to F) Restorations of hyomandibula in lateral view (C and D; digital restoration and line drawing) and mesial view (E and F; digital restoration and line drawing). Not drawn to scale.

characters ($CI < 1$) separating *Styloichthys* from rhipidistians, the node uniting *Styloichthys* and rhipidistians is strongly supported by 16 characters, five of them uniquely shared. These include the presence of a fenestra ventralis (character 50), a maxillary that does not contribute to the posterior margin of cheek (character 129), and three coronoids (character 145).

The well-resolved position of the *Guiyu* clade in the sarcopterygian stem group allows us to identify a number of characters, shared between the *Guiyu* clade and certain members of the crown group (chiefly onychodonts, porolepiforms, *Powichthys*, and *Youngolepis*), as primitive for the sarcopterygian crown group. These include deep internasal pits that receive the teeth of the parasymphysial tooth whorls of the lower jaw, widely spaced vomers, and possibly a short rhomboidal parasphenoid. Other characters of the *Guiyu* clade, such as a hypophysial canal situated at the same level or slightly anterior to the ethmoid articulation, lack of a processus connectens, and a posteriorly reclined intracranial joint, may also be primitive for Sarcopterygii, although this cannot be demonstrated at present. A processus connectens, a vertical or posteroventrally slanting intracranial joint, and a double-headed hyomandibula are characteristic of crown sarcopterygians and are probably synapomorphies of this clade.

Well-developed intracranial joint in onychodonts and coelacanth

The intracranial joint, comprising dermal and endoskeletal parts, is a conspicuous feature of the sarcopterygian neurocranium, except in lungfishes and tetrapods, where it has been lost secondarily. The endoskeletal articulation, which lies just below the cranial cavity, is formed by the otic shelf of the otoccipital and the processus connectens of the

basisphenoid (44). It is most strongly developed in coelacanth, in which the anteroventrally inclined processus connectens reaches the level of parasphenoid and forms a track-and-groove intracranial joint with the prominent otic shelf from the lateral commissure (44) (Fig. 4). The processus connectens in *Qingmenodus* is anteroventrally elongated, reaching the level of the basiptyergoid process, similar to that of Devonian coelacanth (15, 44) (Fig. 4). The rough surface of the processus connectens in *Qingmenodus* suggests a ligamentous attachment to the otic shelf of the otoccipital braincase. By contrast, in *Onychodus*, the notochord is so greatly enlarged that the otic shelves clasp the lateral sides of the notochordal facet and no true processus connectens is present. *Qingmenodus* demonstrates that this strange morphology is a modification of a typical crown sarcopterygian intracranial joint, with some specific coelacanth-like characteristics. The well-developed processus connectens of *Qingmenodus* and coelacanth suggest similar high mobility of the intracranial joint in both.

The intracranial joint in stem sarcopterygians (for example, *Psarolepis*, *Achoania*, and *Guiyu*) is anteriorly reclined (20, 21, 46), without a processus connectens. This arrangement suggests that the endoskeletal intracranial joint in stem sarcopterygians is probably articulated by the posterodorsal articular process of ethmosphenoid and the anterodorsal articular process of otoccipital (21), which is significantly different from the condition in crown sarcopterygians.

Implications for neurocranial evolution in sarcopterygians

The virtual endocast of *Qingmenodus* provides a more direct comparison with similar reconstructions available for other sarcopterygians, and early actinopterygians as well (Fig. 4 and fig. S7). *Qingmenodus* is suggestive of coelacanth in the following neurocranial traits: (i) the

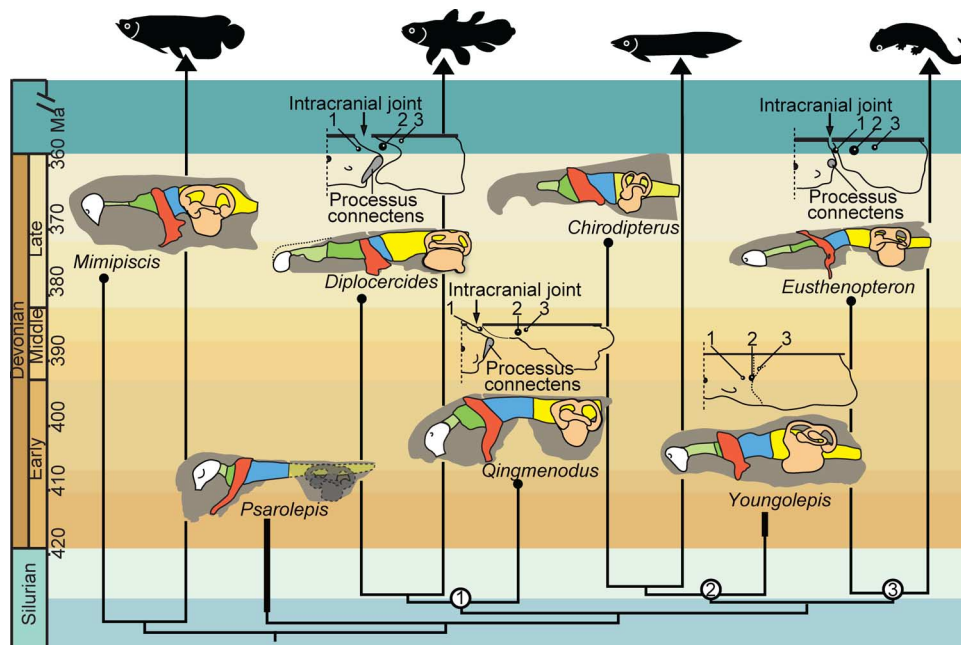


Fig. 4. Comparison of the brain cavities of selected Devonian sarcopterygians in a temporally calibrated cladogram. Node 1, Actinistia (coelacanth lineage); node 2, Dipnomorpha (lungfish lineage); node 3, Tetrapodomorpha (tetrapod lineage). 1, $V_{1,prof}$ profundus nerve; 2, $V_{2,tri}$ trigeminal nerve; 3, $V_{7,oph}$ ophthalmic branch for facial nerve. Main color key: white, olfactory capsule; green, telencephalic cavity; red, diencephalic cavity; blue, mesencephalic cavity; yellow, rhombencephalic cavity; orange, labyrinth cavity. Illustrations are redrawn from the studies of Jarvik (15), Chang (17), Stensiö (29), Säve-Söderbergh (32), Thomson and Campbell (37), and Giles and Friedman (47). Not drawn to scale.

top of the labyrinth cavity is no higher than that of the brain cavity; (ii) the sacculus of the inner ear cavity is large and laterally expanded, so that it is visible on dorsal view; and (iii) the oculomotor and trochlear nerves issue from the diencephalic cavity (fig. S7).

In early actinopterygians (for example, *Mimipiscis*, *Kentuckia*, and *Lawrenciella*) (47, 48), the rhombencephalic cavity anterior to the labyrinth cavity is very short, and the exit of the facial nerve is immediately posterior to the mesencephalic cavity. By contrast, in Devonian sarcopterygians, the rhombencephalic cavity anterior to the inner ear is well developed, and the exit of the facial nerve is far behind the boundary between the mesencephalic and the rhombencephalic cavities (Fig. 4 and fig. S7) (15, 17, 29). The elongate anterior part of the rhombencephalic cavity is a sarcopterygian character, which might be related to increased functional demand for a precise sensitivity to movement in the group.

The hypophysial fossa in sarcopterygians shows three different patterns: (i) vertically extended, triangular-shaped with a posterior lobe, and approximately equal length and depth, as in the coelacanth *Diplocercides* and the dipnomorph *Youngolepis* (17, 29); (ii) vertically extended, greater depth than length, and without a posterior lobe, as in onychodonts (for example, *Qingmenodus* and *Onychodus*) (12) and tetrapodomorphs (for example, *Gogonasmus* and *Eusthenopteron*) (15, 41); and (iii) anteroventrally extended, elongated, and with distinct vertical and horizontal limbs, as in *Powichthys* (31) and *Latimeria* (49). The first type, the triangular-shaped hypophysial fossa, recalls that of early actinopterygians (47), which may indicate a primitive osteichthyan condition. However, the polarity of the different types of the hypophysial fossa in sarcopterygians needs further investigation.

Qingmenodus, one of the oldest known onychodonts, shows a virtually complete set of neurocranial structures of an onychodont. It exhibits a mosaic of features present in both stem sarcopterygians (such as large pear-shaped internasal pits, absence of a ventral fenestra, short sphenoid region, and lozenge-shaped parasphenoid) and coelacanth (such as long and well-developed processus connectens, well-developed posteroventrally slanting intracranial joint, posteriorly situated attachment for basicranial muscle on the otoccipital, and similar neurocranial features in the otic region). It thus further bridges the morphological gap between stem sarcopterygians (*Guiyu*, *Psarolepis*, and *Achoania*) and crown sarcopterygians and provides unique insights into the sequence of neurocranial character acquisition involved in the origin and early diversification of the latter. Remarkably, it appears that the distinctive onychodont ethmosphenoid morphology is not autapomorphic but is, in most respects, a primitive character complex retained from the sarcopterygian stem group. The occurrence of a less extreme version of the same character suite (widely separated vomers, paired internasal pits receiving parasymphysial tooth whorls of the lower jaw) in basal dipnomorphs, such as porolepiforms, *Powichthys*, and *Youngolepis* further supports this hypothesis and leads to the unexpected conclusion that the gross similarities in ethmosphenoid morphology between actinopterygians, coelacanth, *Styloichthys*, and tetrapodomorphs (for example, long parasphenoid, vomers positioned close together, and absence of paired internasal pits) may be convergences, not osteichthyan symplesiomorphies.

MATERIALS AND METHODS

Specimen collection

The new specimens in this study, including a completely ossified anterior cranial portion (IVPP V16003.5) and a posterior cranial por-

tion (IVPP V16003.6), were collected from the type site of *Q. yui* (Pragian, ~409 million years ago) during 2009 to 2012 field trips. These specimens were both mechanically prepared to remove rock matrix. A posteriorly extending triangular-shaped matrix block attached to the posterior part of the anterior cranial portion, which had been left by the preparator, was removed digitally during modeling. The specimens are housed in the IVPP. The anterior cranial portion (IVPP V16003.5) is referred to as *Q. yui* based on the shared ornamentation and comparable size with the holotype of *Q. yui* (IVPP V16003.1). The new posterior cranial portion (IVPP V16003.6) has not preserved the ventral part of the otic capsules; however, its preserved part matches well with the holotype (IVPP V16003.1), such as vermiculate impressions on the dermal surface, and the elongate otic shelf.

Phylogenetic analysis

To explore the phylogenetic position of *Qingmenodus*, we conducted phylogenetic analyses using a modified data set with 242 characters and 37 taxa (see Supplementary Materials and Methods). This data set is based on the work of Cloutier and Ahlberg (2), Zhu and Yu (3), Friedman (5), Lu and Zhu (7), Zhu *et al.* (19), Forey (44), and Zhu and Schultze (45). Thirteen new cranial characters (11 of them based on CT data) were added in the character data (characters 65, 66, and 232 to 242 based on HRCT). The actinopterygians (*Dialipina*, *Howqualepis*, *Cheirolepis*, *Mimipiscis*, and *Moythomasia*) plus *Ligulalepis* were designated as the outgroup.

Character data entry and formatting were performed in Mesquite (version 3.04) (50). The data matrix was subjected to parsimony analysis in PAUP* (version 4.0b10) (51) using the heuristic algorithm. All characters were treated as unordered and weighted equally. The synapomorphies listed (fig. S12) were obtained under DELTRAN (delayed transformation) optimization. MacClade 4.0 (52) was used to trace the character transformation in the selected cladogram. Bremer decay indices were obtained using command files composed by TreeRot (53) in conjunction with the heuristic search algorithm in PAUP*.

The strict consensus tree of 845 shortest trees (fig. S11) places the onychodonts, excluding *Bukkanodus*, as the sister group of coelacanth, within the crown sarcopterygians. *Bukkanodus* is placed as the sister clade of onychodonts plus coelacanth. The 50% majority consensus tree resolves *Strunius* as the most basal onychodont. The crownward *Qingmenodus*, *Grossius*, and *Onychodus* form a trichotomy (fig. S12). The interrelationship of coelacanth is not fully resolved in the current analysis.

X-ray microtomography

We analyzed three detached cranial elements (one ethmosphenoid and two otoccipital regions) of *Q. yui*, using three-dimensional models constructed with the 225-kV micro-CT [developed by the Institute of High Energy Physics, Chinese Academy of Sciences (CAS)] at the Key Laboratory of Vertebrate Evolution and Human Origin of CAS, IVPP, CAS, Beijing, China. The specimens were scanned with a beam energy of 130 kV and a flux of 90 μ A at a detector resolution of 10.8 μ m per pixel, using a 720° rotation with a step size of 0.5° and an unfiltered aluminum reflection target. A total of 1440 transmission images were reconstructed in a 2048 \times 2048 matrix of 1536 slices in a two-dimensional reconstruction software developed by the Institute of High Energy Physics, CAS.

Anatomical reconstruction

The three-dimensional reconstructions were created with the software Mimics (version 16.1). The images of the reconstructions were exported from Mimics and finalized in Adobe Photoshop and Adobe Illustrator, and the restorations were carried out in Adobe Photoshop and Adobe Illustrator. In addition to neurocranial structures that were modeled as preserved, the final three-dimensional model included one area of reconstruction produced by application of a prosthetic. This was the floor of the anterior part of the brain cavity of the otoccipital portion, which was not bounded by skeleton because it lay within the basicranial fenestra. The level of this floor was reconstructed from preserved correlates, such as the level of the brain cavity floor of the ethmosphenoid portion. The retrodeformation of the posterior part of the ethmosphenoid was based on the perimeter of the notochordal facet as a parameter, working on the assumption that the facet would have been approximately circular in life.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/2/6/e1600154/DC1>

Supplementary Materials and Methods

- fig. S1. The anterior cranial portion of *Qingmenodus* (IVPP V16003.5).
 fig. S2. Rendered anterior cranial portion of *Qingmenodus* (IVPP V16003.5).
 fig. S3. The posterior cranial portions of *Qingmenodus*.
 fig. S4. Rendered posterior cranial portion of *Qingmenodus* (holotype, IVPP V16003.1) showing the position of the hyomandibula.
 fig. S5. Tentative restoration of the cranium of *Qingmenodus* in right lateral view.
 fig. S6. Rendered brain cavity with the transparent braincase of *Qingmenodus* in left lateral view.
 fig. S7. Comparative brain cavity morphology of selected Palaeozoic osteichthyans.
 fig. S8. Digital restorations of the anterior cranial portion of *Qingmenodus*.
 fig. S9. Comparison of the tubule system in selected sarcopterygians.
 fig. S10. Previously sarcopterygian phylogenetic hypotheses showing the different positions of onychodonts.
 fig. S11. Strict consensus of 845 most parsimonious trees resulting from a modified data set.
 fig. S12. Phylogenetic placement of *Qingmenodus* shown in a 50% majority consensus tree of the 845 most parsimonious trees.
 fig. S13. One selected most parsimonious tree.

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