

# An onychodont fish (Osteichthyes, Sarcopterygii) from the Early Devonian of China, and the evolution of the Onychodontiformes

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Although the superbly preserved specimens of *Onychodus jandemarrai* have greatly advanced our understanding of the Onychodontiformes, a primitive sarcopterygian group with large parasymphysial tooth whorls, the scarcity of the otoccipital material in the group hampers further morphological comparisons between onychodonts and other sarcopterygian groups. Here we report a new onychodont *Qingmenodus yui* gen. et sp. nov. from the Early Devonian (Pragian) of South China that comprises well-ossified otoccipital and upper and lower jaw material. As one of the oldest known onychodonts, *Qingmenodus* shows for the first time the nearly complete structure of the otoccipital in onychodonts and provides an additional basis to address the phylogenetic position of the group. Its elongated otic shelf exhibits the posterior shift of the attachment for the basicranial muscle as in coelacanth and sheds light on the feeding mechanism of onychodonts. *Qingmenodus* displays a mosaic of primitive and derived onychodont features. The phylogenetic analysis places *Qingmenodus* immediately basal to the clade comprising *Onychodus* and *Grossius*.

**Keywords:** onychodonts; evolution; Early Devonian; otoccipital; feeding mechanism; phylogenetic analysis

## 1. INTRODUCTION

The Onychodontiformes (or 'Strunioformes') are a Devonian sarcopterygian group, with five genera currently described (*Onychodus*, Newberry 1857; *Strunius*, Jessen 1966; *Grossius*, Schultze 1973; *Lukeus*, Young & Schultze 2005; *Bukkanodus*, Johanson *et al.* 2007). Two mandibles, respectively, from the Lochkovian and Pragian of South China (Zhu & Janvier 1994; Zhu & Yu 2004), and *Bukkanodus* from the Pragian of Australia (Johanson *et al.* 2007), are among the oldest known onychodonts. The most well-known onychodont is *Onychodus jandemarrai* from the Frasnian of Western Australia (Andrews *et al.* 2006).

It is widely recognized that the Onychodontiformes are a monophyletic group (Cloutier & Ahlberg 1996; Janvier 1996; Andrews *et al.* 2006; Campbell & Barwick 2006), except by Friedman (2007), who reconstructed *Strunius* and *Onychodus* as a paraphyletic grade that forms the immediate sister group to the crown group Sarcopterygii. Opinions differ mainly in the affinities of the group within the Sarcopterygii, which fall in one of the three positions: (i) together with *Psarolepis*, sister to the crown group Sarcopterygii (Long 2001); (ii) sister to the actinistians (Zhu & Schultze 1997, 2001; Zhu *et al.* 1999, 2001,

2006); and (iii) above actinistians, sister to the clade containing dipnomorphs and tetrapodomorphs (Cloutier & Ahlberg 1996), or tetrapodomorphs plus a subset of dipnomorphs (Schultze 1987; Long 1989; Young *et al.* 1992). The superbly preserved specimens of *O. jandemarrai* have provided a wealth of anatomical information for the understanding of the group; however, few data are known of the otoccipital (Schultze 1973; Andrews *et al.* 2006), thus the posterior extent of the basicranial muscle and its relationship to the intracranial joint and feeding mechanism remain enigmatic. The scarcity of the otoccipital material also hampers further morphological comparisons between onychodonts and other sarcopterygian groups.

Here we report a new onychodont from the Pragian of Yunnan, South China (see electronic supplementary material A), exemplified by a posterior cranial portion with extensively ossified otoccipital and some disarticulated bones. The new form reveals some features of onychodont affinity; for example, elongated postparietal, anteriorly positioned tabular, mandibular sensory canal through the lowermost part of the infradentary series with many tubes and striated enamel on the parasymphysial tusk. It is unique in its dermal surface covered with closely spaced tiny pores and vermiculate branches of the otic canal. The new form is among the oldest known onychodonts and exhibits for the first time the nearly complete structure of the otoccipital in onychodonts, thus improving our understanding of the feeding mechanism and evolution of the Onychodontiformes.

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## 2. SYSTEMATIC PALAEOLOGY

Osteichthyes, Huxley (1880)

Sarcopterygii, Romer (1955)

Onychodontiformes (i.e. Onychodontida, Andrews 1973)

Onychodontidae, Woodward (1891)

*Qingmenodus yui* gen. et sp. nov.

### (a) *Holotype*

IVPP V 16003.1, a posterior cranial portion.

### (b) *Referred specimen*

A maxillary (IVPP V 16003.2), an incomplete mandible (IVPP V 16003.3) and a detached parasymphysial tusk (IVPP V 16003.4).

### (c) *Etymology*

The generic name is after the type locality 'Qingmen' and Greek 'odus', tooth. The specific name is after Dr Yu Xiaobo (Kean University), to acknowledge his contribution to the study of early sarcopterygians.

### (d) *Locality and horizon*

All of the specimens were recovered in 2005–2006 from an outcrop near the Qingmen reservoir in the suburb of Zhaotong, northeastern Yunnan, China. The horizon belongs to the Posongchong Formation, which is of late Pragian age (Liao *et al.* 1978; Hao *et al.* 2004).

### (e) *Diagnosis*

A small onychodont with the following suite of characters that distinguish it from other members of this group (autapomorphies marked with an asterisk): dermal surface covered with closely spaced tiny pores\*; elongated postparietal (about four times as long as wide, different from *Strunius* and *Bukkanodus*); vermiculate branches of the otic canal\*; postparietals extending posteriorly between lateral extrascapulars (as in *Strunius*, *Onychodus* and *Grossius*, unknown in *Bukkanodus*); large attachment area for the basicranial muscle behind the lateral commissure (unknown in other onychodonts); saccular bulge dorsal to the posterior portion of the otic shelf\*; cluster of large pits (as in *Bukkanodus*); mandibular sensory canal through the lowermost part of the infradentary series with many tubes (as in *Strunius* and *Onychodus*, unknown in *Bukkanodus* and *Grossius*); and striated enamel on the parasymphysial tusk (as in other onychodonts).

## 3. DESCRIPTION

The holotype of *Q. yui* has preserved paired postparietals and tabulars, but lacks the supratemporals (figure 1a). The dermal ornament consists of tiny pores, which are much smaller and more closely spaced than those in *Bukkanodus* (Johanson *et al.* 2007). However, whether the surface bears the enameloid covering needs histological examination. In other onychodonts, the dermal surface is ornamented with tubercles. The bone pattern of the skull roof agrees with that of *Onychodus* (Andrews 1973; Andrews *et al.* 2006) and *Grossius* (Schultze 1973). The postparietal (figure 1a, Pp) is elongated with the length/width index of approximately 400. By out-group comparison, the elongation of the postparietal in *Qingmenodus*,

*Onychodus* and *Grossius* (Jessen 1966; Andrews 1973; Schultze 1973; Andrews *et al.* 2006) should be derived in onychodonts. The postparietal in *Strunius* and *Bukkanodus* with the length/width index of approximately 200 represents a plesiomorphic condition. As in rhizodonts (Andrews 1985; Long 1989; Johanson & Ahlberg 1998, 2001) and some onychodonts (*Onychodus* and *Grossius*), the posteriorly tapering postparietals of *Qingmenodus* are placed between the lateral extrascapulars (figure 1a, Ext.l). Anteriorly, the postparietal is bordered laterally by the tabular (figure 1a, Ta) and putative supratemporal (figure 1a, St). Medially, the postparietal has two pairs of pit-lines, the middle and posterior pit-lines (figure 1a, pl.m, pl.p), as in other onychodonts. The tabular seems to be rectangular in shape, although its anterior extremity on both sides was broken. The tabular pit-line (figure 1a, pl.Ta) is behind the level of the middle pit-line as in *Strunius* and *Bukkanodus* (Jessen 1966; Johanson *et al.* 2007). Noteworthy are many vermiculate impressions on the surface of the posterior half of the postparietal shield, along the sutures between the postparietals and tabulars. These impressions are formed by the branches of the otic canal (figure 1a, br.otc), exposed where the dermal surface has been eroded. There are clusters of large pits scattered on the postparietal shield, as in *Bukkanodus*. The overlapped areas along the posterior and posterolateral margins of the shield suggest that the lateral extrascapular extends forwards and contacts the posterolateral margin of the postparietal, as in *Onychodus* and *Grossius*.

The well-ossified otoccipital resembles that of coelacanths in overall shape and proportion. Most striking is that the otic shelf (figure 1b, ot.sh) increases posteriorly in breadth to form a distinct depressed area (figure 1b, or.m.bc), which agrees well with the area of origin of the basicranial muscle (or subcranial muscle) in coelacanths (Bjerring 1967, 1972; Jarvik 1980; Forey 1998). This attachment area in *Qingmenodus* and coelacanths is posterior to the lateral commissure, relating to the high mobility of their intracranial joints. In other sarcopterygians, the attachment area of the basicranial muscle, if present, is usually anterior to or level with the lateral commissure. The largest ossification of the otoccipital is the prootic, which forms the lateral commissure (figure 1b, lc), the otic shelf, the anterior wall of the otic capsule and part of the lateral wall of the notochordal canal. The lateral commissure seems to carry only one articulation facet for the hyomandibular (figure 1b, art.hy). The single-headed hyomandibular is also seen in *Psarolepis* (Yu 1998), *Onychodus* (Andrews *et al.* 2006) and actinopterygians. Medial to the articulation facet for the hyomandibular, the jugular canal (figure 1b, c.ju) runs through the lateral commissure. The ventral view of the otoccipital shows it to be remarkable in its basicranial fenestra (figure 1b, fe.bc), otic shelf and basioccipital ossification. The basicranial fenestra, the opening of the notochordal canal in the otoccipital area, is oblong in outline. The otic shelf is remarkably elongated and occupies a majority of the ventral surface of the otoccipital. The ossified otic capsules display the external ampulla (figure 1b, am.e) and part of the impression for semicircular canals. A putative vestibular fontanelle is found in *Qingmenodus*. Dorsal to the posterior portion of the otic shelf, there is a well-developed process covered with a very thin bone. This process, which we term the

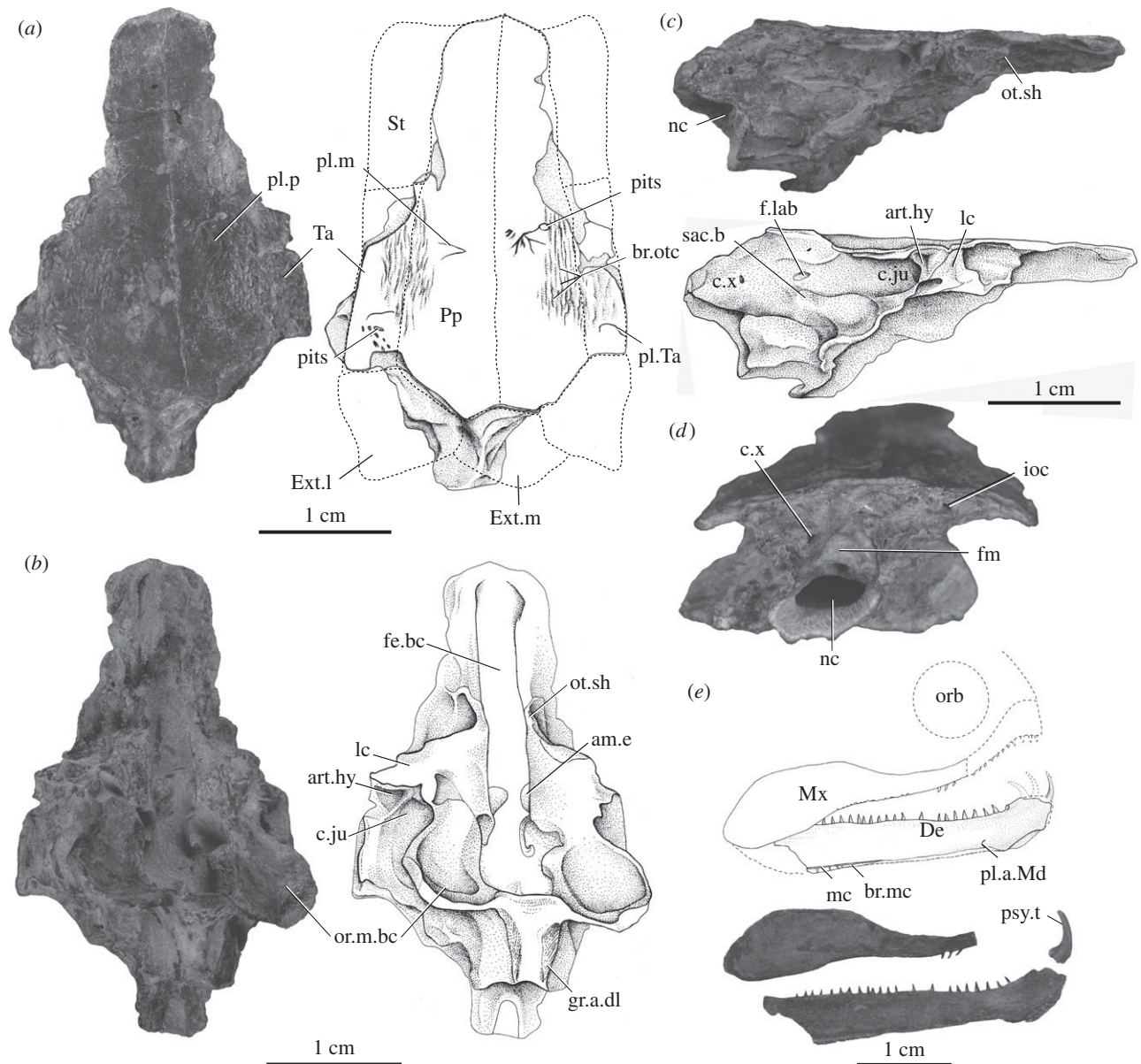


Figure 1. *Qingmenodus yui* gen. and sp. nov., late Pragian, Zhaotong, South China. Posterior cranial portion (holotype, IVPP V 16003.1) in (a) dorsal, (b) ventral, (c) lateral and (d) posterior views, and (e) mandible (IVPP V 16003.3, reversed for ease of reconstruction), maxillary (IVPP V 16003.2), parasymphysial tusk (IVPP V 16003.4) and their reconstruction. Scale bar, 1 cm; the reconstruction of the parasymphysial tusk is not to scale. am.e, external ampulla; art.hy, articulation facet for hyomandibular; br.mc, branches of mandibular canal; br.otc, branches of otic canal; c.ju, jugal canal; c.x, canal for *N. vagus*; De, dentary; Ext.l, lateral extrascapular; Ext.m, median extrascapular; fe.bc, basicranial fenestra; f.lab, fenestra in wall of otic capsule; fm, foramen magnum; gr.a.dl, groove for lateral dorsal aorta; ioc, infraorbital canal; lc, lateral commissure; mc, mandibular canal; Mx, maxillary; nc, canal for notochord; orb, orbit; or.m.bc, origin of the basicranial muscle; ot.sh, otic shelf; pl.a.Md, anterior pit-line of mandible; pl.m, middle pit-line; pl.p, posterior pit-line; pl.Ta, tabular pit-line; Pp, postparietal; psy.t, parasymphysial tusk; sac.b, saccular bulge; St, supratemporal; Ta, tabular.

saccular bulge (figure 1c, sac.b), corresponds topologically to the vestibular fontanelle of other sarcopterygians and might result from the lateral wall of the sacculus filling in the vestibular fontanelle. A large foramen dorsal to the saccular bulge represents the fenestra on the lateral wall of the otic capsule (figure 1c, f.lab). A similar fenestra is also present in *Youngolepis*, *Onychodus*, *Styloichthys* and some coelacanths (Bjerring 1972; Chang 1982; Forey 1998; Zhu & Yu 2002; Andrews *et al.* 2006; Friedman 2007). The basioccipital extends forward to suture with the otic shelf. Posteriorly, the basioccipital represents a rather stout, smooth basicranial plate. The midline of the plate is somewhat elevated, and

a distinct groove (figure 1b, gr.a.dl) on each side of the elevation represents the course of the dorsal aorta.

The maxillary (figure 1e, Mx, V 16003.2) is found from the same site as the holotype. Its assignment to *Qingmenodus* is mainly supported by the dermal surface covered with closely spaced tiny pores. The overall shape of the maxillary agrees with that of stem sarcopterygians (Zhu *et al.* 2009). It possesses a posterior expansion, as in actinopterygians, *Psarolepis* and other onychodonts (Jessen 1966; Gardiner 1984; Zhu *et al.* 1999; Andrews *et al.* 2006). The anterior part of the maxillary is low and adjoins the lachrymal and jugal. The anterior extremity is broken but, as judged from

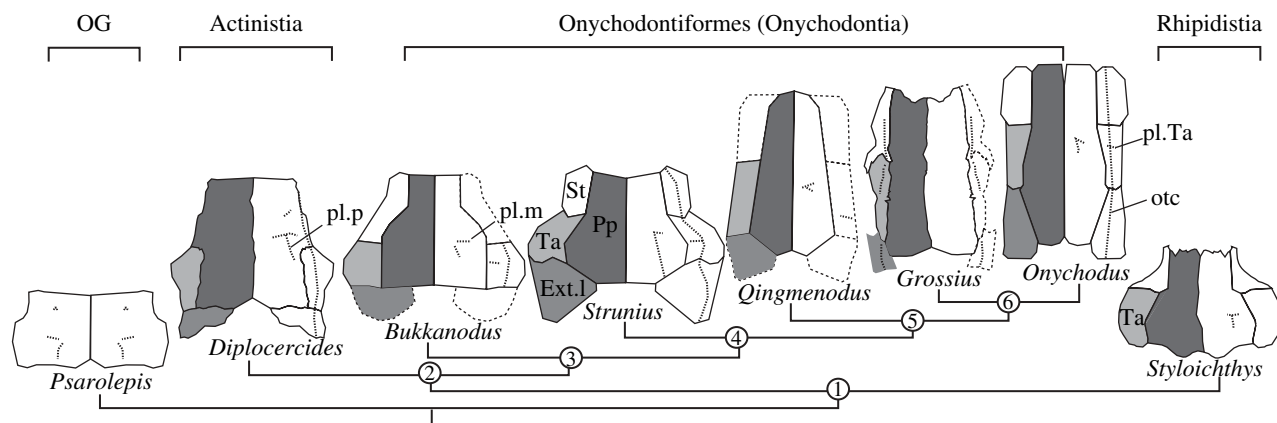


Figure 2. Phylogenetic relationships of the Onychodontiformes. A single most parsimonious tree is based on a PAUP v. 4.0b10 (Swofford 2003) analysis of the data matrix in electronic supplementary material B. Tree length, 46 steps; consistency index (CI), 0.8696; homoplasy index (HI), 0.1304; retention index (RI), 0.8235; rescaled consistency index (RC), 0.7161. Equally weighted solution places *Bukkanodus*, *Strunius*, *Onychodus*, *Grossius* and *Qingmenodus* as a monophyletic group (Onychodontiformes), and *Qingmenodus* forms a sister clade with *Grossius* + *Onychodus*. Ext.l, lateral extrascapular; OG, outgroup; etc, otic canal; pl.m, middle pit-line; pl.p, posterior pit-line; pl.Ta, tabular pit-line; Pp, postparietal; St, supratemporal; Ta, tabular. Drawings not to scale. For a detailed list of synapomorphies for each node, refer to the electronic supplementary material.

the preserved part and by reference to *Strunius*, the missing part should be very short. The maxillary teeth form a continuous row along its ventral edge. Anteriorly, three large marginal teeth are well preserved. They curve slightly backwards and inwards as in *O. jandemarrai*. The marginal teeth are reduced in size posteriorly, but no tooth is observed on the posterior quarter of the bone.

The mandible (V 16003.3) is exposed in external view, with the posterior part missing. It shares the same ornamentation with the postparietal shield and maxillary, and is compatible to other referred specimens in size. From the same site, Zhu & Janvier (1994) described an unnamed onychodont mandible, which is much smaller and thinner than V 16003.3. Based on the available data, we cannot decide whether the differences between these two mandibles result from the allometric growth of the same species or the taxonomic discrimination. No suture is visible between the dentary (figure 1e, De) and infradentaries. The dentary teeth are large and cone-shaped, forming a single tooth row. As in other onychodonts, the pulp cavity of the conical tooth is quite large and without folding. The height of the mandible decreases anteriorly, but increases in the symphyseal region, where the Meckelian attachment base for the parasymphysial tooth whorl is not preserved. The sutures between the bones of the infradentary series are indiscernible, yet the mandibular sensory canal (figure 1e, mc) is evidently shown to run through the lowest part of the infradentary series with many tubes (figure 1e, br.mc), as in other onychodonts (Jessen 1966; Andrews *et al.* 2006). One detached parasymphysial tusk (figure 1e, psy.t), with the characteristic enamel striations of onychodonts, is referred to the new form. The tusk is slender, sigmoidally curved and swollen on the base. Unlike *Onychodus jaekeli* and *Strunius* (Jessen 1966; Upeniece 1995), *Qingmenodus* bears no harpoon-shaped tip in the tusk.

#### 4. DISCUSSION

##### (a) *Phylogenetic analysis*

Discovery of *Qingmenodus* adds to our knowledge of the onychodont morphology that forms the basis for the

understanding of onychodont evolution. In order to make a proper assessment of the phylogenetic position of *Qingmenodus*, we proceeded by assembling a data matrix of 39 characters and 8 taxa (see electronic supplementary material B for a complete character list and codings for all included taxa). Our data matrix is mainly based on skull roof and mandibular anatomical characters.

Phylogenetic analysis yields a single most parsimonious tree (figure 2), in which *Qingmenodus* is placed as the sister taxon to the clade comprising *Onychodus* and *Grossius*. The close relationship of *Qingmenodus* and *Onychodus* + *Grossius* is supported by the posteriorly tapering and elongated postparietal, the length of which is about four times the width. *Bukkanodus* represents the most basal taxon among onychodonts. *Diplocercides* (a primitive coelacanth) forms the sister taxon of onychodonts, and *Styloichthys* is resolved as the sister pair to *Diplocercides* + onychodonts.

##### (b) *Intracranial joint and basicranial muscle in Qingmenodus*

The intracranial joint is a debatable feature of sarcopterygians with respect to its function or its evolution (Janvier 1996). The coelacanth *Latimeria* is the only living vertebrate with a movable intracranial joint, the function of which is closely associated with the lengthened basicranial muscle (Thomson 1966, 1967; Nelson 1970; Lauder 1980; Forey 1991, 1998). The basicranial muscle spans the ventral portion of the intracranial joint and mainly functions for the intracranial joint movements (Bemis & Northcutt 1991; Northcutt & Bemis 1993). Previously, studies have revealed that the joint is well developed in coelacanths, yet less movable in rhipidistians (Thomson 1967; Alexander 1973; Lauder 1980; Forey 1998). In rhipidistians and stem sarcopterygians with the otoccipital preserved, such as *Psarolepis*, the attachment area of the basicranial muscle is usually anterior to, or level with, the lateral commissure. This marks a striking difference from the posterior location of the attachment of the basicranial muscle in coelacanths. Onychodonts are extraordinary in their highly kinetic intracranial joint, as

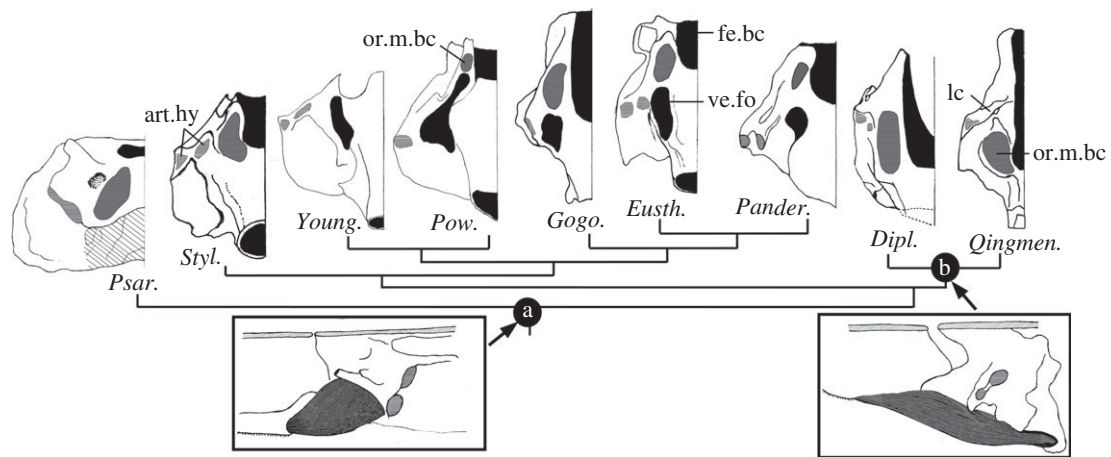


Figure 3. Simplified cladogram of major sarcopterygian groups after Zhu & Yu (2002) and Ahlberg & Johanson (1998), showing the relative position of the attachment for the basicranial muscle and the lateral commissure. The attachment for the basicranial muscle is shaded in grey; the articulation facet(s) for the hyomandibular are in hatched shading. *Dipl.*, *Diplocercides* (from Jarvik 1980); *Eusth.*, *Eusthenopteron* (from Jarvik 1980); *Gogo.*, *Gogonassus* (from Long *et al.* 1997); *Pander.*, *Panderichthys* (from Ahlberg *et al.* 1996); *Pow.*, *Powichthys* (from Jessen 1980); *Psar.*, *Psarolepis* (from an unpublished specimen, IVPP V16005); *Qingmen.*, *Qingmenodus*; *Styl.*, *Styloichthys* (from Zhu & Yu 2002); *Young.*, *Youngolepis* (from Chang 1982); art.hy, articulation facet for hyomandibular; fe.bc, basicranial fenestra; lc, lateral commissure; or.m.bc, origin of the basicranial muscle; ve.fo, vestibular fontanelles. Inset (a) shows the basicranial muscle in stem sarcopterygian *Psarolepis* and rhipidistians (based on *Eusthenopteron*, from Bjerring 1972). Inset (b) shows the elongated basicranial muscle in *Qingmenodus* and coelacanth (based on *Latimeria*, from Bjerring 1972). Drawings not to scale.

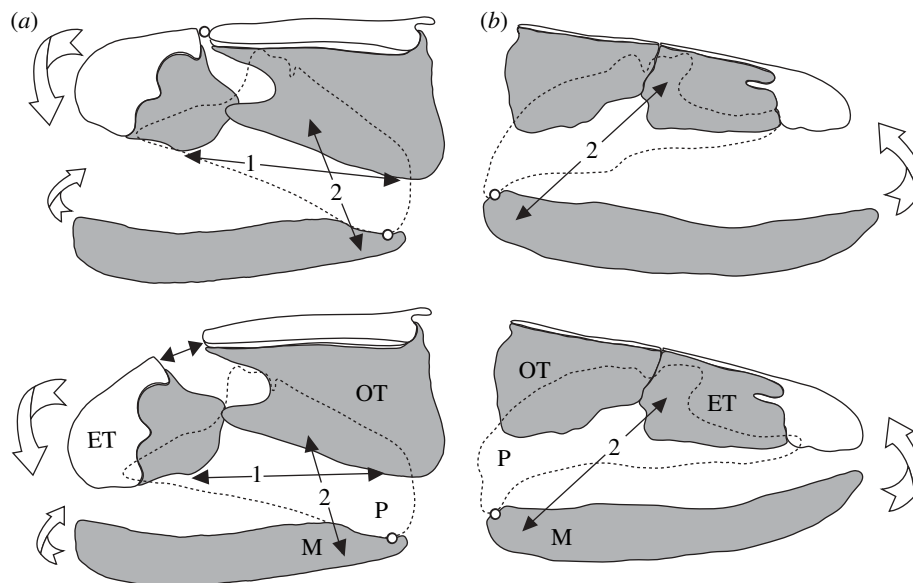


Figure 4. Two hypotheses of jaw-closing mechanism in sarcopterygian fishes. Solid circles represent the rotational joints. (a) Hypothesis of *Onychodus* (Andrews *et al.* 2006) jaw-closing mechanism, assuming that *Onychodus* possesses an elongated basicranial muscle as in *Qingmenodus*. The closing involves the adduction of the mandible and the movement of the intracranial joint (lowering of the snout), and is effected by the collaboration of the basicranial muscles (1) and adductor muscle (2). (b) Hypothesis of *Eusthenopteron* (Jarvik 1980) jaw-closing mechanism. The closing is mainly conducted by the contraction of adductor muscle (2). ET, ethmosphenoid; M, mandible; OT, otoccipital. Drawings not to scale.

inferred from the skull roof and available braincase material (Andrews *et al.* 2006). However, the condition of the basicranial muscle relating to the joint remains unknown, because the otoccipital in the best-known *O. jandemarrai* is not extensively ossified.

Here, we show for the first time the nearly complete structure of the otoccipital in onychodonts. *Qingmenodus* has the lengthened otic shelf with the posterior shift of the attachment for the basicranial muscle, which has

greatly increased the length of the basicranial muscle. This arrangement is quite similar to that in coelacanth, in which the basicranial muscle is lengthened by the anterior extension of the untoothed parasphenoid region and the posterior shift of the muscle (Forey 1991). Thus, we propose that the posterior shift of the attachment in *Qingmenodus* and coelacanth is a derived sarcopterygian feature (figure 3) and functions for more flexible intracranial joint in these taxa.

**(c) Feeding mechanism in onychodonts**

When analysing the jaw-closing mechanism of *Latimeria*, previous studies showed that the basicranial muscle in coelacanth plays an important role in mouth closing by executing movement at the intracranial joint (Thomson 1966, 1967; Alexander 1973; Lauder 1980; Forey 1991; 1998; Bernstein 2003; Levine *et al.* 2004). The similar arrangement of the basicranial muscle in *Qingmenodus* suggests the same function of the muscle as in *Latimeria*. Considering the length of the basicranial muscle relative to the total skull length, the basicranial muscle in *Qingmenodus* should be more powerful than that in coelacanth.

Andrews *et al.* (2006) discussed the unconstrained adductor muscle attachment and the mandibular articulation in *Onychodus*, and proposed that the flexible jaw apparatus is responsible for the powerful and highly kinetic biting in *Onychodus*. The available incomplete otoccipital of *Onychodus* does not provide any evidence about the arrangement of the basicranial muscle; however, its elongated postparietal shield, as in *Qingmenodus*, indicates a lengthening of the otoccipital. If *Onychodus* has its attachment area for the basicranial muscle on the posterior half of the otoccipital as *Qingmenodus* and coelacanth have, its putative well-developed basicranial muscle must play an important role in feeding through the movement of the intracranial joint (figure 4). Based on this assumption, the feeding mode proposed by Andrews *et al.* (2006) might be modified. We suggest that the rapid and powerful bite in *Onychodus*, the best representative of onychodonts, was achieved by the collaboration of the adductor muscle and the basicranial muscle. However, the jaw-opening mechanism in *Onychodus* needs further investigation (Andrews *et al.* 2006).

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**REFERENCES**

- Ahlberg, P. E. & Johanson, Z. 1998 Osteolepiformes and the ancestry of tetrapods. *Nature* **395**, 792–794. (doi:10.1038/27421)
- Ahlberg, P. E., Clack, J. A. & Lukševičs, E. 1996 Rapid braincase evolution between *Panderichthys* and the earliest tetrapods. *Nature* **381**, 61–64. (doi:10.1038/381061a0)
- Alexander, R. M. 1973 Jaw mechanisms of the coelacanth *Latimeria*. *Copeia* **1973**, 156–158. (doi:10.2307/1442379)
- Andrews, S. M. 1973 Interrelationships of crossopterygians. In *Interrelationships of fishes* (eds P. H. Greenwood, R. S. Miles & C. Patterson), pp. 137–177. London, UK: The Linnean Society of London, Academic Press.
- Andrews, S. M. 1985 Rhizodont crossopterygian fish from the Dinantian of Foulden, Berwickshire, Scotland, with a re-evaluation of this group. *Trans. R. Soc. Edinb. Earth Sci.* **76**, 67–95.
- Andrews, S. M., Long, J. A., Ahlberg, P. E., Barwick, R. & Campbell, K. 2006 The structure of the sarcopterygian *Onychodus jandemarraii* n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. *Trans. R. Soc. Edinb. Earth Sci.* **96**, 197–307.
- Bemis, W. E. & Northcutt, R. G. 1991 Innervation of the basicranial muscle of *Latimeria chalumnae*. *Environ. Biol. Fish.* **32**, 147–158. (doi:10.1007/BF00007450)
- Bernstein, P. 2003 The ear region of *Latimeria chalumnae*: functional and evolutionary implications. *Zoology* **106**, 233–242. (doi:10.1078/0944-2006-00119)
- Bjerring, H. C. 1967 Does a homology exist between the basicranial muscle and the polar cartilage? *Colloq. Intern. Centre Natl. Rech. Sci.* **163**, 223–267.
- Bjerring, H. C. 1972 The *nervus rarus* in coelacanthiform phylogeny. *Zoo. Scr.* **1**, 57–68. (doi:10.1111/j.1463-6409.1972.tb00569.x)
- Campbell, K. S. W. & Barwick, R. E. 2006 Morphological innovation through gene regulation: an example from Devonian Onychodontiform fish. *Int. J. Dev. Biol.* **50**, 371–375. (doi:10.1387/ijdb.052125kc)
- Chang, M.-M. 1982 *The braincase of Youngolepis, a Lower Devonian crossopterygian from Yunnan, South-Western China*. Stockholm, Sweden: University of Uppsala.
- Cloutier, R. & Ahlberg, P. E. 1996 Morphology, characters, and the interrelationships of basal sarcopterygians. In *Interrelationships of fishes* (eds M. L. J. Stiasny, L. R. Parenti & G. D. Johnson), pp. 445–479. San Diego, CA: Academic Press.
- Forey, P. L. 1991 *Latimeria chalumnae* and its pedigree. *Environ. Biol. Fish.* **32**, 75–97. (doi:10.1007/BF00007446)
- Forey, P. L. 1998 *History of the coelacanth fishes*. London, UK: Chapman & Hall.
- Friedman, M. 2007 *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *J. Syst. Palaeontol.* **5**, 289–343. (doi:10.1017/S1477201907002052)
- Gardiner, B. G. 1984 The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bull. Br. Mus. Nat. Hist. (Geol.)* **37**, 173–428.
- Hao, S.-G., Wang, D.-M. & Wang, Q. 2004 A new species of *Estinnophyton* from the Lower Devonian Posongchong Formation, Yunnan, China; its phylogenetic and palaeophytogeographical significance. *Bot. J. Linn. Soc.* **146**, 201–216. (doi:10.1111/j.1095-8339.2004.00327.x)
- Huxley, T. H. 1880 On the application of the laws of evolution to the arrangement of the vertebrata, and more particularly of the mammalia. *Proc. Zool. Soc. Lond.* **1880**, 649–661.
- Janvier, P. 1996 *Early vertebrates*. Oxford, UK: Oxford University Press.
- Jarvik, E. 1980 *Basic structure and evolution of vertebrates*, vol. 1. London, UK: Academic Press.
- Jessen, H. L. 1966 Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischem und europäischem *Onychodus*-material. *Arkiv. Zool.* **18**, 305–389.
- Jessen, H. L. 1980 Lower Devonian Porolepiformes from the Canadian Arctic with special reference to *Powichthys thorstheimsoni* Jessen. *Palaeontographica A* **167**, 180–214.
- Johanson, Z. & Ahlberg, P. E. 1998 A complete primitive rhizodontid from Australia. *Nature* **394**, 569–572. (doi:10.1038/29058)
- Johanson, Z. & Ahlberg, P. E. 2001 Devonian rhizodontids and tristichopterids (Sarcopterygii; Tetrapodomorpha) from East Gondwana. *Trans. R. Soc. Edinb. Earth Sci.* **92**, 43–74. (doi:10.1017/S0263593300000043)

- Johanson, Z., Long, J. A., Talenet, J. A., Janvier, P. & Warren, J. W. 2007 New onychodontiform (Osteichthyes; Sarcopterygii) from the Lower Devonian of Victoria, Australia. *J. Paleontol.* **81**, 1031–1043. (doi:10.1666/pleo05-023.1)
- Lauder, G. V. 1980 The role of the hyoid apparatus in the feeding mechanism of the coelacanth *Latimeria chalumnae*. *Copeia* **1**, 1–9. (doi:10.2307/1444128)
- Levine, R. P., Monroy, J. A. & Brainerd, E. L. 2004 Contribution of eye retraction to swallowing performance in the northern leopard frog, *Rana pipiens*. *J. Exp. Biol.* **207**, 1361–1368. (doi:10.1242/jeb.00885)
- Liao, W.-H., Xu, H.-K. & Wang, C.-Y. 1978 The subdivision and correlation of the Devonian stratigraphy of S.W. China. *Symp. Devonian System of South China*, pp. 193–213. Beijing, China: Geological Publishing House.
- Long, J. A. 1989 A new rhizodontiform fish from the Early Carboniferous of Victoria, Australia, with remarks on the phylogenetic position of the group. *J. Vert. Palaeontol.* **9**, 1–17.
- Long, J. A. 2001 On the relationships of *Psarolepis* and the onychodontiform fishes. *J. Vert. Palaeontol.* **21**, 815–820. (doi:10.1671/0272-4634(2001)021[0815:OTROPA]2.0.CO;2)
- Long, J. A., Campbell, K. S. W. & Barwick, R. E. 1997 Osteology and functional morphology of the osteolepiform fish *Goganasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia. *Recs. W. A. Mus. Suppl.* **53**, 1–89.
- Nelson, G. J. 1970 Subcephalic muscles and intracranial joints of sarcopterygian and other fishes. *Copeia* **3**, 468–471. (doi:10.2307/1442274)
- Newberry, J. S. 1857 New fossil fishes from the Devonian rocks of Ohio. *Am. J. Sci. Ser. 2* **24**, 147–149.
- Northcutt, R. G. & Bemis, W. E. 1993 Cranial nerves of the coelacanth, *Latimeria chalumnae* (Osteichthyes, Sarcopterygii, Actinistia), and comparisons with other Craniata. *Brain Behav. Evol.* **42**(Suppl. 1), 1–76.
- Romer, A. S. 1955 Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? *Nature* **176**, 126. (doi:10.1038/176126a0)
- Schultze, H.-P. 1973 Crossopterygier mit heterozeker Schwanzflosse aus dem Oberdevon Kanadas, nebst einer Beschreibung von Onychodontida-Resten aus dem Mitteldevon Spaniens und aus dem Karbon der USA. *Palaeontogr. Abt. A* **143**, 188–208.
- Schultze, H.-P. 1987 Dipnoans as sarcopterygians. In *The biology and evolution of lungfishes*, *J. Morphol. Suppl.* **1** (eds W. E. Bemis, W. W. Burggren & N. E. Kemp), pp. 39–74. New York, NY: Alan R. Liss Inc.
- Swofford, D. L. 2003 *PAUP\*: Phylogenetic Analysis Using Parsimony (\*and other methods)*, Version 4.0b10. Sunderland, MA: Sinauer Associates.
- Thomson, K. S. 1966 Intracranial mobility in the coelacanth. *Science* **153**, 999–1000. (doi:10.1126/science.153.3739.999)
- Thomson, K. S. 1967 Mechanisms of intracranial kinetics in fossil rhipidistian fishes (Crossopterygii) and their relatives. *Zool. J. Linn. Soc.* **46**, 223–253. (doi:10.1111/j.1096-3642.1967.tb00505.x)
- Upeniece, I. 1995 A new species of *Strunius* (Sarcopterygii, Onychodontida) from Latvia, Lode Quarry (Upper Devonian). *Geobios* **19**, 281–284. (doi:10.1016/S0016-6995(95)80127-8)
- Woodward, A. S. 1891 *Catalogue of the fossil fishes in the British Museum (Natural History). Part II*. London, UK: British Museum (Natural History).
- Young, G. C. & Schultze, H.-P. 2005 New osteichthyans (bony fishes) from the Devonian of Central Australia. *Mitt. Mus. Nat.kd. Berl. Geowiss. Reihe* **8**, 13–35. (doi:10.1002/mmng.200410002)
- Young, G. C., Long, J. A. & Ritchie, A. 1992 Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Rec. Aust. Mus. Suppl.* **14**, 1–77.
- Yu, X.-B. 1998 A new porolepiform-like fish, *Psarolepis romeri* gen. et sp. nov. (Sarcopterygii, Osteichthyes) from the Lower Devonian of Yunnan, China. *J. Vert. Paleontol.* **18**, 261–274.
- Zhu, M. & Janvier, P. 1994 Un onychodontide (Vertebrata, Sarcopterygii) du Dévonien inférieur de Chine. *Compt. Rend. Sci., Ser. II* **319**, 951–956.
- Zhu, M. & Schultze, H.-P. 1997 The oldest sarcopterygian fish. *Lethaia* **30**, 293–304.
- Zhu, M. & Schultze, H.-P. 2001 Interrelationships of bony osteichthyans. In *Major events in early vertebrate evolution: palaeontology, phylogeny and development* (ed. P. E. Ahlberg), pp. 289–314. London, UK: Taylor & Francis.
- Zhu, M. & Yu, X.-B. 2002 A primitive fish close to the common ancestor of tetrapods and lungfish. *Nature* **418**, 767–770. (doi:10.1038/nature00871)
- Zhu, M. & Yu, X.-B. 2004 Lower jaw character transitions among major sarcopterygian groups—a survey based on new materials from Yunnan, China. In *Recent advances in the origin and early radiation of vertebrates* (eds G. Arratia, M. V. H. Wilson & R. Cloutier), pp. 271–286. Munich, Germany: Dr Friedrich Pfeil.
- Zhu, M., Yu, X.-B. & Janvier, P. 1999 A primitive fossil fish sheds light on the origin of bony fishes. *Nature* **397**, 607–610. (doi:10.1038/17594)
- Zhu, M., Yu, X.-B. & Ahlberg, P. E. 2001 A primitive sarcopterygian fish with an eyestalk. *Nature* **410**, 81–84. (doi:10.1038/35065078)
- Zhu, M., Yu, X.-B., Wang, W., Zhao, W.-J. & Jia, L.-T. 2006 A primitive fish provides key characters bearing on deep osteichthyan phylogeny. *Nature* **441**, 77–80. (doi:10.1038/nature04563)
- Zhu, M., Zhao, W.-J., Jia, L.-T., Lu, J., Qiao, T. & Qu, Q.-M. 2009 The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature* **458**, 469–474. (doi:10.1038/nature07855)