The posterior cranial portion of the earliest known Tetrapodomorph Tungsenia paradoxa and the early evolution of tetrapodomorph endocrania (postprint)

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Abstract

Here the posterior cranial portion of the tetrapodomorph Tungsenia from the Lower Devonian (Pragian, ~409 million years ago) of Yunnan, southwest China, is reported for the first time. The pattern of posterior skull roof and the morphology of the otoccipital region of the neurocranium are described in detail, providing precious insight into the combination of cranial characters of the earliest known tetrapodomorph to date. The posterior cranium of Tungseniadisplays a mosaic of features previously linked either to basal dipnomorphs such as Youngolepis(e.g., the well-developed subjugular ridge, the strong adotic process, and the poorly developed fossa bridgei) or to typical tetrapodomorphs (e.g., the lateral dorsal aortae commenced from the median dorsal aorta postcranially). The independent ventral arcual plate is also found in the advanced tetrapodomorph Eusthenopteron. The new endocranial material of Tungsenia further fills in the morphological gap between Tetrapodomorpha (tetrapod lineage) and Dipnomorpha (lungfish lineage) and unveils the sequence of character acquisition during the initial diversification of the tetrapod lineage. The new phylogenetic analysis strongly supports the basalmost position of Tungsenia amongst the tetrapod lineage.

Full Text

Preamble

The Posterior Cranial Portion of the Earliest Known Tetrapodomorph Tungsenia paradoxa and the Early Evolution of Tetrapodomorph Endocrania

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Abstract

Here we report for the first time the posterior cranial portion of the tetrapodomorph Tungsenia from the Lower Devonian (Pragian, ~409 million years ago) of Yunnan, southwest China. The pattern of the posterior skull roof and the morphology of the otoccipital region of the neurocranium are described in detail, providing valuable insight into the combination of cranial characters present in the earliest known tetrapodomorph to date. The posterior cranium of Tungsenia displays a mosaic of features previously linked either to basal dipnomorphs such as Youngolepis (e.g., the well-developed subjugular ridge, strong adotic process, and poorly developed fossa bridgei) or to typical tetrapodomorphs (e.g., the lateral dorsal aortae branching from the median dorsal aorta postcranially). The independent ventral arcual plate is also found in the advanced tetrapodomorph Eusthenopteron. This new endocranial material of Tungsenia further fills the morphological gap between Tetrapodomorpha (tetrapod lineage) and Dipnomorpha (lungfish lineage) and reveals the sequence of character acquisition during the initial diversification of the tetrapod lineage. New phylogenetic analysis strongly supports the basalmost position of Tungsenia among the tetrapod lineage.

Key words: Yunnan, Early Devonian, Sarcopterygii, Tetrapodomorpha, endocranial character transition

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1 Introduction

Tetrapodomorpha, also known as the tetrapod lineage or tetrapod total group, includes all representatives more closely related to living tetrapods than to living lungfishes (Ahlberg, 1991). Hitherto, only two undisputed Early Devonian stem-tetrapods were known: Kenichthys and Tungsenia from Yunnan, China (Chang and Zhu, 1993; Zhu and Ahlberg, 2004; Lu et al., 2012). However, the otoccipital region of these two early representatives has never been described due to insufficient material (Chang and Zhu, 1993; Zhu and Ahlberg, 2004; Lu et al., 2012). The recent discovery of the oldest known tetrapodomorph fish, Tungsenia, provides unique information that improves our understanding of the origin and early evolution of the tetrapod lineage, based on well-preserved anterior cranial region (ethmosphenoid shield), lower jaws, and cheek bones (Lu et al., 2012). Nevertheless, our knowledge of the posterior cranial portion (otoccipital shield) of Tungsenia and the early evolution of this region in the tetrapod lineage remains limited due to the scarcity of known fossils.

During fieldwork conducted from 2011–2015, we collected additional Tungsenia cranial materials from the same site, including a well-preserved posterior cranial portion (IVPP V 15132.50). This new posterior cranial material possesses fine pores on the skull roof, and its size is comparable to the anterior cranial portion of Tungsenia. Based on shared ornamentation and comparable size with the reported anterior cranial portions, we assigned the new posterior cranial portion to Tungsenia.

After preparation, we found that the posterior cranial portion of Tungsenia resembles that of Youngolepis in having a well-developed subjugular ridge and adotic process (Chang, 1982), while other endocranial features are quite similar to those of ‘osteolepids’ . This combination of characters sheds light on the early evolution of the tetrapod lineage.

2 Materials and Methods

All specimens of Tungsenia are housed in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China (IVPP). The specimen was mechanically prepared to remove rock matrix.

High-resolution computed tomography: The posterior cranial portion (IVPP V 15132.50) was scanned at IVPP using 225 kV microCT. The specimen was scanned with a beam energy of 180 kV and a flux of 100 mA at a detector resolution of 7.4 m per pixel, using a 1440° rotation with a step size of 0.25° and an unfiltered aluminum reflection target. A total of 1440 transmission images were reconstructed in a 2048 × 2048 matrix of 1536 slices.

Scan data were analyzed using Mimics v.18.01 (http://biomedical.materialise.com/mimics; Materialize). The CT data, as well as 3D surface files of the posterior cranial portion (V 15132.50), are available in the IVPP Digital data repository AD-Morph <Archives of Digital Morphology, http://dx.doi.org/10.12112/F.12>.

Phylogenetic analysis: The phylogenetic analysis was performed on a matrix of 263 characters scored for 38 taxa (see online supplementary appendix 3; taxon-by-character matrix). All characters were treated as unordered and weighted equally. The resulting data matrix was subjected to parsimony analysis in PAUP* (version 4.0b10) (Swofford et al., 2001) using a heuristic search, with Guiyu, Psarolepis, and Achoania (basal osteichthyans) specified as the outgroup. The analysis generated 24 most parsimonious trees (MPTs) with 581 steps (Consistency index (CI) = 0.5232; Homoplasy index (HI) = 0.4768; Retention index (RI) = 0.7247; Rescaled consistency index (RC) = 0.3792). All trees show Tungsenia as the most basal stem-tetrapod. The strict consensus tree highlights the poor phylogenetic resolution of the lower part of the tetrapodomorph lineage.

3 Systematics

Osteichthyes Huxley, 1880
Sarcopterygii Romer, 1955
Tetrapodomorpha Ahlberg, 1991 (= total group Tetrapoda)
Tungsenia Lu et al., 2012
Tungsenia paradoxa (Lu et al., 2012)

Holotype: IVPP V 10687, an anterior cranial portion.
Type locality and horizon: Zhaotong, Yunnan Province, China; Posongchong Formation (Pragian, Early Devonian).
New material: IVPP V 15132.50, a posterior cranial portion.
Locality and horizon: The same as type locality and horizon.

Diagnosis (emended): The posterior cranial portion (otoccipital or postparietal shield) is as long as it is wide; W-shaped postparietals extend much further posteriorly than the tabulars; the tabulars turn down anterolaterally, forming the inner margin of the spiracular slit; the extratemporals are large; the basicranial fenestra is large; the ventral fenestra is present, with well-developed subjugular ridge; a notch for the middle process of median extrascapular is present; the posterior dorsal fontanelle is present; the fossa bridgei is poorly developed.

Description: The posterior cranial portion of Tungsenia (IVPP V 15132.50) is well-preserved except for the broken left anterior part of the shield (Figs. 1-3). The length of the shield is about 8 mm, and is basically equal to its width. In dorsal view, the dermal skull roof is covered with a continuous layer of cosmine, and the sutures between the postparietals and the marginal bones of the skull roof (supratemporals, temporals, and tabulars) cannot be traced. The typical anterolateral overlapped area for the postorbital plate of the anterior cranial portion in tetrapodomorphs has not been observed due to incomplete preservation. The posterior edge of the skull roof is well-preserved, showing a curved embayment in the mesial part of the postparietals that may indicate the outline of the anterior margin of the median extrascapular. The tabular and the outer part of the postparietal have a slit in the edge of the bone; the lip below the slit extends posteriorly to form a shelf for articulation of the lateral extrascapulars. A distinct posterolateral protruding corner suggests the presence of an extratemporal, which is common in 'osteolepiforms' (Jarvik, 1948). This extratemporal, if present, is fused with the tabular and thus strongly supports the hypothesis that the extratemporal is part of the skull table, rather than an element of the hyoid area. The pores of the otic branch of the main sensory canal indicate that the course of the lateral line canal passes through the marginal bones of the skull roof. However, it should be noted that the lateral line sensory canal passes through the lateral margin of the extratemporal, which differs from other known sarcopterygians in which the sensory canal passes through the tabular. No pore cluster or pit-line has been found in the dermal skull roof.

In ventral view, the otoccipital region of Tungsenia is composed of two main elements: the basicranial fenestra (bs.fn, Figs. 1B, 2B) and the otoccipital ossification (Figs. 1, 2). The basicranial fenestra is oblong in outline and occupies about half of the whole length of the otoccipital region. Anteriorly, it is bounded by the posteroventral parts of the ethmosphenoid below the notochordal pit. Laterally, the fenestra reaches the medial margin of the anteroventral articular process of the otoccipital and of the otic shelf (ot.sh, Fig. 2B), while posteriorly its extension is delimited by the independent ventral arcual plate, which lies anterior to the otoccipital ossification. The ventral margin of the otic shelf is not fully preserved, so the natural shape of the otic shelf remains unclear. The lateral commissure continues with the otic shelf, extending laterally to the skull roof. The facets for hyomandibular articulation are not well shown due to poor preservation. An independent arched ventral arcual plate is present anterior to the otoccipital, and the suture between the ventral arcual plate and the otoccipital is well defined. The otoccipital is of polygonal, symmetrical shape and represents a single stout basicranial plate immediately behind the ventral arcual plate. A paired longitudinal groove for the dorsal aorta (gr.a.dl, Figs. 2B, 3B) is obvious at the posterolateral margin. At the same level as the ventral arcual plate, a large vestibular fontanelle (v.font, Fig. 2B) is present on the lateral braincase wall. A well-developed subjugular ridge (r.sub, Figs. 2B, 3) forms the lateral and posterior boundary for the vestibular fontanelle. The adotic process (pr.ad, Fig. 3) is situated at the end of the subjugular ridge, posterolateral to the otic capsule, as in Youngolepis (Chang, 1982). Based on its relative position to the vestibular fontanelle, the subjugular ridge corresponds to the jugular ridge in Eusthenopteron, and the adotic process could be compared to the areas articulating with branchial arches in Eusthenopteron (Jarvik, 1980).

The dorsal margin of the jugular groove is bounded by a suprajugular ridge, as in Youngolepis. Due to preservation limitations, the foramina for nerves or vessels in the otoccipital region are not visible.

In posterior view, the specimen is deformed along the right axis. The dorsomedian part of the posterior face of the otoccipital has a large foramen representing the posterior dorsal fontanelle (pdf, Fig. 3B, D), a structure commonly present in osteichthyans (Chang, 1982; Yu, 1998; Zhu and Yu, 2002; Lu et al., 2016, 2017; Clement et al., 2018). Lateral to the posterior dorsal fontanelle are well-defined paired depressions called fossa tectosynotica (f.tect, Fig. 3). The poorly developed fossa bridgei (f.br, Fig. 3) lies lateral to the fossa tectosynotica. The fossa bridgei and fossa tectosynotica are separated by a short ridge. The occipitalis lateralis fissure, indicating the boundary between the otic and occipital regions, could not be traced. The suture between the notochordal canal (nc, Fig. 3) and the foramen magnum (fm, Fig. 3) is not visible.

4.1 Phylogenetic Implications of Tetrapodomorph Evolution

To re-examine the phylogenetic position of Tungsenia in light of the new morphological data, we conducted phylogenetic analysis using a modified data matrix from Lu et al. (2012) (see online supplementary appendix 1). Our parsimony analysis recovers 12 trees with a length of 581 steps (Fig. 4) (character optimization for a single MPT given in online supplementary appendix 2). Our result shows Tungsenia is consistently resolved as the basalmost stem tetrapod and shares with other tetrapodomorphs the following unambiguous characters:

1. The exit of the pituitary vein situated in front of the basipterygoid (Ch. 50, code 0) represents a derived arrangement for the tetrapod lineage. In other sarcopterygians (e.g., Styloichthys, Youngolepis), the pituitary vein foramen lies dorsal to the basipterygoid process.
2. In tetrapodomorphs, accessory fenestration in the otic capsule is absent (Ch. 62, code 0). Accessory fenestration is present in Styloichthys, coelacanths, the onychodont Qingmenodus, and basal dipnomorphs.
3. The parasymphysial tooth whorl is a feature of non-tetrapodomorph sarcopterygians. In tetrapodomorphs, the parasymphysial plate bears either a tooth pavement or paired tusks (Ch. 139, code 1).
4. In tetrapodomorphs, the anterior mandibular (precoronoid) fossa is widely present (Ch. 161, code 1).
5. The otic and supraorbital canals are in contact in the tetrapod lineage through the dermal demosphenoid bone (Ch. 183, code 1).

Previous to the discovery of Tungsenia, the tetrapodomorph clade was supported by the following characters:

1. The absence of internasal pits (Ch. 40). Tungsenia is the only known tetrapodomorph with paired internasal pits. Usually, an unpaired prenasal pit is present in the snout region of tetrapodomorphs.
2. The intracranial joint running through the profundus foramen (Ch. 55). In Tungsenia and some basal dipnomorphs, such as Powichthys, the profundus foramen lies in front of the intracranial joint.
3. Posttemporal fossae present (Ch. 67). The posttemporal fossa is poorly developed in Tungsenia and in the basal dipnomorph Youngolepis.
4. Parasphenoid slender and splint-shaped (Ch. 96). The shape of the parasphenoid in Tungsenia is quite different compared with other

tetrapodomorphs. A broad parasphenoid is present in Tungsenia and other primitive sarcopterygians.

5. Lateral sides of the parasphenoid converging anteriorly (Ch. 97). The lateral sides of the parasphenoid in Tungsenia are similar to those of Styloichthys and basal dipnomorphs (e.g., Youngolepis, Powichthys), being parallel or slightly diverging anteriorly.

The strict consensus tree shows that the 'lower part' of the tetrapodomorph lineage—formed by a heterogeneous group traditionally referred to as 'osteolepiforms' —remains significantly problematic. The evolutionary relationships among the four 'osteolepiform' groups (i.e., osteolepids, megalepids, canowindrids, and tristichopterids) remain unresolved as a polytomy due to insufficient information, particularly from key taxa representing early diverging members of these groups. Many known 'osteolepiform' representatives are entirely restricted to the Middle-Late Devonian. The rhizodonts surveyed in the current analysis appear stable in the second basalmost position of the lineage. However, it is still worth noting that the anatomical similarities between rhizodonts and advanced representatives of the tetrapodomorph lineage should not be underestimated and indicate the possibility that the group might occupy a much higher position in the tree (Zhu et al., 2017).

Hitherto, only two undisputed Early Devonian tetrapodomorph fishes were known (Chang and Zhu, 1993; Zhu and Ahlberg, 2004; Lu et al., 2012). This apparent low diversity is now augmented by the Australian Early Devonian tetrapodomorph 'Gyroptychius?' australis (Young and Gorter, 1981), which shares some unique features with Kenichthys (Chang and Zhu, 1993). In addition, numerous new tetrapodomorph fishes from the Early-Middle Devonian have been found in Hatchery Creek, New South Wales, Australia, but have never been properly described (Hunt and Young, 2012). Further investigations into the early representatives from both China and East Gondwana (Australia-Antarctica) will help resolve ancestral conditions for tetrapod origins.

4.2 Endocranial Evolution in Tetrapodomorphs

The endocranium is one of the most important components of the body plan, and more than 70% of characters in previous phylogenetic analyses are related to cranial features. However, due to the lack of primitive tetrapodomorph material, our understanding of endocranial evolution in the tetrapod lineage remains obscure. The discovery of Tungsenia, the basalmost and oldest known tetrapodomorph, provides a unique opportunity to investigate endocranial evolution at the initial stage of the tetrapod lineage.

The endocranium of Tungsenia shares many features with Youngolepis (Chang, 1982), as well as to a lesser extent with Styloichthys (Zhu and Yu, 2002) and Powichthys (Jessen, 1980), such as the ventrally opened anterior nostril; presence of paired internasal cavities; elongate and broad parasphenoid that is parallel or slightly diverging anteriorly; vomers separated by the parasphenoid; attachment for the basicranial muscle covered by the parasphenoid, which cannot be seen in ventral view; broad orbital tectum; and well-developed basipterygoid.

Furthermore, the typical crista suspendens is poorly developed in Tungsenia, which differs from the well-developed crista suspendens in other tetrapodomorphs (e.g., Kenichthys, Gogonasus, Osteolepis, Meglichthys) (Thomson, 1964; Fox et al., 1995; Lebedev, 1995; Long et al., 1997; Zhu and Ahlberg, 2004; Borgen and Nakrem, 2016). The similarity between Tungsenia and other tetrapodomorph fishes lies in the opening of the pituitary vein, which is situated at the base of the basipterygoid (Coates and Friedman, 2010). However, the exit for the profundus nerve in Tungsenia opens in the posterior part of the ethmosphenoid region, recalling the condition in Youngolepis. It is worth mentioning that the parasphenoid in Tungsenia, Styloichthys, Youngolepis, and some basal tetrapodomorphs (e.g., Kenichthys and an undescribed Early Devonian tetrapodomorph from Australia) extends posteriorly, reaching the ventral opening of the notochord canal and covering the attachment for the basicranial muscle (Chang, 1982; Zhu and Yu, 2002; Zhu and Ahlberg, 2004; Hunt and Young, 2012).

Although a large basicranial fenestra is present in Tungsenia, the general features of the otoccipital region agree quite well with those of Youngolepis, such as the well-developed subjugular ridge, strong adotic process situated at the end of the subjugular ridge, and poorly developed fossa bridgei (Chang, 1982). On the other hand, Tungsenia agrees with other tetrapodomorphs in that the lateral dorsal aortae emerge from the median dorsal aorta postcranially, so the impression for the median dorsal aorta is not preserved on the ventral side of the occipital unit (Long et al., 1997). An independent ventral arcual plate is also seen in Eusthenopteron (Jarvik, 1980).

It is remarkable that Tungsenia displays more primitive rather than advanced features in the endocranium, indicating that the tetrapodomorph endocranium retains the primitive condition present at the initial stage of tetrapod evolution. The major endocranial modifications characteristic of the tetrapod lineage, such as elongation of the olfactory tract, anterior-posterior positioning of pineal and parapineal organs, anteriorly converging sword-like parasphenoid, well-developed crista suspendens, and well-developed fossa bridgei, occurred later, after the Pragian stage of the Devonian period (Jarvik, 1980; Zhu and Ahlberg, 2004).

5 Conclusion

The posterior cranial portion of Tungsenia provides unique evidence for understanding otoccipital region evolution in the tetrapod lineage, and the new data strongly support the basalmost position of Tungsenia among tetrapodomorphs. However, the phylogenetic relationships of the lower part of the tetrapod lineage remain poorly resolved. Further investigations into early representatives from both China and East Gondwana (Australia–Antarctica) will help resolve ancestral conditions for tetrapod origins.

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Note: Figure translations are in progress. See original paper for figures.