A new tetrapodomorph specimen from the Middle Devonian of Qujing, Yunnan, China

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Abstract

Tetrapodomorphs include all terrestrial vertebrates and their closest fish relatives. The oldest and most primitive tetrapodomorphs currently known are from the Early Devonian of South China, indicating that South China was the center of origin of the tetrapod lineage. However, the phylogenetic relationships among early members of this lineage, especially those of "osteolepiforms" (i.e., Osteolepidae), remain unclear. This paper describes a new tetrapodomorph specimen from the Middle Devonian Zhujiangyuan Scenic Area of Qujing, Yunnan, China. The material includes two anterior cranial portions and a lower jaw, with an overall morphology similar to that of the Wuding tetrapodomorph from the Middle Devonian of Wuding, Yunnan. High-resolution computed tomography (HRCT) reveals that the dermal surfaces of the skull roof and lower jaw of this specimen are extremely similar to those of the Wuding tetrapodomorph. In contrast, the neurocranial anatomy of this specimen differs from that of other tetrapodomorphs, particularly in the morphology of the parasphenoid and the position of the buccohypophyseal foramen. Phylogenetic analysis indicates that the new specimen may represent a possible sister group of the Wuding tetrapodomorph, whereas the relationships among "osteolepiforms" remain unclear. To further evaluate morphological variation and evolutionary relationships among osteolepiforms, a principal component analysis (PCA) was conducted on the morphology of the parietal shield of "osteolepiforms," including representatives of Osteolepidae, Canowindridae, and Megalichthyidae. The PCA results are consistent with the phylogenetic analysis, placing the new specimen near the Wuding tetrapodomorph. The new tetrapodomorph material from the Middle Devonian of the Zhujiangyuan Scenic Area provides new insights into the early evolution of the tetrapod lineage.

Full Text

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A new tetrapodomorph specimen from the Middle Devonian of Qujing, Yunnan, China

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Abstract Tetrapodomorpha comprises all terrestrial vertebrates and their closest fish relatives. The oldest and most basal tetrapodomorphs are known from the Early Devonian of South China, suggesting that South China was a center for the origin of the tetrapod lineage. However, the phylogenetic relationships among early members of the lineage, particularly "osteolepids" (that is equivalent to Osteolepididae), remain poorly resolved. Here we describe a new tetrapodomorph specimen from the Middle Devonian Pearl River Source Scenic Area, Qujing, Yunnan, China. The material includes two anterior cranial portions and a lower jaw, which show overall similarity to *Thursius wudingensis* from the Middle Devonian of Wuding, Yunnan. High-resolution computed tomography (HRCT) reveals that the skull roof and dermal surface of the lower jaw of the material closely resemble those of *T. wudingensis*. In contrast, the neurocranial anatomy of the new material differs from those of other *Thursius*, especially in the morphology of the parasphenoid and the position of the buccohypophyseal foramen. Phylogenetic analysis recovers the new material as a possible sister taxon to *T. wudingensis*, while the interrelationships of "osteolepids" remain poorly resolved. To further assess the morphological variation and evolutionary relationship among the osteolepiforms, a principal component analysis (PCA) of parietal shield morphology for "osteolepiforms" was conducted, including representatives of Osteolepididae, Canowindridae, and Megalichthyidae. The PCA results are consistent with the phylogenetic analysis, placing the new material in close proximity to *T. wudingensis*. The new tetrapodomorph material from the Middle Devonian of the Pearl River Source Scenic Area provides new insights into the early evolution of the tetrapod lineage.

Key words South China, Middle Devonian, Tetrapodomorpha, Osteolepiformes, phylogeny, morphometrics

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1 Introduction

Tetrapodomorpha, the sarcopterygian lineage leading to tetrapods, comprises "Osteolepiformes" , Rhizodontida, Panderichthyidae, and Tetrapoda (Ahlberg, 1991). Among these, "osteolepiforms" represent the dominant tetrapodomorph

Fig. 1 Geological setting of Pearl River Source Scenic Area, Qujing, China. A. regional geological map; B. the fish-bearing lithological column

Figure 1: Fig. 1 Geological setting of Pearl River Source Scenic Area, Qujing, China. A. regional geological map; B. the fish-bearing lithological column

assemblage during the Middle Devonian (Long et al., 2018). However, phylogenetic relationships within this grade remain poorly resolved, particularly among "osteolepids" (Ahlberg and Johanson, 1998). A major limitation underlying this uncertainty is the scarcity of well-preserved Middle Devonian material with informative internal anatomy, especially from key regions such as South China. The earliest and most basal tetrapodomorphs, *Tungsenia* and *Kenichthys* from the Early Devonian of South China, indicate that South China played a crucial role in the early evolution of the tetrapod lineage (Chang and Zhu, 1993; Zhu and Ahlberg, 2004; Lu et al., 2012). In contrast, Middle Devonian tetrapodomorph fossils from China remain scarce and are mostly known from dermal remains. To date, *Thursius wudingensis* (Fan, 1992) from Wuding, Yunnan Province is the only well-recognized taxon from China. Although *T. wudingensis* preserves abundant dermal cranial elements, its neurocranial anatomy and internal structures remain poorly known, limiting assessment of its phylogenetic position.

Here we report new tetrapodomorph specimens from the Middle Devonian of Pearl River Source Scenic Area of Qujing, South China. The dermal surface of the skull roof and lower jaw of the new material closely resemble those of *T. wudingensis*. However, high-resolution computed tomography (HRCT) reveals the internal anatomical features that differ from those of previously described *Thursius*, particularly in the configuration of the braincase.

To clarify the phylogenetic position of the new material, we conducted a phylogenetic analysis of the "osteolepiforms" . In addition, a principal component analysis (PCA) of skull roof morphology was performed to quantify morphometric variation among osteolepiforms. Together, these analyses provide new data on internal cranial anatomy and offer further insights into the phylogenetic relationships and morphological diversification of Middle Devonian tetrapodomorphs.

2 Geological setting

The new tetrapodomorph material was collected from a purplish-red silty mudstone in the Xichong Formation (also known as 'Haikou' Formation, representing the same stratigraphic unit under different names, Givetian, Middle Devonian) at Locality 4 (25.91°N, 103.82°E), Pearl River Source Scenic area, Qujing, Yunnan Province (Fig. 1). The same horizon also yields placoderm and sarcopterygian fossils, such as *Xichonolepis qujingensis*, *Dianolepis liui* and *T. wudingensis* (Zhao and Zhu, 2010, Xian et al., 2025).

Fig. 1 Geological setting of Pearl River Source Scenic Area, Qujing, China

A. regional geological map; B. the fish-bearing lithological column
Abbreviations: D_1x. Xishancun Formation; D_1xl. Lower Member of the Xishancun Formation; D_1xt. Upper Member of the Xishancun Formation; D_2h. Haikou Formation; D_3zg. Zaige Formation; S_3m. Miaokao Formation; S_3y. Yulungssu Formation; Q_c^{al}. Quaternary alluvial deposits

3 Materials and methods

3.1 Material

Two parietal shields (IVPP V34447, V34448) and one mandible (V34449) (Fig. 2) from the Xichong Formation (Givetian, Middle Devonian) of Qujing, Yunnan, China. V34447 preserves well-developed internal cranial structures, revealed by HRCT data, whereas V34448 primarily preserves external dermal morphology. The mandible, V34449, retains both external surface features and limited internal anatomical information. All specimens are housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP).

3.2 Methods

3.2.1 High-resolution CT scanning

The anterior cranial portion (V34447) was scanned using a high-resolution micro-CT system (225 micro-CT) at the Key Laboratory of Vertebrate Evolution and Human Origins, IVPP, with a beam energy of 130 kV and a flux of 150 mA at a detector resolution of 7.981 μm per pixel, and the lower jaw (V34449) was scanned with a beam energy of 135 kV and a flux of 100 mA at a detector resolution of 6.007 μm per pixel. The three-dimensional reconstructions were created in the Mimics (v19.0) software. The images of the reconstructions were exported

from Mimics and VG Studio Max (v2.0) and the three-dimensional surface data were rendered using Vayu (v1.1) (Lu, 2023).

3.2.2 Phylogeny

We performed a phylogenetic analysis based on a matrix comprising 204 morphological characters across 47 taxa, modified from Choo et al. (2024). We coded the characters using the dataset of Choo et al. (2024), based on Cloutier et al. (2020). All characters were treated as unordered and equally weighted. Character coding and matrix assembly were carried out using Mesquite (v.3.8.1), and the final data matrix is provided in Supplementary File 2 as a NEXUS (.nex) file. The outgroup included the basal dipnomorphs, *Youngolepis*, *Diabolepis*, *Powichthys*, *Porolepis*, and *Glyptolepis*. Parsimony analysis was conducted in TNT (v.1.6).

Fig. 2

Figure 2: Fig. 2

3.2.3 Geometric morphometrics

To investigate the shape variation of the parietal shield region among tetrapodomorphs, particularly in "osteolepiforms" , 21 parietal shields were sampled for geometric morphometric analysis. 31 landmarks were digitized using the software tpsDig2 (Supplementary File 3), including Type I (anatomically homologous points), Type II (points with some biological meaning defined geometrically), and semi-landmarks (points along curves representing the ethmoidal margin) (Zelditch et al., 2012; Ferrón et al., 2020). Procrustes superimposition and principal component analysis (PCA) were subsequently performed in PAST (Hammer et al., 2001) (Supplementary File 4).

Semi-landmarks were allowed to slide along their respective curves to minimize Procrustes distance, ensuring that shape variation was captured while reducing the influence of arbitrary landmark placement. Due to bilateral symmetry in the data and frequent preservation

Fig. 2 Photographs of osteolepid gen. et sp. indet. from the Middle Devonian of China. A, B. parietal shields IVPP V34447 (A) and V34448 (B) in dorsal views; C. the lower jaw V34449 in external view. Scale bars = 5 mm

of only one well-defined side, specimens underwent mirror imaging before landmark digitization.

31 landmarks were defined, their descriptions and locations are illustrated and described in Supplementary File 1. Type I Landmarks: Landmark 2-5, the subnarial corner and the preorbital corner; Landmark 6 and 7, the postorbital corner; Type II Landmarks: Landmark 1, the most anterior point of the ethmoidal shield; Landmark 11 and 12, the most anterior and most posterior medial points of the pineal foramen; Landmark 10, the middle point of the posterior margin of frontal; Landmark 8 and 9, the most posterior point of the ethmoidal shield; Semi-Landmarks: Landmark 13-31, situated between Type I and Type II Landmarks.

4 Results

4.1 Systematic paleontology

Sarcopterygii Romer, 1955
Tetrapodomorpha Ahlberg, 1991
Osteolepididae Cope, 1887
osteolepid gen. et sp. indet.

Materials Two anterior cranial portions (IVPP V34447 and V34448) and a mandible (V34449)

Fig. 3

Figure 3: Fig. 3

Fig. 4

Figure 4: Fig. 4

Locality and horizon Locality 4, Pearl River Source Scenic Area, Qujing, Yunnan, China; Xichong Formation, Middle Devonian.

Comparison Owing to the limited information preserved, the taxonomic assignment of the new material remains uncertain. Nevertheless, the presence of cosmine covering the external surface and the overall morphology of the ethmoidal shield support its assignment to Osteolepiformes. A well-developed subnarial corner is present, as also observed in *T. wudingensis* and *Kenichthys* (Fan, 1992). The anteriormost portion of the ethmosphenoid shield is strongly ventrally deflected, such that the anterior naris is partially visible in dorsal view. The pineal foramen is positioned approximately at the level of the posterior orbital margin, and no distinct pineal plate is observed, a condition comparable to that in *T. wudingensis*.

4.2 Description

4.2.1 The dermal skull roof The dermal surface of the anterior cranial portion is covered with fine pores, and sutures are not discernible externally (Fig. 3). A well-developed subnarial corner is present (Fig. 4), comparable to that in *Thursius wudingensis* and *Kenichthys* (Fan, 1992, Chang and Zhu, 1993). The anteriormost part of the skull roof is ventrally bent, and the anterior nostril is only partially visible in dorsal view (Fig. 3C). The processus dermintermedius is not clearly visible. The preorbital corner is acutely pointed and directed posteriorly, whereas the postorbital

corner is obtuse. The orbital notch occupies approximately 30% of the length of the anterior cranial portion. The pineal foramen is positioned approximately along the midline connecting the two postorbital corners, and no distinct pineal plate is observed. The supraorbital sensory canal connects with the infraorbital sensory canal at the dermosphenotic, and the anterior and posterior pit-lines are present.

Fig. 3 Osteolepid gen. et sp. indet. (IVPP V34447) from Xichong Formation (Givetian, Middle Devonian) of Qujing, Yunnan, China
Photograph (A) and interpretative drawing (C) of the parietal shield from dorsal view; Micro-CT 3D rendering (B) and interpretative drawing (D) of the braincase from ventral view. Scale bars = 5 mm

Fig. 4 Micro-CT 3D rendering of IVPP V34447 in lateral (A) and anterior (B) views

Fig. 5 Micro-CT 3D rendering and interpretative drawing of IVPP V34449 right mandible in external and internal views

Figure 5: Fig. 5 Micro-CT 3D rendering and interpretative drawing of IVPP V34449 right mandible in external and internal views

Scale bar = 5 mm

4.2.2 Endocranium The general shape of the braincase agrees with that of osteolepids. The fenestra ventralis is broad (Fig. 3D). The parasphenoid is slender and splint-shaped, with its denticulated field narrowing towards both the anterior and posterior ends, a feature that provides an important diagnostic character for distinguishing related taxa. Anteriorly, the parasphenoid extends to the level of the autopalatine articulation. In contrast, in *T. estonicus* and *Gyroptychius pauli*, the parasphenoid does not extend anteriorly beneath the ethmoidal region, instead, it expands posteriorly and partially contacts the basipterygoid process (Chang and Yu, 1997). The basipterygoid process is positioned posteriorly and is well separated from the cranial cavity. The opening of the buccohypophyseal canal is located anterior to the basipterygoid process.

4.2.3 Lower jaw In dorsal view, the surface of the lower jaw agrees well with that of *T. wudingensis*. The anterior margin of the mandible is blunt and rounded. Both horizontal and vertical pit-lines are shown (Fig. 5C), with the vertical pit-line concave anteriorly. The mandibular sensory canal is clearly shown.

In mesial view, the ventral margin of the inner side of the lower jaw has an extensive anterior infradentary (splenial) flange, as in *Youngolepis*, *Powichthys* (Chang and Yu, 1997). Three coronoids are visible, showing a pair of coronoid tusks. The spacing between coronoid 1 and coronoid 2 is greater than that of coronoid 2 and coronoid 3 with the ratio between these two distances being approximately 8:3, measured between the central points of each coronoid element (Fig. 6), which is similar to that of *Kenichthys*. coronoid 1 bears two bigger tusks in its posteroventral corner. coronoid 2 shows a well-developed tusk and a socket. coronoid 3 holds a small growing tooth in the socket in addition to the tusk, as in some *Kenichthys* and *Youngolepis* (Chang, 1991, Chang and Zhu, 1993). A well-developed intercoronoid fossa is situated between coronoid 1 and coronoid 2, similar to that of *Gogonasus* (Long et al., 1997). The lateral portions of the anterior coronoids are studded with numerous teeth, which can also

Fig. 5 Micro-CT 3D rendering (A, B) and interpretative drawing (C, D) of IVPP V34449 (right mandible) in external (A, C) and internal (B, D) views
Scale bar = 5 mm

be observed in *Kenichthys* and in *Youngolepis* and *Powichthys* (Chang and Yu, 1997). The prearticular is highest and widest posteriorly, gradually tapering anteriorly.

Fig. 6 Measurement of distances between the coronoids of the lower jaw (IVPP V34449)
a. The spacing between coronoid 1 and coronoid 2; b. The spacing between coronoid 2 and coronoid 3
Not to scale

4.3 Phylogenetic analysis

To assess the phylogenetic position of the new material and its relationships among osteolepiforms, a cladistic analysis was conducted using TNT, based on the matrix of Choo et al. (2024), which was modified from Cloutier et al. (2020). A traditional search was performed using tree bisection–reconnection (TBR) branch swapping, with 1000 replicates and 10 trees retained per replication. The analysis recovered 80 most parsimonious trees (MPTs) of 446 steps in length. The best score was found once, and a total of 5447003 rearrangements were examined. Strict and 50% majority-rule consensus trees were calculated to summarize the common topology among the MPTs (Fig. 7).

In the present morphological matrix, the character 69 (“Lateral sides of the parasphenoid”) was revised by redefining state (1) as converging anteriorly only, and by introducing a new state (2), in which the lateral margins converge both anteriorly and posteriorly. In addition, two new characters were added:

Character 203: Buccohypophyseal canal opening position: at the same level as the basipterygoid process (0); anterior to the basipterygoid process (1).

Character 204: Relative distances between the coronoids: the distance between coronoid 1 and coronoid 2 is greater than that between coronoid 2 and coronoid 3 (0); the distances between coronoids are approximately equal (1).

Characters 203 and 204 were treated as discrete, independent characters. Specifically, Character 203 describes the relative positional relationship between the buccohypophyseal canal opening and the basipterygoid process, which reflects a discrete anatomical arrangement of neurocranial structures rather than a simple proportional change. Character 204 captures the relative spacing pattern among the coronoids, which is based on the qualitative configuration of the lower jaw rather than absolute size differences. In both cases, the character states are defined by non-overlapping conditions that can be objectively scored, supporting their treatment as independent phylogenetic characters.

The strict consensus tree places the new material within Osteolepididae, but does not resolve its relationships, recovering it as part of an unresolved polytomy with other osteolepids

(Fig. 7A). In contrast, the 50% majority-rule consensus tree (Fig. 7B) provides a more resolved hypothesis, in which the new material is recovered as the sister taxon to *T. wudingensis* within Osteolepididae. However, this sister-group relationship is only supported under the majority-rule criterion and does

Fig. 7. Proposed phylogenetic interrelationships among early Tetrapodomorpha incorporating new data from osteolepid gen. et sp. indet. A. strict consensus tree, numbers represent Bremer support values; B. 50% majority-rule consensus tree, numbers are node support bootstrap values

Figure 6: Fig. 7. Proposed phylogenetic interrelationships among early Tetrapodomorpha incorporating new data from osteolepid gen. et sp. indet. A. strict consensus tree, numbers represent Bremer support values; B. 50% majority-rule consensus tree, numbers are node support bootstrap values

not appear in the strict consensus. Despite this difference, the broader interrelationships within Osteolepididae remain unresolved in both trees, forming a polytomy with *Thursius macrolepidotus*, *Medoevia lata*, *Gogonasus andrewsae*, *Osteolepis macrolepidotus*, and *Gyroptychius agassizi*. The persistent lack of resolution within Osteolepididae may reflect a high degree of morphological homoplasy among early tetrapodomorphs (Choo et al., 2024). This pattern highlights the morphological complexity of the group and indicates that additional well-preserved material, particularly with internal anatomical information, will be critical for resolving their phylogenetic relationships.

This phylogenetic placement is supported by the following combination of characters: the new material shares with *T. wudingensis* a combination of features, including well-developed subnarial corners, a strongly ventrally bent anteriormost portion of the parietal shield, an anterior external naris positioned ventrally on the skull, an acutely pointed preorbital corner, an obtuse postorbital corner, and a pineal foramen located approximately along the line connecting

Fig. 7 Proposed phylogenetic interrelationships among early Tetrapodomorpha incorporating new data from osteolepid gen. et sp. indet.
A. strict consensus tree, numbers represent Bremer support values;
B. 50% majority-rule consensus tree, numbers are node support bootstrap values

the postorbital corners. It also exhibits a buccohypophysieal canal opening positioned anterior to the basipterygoid process (Character 203, state 1), and the distance between coronoid 1 and coronoid 2 is greater than that between coronoid 2 and coronoid 3 (Character 204, state 0), distinguishing it from *Thursius macrolepidotus* and other osteolepiform taxa.

4.4 Principal component analysis

Morphological disparity of the skull roof of the parietal shield was assessed using principal component analysis (PCA), with the results shown in the scatterplot (Fig. 8). The first two principal components (PC1 and PC2) together account for 70.4% of the total variance. PC1 primarily reflects variation in overall skull roof proportions, particularly the relative length and width of the parietal shield and the degree of anterior–posterior elongation, whereas PC2 captures variation in the shape and relative expansion of the ethmoidal and posterior regions, in-

Fig. 8 Principal component analysis scatter plot

Figure 7: Fig. 8 Principal component analysis scatter plot

cluding the configuration of the pineal and postorbital areas. Canowindridae and Osteolepididae occupy partially overlapping regions in morphospace, indicating limited morphological differentiation between these groups. In contrast, Megalichthyidae and Osteolepididae are clearly separated, showing distinct morphospace occupation. This pattern suggests that, although some osteolepiform clades share similar cranial morphologies, others exhibit pronounced divergence. Such differentiation may reflect different evolutionary trajectories in cranial morphology, consistent with patterns of morphological disparity discussed by Stayton (2005).

The morphospace occupied by Osteolepididae is consistently larger than that of Megalichthyidae, indicating a higher degree of morphological disparity in parietal shield

Fig. 8 Principal component analysis scatter plot, visualizing the dataset reduced to its first two principal components (PC1 and PC2)
Each point represents an individual sample or observation

morphology (Wills et al., 1994). The inclusion of *Thursius* and *Gogonasus* notably expands the boundaries of osteolepid morphospace. The new material plots in close proximity to *T. wudingensis*, consistent with their overall similarity in anterior cranial morphology. These results illustrate both overlap and differentiation among major tetrapodomorph groups and further support a close relationship between the new material and *T. wudingensis*. The observed patterns highlight the parietal shield as an informative source of morphological variation and phylogenetic signal in early tetrapodomorphs. However, proximity in morphospace should be interpreted as reflecting descriptive morphological similarity rather than phylogenetic affinity, and it cannot be used as a substitute for explicit phylogenetic evidence.

5 Discussions

The new tetrapodomorph material from the Pearl River Source Scenic Area shows close morphological similarity to *Thursius wudingensis* in many aspects (Fig. 9). Both share a suite of characters, including well-developed subnarial corners, a strongly ventrally bent anteriormost portion of the parietal shield, an anterior external naris positioned ventrally on the skull, an acutely pointed preorbital corner, an obtuse postorbital corner, and a pineal foramen located approximately along the line connecting the postorbital corners. However, it should be noted that the internal anatomy of *T. wudingensis* has not yet been formally described, limiting direct comparison of internal cranial structures between the two forms.

Fig. 9 Parietal shields of *T. wudingensis* (A) and IVPP V34447 (B)

Figure 8: Fig. 9 Parietal shields of *T. wudingensis* (A) and IVPP V34447 (B)

Fig. 10 Endocrania of osteolepids in ventral views

Figure 9: Fig. 10 Endocrania of osteolepids in ventral views

The parietal shield morphospace, as revealed by PCA, further supports this affinity, with the new material occupying a region overlapping with *T. wudingensis* but clearly separated from Megalichthyidae and other osteolepiform clades. In contrast, some osteolepiform taxa such as *Gyroptychius* exhibit distinct cranial features, including a strongly ventrally deflected

Fig. 9 Parietal shields of *T. wudingensis* (A) and IVPP V34447 (B)
A. *T. wudingensis* (Fan, 1992); B. osteolepid gen. et sp. indet.
Abbreviations: dsph. dermosphenotic; f.pin. pineal foramen; fe.exa. fenestra exonarina anterior; gp.so. groups of pores for cutaneous sensory organs; i.o. orbital notch; ioc. infraorbital sensory canal; pl. pit-line; pmx. premaxillary; soc. supraorbital sensory canal. Not to scale

anteriormost skull roof, an anterior naris only partially visible in dorsal view, and a well-developed orbital depression. These differences further highlight the morphological divergence among osteolepiform taxa. Phylogenetic analysis likewise recovers the new material as the sister taxon to *T. wudingensis*. However, it differs from other species of *Thursius* in several neurocranial features, particularly in the morphology of the parasphenoid and the position of the buccohypophyseal canal opening. These differences suggest that, although closely related to *T. wudingensis*, the new material may represent a distinct lineage within Osteolepididae. Taken together, these observations raise the possibility that the Chinese "*Thursius*" -type taxa may represent a separate evolutionary lineage distinct from *Thursius* sensu stricto; however, this hypothesis remains tentative and requires testing with additional well-preserved material, particularly specimens preserving internal cranial anatomy. It is also worth noting that some of the observed differences may potentially reflect ontogenetic variation or taphonomic distortion, especially given the limited number of specimens currently available; therefore, their taxonomic significance should be treated with caution.

The new tetrapodomorph material also exhibits a set of distinctive features that differ from other osteolepids, including a parasphenoid that tapers towards both its anterior and posterior ends, and a greater distance between coronoid 1 and coronoid 2 than between coronoid 2 and coronoid 3. In contrast (Fig. 10), the parasphenoid of *Gogonasus* is subequal in

Fig. 10 Endocrania of osteolepids in ventral views
A. *Gogonasus* (Long et al., 1997); B. *Thursius estonicus* (Vorobyeva, 1977); C. osteolepid gen. et sp. indet.;

Fig. 11 Lower jaws of osteolepids in internal views

Figure 10: Fig. 11 Lower jaws of osteolepids in internal views

D. *Gyroptychius* (Borgen and Nakrem, 2017); E. *Medoevia* (Lebedev, 1995); F. *Eusthenopteron* (Borgen and Nakrem, 2017)

width anteriorly and posteriorly, being nearly ellipsoid, whereas in *Eusthenopteron*, the dental plate is elongate and narrow (Borgen and Nakrem, 2017). The spacing between coronoid 1 and coronoid 2 is greater than that of coronoid 2 and coronoid 3, with the ratio between these two distances being approximately 8:3, a condition similar to that observed in *Kenichthys*, and differing from the condition seen in other osteolepiforms (Fig. 11). These differences indicate notable variation in parasphenoid and coronoid morphology among osteolepiform taxa. They further suggest that the generic assignment of both the new material and *T. wudingensis* requires re-evaluation, and that their relationships to *Thursius* sensu stricto remain uncertain pending additional data.

Fig. 11 Lower jaws of osteolepids in internal views
A. *Eusthenopteron* (Jarvik, 1980); B. *Gogonasus* (Long et al., 1997); C. osteolepid gen. et sp. indet.;
D. *Kenichthys* (Zhu and Yu, 2004)

Abbreviations: a.i.f. anterior infradentary flange; Co 1. coronoid 1; Co 2. coronoid 2; Co 3. coronoid 3; fo.add. adductor fossa; fo.gl. glenoid fossa; ic.fs. intercoronoid fossae; l.t. lateral row of small tooth; Pra. prearticular; t. De. dentary teeth. Not to scale

6 Conclusions

The new tetrapodomorph from the Pearl River Source Scenic Area expands the known diversity of Middle Devonian osteolepiforms in South China and provides new evidence for understanding early tetrapodomorph diversification. Phylogenetic analyses indicate that the new material is closely related to *T. wudingensis*, with this affinity further supported by both morphological and morphometric data. The two taxa share key features and occupy similar regions of skull roof morphospace, yet can be distinguished from *Thursius macrolepidotus* and other osteolepiforms by differences in cranial, parasphenoid, and mandibular characters. These results indicate that the new material and *T. wudingensis* form a closely related lineage within Osteolepididae. However, given the limited resolution of the phylogenetic analyses and the absence of comprehensive internal anatomical data for *T. wudingensis*, broader evolutionary interpretations and higher-level taxonomic conclusions remain provisional.

Within this framework, the present study primarily refines the morphological and phylogenetic understanding at the species- to genus-level, and provides

evidence for previously unrecognized diversity within Chinese osteolepids, rather than resolving deeper relationships within Osteolepiformes. Although formal taxonomic revision requires additional material, this study reveals previously unrecognized morphological heterogeneity within *Thursius* and highlights the need to reassess its generic boundaries.

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New Knowledge of Middle Devonian Tetrapodomorph Fossils from the Qujing Basin, Yunnan

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Abstract: Tetrapodomorpha represents all terrestrial vertebrates and their closest common ancestor. The earliest known tetrapodomorphs have been found in the Early Devonian strata of South China. However, the systematic evolutionary relationships of tetrapodomorphs that are relatively primitive in morphology remain incompletely clear. This study reports tetrapodomorph fossils from the Middle Devonian of the Zhujiangyuan area, Qujing, Yunnan, China. The skull roof and lower jaw of the new fossil material are similar in many respects to those of *Thursius wudingensis*, previously reported from the Middle Devonian strata of Wuding, Yunnan. High-resolution CT scanning and computerized three-dimensional reconstruction show that the new material has a well-developed nasal notch similar to that of *Thursius wudingensis*, but differs from other known ostrolepidid-related information in the morphology of the extrascapular bone and the position of the spiracular region. To further explore the phylogenetic position of the new material, we conducted a phylogenetic analysis. The results indicate that the new material and *Thursius wudingensis* form a sister group; "osteolepiforms" are monophyletic, but the evolutionary relationships among the various families remain incompletely clear. In addition, to further investigate the phylogenetic relationships among osteolepiforms, we performed a principal component analysis of the skull roofs of the new tetrapodomorph material, *Thursius wudingensis*, Osteolepididae, Canowindridae, and Megalichthyi-

dae. The principal component analysis supports the phylogenetic analysis: the new material is more closely related to *Thursius wudingensis* and is separated from other osteolepiforms. The new Middle Devonian tetrapodomorph material from the Zhujiangyuan Basin provides new insight into the early evolution of the tetrapod lineage.

Keywords: South China, Middle Devonian, Tetrapodomorpha, "osteolepiforms," phylogenetic analysis, morphometrics

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