Novel Mid-Paleozoic dataset of antiarch placoderms (the most basal jawed vertebrates)

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Abstract. Antiarcha data are essential to quantitative studies of basal jawed vertebrates. The absence of structured data on key groups of early vertebrates, such as Antiarcha, has lagged in understanding their diversity and distribution patterns. Previous works of early vertebrates usually focused on anatomy and phylogeny, given their significant impacts on the evolution of key characters but lacked comprehensive structured data. Here, we contribute an unprecedented open access Antiarcha dataset covering 60 genera of 6025 specimens from the Ludfordian to the Famennian globally. We have organized an expert team to collect and curate 142 publications spanning from 1939 to 2021. Additionally, we have two-stage quality controls in the process, domain experts examined the literature, and senior experts reviewed the results. In this paper, we give details of the data storage structure, visualize these antiarch fossil sites on the paleogeographic map, and present the biodiversity of the Antiarcha. The novel Antiarcha dataset has tremendous research potential, including testing previous qualitative hypotheses in biodiversity changes, spatiotemporal distribution, evolution, and community composition. It is now an essential part of the DeepBone database and will update with the latest publication, also available on https://zenodo.org/record/6536446 (Pan and Zhu, 2021).

1 Introduction

Placodermi is an extinct group of jawed vertebrates that first occurred in the Silurian, then dominated the Devonian and constituted a prevalent biotic component of the marine vertebrate ecosystem from

425.0 to 358.9 million years ago (Carr, 1995; Denison, 1978; Janvier, 1996; Young, 2010; Zhu, 1996). Recent prevailing phylogenetic hypotheses placed Placodermi as jawed stem-Gnathostomata that is sister to crown-Gnathostomata or modern jawed vertebrates (Brazeau, 2009; Davis et al., 2012; Dupret et al., 2014; Giles et al., 2015; King, 2021; Long et al., 2015; Qiao et al., 2016; Trinajstic et al., 2015; Zhu et al., 2013, 2016). In this scenario, Antiarcha has usually been placed at the most basal position in the Placodermi (Fig. 1), representing the most basal jawed vertebrates. The spatiotemporal distribution of Antiarcha will thus help us understand the origin and early evolution of jawed vertebrates. For example, Sallan et al. (2018) found that vertebrate diversification occurred primarily in nearshore environments by analyzing early vertebrate occurrence and habitat data. Historically, antiarchs resided in various paleo-environments across all paleo-continents, including marine and freshwater environments close to shore. As a successful vertebrate group during the Devonian (Long, 2011; Young, 2010), Antiarcha has contributed significantly to the Devonian stratigraphic correlation. For instance, the biozonation of the East Baltic and southern East Antarctica Devonian succession is partly based upon the antiarchs *Bothriolepis*, *Asterolepis*, and *Pambulaspis* (Young, 1974, 1988). Lukševičs (1996) identified 14 bothriolepid species (12 *Bothriolepis* and 2 *Grossilepis*) in the Frasnian-Famennian formations of the East European Platform, proposed nine antiarch assemblages, and set up the most detailed zonation of the Main Devonian Field, north-western part of the East European Platform (Latvia and NW Russia).

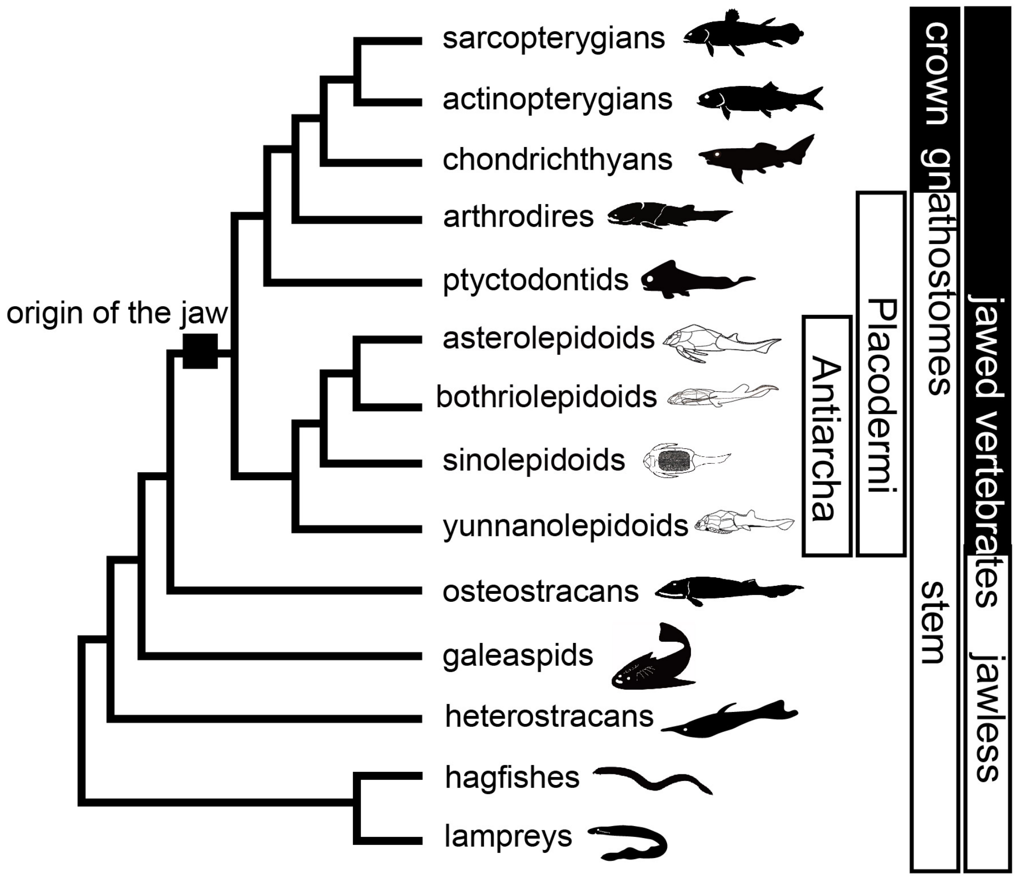


Figure 1 Phylogenetic relationships of major early vertebrate groups from Qiao et al. (2016) and Pan et al. (2018). Silhouettes indicate groups of Antiarcha.

Collecting and visualizing the data of Antiarcha is a prerequisite to explaining the spatial and temporal distribution of early vertebrates. With the help of data visualization, we could better understand the biogeographic evolution of early vertebrates. Although Zigaite and Blieck (2013) advocated a quantitative analysis to define early vertebrates' biogeographic patterns, efficient quantitative analysis is still lacking to understand the dispersal of early vertebrates. This occurs mainly because no comprehensive data collection of early vertebrates was accomplished. The disadvantages of unstructured data are clear: the absence of schema and structure makes them difficult to manage, and the lack of predefined attributes makes them difficult to be reused or extended.

In this paper, we present an unprecedented structured dataset of Antiarcha that potentially facilitates understanding the spatiotemporal distribution pattern and quantifying the variety of antiarchs. This dataset is open access and follows the FAIR principles (findability, accessibility, interoperability, and reusability). This dataset complements existing fossil records of early vertebrates. Moreover, it is the first step to accomplishing the global coverage of the vertebrate fossil dataset to analyze the Middle Paleozoic biogeography and paleogeography. Understanding the distribution of antiarchs in the paleogeographic background with reference to the global paleogeographic reconstructions of Scotese (2021), our preliminary results can also be used to test the hypothesis of paleogeographic reconstructions.

2. Method

2.1 Overview

Comprehensive data are essential for quantitative studies and simulation analysis on early vertebrates. Sallan et al. (2018) pointed out that a lack of early vertebrate fossil data has limited quantitative approaches and hindered the resolution of issues regarding ancestral habitat in vertebrate evolution. To bring the study of Vertebrate Paleontology into the next phase of macroevolutionary, we built the DeepBone database with the implementation of a project entitled "Big Earth Data Science Engineering (CASEarth)" in 2018 (Guo, 2017; Pan and Zhu, 2019).

With continuously refining data, the Antiarcha dataset of the DeepBone database is the first and most comprehensive dataset endorsed by Chinese researchers at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. The Antiarcha dataset of DeepBone differs from that of PBDB (https://paleobiodb.org/) in its basic unit, which is the specimen ID coupled with the occurrence and other detailed data. All the specimens are referenced in taxa and literature to guarantee accuracy. Because the data format was designed as specimen-based, we input the metadata according to the published specimen ID or virtual specimen ID. The literature on classic systematic paleontology always has real specimen IDs. When it handled stratigraphic topics, the authors usually cited fossil records instead of real specimens. We introduce a virtual specimen ID to store the taxon information in this kind of literature containing no real specimens.

Since no satisfactory approach can automatically extract paleontological data from the literature, we recruit several data entry assistants, including researchers, master's and Ph.D. students, to collect and curate the data. In order to guarantee the quality of the data, we designed a four-step data processing procedure (Fig. 2):

1. Experts who obtained his/her Ph.D. degree in Paleontology collected and sifted the Data source.

2. Data entry assistants read the related references, extracted the antiarch placoderm data, and manually filled them into the online record file under the supervision of vertebrate paleontology experts.
3. According to the references, experts reviewed and cleaned the data line by line as the quality control procedure.
4. Senior experts, who have outstanding achievements in vertebrate paleontology, reviewed the data again to guarantee quality.
5. DeepBone.org published the dataset with visualization. A better user interface helps dissemination.

Next, we provide more details on the data processing and visualization.

Figure 2 Workflow of the data processing. 1, collecting and sifting lectures by experienced experts. 2, data entry assistants digitalize paleontological descriptions from the page into the DeepBone database. 3, According to the reference, experts are accountable for data review and cleaning to implement quality control. 4, senior researchers review the data again. 5, data managers release the data to the public through DeepBone.org.

2.2 Data Source

The data were extracted from the published literature containing information on antiarch specimens. Most of the journals are professional journals on Paleontology. The main journals include Alcheringa, Acta Geologica Polonica, Bulletin of the Geological Society of China, Estonian Journal of Earth Sciences, Journal of Vertebrate Paleontology, Journal of Paleontology, Palaeontologia Electronica, Palaeontology, Palaeoworld, and Vertebrata PalAsiatica. Totally we have collected 142 publications spanning from 1939 to 2021 (see dataset for more details). The satisfactory literature should include an accurate description or revision of the specimen and taxon. We accepted the latest peer-reviewed literature to deal with the inconsistent descriptions of stratigraphy and taxonomy.

2.3 Data Processing and Quality Control

We made a tailored web page that provides a better user interface for data entry assistants to fill in the rows of paleontological data. After that, the other related experts would review the data so that a researcher could quickly access them to perform quantitative analysis (Fig. 2). This workflow was adopted from the Geobiodiversity Database (GBDB) (Xu et al., 2020). Almost all antiarch literature was published in English, Russian, French, German, and Chinese. The data entry assistant could handle the literature in Chinese and English well. Many fossils were documented in French, Russian, and German. We invited paleontology postgraduates, who know French, Russian, or German, to deal with the literature in these languages.

2.4 Data Visualization

Due to the easy access of the paleo-geographic coordinates calculator (PointTrack version 7.0) (Scotese, 2021) and its widely used in Paleontology (Ke et al., 2016; Kiel, 2017), we decided to use Scotese's paleocontinent reconstruction to perform the plot map, although many paleogeographic reconstructions were proposed (Heckel and Witzke, 1979; Li and Powell, 2001). Using the TrackPoint software, we converted the excavation locations from the current GPS to paleo-GPS and visualized the locations using the Web Mercator algorithm (Battersby et al., 2014).

2.5 Biodiversity Visualization

We calculated Antiarcha biodiversity (the genus richness) by the divDyn R package (Kocsis et al., 2019). Range-through diversity is all taxa in the interval, based on the range-through assumption: *tSing + tOri + tExt + tThrough*. Boundary-crosser diversity is the number of taxa with ranges crossing the boundaries of the interval: *tExt + tOri + tThrough*. Sampled-in-bin diversity is the number of genera sampled in the focal bin.

The timescale follows the International Commission on Stratigraphy International Chronostratigraphic Chart version 2021/07 (Cohen et al., 2021).

3. Results

3.1 Data Overview

This dataset consists of 60 genera of 6025 specimens, covering all known antiarch lineages. The 6025 specimens include 5867 fossil specimens that have been systematically described and documented and 158 virtual specimens introduced to describe the taxon information when no specimen was assigned for the referred fossil records. Each specimen has at least one reference within our dataset, and the specimens lacking precise age are excluded. We followed the lithostratigraphic information of the original authors, except we found a revision. We accepted the latest revision in the literature to modify our dataset. The amendments were linked to the latest reference as an endorsement. We took the geological background data in our dataset unless it was missing from the original literature. We transferred the unstructured data from the literature to structured data for further research in as much detail as possible. Table 1 shows the data structure of our dataset. Among all the referred specimens, 6.51% belong to Yunnanolepidoidei, 2.86% belong to Sinolepidoidei, 78.92% belong to 'Bothriolepidoidei', 11.71% belong to Asterolepidoidei. We plotted all the fossil sites of the constituent groups in Figure 3.

Specimen	
Specimen ID	Genus
Lithostratigraphy_formation	Species
Lithostratigraphy_member	Custodian institute
Fossil site	Custodian country
Discovery country	System / Period
Latitude	Series / Epoch
Longitude	Stage / Age
Paleo-latitude	Reference age to calculate paleo-coordinates
Paleo-longitude	

Reference
Literature type
Title
Keywords
Volume
Issue
Pages
Authors
Year
Journal
Doi

Table 1 The structure of Antiarcha dataset.

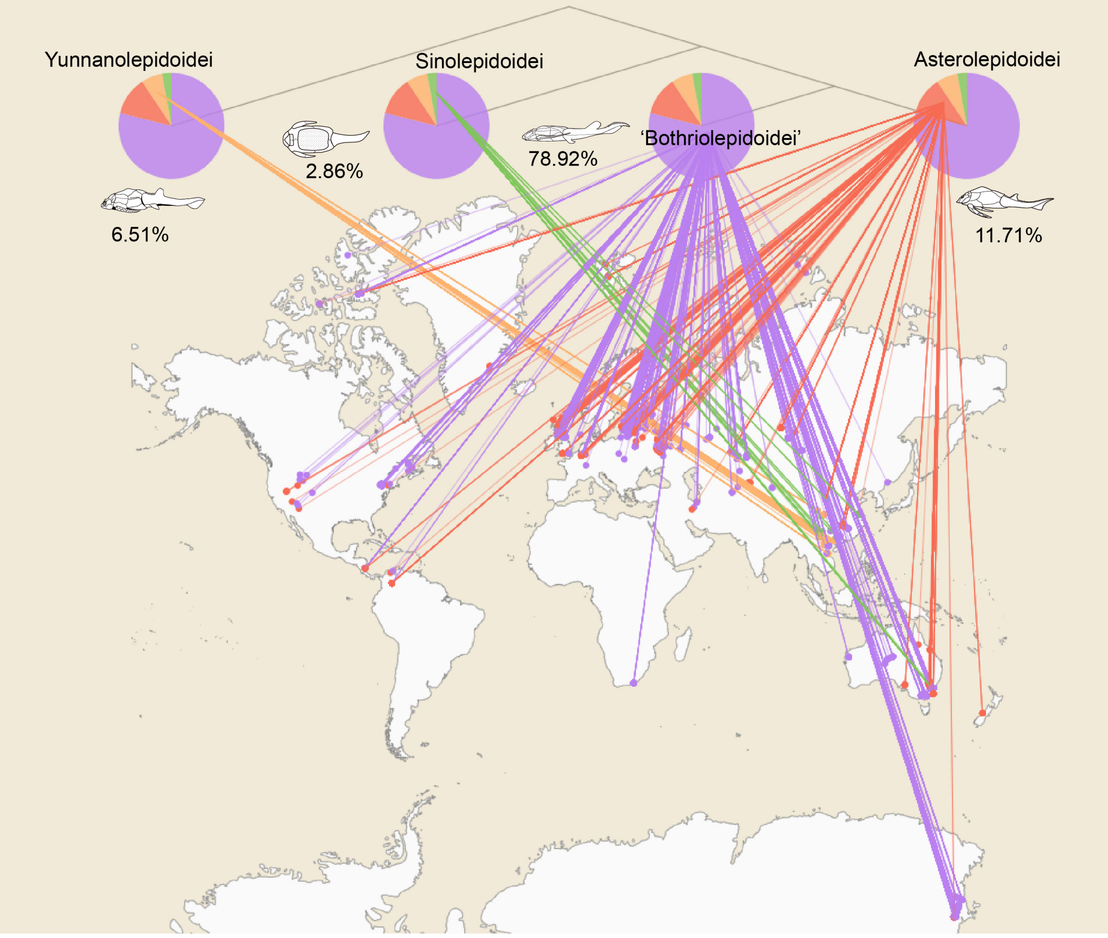
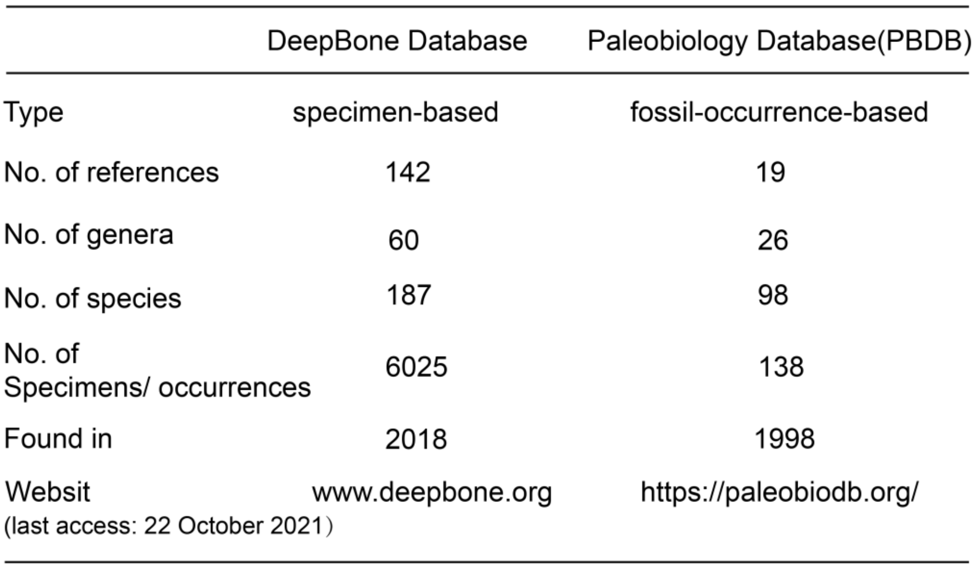


Figure 3 Antiarch placoderm spatial distribution and richness. The tree topology is simplified from the phylogenetic result in Pan et al. (2018). Numbers under the pie chart represent each group's relative amounts of specimens. Terminal groups are linked with their geographic distributions. Each node represents a single specimen. Specimens from one locality overlap each other.

GBDB is a stratigraphic and palaeontological database, but no antiarch record exists. Compared to the 138 records of Antiarcha in the Paleobiology Database (PBDB, 2021-08-12), this is the most comprehensive dataset of Antiarcha up to now (Table 2). Only taxon rank, reference, and occurrence location are available in PBDB. DeepBone dataset has more fields on the structured information of the specimen than that is in the PBDB, such as lithostratigraphic fields (Table 1）. Some records in PBDB are not stored at the genus or species level. There are some typing errors in PBDB, for instance, '*Jiangxilepus*', 'Bothriolepiodei' and '*Pterichthys*'. *Jiangxilepis,* 'Bothriolepidoidei' and *Pterichthyodes* are correct spellings. *Macrodontophion* is not a genus of Antiarcha, but PBDB adopts it in antiarchs. PBDB also adopts *Silurolepis* as an antiarch ignoring the latest research of Zhu et al. (2019). To ensure accuracy, every specimen of DeepBone is endorsed by the latest publication and reviewed by the experts who have focused on Antiarcha. It is open to access through the website of the DeepBone database or https://doi.org/10.5281/zenodo.6478602.



	DeepBone Database	Paleobiology Database(PBDB)
Type	specimen-based	fossil-occurrence-based
No. of references	142	19
No. of genera	60	26
No. of species	187	98
No. of Specimens/ occurrences	6025	138
Found in	2018	1998
Websit (last access: 22 October 2021）	www.deepbone.org	https://paleobiodb.org/

Table 2 Comparison of Antiarcha data in two paleontological databases.

3.2 The Geospatial Distribution of the Antiarcha Dataset

Yunnanolepidoidei is endemic in the South China block (comprising southern China and northern Vietnam) regarding the fossil site distribution. Sinolepidoidei is limited in South China and Australia (East Gondwana). In contrast, 'Bothriolepidoidei' and Asterolepidoidei are cosmopolitan, especially *Bothriolepis.* The faunistic elements in the communities are used herein at the genus level for their distributions because many *Bothriolepis* species were described based on isolated plates lacking diagnostic characters (Blieck and Janvier, 1993; Downs, 2011). The heat map of fossil sites (Fig. 4) shows that Europe, Australia, and China account for the most fossil sites globally, partly due to their long research history.

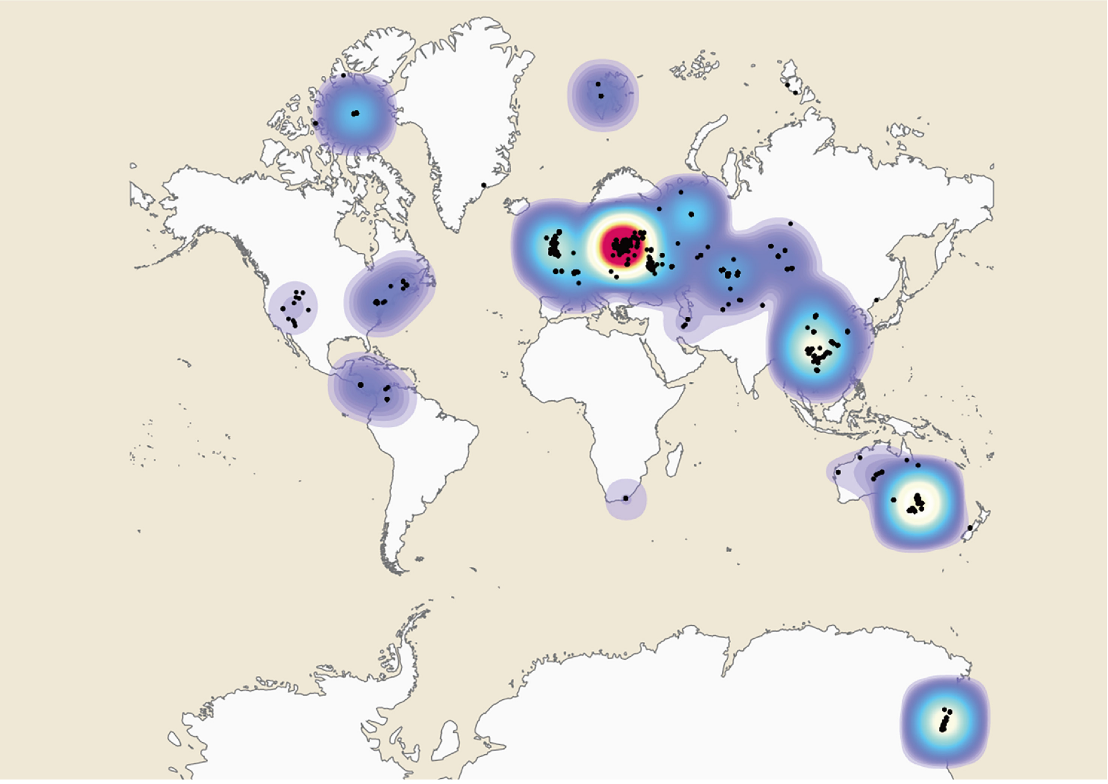


Figure 4 Heat map of Antiarcha fossil sites based on the modern world map. Each spot represents a single fossil site. The blue color indicates the area with sparse fossil sites. The red color indicates the area with dense fossil sites.

As Young (1990a) mentioned that biogeographic data must be interpreted in the context of paleogeographic hypotheses, we plot our data on paleogeographic atlas（Fig. 5) to generate an outline of their past. The continental reconstructions of Scotese place Baltica, China, and Australia in the tropic and subtropic near the equator from Llandovery to Famennian.

3.3 The Paleogeographic Distribution of the Antiarcha Dataset

We plotted these fossil sites on the paleogeographic map (Fig. 5) except the Silurian *Shimenolepis*, the earliest record of Yunnanolepidoidei and the only documented antiarch specimen before the Devonian (Wang, 1991; Zhao et al., 2016). Most of the fossil sites were positioned around the paleo equator. In the present scenario, the suborder Yunnanolepidoidei apparently originated as early as the Silurian in the South China block, forming a highly endemic fauna. All fossil sites of Yunnanolepidoidei lay in southern

China and northern Vietnam (Wang et al., 2010). From Ludlow (Silurian) to the Early Devonian, Yunnanolepidoidei formed dominant antiarchs. Sinolepidoidei and 'Bothriolepidoidei' first appeared in Pragian in South China, and Asterolepidoidei first evolved in Emsian in Australia or East Gondwana. During the middle Devonian, along with lessened isolation of South China, Yunnanolepidoidei became extinct. Euantiarcha ('Bothriolepidoidei' + Asterolepidoidei) dominated Middle and Late Devonian antiarchs, and only a few members of Sinolepidoidei coexisted with them in China and Australia. In Eifelian, Asterolepidoidei suddenly bloomed in Baltica without any clue from the older horizons based on existing research. The distribution and diversity of Antiarcha reached a peak in Givetian. 'Bothriolepidoidei' and Asterolepidoidei represent the main groups of Antiarcha in Givetian, comprising five bothriolepidoid genera with 42 fossil locations and nine asterolepidoid genera with 49 fossil locations. The records of antiarchs decreased in the Pan-Cathaysian and East Gondwana in the Late Devonian, contrary to those increased in Baltica. Antiarchs in Baltica went through an independent evolution in the Late Devonian.

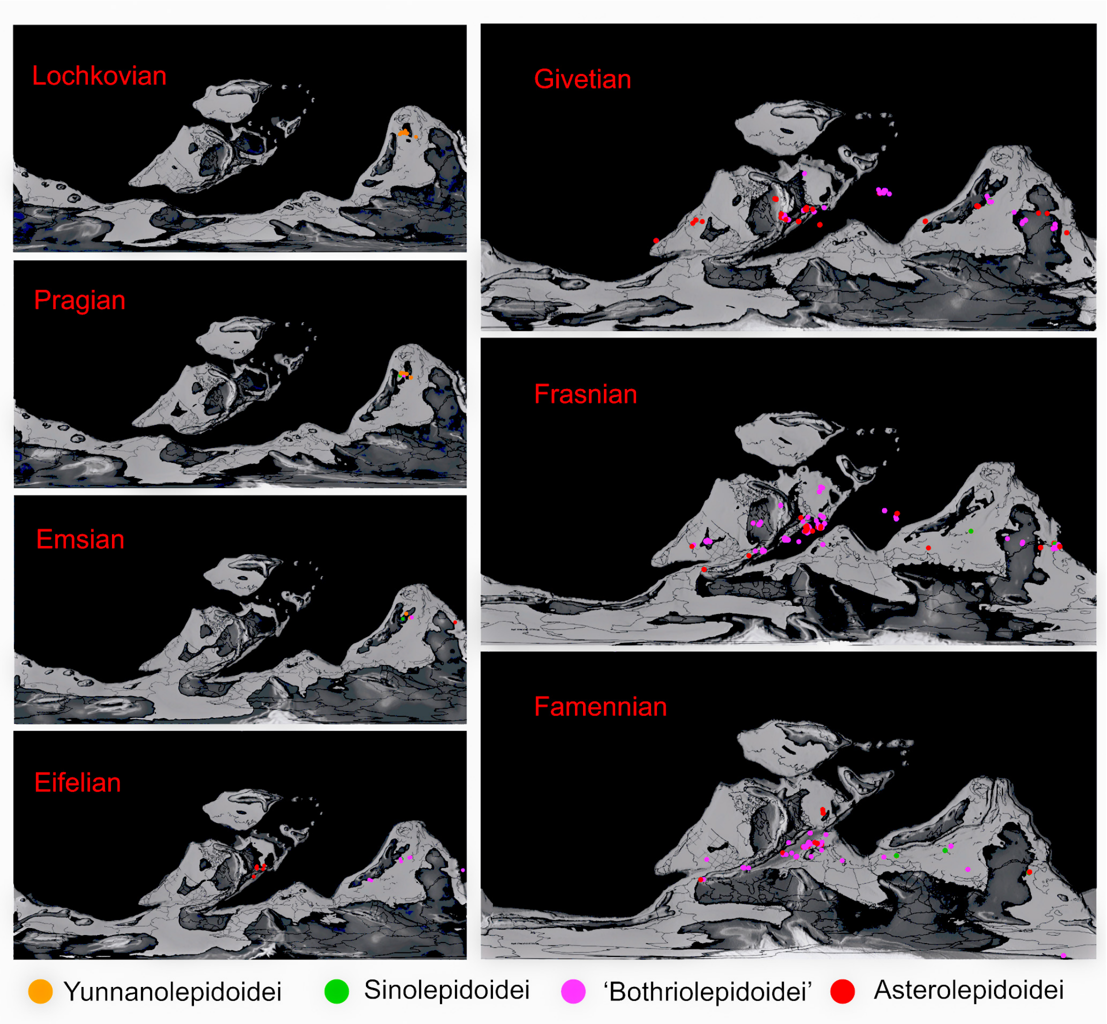


Figure 5 The distributions of Antiarcha during Devonian. Each spot represents the location of one specimen on the paleogeographic map. Specimens from the same locality and the same age overlap each other. The paleo-coordinates are calculated by TrackPoint. Colors denoting respective groups follow Figure 3.

4 Discussion

4.1 First Appearance Record

A taxon's first appearance record or lineage is important in Paleontology and Evolutionary Biology. It renders a hard minimum constraint on molecular clock calibration for a taxon (Benton and Donoghue, 2007; Benton et al., 2009; Donoghue and Benton, 2007). Based on our dataset, the oldest record of yunnanolepidoids or antiarchs is *Shimenolepis graniferus* from the Xiaoxi Formation at Shanmen Reservoir, Lixian County, Hunan, China. *Shimenolepis* was first described as the oldest known placoderm, dated as Telychian of Llandovery (Janvier, 1996; Wang, 1991). However, after a detailed stratigraphic work, Zhao et al. (2016) suggested that the age of *Shimenolepis* is late Ludlow rather than late Llandovery. Janvier and Tông-Dzuy (1998) also documented an indeterminate yunnanolepidoid (Antiarcha gen. sp. indet.) from the Do Son Formation of northern Vietnam, which could be another earliest antiarch potentially.

The oldest sinolepid is *Liujiangolepis suni*, from the Nakaoling Formation (Pragian), Xiangzhou, Guangxi, China (Wang, 1987). The oldest bothriolepidid is *Houershanaspis zhangi,* documented from the Danlin Formation (Pragian) in Houershan, Dushan county, Guizhou, southwestern China, based on a bothriolepid-like anterior median dorsal plate (Lu et al., 2017). The earliest asterolepidoid records are represented by *Wurungulepis* and some disarticulated specimens, which have been documented from the Broken River Formation, Broken River, Australia. The age of the Broken River Formation was first referred to Eifelian and then reassigned to Emsian (*serotinus* Zone) (Burrow, 1996; De Pomeroy, 1996; Young, 1984a, 1990b).

4.2 Origin and Differentiation of Euantiarcha

Houershanaspis, Wudinolepis, and *Wufengshania* from the Pragian and Emsian represent the earliest members of 'Bothriolepidoidei' (Chang, 1965; Lu et al., 2017; Pan et al., 2018), highlighting the origin and early diversification of this group in South China. In Eifelian, the distribution range of 'Bothriolepidoidei' extended from South China to Iran, which was positioned at the northern margin of East Gondwana with the discovery of *Hyrcanaspis* (Janvier and Pan, 1982). 'Bothriolepidoidei' became cosmopolitan during the Givetian and Late Devonian. The earliest asterolepidoid records are from Australia or East Gondwana in Emsian (Burrow, 1996; Young, 1984a, 1990b). In Eifelian, asterolepidoids occurred in Baltica, in addition to East Gondwana. Compared to the abundant Early and Middle Devonian fish faunas in South China, asterolepidoids were late arrivals to South China (Young, 1984a) since no asterolepidoid was known from this province before Givetian. It could be inferred that Asterolepidoidei originated and differentiated in East Gondwana.

4.3 Biodiversity Changes of Antiarcha

The observed genus and species numbers over time were summarized in histograms (Fig. 6). The comprehensive dataset of Antiarcha specimens allows us to generate its biodiversity changes throughout its life span at the genus level (Fig. 7). Numerous metrics were proposed to estimate diversity, given such distorting effects of incomplete sampling and the discretized time dimension (Gotelli and Colwell, 2001). Since all the richness metrics cannot be consensus, we choose the traditional range-based methods (Fig 7a) to illustrate the data. The biodiversity curve reached its peak at Givetian. The curve identified two sharp risings in the Pridoli and Eifelian. The first rise in Pridoli coincided with the rising of the jawed vertebrate and resulted in Yunnanolepidoidei reaching its diversity peak in Lochkovian. Walliser (1996) proposed the E'Em event as a faunal turnover from endemic taxa to more cosmopolitan ones in the transition between Emsian and Eifelian. Changes in the diversity of antiarchs coincided with the E'Em Event. After the E'Em event, the second increase was recognized by a faunal turnover from endemics to cosmopolitans (Zhu, 2000) due to the broader geographical ranges. Before this event, Petalichtyida and Antiarcha were endemic to China (Pan et al., 2015). *Wurungulepis* was the only documented antiarch outside China in the Early Devonian (Young, 1990b). Yunnanolepidoidei was extinct after the E'Em event, coinciding with the differentiation of euantiarchs. Zhu (2000) proposed the Late Eifelian event (Walliser, 1996) for the Chinese placoderm extinction in the late Eifelian. Although decreasing in the Pan-Cathaysian, the genus and species diversity of Antiarcha in other parts of the world kept rising after the Late Eifelian event. Walliser (1995) proposed that the Mid-Famennian Event was characterized by an increase in the species diversity of Antiarcha, which is also visible at the genus level based on this dataset.

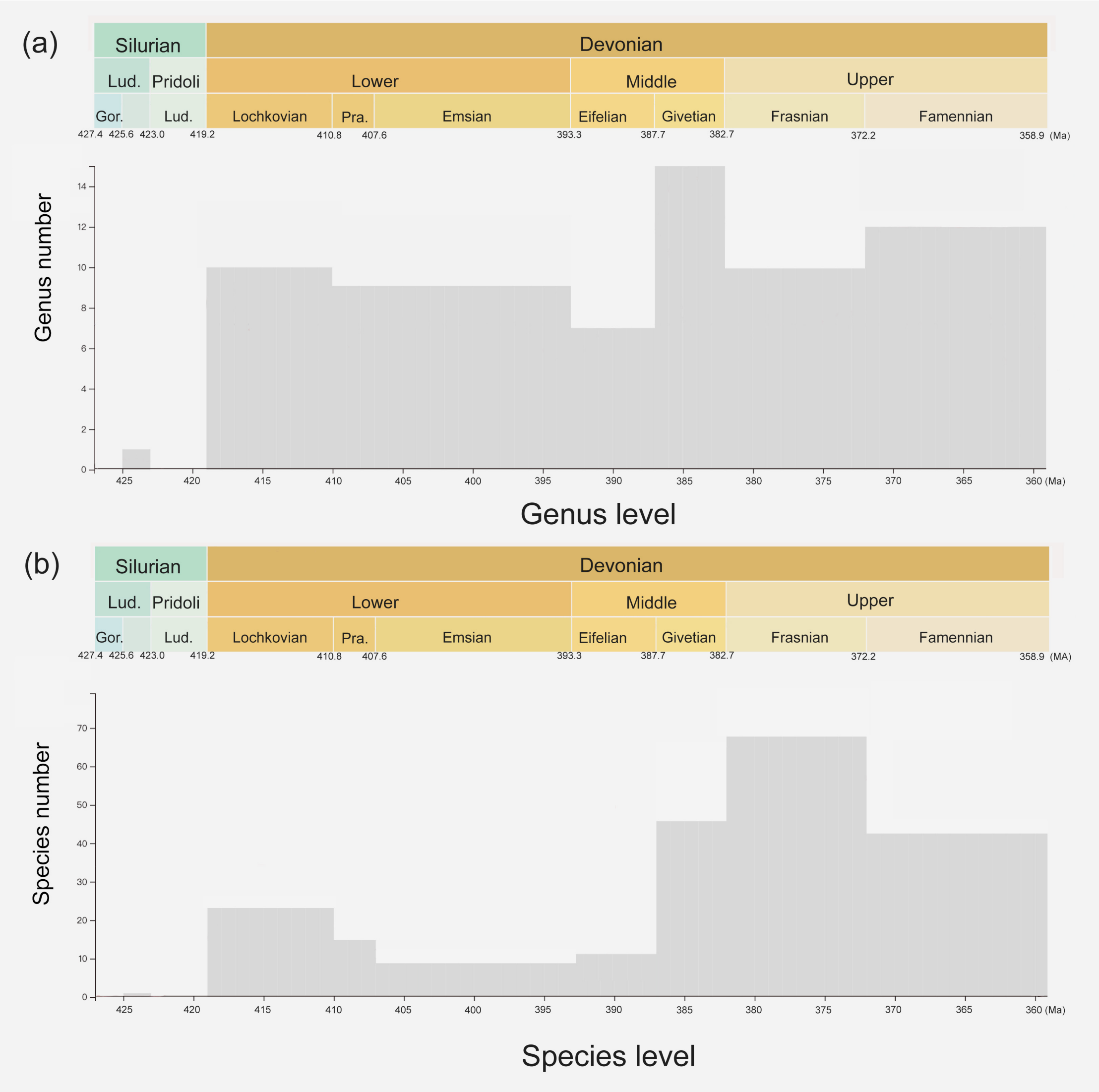


Figure 6 Histogram of observed specimen number. (a) The genus number at different time intervals, and (b) the species number at different time intervals.

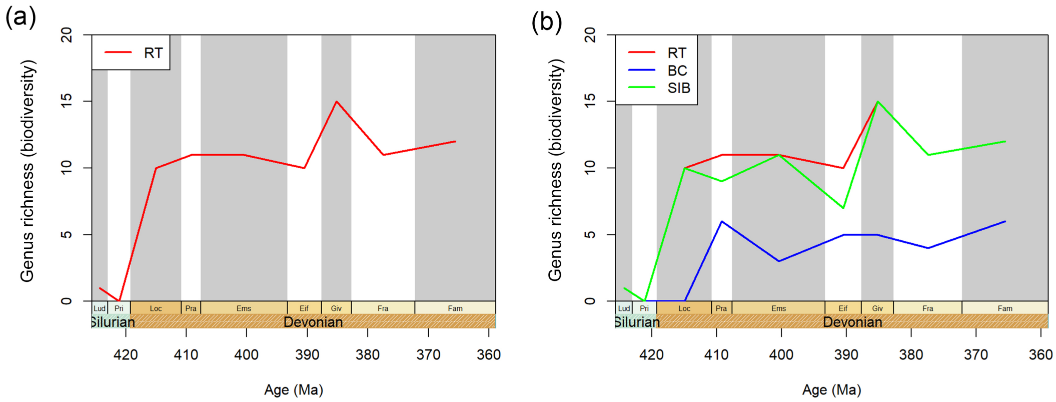


Figure 7 The trajectory of antiarchs diversity over the middle Paleozoic interval. (a) The range-through diversity of antiarchs, (b) Results of different approaches that estimate diversities. RT, the range-through

diversity, all taxa in the interval, based on the range-through assumption; BC, the boundary-crosser diversity, the number of taxa with ranges crossing the boundaries of the interval; SIB, the sampled-in-bin diversity, the number of genera sampled in the focal bin; Lud, Ludlow; Pri, Pridoli; Loc, Lochkovian; Pra, Pragian; Ems, Emsian; Eif, Eifelian; Giv, Givetian; Fra, Frasnian; Fam, Famennian.

5 Data Availability

The current dataset achieved via Zenodo represents a static version of the dataset in June 2022：https://zenodo.org/record/6536446 (Pan and Zhu, 2021). The latest version of the dataset is always freely available via https://deepbone.org/ (last access: June 2022).

6 Conclusions

We presented here an open-access dataset of Antiarcha, the most basal jawed vertebrate, from the late Silurian to the Late Devonian. This dataset significantly expands the previously available data of antiarch fossils. Paleontologists, stratigraphers, and evolutionary biologists could import the tab-delimited file for future research studies, especially for biodiversity analysis, stratigraphic correlation, and molecular clock calibration. With the information of 6025 specimens, our Antiacha dataset is far more comprehensive than the other sources in lithostratigraphy and specimen details. Data are significant for quantitative analysis and potentially contribute to data-driven paleontology research. We performed a visualization of the data to understand the spatiotemporal distribution of Antiarcha. In brief, Antiarcha first appeared in the Pan-Cathaysian province and then boomed around the world. The distribution and diversity of Antiarcha reached a peak in Givetian. The diversity changes of Antiarcha coincided with the E'Em Event, which is a faunal turnover from endemic taxa to more cosmopolitan ones in the Early Devonian. The diversity changes of Antiarcha also identified the Late Eifelian Event, which is the Chinese placoderm extinction in the late Eifelian. The available Antiarcha data may be just the tip of the historical reality due to the incomplete fossil record. We will continue to update the dataset with the latest publication.

Author contributions. MZ supervised the project. ZHP and ZBN developed the model and performed the simulations. ZHP prepared and revised the manuscript with contributions from MZ and ZBN. ZHP and ZMX prepared the data.

Competing interests. The authors declare that they have no conflicts of interest.

Acknowledgment. We thank Wenjin Zhao, Zhikun Gai, and Tuo Qiao, Institute of Vertebrate Paleontology and Paleoanthropology (CAS); Junxuan Fan, School of Earth Sciences and Engineering, Nanjing University; Honghe Xu, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS); Junqi Wu, Yaqi Xue, College of Intelligence and Computing, Tianjin University for discussion and help.

Financial support. This project was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA19050102, XDB26000000), National Science Foundation of China (No. 42002015), Youth Innovation Promotion Association CAS (No. 2021070), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (No. 193121).

Reference

Battersby, S. E., Finn, M. P., Usery, E. L., and Yamamoto, K. H.: Implications of web Mercator and its use in online mapping, Cartographica: J. Geogr. Inf. Geovis., 49(2), 85-101, doi: 10.3138/carto.49.2.2313, 2014.

Benton, M. J. and Donoghue, P. C. J.: Paleontological evidence to date the tree of life, Mol. Biol. Evol., 24(1), 26-53, doi:10.1093/molbev/msl150, 2007.

Benton, M. J., Donoghue, P. C. J., and Asher, R. J.: Calibrating and constraining molecular clocks, in: The Timetree of Life , edited by: Hedges, S. B. and Kumar, S., pp.35-86, Oxford Univ. Press, Oxford, 2009.

Blieck, A., and Janvier, P.: Silurian-Devonian vertebrate biostratigraphy of Siberia and neighbouring areas, in: Palaeozoic Vertebrate Biostratigraphy and Biogeography, edited by: Long J. A., pp. 87-103, Bellhaven Press, London, 1993.

Brazeau, M. D.: The braincase and jaws of a Devonian 'acanthodian' and modern gnathostome origins. Nature, 457, 305-308, doi:10.1038/nature07436, 2009.

Burrow, C. J.: Placoderm scales from the Lower Devonian of New South Wales, Australia, Mod. Geol., 20, 351-369, 1996.

Carr, R. K.: Placoderm diversity and evolution. Bull. Mus. Natl. Hist. Nat., Sect. C, 17(1-4), 85-125, 1995.

Cohen, K.M., Harper, D.A.T., Gibbard, P.L., Car, N.: International Commission on Stratigraphy, 2021.

Chang, K. J.: New antiarchs from the Middle Devonian of Yunnan, Vertebr. Palasiat., 9(1), 1-9, 1965.

Davis, S. P., Finarelli, J. A., and Coates, M. I.: *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes, Nature, 486(7402), 247-250, doi:10.1038/nature11080, 2012.

De Pomeroy, A. M.: Biostratigraphy of Devonian microvertebrates from the Broken River region, north Queensland, West. Aust. Mus. Rec., 17, 417-437, 1996.

Denison, R.: Placodermi. Handbook of Paleoichthyology, vol. 2, 128, 1978.

Donoghue, P. C. J.and Benton, M.: Rocks and clocks: calibrating the tree of life using fossils and molecules, Trends Ecol. Evol., 22(8), 424-431, doi:10.1016/j.tree.2007.05.005, 2007.

Downs, J. P.: Mass mortality of juvenile antiarchs (*Bothriolepis* sp.) from the Catskill Formation (Upper Devonian, Famennian Stage), Tioga County, Pennsylvania, Proc. Acad. Nat. Sci. Phila., 161, 191-203, 2011.

Dupret, V., Sanchez, S., Goujet, D., Tafforeau, P., and Ahlberg, P. E.: A primitive placoderm sheds light on the origin of the jawed vertebrate face, Nature, 507, 500-503, doi:10.1038/nature12980, 2014.

Giles, S., Friedman, M., and Brazeau, M. D.: Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome., Nature, 520, 82-85, doi:10.1038/nature14065, 2015.

Gotelli, N. J., and Colwell, R. K.: Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness, Ecology letters, 4(4), 379-391, doi: 10.1046/j.1461-0248.2001.00230.x, 2001.

Guo, H. D. : Big Earth data: A new frontier in Earth and information sciences, Big Earth Data, 1(1-2), 4-20, doi: 10.1080/20964471.2017.1403062, 2017.

Heckel, P. H., and Witzke, B. J.: Devonian world palaeogeography determined from distribution of carbonates and related lithic palaeoclimatic indicators, in: The Devonian System, edited by: House M. R., pp. 99-123, Vol. Spec. Pap. Paleontol. 23, 1979.

Janvier, P. (Ed.): Early Vertebrates, Clarendon Press, Oxford, United States, 1996.

Janvier, P. and Pan, J.: *Hyrcanaspis bliecki* n.g. n.sp., a new primitive euantiarch (Antiarcha, Placodermi) from the Middle Devonian of northeastern Iran, with a discussion on antiarch phylogeny, Neues. Jahrb. Geol. Palaontol. Abh., 164(3), 364-392, 1982.

Janvier, P. and Tông-Dzuy, T.: The Silurian and Devonian vertebrates of Viêt Nam: a review, J. Geol., Series B, 1998(11-12), 18-28, 1998.

Ke, Y., Shen, S. Z.., Shi, G. R., Fan, J. X., Zhang, H., Qiao, L., and Zeng, Y.: Global brachiopod palaeobiogeographical evolution from Changhsingian (Late Permian) to Rhaetian (Late Triassic), Paleogeogr. Paleoclimatol. Paleoecol., 448, 4-25, doi:10.1016/j.palaeo.2015.09.049, 2016.

Kiel, S.: Using network analysis to trace the evolution of biogeography through geologic time: A case study, 45(8), 711-714, 2017.

King, B.: Bayesian tip-dated phylogenetics in paleontology: topological effects and stratigraphic fit, Syst. Biol., 70(2), 283-294, doi: 10.1093/sysbio/syaa057, 2021.

Kocsis, Á. T., Reddin, C. J., Alroy, J., and Kiessling, W.: The R package divDyn for quantifying diversity dynamics using fossil sampling data. Methods in Ecology and Evolution, 10(5), 735-743, doi: 10.1111/2041-210X.13161, 2019.

Li, Z. X. and Powell, C. M.: An outline of the palaeogeographic evolution of the Australasian region since the beginning of the Neoproterozoic, Earth-Sci. Rev., 53(3-4), 237-277, doi: 10.1016/S0012-8252(00)00021-0, 2001.

Long, J. A.: Dawn of the Deed. Sci. Am., 304(1), 34-39, 2011.

Long, J. A., Mark-Kurik, E., Johanson, Z., Lee, M. S., Young, G. C., Zhu, M., Ahlberg, P. E., Newman, M., Jones, R., Blaauwen, J., Choo, B., and Trinajstic, K.: Copulation in antiarch placoderms and the origin of gnathostome internal fertilization, Nature, 517, 196-199, doi:10.1038/nature13825, 2015.

Lu, L., Tan, K., and Wang, X.: A New Antiarchi (placoderm fishes) from Devonian Strata of Dushan, Guizhou Province, Acta Geosci. Sin., 38(2), 144-148, 2017.

Lukševičs, E.: Bothriolepid antiarchs (Placodermi, Bothriolepididae) from the north-western part of East European platform, Ph.D. thesis, Ģeogrāfijas un Zemes zinātņu fakultāte, University of Latvia, Latvia, 196 pp., 1996.

Pan, J., Lu, L., and Ji, S. A.: A brief review of studies on palaeogeography of Middle Paleozoic vertebrates in China, J. Southeast Asian Earth Sci., 13(3-5), 185-190, 1996.

Pan, Z. H., and Zhu, M. VPPDB: Hosting the data for vertebrate paleoanthropology, Acta Geol. Sin.-Engl., 93(supp.1), 61-63, doi: 10.1111/1755-6724.14246, 2019.

Pan, Z. H., Zhu, M., Zhu, Y. A., and Jia, L. T.: A new antiarch placoderm from the Emsian (Early Devonian) of Wuding, Yunnan, China, Alcheringa, 42, 10-21, doi:10.1080/03115518.2017.1338357, 2018.

Pan, Z. H. and Zhu, M, Dataset of antiarch placoderms (the most basal jawed vertebrates) throughout Middle Paleozoic (Version 31-Aug-2021), Zenodo, 10.5281/zenodo.5347006, 2021.

Qiao, T., King, B., Long, J. A., Ahlberg, P. E., and Zhu, M.: Early gnathostome phylogeny revisited: multiple method consensus, PLoS One, 11(9), e0163157, doi:10.1371/journal.pone.0163157, 2016.

Sallan, L., Friedman, M., Sansom, S. R., Bird, M. C., and Sansom, J. I.: The nearshore cradle of early vertebrate diversification, Science, 362, 460-464, doi: 10.1126/science.aar3689, 2018.

Scotese, C. R.: Tutorial: PALEOMAP paleoAtlas for GPlates and the paleoData plotter program, Technical Report, 56, https://www. earthbyte.org/paleomap, last access: 31 August 2021.

Trinajstic, K., Boisvert, C., Long, J., Maksimenko, A., and Johanson, Z.: Pelvic and reproductive structures in placoderms (stem gnathostomes), Biol. Rev., 90(2), 467-501, doi:10.1111/brv.12118, 2015.

Walliser, O.H.: Global events in the Devonian and Carboniferous, in: Global events and event stratigraphy in the Phanerozoic, edited by: Walliser O.H., pp. 225-250, Springer, Berlin, Heidelberg, New York, 1996.

Wang, J. Q.: The Antiarchi from Early Silurian of Hunan, Vertebr. Palasiat., 29(3), 240-244, 1991.

Wang, S. T.: A new antiarch from the Early Devonian of Guangxi, Vertebr. Palasiat., 25, 81-90, 1987.

Wang, W., Qu, Q. M., and Zhu, M.: A brief review of the Middle Palaeozoic vertebrates from Southeast Asia, Palaeoworld, 19(1-2), 27-36, doi:10.1016/j.palwor.2009.12.005, 2010.

Xu, H. H., Niu, Z. B., and Chen, Y. S.: A status report on a section-based stratigraphic and palaeontological database the Geobiodiversity Database, Earth Syst. Sci. Data, 12, 3443–3452, doi: 10.5194/essd-12-3443-2020, 2020.

Young, G. C.: Stratigraphic occurrence of some placoderm fishes in the Middle and Late Devonian, Newsl. Stratigr., 243-261, 1974.

Young, G. C.: An asterolepidoid antiarch (placoderm fish) from the Early Devonian of the Georgina Basin, central Australia, Alcheringa, 8, 65-80, 1984a.

Young, G. C.: Comments on the phylogeny and biogeography of antiarchs (Devonian placoderm fishes), and the use of fossils in biogeography, Proc. Linn. Soc. N. S. W., 107(3), 443-473, 1984b.

Young, G. C.: Antiarchs (placoderm fishes) from the Devonian Aztec siltstone, southern Victoria Land, Antarctica, Palaeontogr. Abt. A, 202, 1-125, 1988.

Young, G. C.: Devonian vertebrate distribution patterns and cladistic analysis of palaegeographic hypotheses, Geol. Soc. Lond., Mem., 12(1), 243-255, doi:10.1144/gsl.mem.1990.012.01.23, 1990a.

Young, G. C.: New antiarchs (Devonian placoderm fishes) from Queensland, with comments on placoderm phylogeny and biogeography, Mem. Queensland Mus., 28(1), 35-50, 1990b.

Young, G. C.: Placoderms (armored fish): dominant vertebrates of the Devonian period, Annu. Rev. Earth Pl. Sc., 38(1), 523-550, doi:10.1146/annurev-earth-040809-152507, 2010.

Young, G. C., Burrow, C. J., Long, J. A., Turner, S., and Choo, B.: Devonian macrovertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica), Palaeoworld, 19, 55-74, doi: 10.1016/j.palwor.2009.11.005, 2010.

Zhao, W. J., Zhu, M., Liu, S., Pan, Z. H., and Jia, L. T.: A new look at the Silurian fish-bearing strata around the Shanmen Reservoir in Lixian, Hunan province, J. Stratigr., 40(4), 341-350, 2016.

Zhu, M.: The phylogeny of the Antiarcha (Placodermi, Pisces), with the description of Early Devonian antiarchs from Qujing, Yunnan, China, Bull. Mus. Natl. Hist. Nat., Sect. C, 18, 233-347, 1996.

Zhu, M.: Catalogue of Devonian vertebrates in China, with notes on bio-events, CFS, Cour. Forschungsinst. Senckenberg, 223, 373-390, 2000.

Zhu, M., Ahlberg, P. E., Pan, Z. H., Zhu, Y. A., Qiao, T., Zhao, W. J., Jia, L. T., and Lu, J.: A Silurian maxillate placoderm illuminates jaw evolution, Science, 354(6310), 334-336, doi:10.1126/science.aah3764, 2016.

Zhu, M., Yu, X. B., Ahlberg, P. E., Choo, B., Lu, J., Qiao, T., Qu, Q. M., Zhao, W. J., Jia, L. T., Blom, H., and Zhu, Y. A.: A Silurian placoderm with osteichthyan-like marginal jaw bones, Nature, 502(7470), 188-193, doi:10.1038/nature12617, 2013.

Zhu, Y. A., Lu, J., and Zhu, M.: Reappraisal of the Silurian placoderm *Silurolepis* and insights into the dermal neck joint evolution, R. Soc. Open Sci. ,6(9), 191181, doi: 10.1098/rsos.191181, 2019.

Zigaite, Z. and Blieck, A.: Chapter 28 Palaeobiogeography of Early Palaeozoic vertebrates, Geol. Soc. Lond., Mem., 38(1), 449-460, doi:10.1144/m38.28, 2013.