

RESEARCH

Open Access



Late Ordovician cephalopods from Morocco and their implications

Xiang Fang^{1,2*}, Björn Kröger³, Kun Liang^{1,2}, Qing Chen^{1,2}, Jiaqi Song^{1,2}, Lan Jiang^{1,2}, Yaoyan He⁴, Chenggang Wang⁴, Xiongwei Zeng⁴, Hao Liu⁴, Kai Wei⁴, Fafu Wu⁴ and Wenkun Qie^{1,2}

Abstract

The present paper describes the latest cephalopod fauna from the Upper Ordovician in the Anti-Atlas region, Morocco. Two species are reported herein belonging to two genera including one new species, *Tafadnatoceras elfechtense* sp. nov. and *Isorthoceras* sp.; the latter of which marks the first occurrence of the genus in Morocco. The discovery extends the distribution of late Katian cephalopod faunas globally, correlative with other high-latitude cephalopod faunas such as those from the Zagros region of Iran. After the evolutionary peak of the Great Ordovician Biodiversification Event in the Middle to early Late Ordovician, a marine ecosystem crisis led to a decline in biodiversity afterwards. Although the cephalopods continued to flourish in low-latitude regions, the palaeogeographic differentiation was observed in the Anti-Atlas region, where the faunas in the high-latitude region experienced a significant decline. The pattern aligns with the changes in the latitudinal diversity gradient from the Middle to Late Ordovician. Furthermore, the distributions of the cephalopod faunas in the Late Ordovician may have been influenced by the emergence of the high-latitude cold current.

Keywords Upper Tiouririne Formation, Katian, Anti-Atlas, Palaeogeography, High-latitude cold current

Introduction

The Ordovician cephalopods from Morocco have been studied rarely in the past. Only a few publications focus on discoveries from Ordovician strata in the Anti-Atlas region of Morocco. Kröger and Lefebvre (2012) first described a rich cephalopod association from the Upper Fezouata Formation, from the same horizon yielding the famous Fezouata fauna of the early Floian (Van Roy et al., 2010). Kröger and Lefebvre (2012) introduced a

high-latitude cephalopod fauna interpreted to have been apex predators during the early pulse of the Great Ordovician Biodiversification Event (GOBE). Ebbestad et al. (2022) reported Late Ordovician mollusk faunas from the central and eastern Anti-Atlas regions including tergomyans, gastropods, bivalves and cephalopods. Among the cephalopod assemblage, *Wadema tattai* Ebbestad et al., 2022, *Tafadnatoceras tiouririnense* Ebbestad et al., 2022, and several other taxa in open nomenclature were first systematically described from the Upper Ordovician of the region.

Recently, the colleagues from the Wuhan Center, China Geological Survey (some of the authors) are conducting geological mapping in the Anti-Atlas (Fig. 1; He et al., 2025a, 2025b). Abundant Late Ordovician specimens consisting of cephalopods, bryozoans, echinoderms, etc., from the lower Palaeozoic were obtained. Here, we describe an assemblage of well-preserved cephalopods from the Upper Ordovician Series. This assemblage represents a typical high-latitude cephalopod fauna from

Handling editor: Christian Klug.

*Correspondence:

Xiang Fang
xfang@nigpas.ac.cn

¹ State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

² University of Chinese Academy of Sciences, Beijing 100049, China

³ Finnish Museum of Natural History, University of Helsinki, Helsinki 00014, Finland

⁴ Wuhan Center, China Geological Survey, Wuhan 430205, China

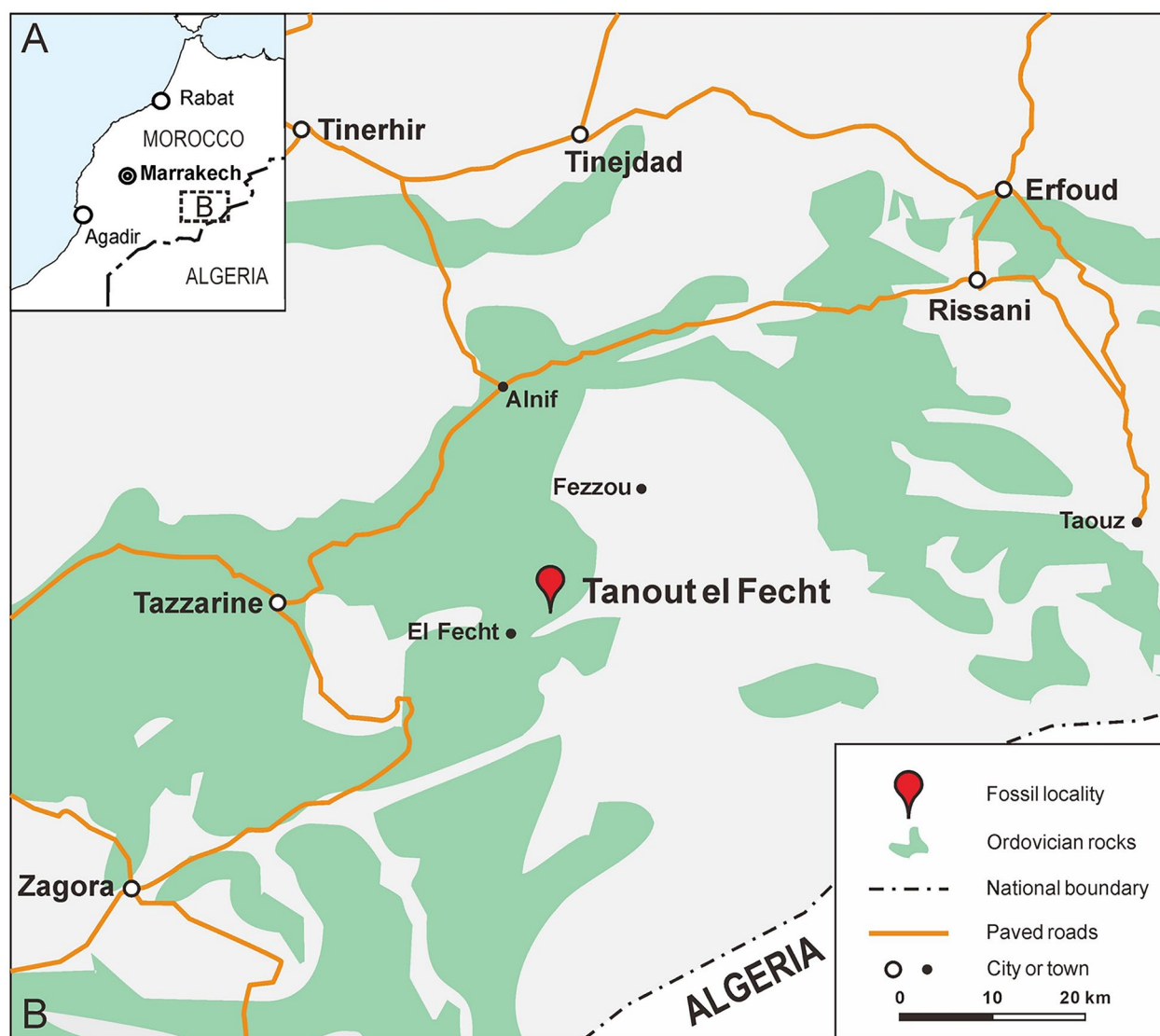


Fig. 1 Fossil locality and outcrops of Ordovician rocks in the Anti-Atlas, Morocco. The distribution of Ordovician deposits is based on Ebbestad et al. (2022)

the late Katian, reflecting the diversity decline after the prominent evolutionary peak of GOBE.

Materials and methods

The materials described and discussed herein were collected during field trips in 2023. A total of 20 cephalopod specimens studied here were extracted from the Upper Tiouririne Formation (Upper Ordovician) at Tanout el Fecht, eastern Anti-Atlas, Morocco (Figs. 1, 2A). The present materials were collected from the upper part of the Upper Tiouririne Formation, from one fossiliferous bed, accompanied by bryozoans and echinoderms (Fig. 2B–D). According to the local and global biostratigraphic correlations (Álvaro et al.,

2022; Goldman et al., 2023), this corresponds to the chitinozoan *Acanthochitina barbata*–*Armoricochitina nigerica* biozones and roughly to the graptolite *Paraorthograptus pacificus* biozone of the late Katian.

All the specimens were cut and polished at the median position and photographed using a Nikon digital camera with Nikkor macro lens in conjunction with a Leica microscope. Furthermore, we used tpsDig2 software (Rohlf, 2015) to measure the morphological characters of the cephalopod specimens. For the applied systematic palaeontological morphological terminology and classification framework comprehensively refer to the published literature (e.g., Ebbestad et al., 2022; Flower,

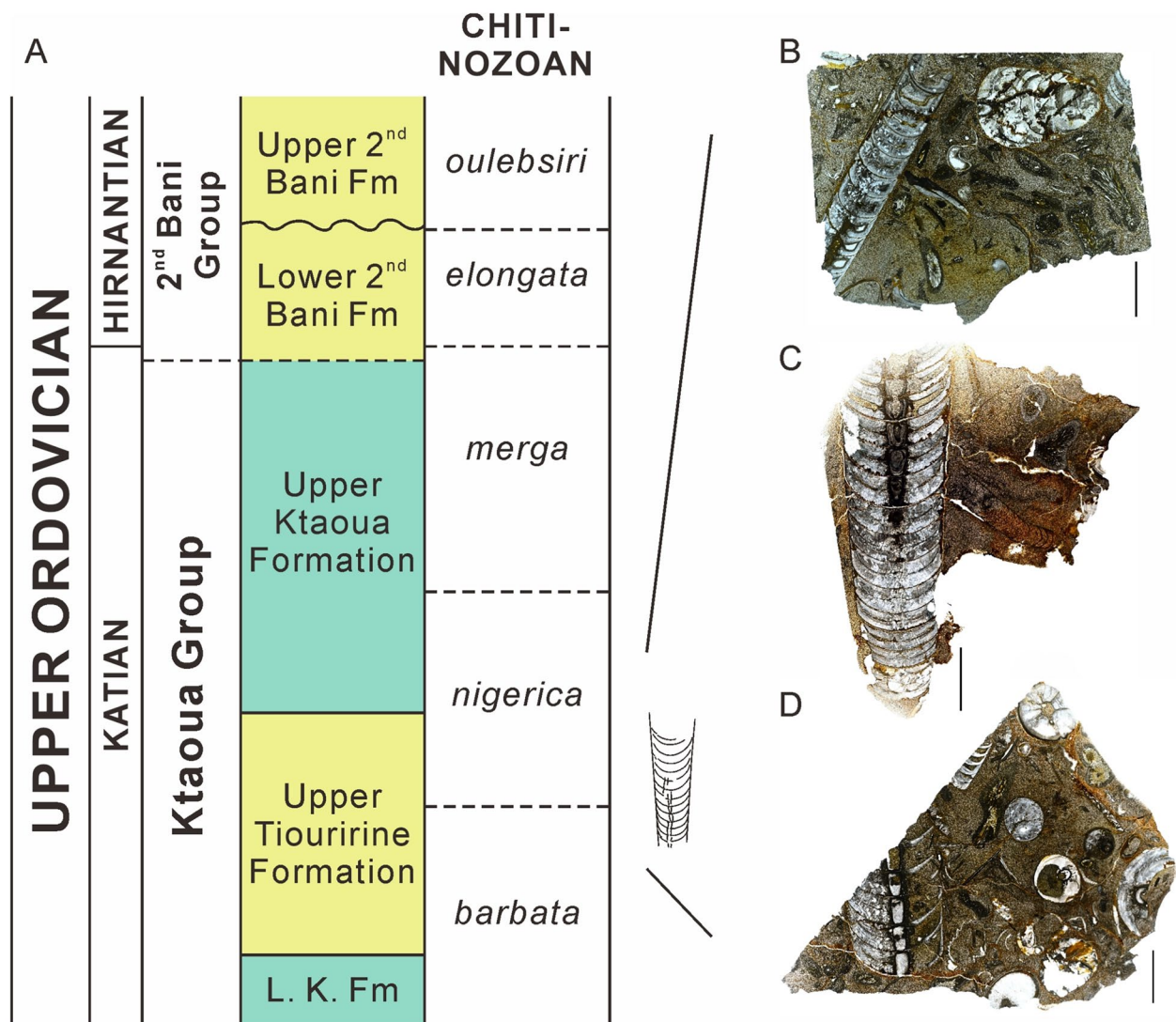


Fig. 2 Stratigraphic column and cephalopod distribution. **A** Lithostratigraphy and biostratigraphy in the study area, chitinozoan biozonation based on Álvaro et al. (2022), L. K. Fm = Lower Ktaoua Formation; **B–D** cephalopods preserved in the Upper Tiouririne Formation accompanied by abundant bryozoans and echinoderms (NIGP207344–NIGP207346); scale bars = 1 cm

1968; Ghavidel-Syooki et al., 2015; King & Evans, 2019; Pohle et al., 2022; Teichert et al., 1964). All specimens are deposited at the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, under the catalogue numbers NIGP207332–207346.

Systematic palaeontology

Class **Cephalopoda** Cuvier, 1797

Subclass **Orthoceratoidea** Teichert, 1967

Order **Orthocerida** Kuhn, 1940

Family **Proteoceratidae** Flower, 1962

Genus **Isorthoceras** Flower, 1962

Type species: *Orthoceras sociale* Hall in Miller, 1877, from the Katian Stage, Upper Ordovician Series, Maquoketa Shale, Iowa, USA.

Diagnosis: Smooth or cancellate orthocones with sub-circular transverse section. Siphuncle subcentral; early segments barrel-shaped and slender, expanding abruptly at septal foramina with cyrtochoanitic to suborthochoanitic septal necks; during ontogeny, later segments become subcylindrical with suborthochoanitic to orthochoanitic septal necks. Endosiphuncular annuli grow forward and backward, joining those of adjacent segments to form continuous parietal lining of nearly uniform



Fig. 3 *Isorthoceras* sp. from the Upper Tiouririne Formation in Anti-Atlas region, Morocco. **A, B** NIGP207332, **A** median section, **B** lateral view; **C, D** NIGP207333, **C** median section, **D** detailed structure of septal necks and connecting rings; scale bars = 1 cm (**A–C**) and scale bar = 1 mm (**D**)

thickness throughout segments (after Ghavidel-Syooki et al., 2015).

Remarks: Typical specimens of *Isorthoceras* display a cancellate sculpture, and longitudinal lirae on the conch surface (Ghavidel-Syooki et al., 2015; Kröger et al., 2009, 2011). According to the spatial and temporal distribution of *Isorthoceras*, Niko (2008) suggested that the taxa

should arise from Laurentia and spread around Baltica during the Boda Event. However, Ghavidel-Syooki et al. (2015) compiled all the occurrences and records of *Isorthoceras* around the world, e.g., Sandbian and Katian of Laurentia, Sandbian of Avalonia and Baltica, and Katian of Arabia and Baltica (Iran and Bohemia). The latter authors accordingly suggested that this genus might have originated from Baltica, or it might be Laurentia. The distribution pattern agrees with the habit of *Isorthoceras* (Kröger et al., 2009).

Isorthoceras sp.

Figure 3

Locality and horizon: Tanout el Fecht, northeastern Anti-Atlas region, Morocco. Upper Tiouririne Formation, Katian Stage, Upper Ordovician Series.

Material: Two specimens, NIGP207332 and NIGP207333, at Tanout el Fecht, northeastern Anti-Atlas, the Upper Tiouririne Formation, Katian Stage, Upper Ordovician Series.

Description: One specimen, NIGP207332 (Fig. 3A, B), comprises portions of the phragmocone and part of the body chamber, 55 mm in maximum diameter and 195 mm in length. The apical angle slightly exceeds 7°. The shell ornament cannot be studied due to the poor preservation of the shell surface. The conch cross-section is circular. The cameral height varies from 6.3 to 13.1 mm (0.18–0.25 of the corresponding conch diameter). The siphuncle is subcentral at the dorsal–ventral median section. The siphuncle is barrel-shaped and expands abruptly at the septal foramen, with a diameter at the septal foramen of 0.07 of the corresponding phragmocone diameter. Septal necks are suborthochoanitic. Siphuncular and cameral deposits are not presented.

The other specimen, NIGP207333 (Fig. 3C, D), comprises portions of a phragmocone 41 mm in maximum diameter and 114 mm in length. The apical angle could not be determined due to the poor preservation of the specimen. The surface of the conch is unknown. The conch cross-section is circular. The cameral height varies between 6.1 and 10.6 mm (0.16–0.27 of the corresponding conch diameter). The siphuncle is subcentral, barrel-shaped, and expands abruptly immediately after the septal foramen, with a diameter at the septal foramen of 0.06 of the phragmocone diameter (Fig. 3D). Septal necks are suborthochoanitic. Connecting rings are adnate at the episeptal surface of the septa. Endosiphuncular and cameral deposits are visible and more developed on the ventral side of the siphuncle and camerae.

Remarks: The material described above does not appear to differ significantly from other specimens of *Isorthoceras* in most internal characters measured, i.e., the large size and

abrupt expansion of the siphuncular segments. Although the present specimens share many characters with the genus *Isorthoceras*, we assign it only in open nomenclature. Furthermore, the species have been suggested to need revision (Ghavidel-Syooki et al., 2015; Kröger et al., 2011).

Family **Stereoplasmoceratidae** Kobayashi, 1934

Genus ***Tafadnatoceras*** Ebbestad et al., 2022

Type species: *Tafadnatoceras tiouririnense* Ebbestad et al., 2022 from the Katian Stage, Upper Ordovician Series, Upper Tiouririne Formation at Tafilalt, eastern Anti-Atlas, Morocco.

Included species: *Tafadnatoceras tiouririnense* Ebbestad et al., 2022; *Tafadnatoceras elfechtense* sp. nov. (this work).

Diagnosis: Slightly curved orthocones with central siphuncle; siphuncle expanded within chambers with adnate area at septa and small septal perforation; septal necks cyrtchoanitic; connecting rings adnate during late growth stages; with siphuncular lining composed of stacked layers of parietal deposits; with cameral deposits (modified after Ebbestad et al., 2022).

Remarks: Ebbestad et al. (2022) proposed that the genus *Tafadnatoceras* is similar to *Adnatoceras* Flower, 1939 and *Paradnatoceras* Chen & Liu, 1974 but differs in having a continuous lining inside the siphuncle. Moreover, the species of *Tafadnatoceras* resemble *Isorthoceras bisignatum* (Barrande, 1877) from Bohemia, Zagros of Iran (Ghavidel-Syooki et al., 2015) and the Moroccan material presented here, but differ in lacking the *Isorthoceras*-like reticulate ornamentation (Ebbestad et al., 2022).

***Tafadnatoceras elfechtense* sp. nov.**

Figures 4, 5, 6, 7

urn:lsid:zoobank.

org:act:33F0B118-CC6D-4AB1-90CF-83D09871B323

Etymology: Referring to the type locality, Tanout el Fecht, Morocco.

Holotype: Body chamber with a rather long part of the phragmocone, NIGP207336 (Figs. 5C, 6B, C, 7).

Paratype: NIGP207334 (Figs. 5A, 6E), NIGP207337 (Figs. 5D, 6A), NIGP207338 (Figs. 5E, 6D), NIGP207343 (Figs. 5J, 6F).

Type locality and horizon: Tanout el Fecht, north-eastern Anti-Atlas. Upper Tiouririne Formation, Katian Stage, Upper Ordovician Series.

Material: Twelve specimens, NIGP207334–NIGP207345 at Tanout el Fecht, northeastern Anti-Atlas region, Morocco, the Upper Tiouririne Formation, Katian Stage, Upper Ordovician Series.

Diagnosis: Orthoconic phragmocone, with an angle of expansion of ca. 10°; conch cross-section circular; siphuncle central with septal perforation diameter ca. 0.05 of the corresponding conch diameter; siphuncular segments expanded, barrel-shaped; connecting rings adnate to septa, adnation wide; septal necks cyrtchoanitic and brim length equal to adnation length; parietal siphuncular deposits form continuous linings; massive episepal and hyposeptal deposits.

Description: The holotype NIGP207336 is a portion of a phragmocone with a length of 47.9 mm and a diameter of 10.9–16.7 mm (angle of expansion ca. 9.6°; Fig. 5C). The conch cross-section is circular. The cameral height varies between 3.1 and 3.7 mm (0.20–0.34 of the corresponding conch diameter). The conch surface



Fig. 4 A rich cephalopod bed yielding *Tafadnatoceras elfechtense* sp. nov. from the Upper Tiouririne Formation in the northeastern Anti-Atlas, Morocco; scale bar = 2 cm



Fig. 5 *Tafadnatoceras elfeichtense* sp. nov. from the Upper Tiouririne Formation in Anti-Atlas region, Morocco. **A** paratype, median section, NIGP207334; **B** median section, NIGP207335; **C** holotype, median section, NIGP207336; **D** paratype, median section, NIGP207337; **E** paratype, median section, NIGP207338; **F** median section, NIGP207339; **G** median section, NIGP207340; **H** median section, NIGP207341; **I** median section, NIGP207342; **J** paratype, median section, NIGP207343; scale bars = 5 mm

is nearly smooth, probably due to poor preservation. The siphuncle is almost central with narrow septal perforation (minimum 0.05 of the corresponding conch

diameter). The septal necks are cyrtchoanitic with a brim ca. 0.22 mm in length and ca. 0.45 mm in width. The connecting rings are barrel-shaped in the median

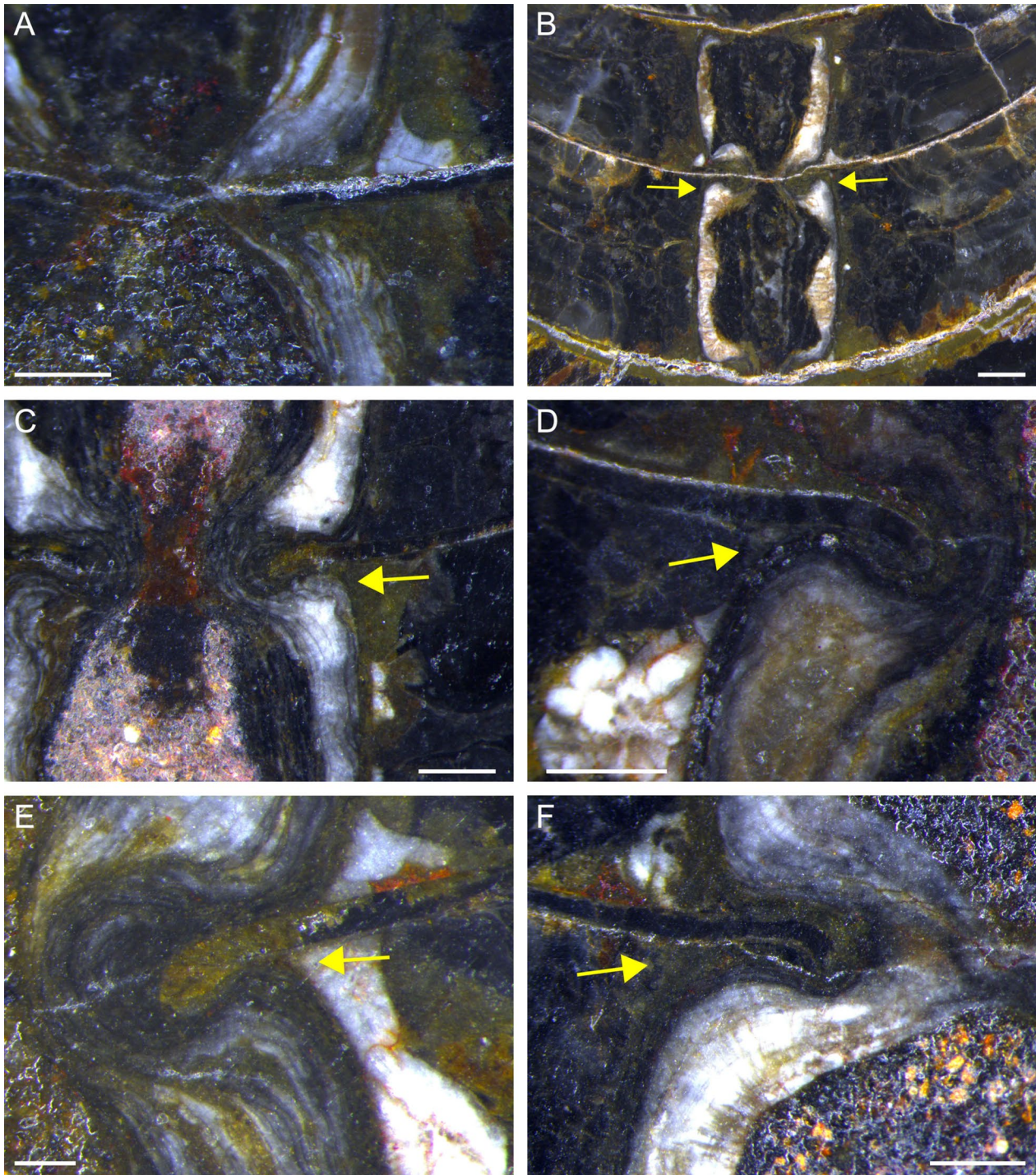


Fig. 6 Detailed structures of *Tafadnatoceras elfeichtense* sp. nov. from the Upper Tiouririne Formation. **A** paratype, NIGP207337; **B**, **C** holotype, NIGP207336; **D** paratype, NIGP207338; **E** paratype, NIGP207334; **F** paratype, NIGP207343; arrows indicate the anteriorly bent connecting rings; scale bars=0.5 mm (**A**–**D**, **F**), scale bar=1 mm (**B**) and scale bar=0.2 mm (**E**)

section (Fig. 6B, C, 7). The expansion of the siphuncular segment at its mid-length has a diameter of 0.18 of the corresponding conch diameter. In this specimen,

the connecting ring is adnate to the episepal surface of the septum for a width of 0.45 mm, equal to the length of corresponding septal necks. Parietal siphuncular

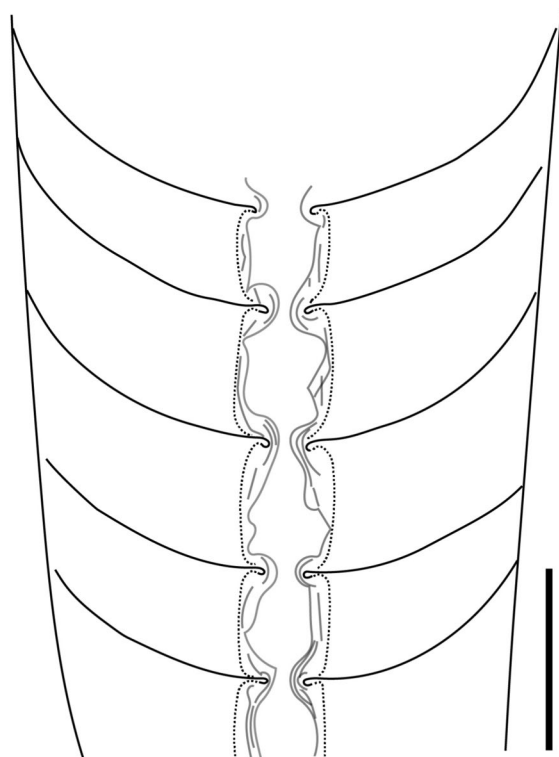


Fig. 7 Interpretative drawing of the *Tafadnatoceras elfeichtense* sp. nov., holotype, NIGP207336, black = conch and septal, grey = siphuncular deposits, dashed line = connecting ring; scale bar = 5 mm

deposits form continuous linings. Massive, irregular episeptal and hyposeptal deposits occur.

Other specimens, paratypes NIGP207334, NIGP207337, NIGP207338 and NIGP207343, reveal siphuncular deposits similar to those of the holotype, containing parietal continuous linings with calcite and argillaceous layers (Fig. 6A, D–F). The calcite layers become thinner or are absent at the septal foramen. The septal necks in NIGP207334 and NIGP207343 are cyrtchoanitic, with an equal width between brim and area of adnation (Fig. 6E, F). The connecting rings expand abruptly and bend anteriorly (Fig. 6E).

Remarks: The ornament of the present material is unknown. The specimens described above are similar to *Tafadnatoceras tiouririnense*, in general features such as the angle of conch expansion, the siphuncular shape and position and with respect to the parietal siphuncular deposits with continuous linings. However, the specimens of *T. elfeichtense* sp. nov. possess a wider septal neck brim and connecting ring adnation compared to the type species *T. tiouririnense*. Moreover, the new species differs in having cameral deposits and anteriorly bent connecting rings.

Discussions

Although the Middle to Late Ordovician was supposed to be the evolutionary peak through GOBE, individual fossil groups varied significantly in diversification patterns (Deng et al., 2021; Servais & Harper, 2018), e.g., brachiopods thrived in the early Middle Ordovician and cephalopods in the early Late Ordovician (Harper & Rong, 2001; Kröger & Zhang, 2009). The diversity evolution pattern and palaeogeographic differentiation of Ordovician cephalopod faunas revealed a global Ordovician diversity increase at the genus level climaxing during the early Katian (Kröger & Zhang, 2009; Kröger, 2013a).

The Late Ordovician cephalopods from Morocco were first systematically described by Ebbestad et al. (2022), and before that, only some in open nomenclature were mentioned (Termier & Termier, 1950). Among the cephalopod fauna reported, *Wadema*, a Middle to early Late Ordovician actinoceroid in low-latitude regions of, e.g., North China, Himalaya, Thailand, was unexpectedly found in Morocco (Chen, 1983; Stait & Burrett, 1984; Wade, 1977). Furthermore, the new genus *Tafadnatoceras* was established by Ebbestad et al. (2022), which is morphologically similar to the Bohemian taxon *Isorthoceras bisignatum* (Barrande, 1877). *I. bisignatum* is also known from high-latitude regions such as the Zagros region of Iran during the Late Ordovician (Ghavidel-Syooki et al., 2015). In the present paper, we improved the faunal portrait by documenting the presence of *Isorthoceras* in the Anti-Atlas region, suggesting a closer relationship between the faunas in the high-latitude regions.

However, the cephalopod faunas had different faunal features from the Middle to Late Ordovician, and the diversity distinctly decreased (Kröger & Zhang, 2009; Kröger, 2013a), especially in the high-latitude regions. In the light of the changes in the latitudinal diversity gradient resulting from the Middle Ordovician global cooling, the tropical cephalopod faunas subsequently experienced a heterogeneous diversified development (Kröger, 2017). Kröger (2013b) recorded 61 species belonging to 31 genera from the latest Katian Boda Limestone in Dalarna, Sweden, where the cephalopod fauna diversified rapidly. Kröger and Ebbestad (2014) analyzed the palaeoecology and palaeogeography of cephalopods from the Boda Limestone, suggesting the similarities between the faunas of Baltica and Avalonia, southwestern Kazakhstan, as well as Laurentia. Recently, Kröger (2025) reviewed the cephalopod collections from northern Estonia, and distinguished 90 species of 35 genera of the late Katian. The palaeogeographic study revealed that the Baltoscandian and Laurentian assemblages are highly similar during the late Katian.

In addition, the most abundant cephalopod fauna during the mid-late Katian was found in South China, particularly

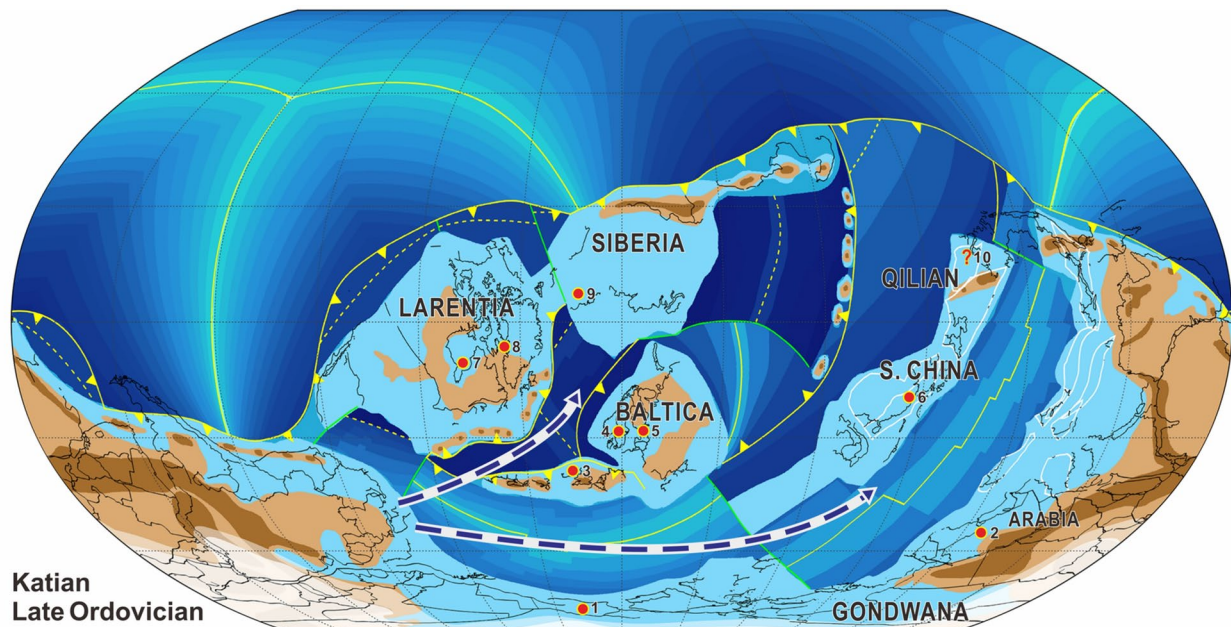


Fig. 8 Palaeogeographic distributions of mid-late Katian cephalopod faunas (based on maps from Scotese, 2023, fig. 11, 450 Ma, Katian Stage). 1. Anti-Atlas, Morocco; 2. High Zagros, Iran; 3. Tyrone, Northern Ireland; 4. Dalarna, Sweden; 5. Northern Estonia; 6. Zhejiang-Jiangxi, South China; 7. Cincinnati Arch, USA; 8. Anticosti Island, Canada; 9. Omulev Mountains, Siberia; 10. Qilian Mountains, Northwestern China. Data sources from Balashov (1962), Lai (1980), The Bureau of Geology and Mineral Resources, Qinghai Province (1991), Evans (1993), Holland (1993), Frey (1995), Holland and Copper (2008), Kröger (2013b, 2025), Ghavidel-Syooki et al. (2015), and Ebbestad et al. (2022). Dark blue arrows indicate the high-latitude cold current (Jin et al., 2018; Zhang et al., 2022)

in the Jiangshan-Changshan-Yushan (JCY) area in the Zhejiang and Jiangxi Provinces (Lai, 1980). In total, 27 species of 17 cephalopod genera have been reported from the latest Katian Xiazhen and Sanjushan formations. Most of them are considered as endemic taxa, but a few were widely distributed, e.g., *Diestoceras*, *Actinoceras*, *Trocholites*, and *Orthonybyoceras*. From Laurentia, only a few cephalopods were described at the species level from the mid-upper Katian Stage (Maysvillian–Richmondian, Cincinnati) in the Cincinnati Arch of USA (Frey, 1995) and in the Anticosti Island of Canada (Holland & Copper, 2008). There are also some genus records in Ireland and northern England, located in Avalonia, including *Trocholites*, *Zitteloceras*, and *Strandoceras* (Evans, 1993; Holland, 1993), and Omulev Mountains of Siberia, i.e., *Rossicoceras*, *Valcouroceras*, and *Charactoceras* (Balashov, 1962). Additionally, several doubtful taxa were recorded in open nomenclature from the Koumenzi Formation of the Qilian Mountain area without any figures or descriptions (The Bureau of Geology & Mineral Resources, Qinghai Province, 1991). We recently obtained new material, and will describe and publish them elsewhere, which will further contribute to the understanding of the mid-late Katian cephalopod palaeogeography or palaeoecology.

The distribution pattern of mid-late Katian cephalopods worldwide can be explained by the high-latitude

cool current during the late Katian (Jin et al., 2018; Zhang et al., 2022). However, due to the global cooling during this time interval, the palaeolatitudinal diversity gradient peaked northward to the mid-low-latitude regions (Kröger, 2017), resulting in a narrower distribution in the high-latitude regions (Fig. 8). At the same time, the cephalopod faunas in the low-latitude regions are rich but with increasing endemicity and only a few widely distributed taxa. However, more information is needed to support this viewpoint, especially in poorly studied areas.

Conclusions

A cephalopod assemblage from the Katian section of the Upper Tiouririne Formation from Tanout el Fecht of northeastern Anti-Atlas, Morocco, has been documented. The assemblage comprises two species of orthoceracones belonging to two families: one proteoceratid (*Isorthoceras* sp.) and one stereoplasmoceratid (*Tafadnatoceras elifechtense* sp. nov.). The genus *Isorthoceras* was identified for the first time from the Anti-Atlas. These taxa suggest a high-latitude palaeogeographical affinity of the late Katian (Late Ordovician) cephalopod fauna. Despite the continued flourishing in low-latitude regions, the palaeogeographic differentiation was pronounced, and the cephalopod fauna in high-latitudes became increasingly scarce. The pattern

coincides with the changes in the latitudinal diversity gradient from the Middle to the Late Ordovician. Additionally, the distributions of the cephalopod faunas in the Late Ordovician were probably caused by the emergence of the high-latitude cold current.

Acknowledgements

We thank Fangchen Zhao, Wenhui Wang, Xuejin Wu, Zhikang Kou, Shouhan Wu, Hongyong Zhang, and Youdong Chen for their assistance with the fossil collection and data preparation. We also thank Vojtěch Turek, René Hoffmann and Christian Klug for their constructive comments and suggestions. This is a contribution to IGCP project 735 (Rocks and the Rise of Ordovician Life).

Author contributions

XF, FFW, and WKQ designed the study. XF, KL, QC, YYH, CGW, XWZ, HL, KW, FFW, and WKQ collected data. XF, BK, JQS, and LJ analyzed the data and prepared the first draft of the paper, and produced the figures. All authors revised the manuscript and approved the final version of the paper.

Funding

This work was supported by the National Key Research and Development Program (Grant Numbers 2023YFF0803703, 2023YFF0803701), the Foreign Aid Project of the Ministry of Commerce of the People's Republic of China (Grant Number 202107), and the National Natural Science Foundation of China (Grant Number 42472018).

Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare no competing interests.

Received: 26 March 2025 Accepted: 12 May 2025

Published online: 09 July 2025

References

- Álvarez, J. J., Benharref, M., Destombes, J., Gutiérrez-Marco, J. C., Hunter, A. W., Lefebvre, B., Van Roy, P., & Zamora, S. (2022). Ordovician stratigraphy and benthic community replacements in the eastern Anti-Atlas, Morocco. *Geological Society, London, Special Publications*, 485, 37–67. <https://doi.org/10.1144/SP485.20>
- Balashov, E. G. (1962). *Nautiloidei ordovika sibirskoi platformy*. Izdatel'stvo Leningradskogo Universiteta.
- Barrande, J. (1877). *Système Silurien du centre de la Bohême. 1ère partie: Recherches Paléontologiques, Vol. II. Classe des Mollusques. Ordre des Céphalopodes. Supplément et Série Tardive. Texte*. Prague: Chez l'auteur et éditeur.
- Chen, J. Y., & Liu, G. W. (1974). *Ordovician and silurian nautiloidea*. Science Press.
- Chen, T. E. (1983). The discovery of *Georgina Wade* from Southern Xizang (Tibet), and its significance. *Bulletin of Nanjing Institute of Geology and Palaeontology, Academia Sinica*, 6, 117–131.
- Cuvier, G. (1797). *Tableau élémentaire de l'histoire naturelle des animaux*. Baudouin.
- Deng, Y. Y., Fan, J. X., Zhang, S. H., Fang, X., Chen, Z. Y., Shi, Y. K., Wang, H. W., Wang, X. B., Yang, J., Hou, X. D., Wang, Y., Zhang, Y. D., Chen, Q., Yang, A. H., Fan, R., Dong, S. C., Xu, H. Q., & Shen, S. Z. (2021). Timing and patterns of the great Ordovician biodiversification event and Late Ordovician mass extinction: Perspectives from South China. *Earth-Science Review*, 220, 103743. <https://doi.org/10.1016/j.earscirev.2021.103743>
- Ebbestad, J. O. R., Polechová, M., Kröger, B., & Gutiérrez-Marco, J. C. (2022). Late Ordovician molluscs of the central and eastern Anti-Atlas, Morocco. *Geological Society, London, Special Publications*, 485, 237–296. <https://doi.org/10.1144/SP485.9>
- Evans, D. H. (1993). The cephalopod fauna of the Killybeg Formation (Ordovician, Ashgill), Pomeroy, County Tyrone. *Irish Journal of Earth Sciences*, 12, 155–189.
- Flower, R. H. (1939). Study of pseudorthoceratidae. *Palaeontographica Americana*, 11, 1–214.
- Flower, R. H. (1962). Notes on the michelinoceratida. *New Mexico Bureau of Mines and Mineral Resources, Memoir*, 10, 21–55.
- Flower, R. H. (1968). Part 1 the first great expansion of the actinoceroids; part 2 some additional whiterock cephalopods. *State Bureau of Mines and Mineral Resources New Mexico, Memoirs*, 19, 1–55.
- Frey, R. C. (1995). Middle and Upper Ordovician Nautiloid Cephalopods of the Cincinnati Arch Region of Kentucky, Indiana, and Ohio. *U.S. Geological Survey Professional Paper*, 1006, 1–126.
- Ghavidel-Syooki, M., Evans, D. H., Ghobadi Pour, M., Popov, L. E., Álvaro, J. J., Rakhmonov, U., Klishevich, I. A., & Ehsani, M. H. (2015). Late Ordovician cephalopods, tentaculitids, machaeridians and echinoderms from Kuh-Faraghan, High Zagros, Iran. *Alcheringa*, 39, 530–549. <https://doi.org/10.1080/03115518.2015.1052677>
- Goldman, D., Leslie, S. A., Liang, Y., & Bergström, S. M. (2023). *Ordovician biostratigraphy: index fossils, biozones and correlation*. Special Publications.
- Harper, D. A. T., & Rong, J. Y. (2001). Palaeozoic brachiopod extinctions, survival and recovery: Patterns within the rhynchonelliformeans. *Geological Journal*, 36, 317–328. <https://doi.org/10.1002/gj.897>
- He, Y. Y., Wu, F. F., Zeng, X. W., Wei, K., Li, B. B., Peng, H., Wang, C. G., Cheng, X., Liu, H., Cui, S., Wang, J. X., & Li, F. L. (2025a). Carte Géologique du Maroc au 1/100 000, feuille de Tarhbalt – Mémoire explicative. *Notes et Mémoires du Service Géologique du Maroc, n° 643 bis*.
- He, Y. Y., Wu, F. F., Zeng, X. W., Wei, K., Li, B. B., Peng, H., Wang, C. G., Cheng, X., Liu, H., Cui, S., Wang, J. X., & Li, F. L. (2025b). *Notes et Mémoires du Service Géologique du Maroc, n° 643*. Carte Géologique du Maroc au 1/100 000, feuille de Tarhbalt.
- Holland, C. H. (1993). Nautiloid cephalopods of the Kildare Limestone (Ashgill), Ireland. *Geological Journal*, 28, 37–44. <https://doi.org/10.1002/gj.3350280104>
- Holland, C. H., & Copper, P. (2008). Ordovician and Silurian nautiloid cephalopods from Anticosti Island: Trajectory across the Ordovician–Silurian (O–S) mass extinction boundary. *Canadian Journal of Earth Science*, 45, 1015–1038. <https://doi.org/10.1139/E08-048>
- Jin, J. S., Zhan, R. B., & Wu, R. C. (2018). Equatorial cold-water tongue in the Late Ordovician. *Geology*, 46, 759–762. <https://doi.org/10.1130/G45302.1>
- King, A. H., & Evans, D. H. (2019). High-level classification of the nautiloid cephalopods: A proposal for the revision of the treatise part K. *Swiss Journal of Palaeontology*, 138, 65–85. <https://doi.org/10.1007/s13358-019-00186-4>
- Kobayashi, T. (1934). The Cambro-Ordovician formations and faunas of South Chosen. *Palaeontology, Part I, Middle Ordovician faunas. Journal of the Faculty of Science, University of Tokyo*, 3, 329–519.
- Kröger, B. (2013a). Cambrian–Ordovician cephalopod palaeogeography and diversity. *Geological Society*, 38, 429–448. <https://doi.org/10.1144/M38.27>
- Kröger, B. (2013b). The cephalopods of the Boda Limestone, Late Ordovician, of Dalarna, Sweden. *European Journal of Taxonomy*, 41, 1–110. <https://doi.org/10.5852/ejt.2013.41>
- Kröger, B. (2017). Changes in the latitudinal diversity gradient during the great Ordovician biodiversification event. *Geology*, 46, 127–130. <https://doi.org/10.1130/G39587.1>
- Kröger, B. (2025). The Lyckholm acme of cephalopods—review of the late Katian (Vormsi–Pirgu regional stages) Ordovician cephalopods of Estonia. *European Journal of Taxonomy*, 978, 1–169. <https://doi.org/10.5852/ejt.2025.978.2801>
- Kröger, B., & Ebbestad, J. O. R. (2014). Palaeoecology and palaeogeography of Late Ordovician (Katian–Hirnantian) cephalopods of the Boda Limestone, Siljan district, Sweden. *Lethaia*, 47, 15–30. <https://doi.org/10.1111/let.12034>
- Kröger, B., Ebbestad, J. O. R., Höglström, A. E. S., & Frisk, Å. M. (2011). Mass concentrations of Hirnantian cephalopods from the Siljan District, Sweden: Taxonomy, palaeoecology and palaeobiogeographic relationships. *Fossil Record*, 14, 35–53. <https://doi.org/10.1002/mmng.201000014>
- Kröger, B., & Lefebvre, B. (2012). Palaeogeography and palaeoecology of early Floian (early Ordovician) cephalopods from the Upper Fezouata

- Formation, Anti-Atlas, Morocco. *Fossil Record*, 15, 61–75. <https://doi.org/10.1002/mmng.201200004>
- Kröger, B., Servais, T., & Zhang, Y. B. (2009). The origin and initial rise of pelagic cephalopods in the Ordovician. *PLoS ONE*, 4, e7262. <https://doi.org/10.1371/journal.pone.0007262>
- Kröger, B., & Zhang, Y. B. (2009). Pulsed cephalopod diversification during the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 273, 174–183. <https://doi.org/10.1016/j.palaeo.2008.12.015>
- Kuhn, O. (1940). *Paläozoologie in tabellen*. G. Fischer.
- Lai, C. G. (1980). Middle and Upper Ordovician cephalopods from Jiangxi and Zhejiang. *Bulletin of the Chinese Academy of Geological Sciences*, 21, 67–99.
- Miller, S. A. (1877). The American Palaeozoic Fossils: A Catalogue of the Genera and Species, with Names of Authors, Dates, Places of Publication, Groups of Rocks in Which Found, and the Etymology and Signification of the Words, and an Introduction Devoted to the Stratigraphical Geology of the Palaeozoic Rocks. Cincinnati: Published by the author
- Niko, S. (2008). *Isorthoceras wahlenbergi*, a new Late Ordovician cephalopod from the Ordovician of Dalarna, Sweden. *Palaeontological Research*, 12, 195–198. [https://doi.org/10.2517/1342-8144\(2008\)12\[195:WANLO\]2.0.CO;2](https://doi.org/10.2517/1342-8144(2008)12[195:WANLO]2.0.CO;2)
- Pohle, A., Kröger, B., Warnock, R. C., King, A. H., Evans, D. H., Aubrechtová, M., Cichowolski, M., Fang, X., & Klug, C. (2022). Early cephalopod evolution clarified through Bayesian phylogenetic inference. *BMC Biology*, 20, 1–30. <https://doi.org/10.1186/s12915-022-01284-5>
- Rohlf, F. J. (2015). *TpsDig2, digitize landmarks and outlines* [software version 2.20]. State University of New York.
- Scotese, C. R. (2023). Ordovician plate tectonic and palaeogeographical maps. *Geological Society*, 532, 91–109. <https://doi.org/10.1144/SP532-2022-311>
- Servais, T., & Harper, D. A. T. (2018). The great Ordovician Biodiversification event (GOBE): Definition, concept and duration. *Lethaia*, 51, 151–164. <https://doi.org/10.1111/let.12259>
- Stait, B. A., & Burrett, C. (1984). Ordovician nautiloid faunas of Central and Southern Thailand. *Geological Magazine*, 121, 115–124. <https://doi.org/10.1017/S0016756800028089>
- Teichert, C. (1967). Major features of cephalopod evolution. In C. Teichert & E. L. Yochelson (Eds.), *Essays in paleontology and stratigraphy: R.C. Moore commemorative volume* (pp. 162–210). University of Kansas Press.
- Teichert, C., Kummel, B., Sweet, W. C., Stenzel, H. B., Furnish, W. M., Glenister, B. F., Erben, H. K., Moore, R. C., & Zeller, D. E. N. (1964). *Treatise on invertebrate Paleontology, part K, Mollusca 3*. The University of Kansas Press.
- Termier, G., & Termier, H. (1950). Paleontologie marocaine. Tome II, Invertébrés de l'Ere primaire, fascicule 3. Mollusques. *Notes Et Mémoires Du Service Géologique Du Maroc*, 78, 1–247.
- The Bureau of Geology and Mineral Resources, Qinghai Province. (1991). *Regional geology of Qinghai Province*. Beijing: Geological Publishing House.
- Van Roy, P., Orr, P. J., Botting, J. P., Muir, L. A., Vinther, J., Lefebvre, B., El Hariri, K., & Briggs, D. E. G. (2010). Ordovician faunas of Burgess Shale type. *Nature*, 465, 215–218. <https://doi.org/10.1038/nature09038>
- Wade, M. (1977). Georginidae, new family of actinoceratoid cephalopods, Ordovician, Australia. *Memoirs of the Queensland Museum*, 18, 1–15.
- Zhang, J. P., Li, C., Fang, X., Li, W. J., Deng, Y. Y., Tu, C. Y., Algeo, T. J., Lyons, T. W., & Zhang, Y. D. (2022). Progressive expansion of seafloor anoxia in the Middle to Late Ordovician Yangtze Sea: Implications for concurrent decline of invertebrate diversity. *Earth and Planetary Science Letters*, 598, 117858. <https://doi.org/10.1016/j.epsl.2022.117858>

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.