

Tohokubelus gen. nov., the Oldest Belemnite from the Olenekian (Lower Triassic) of Northeast Japan

Authors: Niko, Shuji, and Ehiro, Masayuki

Source: Paleontological Research, 26(2): 115-123

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/PR200036

The BioOne Digital Library (<u>https://bioone.org/</u>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<u>https://bioone.org/subscribe</u>), the BioOne Complete Archive (<u>https://bioone.org/archive</u>), and the BioOne eBooks program offerings ESA eBook Collection (<u>https://bioone.org/esa-ebooks</u>) and CSIRO Publishing BioSelect Collection (<u>https://bioone.org/csiro-ebooks</u>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Tohokubelus gen. nov., the oldest belemnite from the Olenekian (Lower Triassic) of Northeast Japan

SHUJI NIKO¹ AND MASAYUKI EHIRO²

¹Department of Environmental Studies, Faculty of Integrated Arts and Sciences, Hiroshima University, Higashihiroshima 739-8521, Japan (e-mail: niko@hiroshima-u.ac.jp)

²The Tohoku University Museum, Sendai 980-8578, Japan

Received August 28, 2020; Revised manuscript accepted November 6, 2020

Abstract. A new sinobelemnitid belemnite genus, *Tohokubelus*, is described based on *T. takaizumii* sp. nov. from the late Olenekian (late Early Triassic) mudstone of the Osawa Formation belonging to the South Kitakami Belt in the Utatsu area, Miyagi Prefecture, Northeast Japan. The present discovery is important because this species is the oldest belemnite and extends downwardly the range of the Belemnitida from the Carnian (early Late Triassic). We concluded that the order appeared first in the earliest Triassic in the low-latitude area of the west-ernmost part of the Panthalassa, then belemnites spread to habitats in the Paleo- and Neo-Tethys in the Early Jurassic by the equatorial currents from the Panthalassa to the Tethys.

Keywords: Belemnitida, Osawa Formation, Sinobelemnitidae, South Kitakami Belt, Triassic

Introduction

The Belemnitida (= belemnites sensu stricto) is an order of cephalopods that evolved probably from the xiphoteuthidid Aulacoceratida (Jeletzky, 1966; Keupp and Fuchs, 2014). Its general body plan is characterized by an internal shell consisting of three parts (rostrum, phragmocone, and pro-ostracum), subcylindrical mantle, paired fins, and ten arms with hooks (Spaeth, 1975; Donovan and Crane, 1992; Fuchs and Hoffmann, 2017; Hoffmann and Stevens, 2020). In comparison with numerous detailed research results in Europe (e.g. Miller, 1829; Riegraf, 1995; Riegraf et al., 1998; Dera et al., 2016), our knowledge about Japanese belemnites is limited, and only six named species have been described previously: Neohibolites mivakoensis Hanai, 1953, from the Lower Cretaceous of Iwate Prefecture, N. kubotai Niko and Hayakawa, 2005, from the Lower Cretaceous of Hokkaido, Acrocoelites (Odontobelus) mantanii Niko and Kameya, 2006, from the Early Jurassic of Yamaguchi Prefecture, Sichuanobelus utatsuensis Iba, Sano, Mutterlose and Kondo, 2012, from the Lower Jurassic of Miyagi Prefecture, Nipponoteuthis katana Iba, Sano and Mutterlose, 2014, from the Lower Jurassic of Miyagi Prefecture, and Eocylindroteuchis? yokoyamai Iba, Sano and Mutterlose, 2014, from the Lower Jurassic of Miyagi Prefecture. This study primarily aims to describe the seventh species, *Tohokubelus takaizumii* gen. et sp. nov., based on material discovered from the Lower Triassic Osawa Formation, Miyagi Prefecture.

Modern researchers agree that the Belemnitida became extinct by the end of the Cretaceous, but its early history is still in debate and the following genera had been proposed for the oldest representative: Eobelemnites (Middle Mississippian; Flower, 1945), Jeletzkya (Early Pennsylvanian; Johnson and Richardson, 1968), Palaeobelemnopsis (late Permian; Chen and Sun, 1982), Sinobelemnites and Sichuanobelus (early Late Triassic; Zhu and Bian, 1984), and Schwegleria (early Early Jurassic; Riegraf, 1980). Among them Eobelemnites and Jeletzkya were excluded by Doyle (1994) and Doyle et al. (1994) who concluded that the stratigraphic information of the former is unreliable and the latter should be placed in the order Phragmoteuthida rather than the Belemnitida. Although assigning Palaeobelemnopsis to the Belemnitida was questioned by Doyle (1994), Doyle et al. (1994) and Riegraf (1995), it remains incertae sedis in the subclass Coleoidea or was questionably placed in the Aulacoceratida without morphological discussion. Iba et al. (2012) confirmed that Sinobelemnites and Sichuanobelus are true belemnites. They were the only genera that indisputably occur from the Triassic before the present new discovery. Limited to Europe, the middle Hettangian genus, Schwegleria, is the oldest belemnite. Doyle (1994), Schlegelmilch (1996), and Weis and Delsate (2006) considered that *Schwegleria* forms the stock of the Belemnitida and attempted reconstructions of early phylogenetic lineages without information from East Asia. Therefore, this study also aims to discuss the origin of the Belemnitida with reexamination of *Palaeobelemnopsis*.

Stratigraphy and ammonoid age of the Osawa Formation

The Osawa Formation in the South Kitakami Belt, Northeast Japan is the second formation of the Lower– Middle Triassic Inai Group, which is divided into the Hiraiso, Osawa, Fukkoshi and Isatomae formations, in ascending order (Onuki and Bando, 1959). The Inai Group, distributed widely in the southern part of the Kitakami Massif (Figure 1), is composed of continuous, fossiliferous, shallow marine (partly alluvial to nearshore marine) clastic sediments, total thickness of which exceeds 2000 m, and therefore, one of the most important reference sequences of the Lower–Middle Triassic of Japan.

The Hiraiso Formation, resting unconformably on the Upper Permian formations, is 200–250 m thick and dominated by coarse- to medium-grained calcareous sandstone with subordinate thin mudstone. Only one age-diagnostic ammonoid, *Tirolites* cf. *ussuriensis* Zharnikova (*in* Buryi and Zharnikova, 1981), has been described from the middle part of the formation (Shigeta and Nakajima, 2017). *Tirolites ussuriensis* was known from the lower part of the Spathian (upper Olenekian) in the South Primorye, Far East Russia (Zakharov and Popov, 2014).

The Osawa Formation is 250-350 m thick and is dominated by laminated mudstones, intercalated with sandstone beds in the lower to middle part. It has yielded rather rich ammonoids, consisting of 27 genera (Bando and Shimoyama, 1974; Ehiro, 1993, 2016; Ehiro et al., 2016a; Ehiro, 2022). The lower to middle part of the formation (the Subcolumbites Zone of Bando and Shimoyama, 1974) is characterized by Columbites parisianus Hyatt and Smith, 1905 and Subcolumbites perrinismithi (Arthaber, 1908), in association with such genera as Hemilecanites, Albanites, Pseudosageceras, Tardicolumbites, Yvesgalleticeras, Hellenites, Metadagnoceras, Procarnites, Olenekoceras, Nordophiceratoides, etc. (Figure 2). The lower part of the upper part (the Arnautoceltites Zone of Bando and Shimoyama, 1974) consists of Arnautoceltites, Nordophiceras, Prenkites, etc. And the uppermost part, the Eodanubites Zone (Ehiro, 2022), yields Pseudosageceras multilobatum Noetling, 1905, Arnautoceltites sp., Procarnites kokeni (Arthaber, 1908), Japonites cf. meridianus Welter, 1915, Eodanubites aff. xinyuanensis Wang, 1978, Procladiscites towaensis (Bando and Ehiro, 1982), etc. (Bando and Ehiro, 1982; Ehiro, 2022). Based on these ammonoids, the lower to upper part and the uppermost part of the Osawa Formation are correlated with the upper Olenekian and the uppermost Olenekian, respectively (Bando and Shimoyama, 1974; Ehiro *et al.*, 2016a; Ehiro, 2022).

The Fukkoshi Formation is composed of thick sandstone and alternating beds of sandstone and mudstone, with a total thickness of 200–300 m. Because of its dominant sandstone facies, the Fukkoshi Formation is almost barren of ammonoids. Only some Anisian species, *Gymnites* cf. *watanabei* (Mojsisovics, 1888), *Hollandites* sp. and *Balatonites* cf. *kitakamicus* (Diener, 1916) were considered to come from the middle part of the Fukkoshi Formation (Onuki and Bando, 1959); however, there are some doubts about the stratigraphic position and locality of these ammonoids (Ishibashi, 2006).

The Isatomae Formation is more than 1,000 m thick and consists of sandy laminated mudstone often with thick sandstones or alternating beds of sandstone and mudstone. From the lowermost part at Kudanohama in Utatsu area, Ishibashi (2006) reported, although not yet described, Grambergia kitakamiensis Ishibashi, 2006, Tropigastrites cf. lahontanus Smith, 1914, Lenotropites isatomaensis Ishibashi, 2006, Ussurites sp., Paracrochordiceras sp. and Leiophyllites pseudopradyumna (Welter, 1915). This Kudanohama ammonoid fauna corresponds to the Lenotropites-Japonites Zone (Aegean: lowermost Anisian) of Qinghai, China (He et al., 1986), Pseudokeyserlingites guexi beds to Lenotropites caurus Zone (lower Anisian) of Nevada (Bucher, 1989), Paracrochordiceras-Japonites beds (Aegean) of Deşli Caira Hill, Romania (Grădinaru et al., 2007) and Chios (Assereto, 1974; Fantini Sestini, 1981). Thus, the Olenekian/Anisian boundary is considered to locate somewhere in the lower part of the Fukkoshi Formation.

Material and methods

The belemnite fossil described here was collected from mudstone float in an outcrop of the Osawa Formation to the north of Heiseinomori, Utatsu area (Figure 1: 38°43′20″N, 141°32′05″E). This outcrop, produced when the preparation work of the athletic field of Heiseinomori was conducted (completed in 1991), is occupied by laminated to poorly laminated, calcareous mudstones (20–30 m in thickness), which strike N-S and dip westerly with moderate angle. The belemnite-bearing boulder is one of the rock lumps scattered by the construction and its lithology is identical with that of the Osawa Formation. The mudstone of the Isatomae Formation, cropping out to the northwest of this outcrop (Figure 1C) is easily distinguished from that of the Osawa Formation and belemnite-



Figure 1. Geological maps of study area, showing distributions of the Pre-Cretaceous tectonic belts in Northeast Japan (A), geology of the southern part of the Kitakami Massif (B), and detailed geology near fossil locality (C). NDB: Nedamo Belt; NKB: North Kitakami Belt; SKB: South Kitakami Belt.



Figure 2. Generalized columnar section of the Inai Group in the South Kitakami Belt and the stratigraphic occurrences of ammonoids. The probable horizon with occurrence of *Tohokubelus takaizumii* gen. et sp. nov. is indicated by asterisk.

bearing mudstone by its rather sandy lithofacies showing remarkable bioturbation. Post-Triassic mudstones distribute far from this site (Figure 1B) and their non-calcareous lithofacies differ from the Osawa Formation. Therefore, it is certain that the belemnite fossil is derived from the Osawa Formation.

The specimen must come from the middle to upper part of the Osawa Formation. But the precise horizon of the belemnite-bearing bed in the Osawa Formation is unknown, because both boundaries of the Hiraiso/ Osawa and Osawa/Fukkoshi formations are not exposed near the fossil site. When the preparation work of the athletic field was conducted, many ammonoid specimens were collected from the present fossil site and its southern extension (present-day Heiseinomori athletic field). They are *Xenoceltites* cf. *crenoventrosus* Chao, 1959, *Nordophiceras* sp., *Preflorianites utatsuensis* Ishibashi, 2006, *Inyoites* aff. *oweni* Hyatt and Smith, 1905, *Stacheites floweri* Kummel, 1969, *Arnautoceltites* sp., *Prenkites* cf. *timorensis* Spath, 1930, and *Leiophyllites pitamaha* (Diener, 1895) (Educational Committee of Utatsu Town, 1996; Ishibashi, 2006). Due to the presence of *Arnautoceltites* species and the absence of *Columbites*, *Subcolumbites* and *Eodanubites* species in this fauna, it is most probable that the fossil horizon belongs to the *Arnautoceltites* Zone (lower part of the upper Osawa Formation: upper Olenekian) (Figure 2).

An almost complete rostrum with an indwelling phragmocone (IGPS coll. cat. no. 112442) was available for study, and it is designated herein as the holotype. We did not adopt any invasive methods, such as preparation of polished and new fracture sections, elimination of the rostrum on the phragmocone, and etching, for the holotype in view is of importance. This specimen sustains the condition when it was donated to the Tohoku University Museum. Although detailed internal structure of the phragmocone, accurate position of the protoconch, and nature of fissure of the rostrum are unknown for this reason, observable characteristics described below are enough for the familial assignment and comparisons with related taxa. Determination of ventral and dorsal sides on the rostrum was made by the siphunclar position observable in fracture section (Figure 3D), where cut surfaces and parts of two septa appeared (Figure 3H). These morphologies serve in identification of a dorsal groove and determinations of septal shape and distance. Measurement of an alveolar angle (= apical angle of phragmocone) can be performed at the exfoliated part of the rostrum (Figure 3A).

Systematic paleontology

Subclass Coleoidea Bather, 1888 Order Belemnitida Zittel, 1895 Suborder uncertain Family Sinobelemnitidae Bian and Zhu *in* Zhu and Bian, 1984

Genus Tohokubelus gen. nov.

Type species.—Tohokubelus takaizumii sp. nov., by monotypy.

Diagnosis.—Rostrum relatively thick with nearly circular transverse sections; apex acute; apical region conical; stem and alveolar regions subcylindrical; outline cylindriconical; profile asymmetrical; a deep groove develops on dorsal surface of rostrum; lateral lines absent; alveolus



Figure 3. *Tohokubelus takaizumii* gen. et sp. nov., holotype, IGPS coll. cat. no. 112442. **A**, ventral view; lower, middle, and upper arrows indicate respectively positions of F, E, and D; **B**, left lateral (ventral on left) view; **C**, dorsal view; **D**, transverse section (fracture surface) at alveolar region, venter down; **E**, transverse section (fracture surface) at alveolar region (near protoconch), venter down; **F**, transverse section (fracture surface) at alveolar region (near protoconch), venter down; **F**, transverse section (fracture surface) at alveolar region (near protoconch), venter down; **F**, transverse section (fracture surface) at alveolar region (near protoconch), venter down; **F**, transverse section (fracture surface) at apical region, venter down; **G**, partial enlargement of F to show concentric growth rings, venter up; **H**, partial enlargement of D to show septa (upper two arrows) and siphuncle (lower arrow). A–F, H; coated with ammonium chloride. G; submerged in water. Scale bar is 12 mm in A–C, 6 mm in D–F, 3 mm in G, 2 mm in H.

(and phragmocone) laterally compressed; alveolar angle moderate, approximately 20°.

Etymology.—The generic name refers to the Tohoku District, from which the type species of the new genus was recovered, and a Greek word " $\beta \epsilon \lambda o \zeta$ " (belus) meaning arrow.

Remarks.—The most diagnostic character of *Tohokubelus* gen. nov. is a single dorsal groove on the rostrum that suggests it should be included within the Sinobelemnitidae. Two genera, *Sinobelemnites* Zhu and Bian (1984; type species, *S. cornutus* Zhu and Bian, 1984) and *Sichuanobelus* Zhu and Bian (1984; type species, *S. longmenshanensis* Zhu and Bian, 1984), were previously known from this family. Among them, *Sichuanobelus* is most similar to the new genus, but its rostrum has a conical outline and laterally compressed transverse sections, and the dorsal groove is somewhat shallower than that of *Tohokubelus*. *Sinobelemnites* clearly differs from *Tohokubelus* by the presence of lateral lines.

Tohokubelus takaizumii sp. nov.

Figure 3

Diagnosis.—As for the genus.

Description.-Rostrum is relatively thick, non-hastate and small sized, having 39 mm in total length. Except for apical region having dorsoventrally depressed oval cross sections, transverse sections of rostrum are nearly circular. Rostral diameters 6.0 mm near estimated position of protoconch and 6.2 mm (maximum diameter) at adoral end. Apex acute with apical angle of 27° and slightly displaced toward dorsal side. Postalveolar region divided into conical apical and subcylindrical stem regions, but their boundary is rather ambiguous. Length of postalveolar region is approximately 24 mm. Alveolar region subcylindrical, short, approximately 15 mm in length. Outline cylindriconical. Profile slightly asymmetrical. Dorsal surface of rostrum marked by a single deep groove that begins posteriorly near boundary of apical and stem regions and reaches adoral end of alveolar region. Profiles of groove are V-shaped with 0.5 mm in depth and 2.1 mm in width at alveolar region. Lateral lines absent.

119

Alveolus (= rostrum cavum; and phragmocone preserved in it) is conical, laterally compressed in transverse section with 0.8 in ratio of lateral diameter per dorsoventral one. Alveolar angle (= apical angle of phragmocone) moderate for the Belemnitida, approximately 20°. Septa are concave adapically and closely spaced. Siphuncle along ventral margin. Diameter of siphuncle is 0.4 mm at lateral phragmocone diameter of 3.1 mm. Apical line (observed in transverse sections) faintly shifts dorsal from central axis of rostrum, indicating position ratio (distance from apical line to ventral surface/diameter of rostrum) of 0.52. Pro-ostracum is not preserved. Microstructure of rostrum consists of radially arranged fibers (presumably calcite) showing concentric growth rings.

Age and occurrence.—Late Olenekian; lower part of the upper Osawa Formation in the Utatsu area, Miyagi Prefecture, Tohoku District, Northeast Japan.

Etymology.—The specific name honors Mr. Yukihiro Takaizumi who found the holotype of this species.

Remarks.—*Sichuanobelus utatsuensis* Iba, Sano, Mutterlose and Kondo (2012, p. 912, 913, figs. 3A–3J) from the Hettangian (Early Jurassic) Niranohama Formation in the Utatsu area was the only representative of the Sinobelemnitidae outside of Southwest China. The cylindriconical outline and a deep dorsal groove of *S. utatsuensis* resembles *Tohokubelus takaizumii* sp. nov. rather than the type species of *Sichuanobelus*. The principal difference between *S. utatsuensis* and *T. takaizumii* is in alveolar angles, the former indicates relatively rapid expansion attaining 30° whereas this value of the latter is moderate for the order. Laterally compressed oval sections with rather flattened lateral sides in *S. utatsuensis* also serve to differentiate.

Discussion

Systematic implications.—Its large alveolar angle (approximately 20°) for the Coleoidea, closely spaced septa, rostrum consisting of radially arranged fibers, and concentric growth rings warrant a placement of *Tohokubelus takaizumii* gen. et sp. nov. in the Belemnitida instead of the Aulacoceratida.

Chen and Sun (1982) stated that a Changhsingian (late Permian) genus *Palaeobelemnopsis* Chen *in* Chen and Sun (1982; type species, *P. sinensis* Chen *in* Chen and Sun, 1982) from the Dalong Formation in Jian-shi County, Hubei Province represents the first Paleozoic and the oldest occurrence of the order Belemnitida. Their view was supported by a subsequent study by Liu and Su (1999) that was based on material recovered from the adjoining Hunan Province. However, the phragmocone of *Palaeobelemnopsis* is a longiconic orthocone with low expansion angle, long camera, and possibly simple cone-like apex, the characteristics of which are apparently beyond the diagnosis of the Belemnitida. Rather, they show affinity to aulacoceratids and xiphoteuthidids belonging to the order Aulacoceratida. Although surface shapes of the rostra in these genera are different, the "double-sphere" transverse sections provided by the paired dorsolateral depressions on the rostra of *Palaeobelemnopsis* may suggest relationship with an aulacoceratid genus, *Miyagiteuthis* Niko and Ehiro (2018; type species, *Dictyoconites nipponicus* Shimizu and Mabuti, 1941) from the Upper Triassic Saragai Group in the South Kitakami Belt. We think, therefore, *Palaeobelemnopsis* should be removed from the Belemnitida and placed in the Aulacoceratida.

Paleogeographic and paleobiogeographic implications.--Undoubted Triassic records of belemnites were limited to Sinobelemnites and Sichuanobelus that occur in the Carnian (lower Upper Triassic) part of the Maantang Formation in the Longmen Mountains, Sichuan Province, South China (Zhu and Bian, 1984; Iba et al., 2012). Furthermore, some uncertain records of Triassic belemnites are present in South China, including Hu et al. (2011; the Middle Triassic of Yunnan Province) and Iba (2016; the Upper Triassic of Yunnan Province), but they remain undescribed. In the subsequent Early Jurassic age, belemnites extended their habitats westward and reached northern Europe in the Paleo-Tethys (Riegraf, 1980; Weis and Delsate, 2006) and Tibet belonging to the northern margin of Gondwana in the Neo-Tethys (Chen, 1982; Iba et al., 2015).

The paleogeography of the South Kitakami Belt, Northeast Japan, where the Inai Group was deposited, has been reconstructed by using paleobiogeographic data, because no valid palaeomagnetic data have been obtained from the Pre-Cretaceous rocks of the belt due to the thermal effect by the Early Cretaceous granites. The belt is thought to have been located near the South China continent during middle Paleozoic to Triassic based on the Silurian-Permian faunal and floral similarities with those of South China (see Ehiro, 2001; Ehiro *et al.*, 2016b). The Early Triassic ammonoids from the Osawa Formation belong to the *Columbites-Subcolumbites* fauna, which is characteristic in the low latitudinal areas (Ehiro, 1997; Brayard *et al.*, 2009).

Thus, it is likely that South Kitakami had been located at or near South China (Ehiro, 2001; Ehiro *et al.*, 2016b). On the other hand, the Late Permian araxoceratid ammonoid fauna of South Kitakami resembles closely that of the western Tethys Province, not with that of South China (Ehiro, 2019). Brayard *et al.* (2009) stated that the ammonoid fauna of the Osawa Formation (Early Triassic) had a close paleobiogeographic relationship with the eastern area of the equatorial Panthalassa (California, Nevada and Idaho), although South Kitakami was located near South China at that time. Ehiro *et al.* (2016b) also stressed that the Osawa ammonoid fauna is most like that of the western United States and next to those in the western Tethys province such as Albania, Croatia and Greece, not to that of South China.

Based on the paleomagnetic data, the South China continent was located in the low latitude near the equator during the Late Permian to Early Triassic, then migrated to the north and reached to the middle latitude at Late Triassic to Jurassic (e.g. Seguin and Zhai, 1992; Yin and Nie, 1993). During this process, the South and North China continents began to collide, initially at the eastern end, during the Late Permian (Yin and Nie, 1993) or Early Triassic (Zhao et al., 2020). Therefore, at the Early Triassic, it is considered that the connection between the Tethys Sea and the Panthalassa Ocean was already closed on the north of South China, and the potential currents between these two oceans passed to the southern side of South China. Brayard et al. (2009) and Ehiro et al. (2016b) considered that South Kitakami was located at the low-latitude area of the westernmost part of the Panthalassa (the Tethys-Panthalassa border) during the Early Triassic and the Early Triassic ammonoid faunal connection among the eastern Panthalassa, South Kitakami and western Tethys was influenced by these potential currents along the equator. We think that the above-mentioned belemnite migrations from the Panthalassa to the Tethys have also related to these equatorial currents.

Conclusions

1) Tohokubelus takaizumii gen. et sp. nov. (Sinobelemnitidae: Belemnitida) is described from the late Olenekian (late Early Triassic) Osawa Formation in the Utatsu area in Miyagi Prefecture, Northeast Japan. This species represents the oldest and the first Early Triassic record of the order Belemnitida, which was previously thought to have appeared in the Carnian (early Late Triassic). This discovery extends the range of the order back at least 17 m.y. 2) Differentiation from the probable ancestor (xiphoteuthidid Aulacoceratida; see above) into the Belemnitida, chanced in the earliest Triassic near South Kitakami and South China, areas which were situated at the low-latitude area of the westernmost part of the Panthalassa. 3) The equatorial currents from the Panthalassa to the Tethys formed by northward migration of a landmass consisting of South Kitakami and South China had an impact on the expansion of the habitats of belemnites to the Paleo- and Neo-Tethys in the Early Jurassic age.

Acknowledgements

We are indebted to Mr. Yukihiro Takaizumi, who pro-

vided the holotype of *Tohokubelus takaizumii* gen. et sp. nov. for this study and donated it to the Tohoku University Museum. We also thank Drs. Dirk Fuchs and Joerg Mutterlose for their valuable suggestions and improvement of the manuscript.

References

- Arthaber, G. von, 1908: Über die Entdeckung von Untertrias in Albanien und ihre faunistische Bewertung. *Mitteilungen der Geologischen Gesellschaft in Wien*, Band 1, p. 245–289, pls. 11–13.
- Assereto, R., 1974: Aegean and Bithynian: Proposal for two new Anisian substages. Schriftenreihe der Erdwissenschaftlichen Kommissionen, Österreichische Akademie der Wissenschaften, Band 2, p. 23–39.
- Bando, Y. and Ehiro, M., 1982: On some Lower Triassic ammonites from the Osawa Formation at Asadanuki, Towacho, Tomegun, Miyagi Prefecture, Northeast Japan. *Transactions and Proceedings of the Palaeontogical Society of Japan*, n. ser., no. 127, p. 375–385, pl. 60.
- Bando, Y. and Shimoyama, S., 1974: Late Schythian ammonoids from the Kitakami Massif. *Transactions and Proceedings of the Palaeontogical Society of Japan*, n. ser., no. 94, p. 293–312, pls. 40–42.
- Bather, F. A., 1888: XXXVII.—Shell-growth in Cephalopoda (Siphonopoda). *The Annals and Magazine of Natural History, Series*, 6, vol. 1, p. 298–309.
- Brayard, A., Escarguel, G., Bucher, H. and Bruhwiler, T., 2009: Smithian and Spathian (Early Triassic) ammonoid assemblages from terranes: Paleoceanographic and paleogeographic implications. *Journal of Asian Earth Sciences*, vol. 36, p. 420–433.
- Bucher, H., 1989: Lower Anisian ammonoids from the northern Humboldt Range (northwestern Nevada, USA) and their bearing upon the Lower–Middle Triassic boundary. *Eclogae Geologicae Helvetiae*, vol. 82, p. 945–1002.
- Buryi, I. V. and Zharnikova, N. K., 1981: Ammonoids from the *Tirolites* Zone of South Primorye. *Paleontologicheskij Zhurnal*, 1981 (3), p. 61–69. (*in Russian with English abstract*)
- Chao, K., 1959: Lower Triassic ammonoids from Western Kwangsi, China. Palaeontologia Sinica, n. ser. B, no. 9, p. 1–355, pls. 1–45.
- Chen, T., 1982: Mesozoic Coleoidea fauna from Xizang. Paleontology of Xizang, vol. 4, p. 282–325, pls. 1–20. (in Chinese with English abstract)
- Chen, T. and Sun, Z., 1982: Discovery of Permian belemnoids in South China, with comments on the origin of (Coleoidea). Acta Palaeontologica Sinica, vol. 21, p. 181–190, pl. 1. (in Chinese with English abstract)
- Dera, G., Toumoulin, A. and De Baets, K., 2016: Diversity and morphological evolution of Jurassic belemnites from South Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 457, p. 80–97.
- Diener, C., 1895: The Cephaolopoda of the Muschelkalk. Paleontologia indica, Series 15, vol. 2, pt. 2, p. 1–118.
- Diener, C., 1916: Japanische Triasfaunen. Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche Klasse, Band, 92, p. 1–30, pls. 1–7.
- Donovan, D. T. and Crane, M. D., 1992: The type material of the Jurassic cephalopod *Belemnotheuthis*. *Palaeontology*, vol. 35, p. 273–296.
- Doyle, P., 1994: Aspects of the distribution of Early Jurassic belemnites. *Palaeopelagos Special Publication*, vol. 1, p. 109–120.
- Doyle, P., Donovan, D. T. and Nixon, M., 1994: Phylogeny and systematics of the Coleoidea. *The University of Kansas Paleontological*

Contributions, n. ser., no. 5, p. 1–15.

- Educational Committee of Utatsu Town, 1996: *Strata and Ichthyosaur Fossils of Utatsu Town*, 30 p. Educational Committee of Utatsu Town, Utatsu. (*in Japanese; original title translated*)
- Ehiro, M., 1993: Spathian ammonoids *Metadagnoceras* and *Keyserlingites* from the Osawa Formation in the Southern Kitakami Massif, Northeast Japan. *Transactions and Proceedings of the Palaeontogical Society of Japan*, n. ser., no. 171, p. 229–236.
- Ehiro, M., 1997: Ammonoid palaeobiogeography of the South Kitakami Palaeoland and palaeogeography of eastern Asia during Permian to Triassic time. *In*, Jin, Y.-G. and Dineley, D. *eds.*, *Proceedings* of the 30th International Geological Congress, vol. 12, p. 18–28.
- Ehiro, M., 2001: Origins and drift histories of some microcontinents distributed in the eastern margin of Asian Continent. *Earth Science*, vol. 55, p. 71–81.
- Ehiro, M., 2016: Additional Early Triassic (late Olenekian) ammonoids from the Osawa Formation at Yamaya, Motoyoshi area, South Kitakami Belt, Northeast Japan. *Paleontological Research*, vol. 20, p. 1–6.
- Ehiro, M., 2019: Two additional araxoceratid ammonoids from the Wuchiapingian (upper Permian) of the South Kitakami Belt, Northeast Japan. *Earth Science*, vol. 73, p. 139–148.
- Ehiro, M., 2022: Latest Olenekian ammonoids from the uppermost part of the Osawa Formation (Inai Group) in the South Kitakami Belt, Northeast Japan. *Paleontological Research*, vol. 26, p. 137–157.
- Ehiro, M., Sasaki, O. and Kano, H., 2016a: Ammonoid fauna of the upper Olenekian Osawa Formation in the Utatsu area, South Kitakami Belt, Northeast Japan. *Paleontological Research*, vol. 20, p. 90–104.
- Ehiro, M., Tsujimori, T., Tsukada, K. and Manchuk, N., 2016b: Chapter 2a. Palaeozoic basement and associated cover. *In*, Moreno, T., Wallis, S., Kojima, T. and Gibbons, W. *eds.*, *The Geology of Japan*, p. 25–60. Geological Society, London.
- Fantini Sestini, N., 1981: Lower Anisian (Aegean) ammonites from Chios island (Greece). *Rivista Italiana di Paleontologia e Stratigrafia*, vol. 87, p. 41–66.
- Flower, R. H., 1945: A belemnite from a Mississippian boulder of the Caney Shale. *Journal of Paleontology*, vol. 19, p. 490–503, pl. 65.
- Fuchs, D. and Hoffmann, R., 2017: Arm armature of belemnoid coleoids. *Treatise Online*, no. 91, p. 1–20.
- Grădinaru, E., Orchard, M. J., Nicora, A., Gallet, Y., Besse, J., Krystyn, L., Sobolev, E. S., Atudorei, N.-V. and Ivanova, D., 2007: The global boundary stratotype section and point (GSSP) for the base of the Anisian stage: Deşli Caira Hill, North Dobrogea, Romania. *Albertiana*, vol. 36, p. 54–71.
- Hanai, T., 1953: Lower Cretaceous belemnites from Miyako district, Japan. Japanese Journal of Geology and Geography, vol. 23, p. 63–80, pls. 5–7.
- He, G.-X., Wang, Y.-G. and Chen, G.-L., 1986: Early and Middle Triassic cephalopods of Mt. Burhan Budai, Central Qinghai. *In*, Geological Institute of Qinghai Province and Nanjing Institute of Geology and Palaeontology *eds.*, *Carboniferous and Triassic Strata and Fossils from the Southern Slope of Mt. Burhan Budai*, *Qinghai*, *China*, p. 171–274, pls. 1–20. Anhui Science and Technology Press, Hefei. (*in Chinese with English abstract*)
- Hoffmann, R. and Stevens, K., 2020: The palaeobiology of belemnites—foundation for the interpretation of rostrum geochemistry. *Biological Reviews*, vol. 95, p. 94–123.
- Hu, S., Zhang, Q., Chen, Z., Zhou, C., Lü, T., Xie, T., Wen, W., Huang, J. and Benton, M. J., 2011: The Luoping biota: Exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proceedings of the Royal Society B*, vol. 278, p. 2274–2282.

- Hyatt, A. and Smith, J. P., 1905: The Triassic cephalopod genera of America. United States Geological Survey Professional Paper 40, p. 1–394
- Iba, Y., 2016: Early evolutionary history of belemnites, revisited: Importance of East Asian fossil records. Report of the Grant-in-Aid for Scientific Research (no. 25800285) by Ministry of Education, Science, Sports and Culture. (in Japanese with English abstract)
- Iba, Y., Sano, S. and Mutterlose, J., 2014: The Early evolutionary history of Belemnites: New data from Japan. *PLOS ONE*, doi: 10.1371/journal.pone.0095632.
- Iba, Y., Sano, S., Mutterlose, J. and Kondo, Y., 2012: Belemnites originated in the Triassic—a new look at an old group. *Geology*, vol. 40, p. 911–914.
- Iba, Y., Sano, S., Rao, X., Fuchs, D., Chen, T., Weis, R. and Sha, J., 2015: Early Jurassic belemnites from the Gondwana margin of Southern Hemisphere—Sinemurian record from South Tibet. *Gondwana Research*, vol. 28, p. 882–887.
- Ishibashi, T., 2006: Triassic cephalopods of Japan. *Bulletin of the Mine City Museum*, no. 21, p. 1–29. (*in Japanese*)
- Jeletzky, J. A., 1966: Comparative morphology, phylogeny, and classification of fossil Coleoidea. *The University of Kansas Paleontological Contributions, Mollusca*, article 7, p. 1–162.
- Johnson, R. G. and Richardson, E. S. Jr., 1968: Ten-armed fossil cephalopod from the Pennsylvanian of Illinois. *Science*, vol. 159, p. 526–528.
- Keupp, H. and Fuchs, D., 2014: Different regeneration mechanisms in the rostra of aulacocerids (Coleoidea) and their phylogenetic implications. *Göttingen Contributions to Geosciences*, vol. 77, p. 13–20.
- Kummel, B., 1969: Ammonoids of the late Scythian (Lower Triassic). Bulletin of the Museum of Comparative Zoology, vol. 137, p. 311–701.
- Liu, Z. and Su, L., 1999: New discovery of Permian belemnoids in Hunan. Journal of Xiangtan Mining Institute, vol. 14, p. 25–29. (in Chinese with English abstract)
- Miller, J. S., 1829: Observations on belemnites. Transactions of the Geological Society of London, Second Series, vol. 2, p. 45–67.
- Mojsisovics, E. von, 1888: Ueber einige japanische Trias-Fossilien. Beiträge zur Geologie und Paläontologie Österreich Ungarns und des Orients, Band 7, p. 163–178, pls. 1–4.
- Niko, S. and Ehiro, M., 2018: Aulacocerid coleoids from the Triassic of the South Kitakami Belt, Northeast Japan. *Bulletin of the Tohoku* University Museum, no. 17, p. 1–8.
- Niko, S. and Hayakawa, H., 2005: A new species of *Neohibolites* (Belemnopseidae, Belemnitida) from the Albian of Hokkaido, Japan. *Bulletin of the Mikasa City Museum*, no. 9, p. 41–44.
- Niko, S. and Kameya, A., 2006: Acrocoelites (Odontobelus) mantanii, a new species of Early Jurassic belemnite from the Toyora Group, Yamaguchi Prefecture, Japan. Bulletin of the Mikasa City Museum, no. 10, p. 37–40.
- Noetling, F., 1905: Untersuchungen über den Bau der Lobenlinie von Pseudosageceras multilobatum Noetling. Palaeontographica, vol. 51, p. 155–260, pls. 19–27.
- Onuki, Y. and Bando, Y., 1959: On the Inai Group of the Lower and Middle Triassic System (Stratigraphical and paleontological studies of the Triassic System in the Kitakami Massif, Northeast Japan: -3). Contributions from the Institute of Geology and Paleontology, Tohoku University, no. 50, p. 1–69. (in Japanese with English abstract)
- Riegraf, W., 1980: Revision der Belemniten des Schwäbischen Jura. Teil 7. Palaeontographica, Abteilung A, vol. 169, p. 128–206, pls. 1–4.

- Riegraf, W., 1995: Cephalopoda dibranchiata fossiles (Coleoidea). In, Westphal, F. ed., Fossilium Catalogus. I: Animalia, p. 1–411. Kugler Publications, Amsterdam and New York.
- Riegraf, W., Janssen, N. and Schmitt-Riegraf, C., 1998: Cephalopoda dibranchiata fossiles (Coleoidea) II. *In*, Westphal, F. *ed.*, *Fossilium Catalogus. I: Animalia*, p. 1–512. Backhuys Publications, Leiden.
- Schlegelmilch, R., 1996: Revision of the belemnites from the Hettangian of Nürtingen (Baden-Württemberg, SW Germany). *Stuttgarter Beiträge zur Naturkunde, Serie B*, no. 238, p. 1–17.
- Seguin, M. K. and Zhai, Y., 1992: Paleomagnetic constraints on the crustal evolution of the Yangtze block, southeastern China. *Tectonophysics*, vol. 210, p. 59–76.
- Shigeta, Y. and Nakajima, Y., 2017: Discovery of the early Spathian (late Olenekian, Early Triassic) ammonoid *Tirolites* in the Hiraiso Formation, South Kitakami Belt, Northeast Japan. *Paleontological Research*, vol. 21, p. 37–43.
- Shimizu, S. and Mabuti, S., 1941: First discovery of *Dictyoconites* from the Upper Triassic of the Kitakami Mountainland, Northeast Japan. *Jubilee Publication in the Commemoration of Professor H. Yabe, M. I. A. Sixtieth Birthday*, vol. 2, p. 919–925, pls. 48–49. Committee of the Commemoration of Professor H. Yabe, M.I.A. Sixtieth Birthday, Sendai.
- Smith, J. P., 1914: The Middle Triassic marine invertebrate faunas of North America. United States Geological Survey Professional Paper 83, p. 1–254.
- Spaeth, C., 1975: Zur Frage der Schwimmverhältnisse bei Belemniten in Abhängigkeit vom Primärgefüge der Hartteile. *Paläontologische Zeitschrift*, vol. 49, p. 321–331.
- Spath, L. F., 1930: The Eo-Triassic invertebrate fauna of East Greenland. Meddelelser om Grønland, vol. 83, p. 1–90.
- Wang, Y.-G., 1978: Latest Early Triassic ammonoids of Ziyun, Guizhou—with notes on the relationship between Early and Middle Triassic ammonoids. *Acta Palaeontologica Sinica*, vol. 17, p. 131–177, pls. 1–3. (*in Chinese with English abstract*)

- Weis, R. and Delsate, D., 2006: The earliest belemnites: New records from the Hettangian of Belgium and Luxembourg. *Acta Universitatis Carolinae–Geologica*, vol. 49, p. 181–184.
- Welter, O. A., 1915: Die Ammoniten und Nautiliden des Ladinischen und Anisischen Trias von Timor. *Paläontologie von Timor*, vol. 5, p. 71–135.
- Yin, A. and Nie, S., 1993: An indentation model for the North and South China collision and the development of the Tan-Lu and Honam fault systems, eastern Asia. *Tectonics*, vol. 12, p. 801–813.
- Zakharov, Y. D. and Popov, A. M., 2014: Recovery of brachiopod and ammonoid faunas following the End-Permian crisis: Additional evidence from the lower Triassic of the Russian Far East and Kazakhstan. *Journal of Earth Science*, vol. 25, p. 1–44.
- Zhao, J., Dong, Y. and Huang, B., 2020: Paleomagnetic constraints of the Lower Triassic strata in South Qinling Belt: Evidence for a discrete terrane between the North and South China blocks. *Tectonics*, doi: 10.1029/2019TC005698.
- Zhu, K. and Bian, Z., 1984: Sinobelemnitidae, a new family of Belemnitida from the Upper Triassic of Longmenshan, Sichuan. Acta Palaeontologica Sinica, vol. 23, p. 300–317, pls. 1–4. (in Chinese with English abstract)
- Zittel, K. A. von, 1895: Grundzüge der Paläontologie (Paläozoologie), I Abteilung, Invertebrata, 971 p. Oldenbourg, München and Leipzig.

Author contributions

S. N. conceived the original idea, designed the project, and contributed to paleontological aspects of the research.

M. E. contributed to geological and paleo-geographical aspects of the research. The two authors discussed the results and wrote the final version of the manuscript.