SCIENCE REPORTS OF NIIGATA UNIVERSITY

(GEOLOGY)

No. 31 (2016)



Published by The Department of Geology, Faculty of Science Niigata University, Niigata, Japan

31 March 2016

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Devonian tabulate corals from pebbles in Mesozoic conglomerate, Kotaki, Niigata Prefecture, central Japan Part 3: Heliolitida

Shuji NIKO*, Yousuke IBARAKI** and Jun-ichi TAZAWA***

Abstract

As the third fascicle, this paper describes two species of heliolitid tabulate corals, namely *Heliolites porosus* (Goldfuss, 1826) and *H*. sp. cf. *H. opacus* (Dubatolov, 1963), from the Kotaki area, Niigata Prefecture, central Japan. The examined specimens were found in Mesozoic conglomerate. This discovery of *H. porosus* suggests that the coral-bearing limestone pebbles are Givetian (late Middle Devonian) in age. Besides the type locality in Europe, this species is widely known to occur from North Africa, Asia and Australia. Another species resembles closely *Heliolites opacus* (Dubatolov, 1963), from the Eifelian to Givetian (lower to upper Middle Devonian) of southern Siberia, with exception of slight differences of tabularium diameters.

Key words: Middle Devonian, heliolitid tabulae corals, *Heliolites*, Kotaki area, Mesozoic conglomerate.

Introduction

Following Niko et al. (2014, 2015), the present paper represents the third fascicle in a series of our descriptive works concerning the Devonian tabulate coral fauna in the Kotaki area of Itoigawa, Niigata Prefecture, central Japan. These coral fossils are preserved in pebbles in a float block of Mesozoic conglomerate. Two species of *Heliolites* are described

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⁽Manuscript received 14 December, 2015; accepted 25 January, 2016)

herein on the basis of nine specimens that housed in the Fossa Magna Museum (abbreviation: FMM).

Systematic Paleontology

Subclass Tabulata Milne-Edwards and Haime, 1850 Order Heliolitida Frech, 1897 Suborder Heliolitina Frech, 1897 Superfamily Heliolitoidea Lindström, 1876 Family Heliolitidae Lindström, 1876 Genus *Heliolites* Dana, 1846

[= *Pachycanalicula* Wentzel, 1895; see Laub, 1979, p. 351; Young and Noble, 1990, p. 49] *Type species.*—*Astraea porosa* Goldfuss, 1826.

> Heliolites porosus (Goldfuss, 1826) Figs. 1-1-4

Astraea porosa Goldfuss, 1826, p. 64, pl. 21, figs. 7a-g.

Heliolites porosa (Goldfuss); Mile-Edwards and Haime, 1851, p. 218, 219; Etheridge, 1899, p. 173, 174, pl. 19, figs. 3, 4, pl. 25, figs. 1, 2.

Heliolites porosus (Goldfuss); Lindström, 1899, p. 53–58, pl. 2, figs. 29–38, 371–VII, pl. 3, figs. 3–7; Lecompte, 1936, p. 93–96, pl. 14, figs. 2, 2a, 3, 3a, b, 4, 5, 5a; Jones and Hill, 1940, p. 204, pl. 9, figs. 3a, b; Termier and Termier, 1950, p. 67, pl. 14, fig. 13, pl. 15, figs. 3, 4; Chernyshev, 1951, p. 88, 89, pl. 22, figs. 3–5; Fontaine, 1954, p. 72, 73, pl. 8, figs. 10, 11; Stasińska, 1958, p. 223, 224, pl. 33, figs. 1–3; Yang et al., 1978, p. 240, pl. 89, fig. 8; Iven, 1980, p. 163, 165, 167; Hill, 1981, figs. 410.2a, b; Nowiński, 1993, figs. 15A, B; Fernández-Martínez, 1999, p. 104–107, 109, 110, figs. 3A, B, 6A–G; Brühl and Pohler, 1999, p. 277, 278, pl. 1, figs. 1–4.

Heliolites (Heliolites) porosus (Goldfuss); Flügel, 1956, p. 72, 73.

Material.—FMM6201–6207. They were recovered from gray to milky white limestone pebbles.

Description.—Seven specimens of incomplete coralla are available for this study; they are probably massive, at least 32 mm in diameter, and consist of cylindrical tabularia (= corallites) surrounded by coenenchyme of prismatic tubules. Tabularia have 1.1–1.5 mm in diameter and separated from one another 2–7 coenenchymal tubules; center to center distances of adjoining tabularia are 1.8–3.4 mm; walls of tabularia are weakly crenulate to smooth; thickness of walls is usually thin, having 0.03–0.05 mm, but it rarely attains to 0.15



Fig. 1. 1–4: *Heliolites porosus* (Goldfuss, 1826), thin sections. 1, 2, 4, FMM6202; 1, 2, transverse sections of corallum; 4, longitudinal section of corallum; 3, FMM6207, transverse section of corallum. **5,** 6: *Heliolites* sp. cf. *H. opacus* (Dubatolov, 1963), FMM6209, thin sections. 5, transverse section of corallum; 6, longitudinal section of corallum. Scale bar = 3 mm.

mm in thickened parts; tabulae complete; septa lamellar or ridge-like in rare cases, 0.05–0.39 mm in length, or absent; basal parts of usual septa are inflated and indicate triangular profiles. Coenenchymal tubules 0.2–0.6 mm in diameter with 0.03–0.08 mm in wall thickness; dissepiments in tubules are complete.

Discussion.—Both in terms of shape and size, morphologies of the Kotaki material fall within the diagnosis of *Heliolites porosus* (Goldfuss, 1826) that indicates wide morphological variations and contains more than 20 subspecies (Flügel, 1956; Iven, 1980). The types of this species were recorded from the Givetian (upper Middle Devonian) of Eifel, Germany. The fragmentary nature of the material precludes confident assignation of subspecies, but the present discovery is useful for age determination of the coral-bearing limestone pebbles. Geographic distributions of *H. porosus* are wide. Except for Europe, it is widely known to occur in North Africa (Morocco; Termier and Termier, 1950). Asia including southern Siberia (Chernyshev, 1951), the Indochinese Peninsula (Fontaine, 1954) and South China (Yang et al., 1978), and Australia including New South Wales (Etheridge, 1899; Brühl and Pohler, 1999) and Queensland (Jones and Hill, 1940).

Heliolites sp. cf. H. opacus (Dubatolov, 1963) Figs. 1-5, 6

Compare with: *Pachycanalicula opaca* Dubatolov, 1963, p. 120, 121, pl. 43, figs. 3a, b, 4a, b.

Material.-FMM6208, 6209. They were recovered from gray limestone pebbles.

Description.—Two available specimens of fragmentary coralla are probably massive in outer form and consist of cylindrical tabularia (= corallites) and surrounding coenenchyme of prismatic tubules. Tabularia are relatively narrow, 1.0–1.2 mm in diameter and separated from one another 3–8 coenenchymal tubules; center to center distances of adjoining tabularia are 1.8–2.2 mm; walls of tabularia are weakly crenulate, thickened with 0.06–0.10 mm; tabulae complete or incomplete, closely spaced; septa thin lamellae with spinose in axial parts to low ridges, or absent; septal length approximately 0.04–0.27 mm. Coenenchymal tubules relatively narrow with 0.2–0.4 mm in diameter; walls of tubules are thin to moderately thick, having 0.03–0.06 mm in thickness; dissepiments in tubules are complete.

Discussion.—The Kotaki species resembles closely *Pachycanalicula opaca* Dubatolov, 1963 (= *Heliolites opacus* in current status) from the Eifelian to Givetian (lower to upper Middle Devonian) of Novokuznetsk, southern Siberia. However, it has slightly smaller diameters of the tabularia than those of the latter that indicates 1.2–1.4 mm.

Acknowledgments

Our sincere thanks extend to Mrs. Kanako Ito, who discovered Devonian tabulate corals from the Kotaki area, allowed us to examine these specimens, and donated them to the Fossa Magna Museum. We also thank Dr. Isao Niikawa and Dr. Atsushi Matsuoka for constructive reviews that improve this manuscript.

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Middle Permian (Wordian) mixed Boreal–Tethyan brachiopod fauna from Kamiyasse–Imo, South Kitakami Belt, Japan

Jun-ichi TAZAWA*

Abstract

A middle Permian (Wordian) brachiopod fauna, consisting of 10 species in 10 genera, is described from the lower part of the Kamiyasse Formation in the Kamiyasse-Imo area, South Kitakami Belt, northeastern Japan. The Kamiyasse-Imo fauna is a mixed Boreal-Tethyan brachiopod fauna, and has some affinities with the middle Permian brachiopod faunas of central Japan (Hida Gaien Belt), eastern Russia (South Primorye), northeastern China (Jilin and Heilongjiang), northern China (Inner Mongolia) and northwestern China (Qinghai). Palaeobiogeographical data for the Kamiyasse-Imo fauna suggest that during the Wordian South Kitakami was probably located at mid-latitudes in the Northern Hemisphere, immediately east of North China (Sino-Korea).

Key words: Brachiopoda, Kamiyasse-Imo, mixed Boreal-Tethyan fauna, South Kitakami Belt, Wordian.

Introduction

The Kamiyasse-Imo area, South Kitakami Belt, northeastern Japan (Fig. 1) is famous for the vast Permian marine invertebrate fossils. Seventy-eight brachiopod species have been previously described from the middle Permian (Wordian) of Kamiyasse-Imo by the following authors: Hayasaka (1917, 1922a, 1925, 1937, 1963, 1966, 1967), Minato (1955), Hayasaka and Minato (1956), Minato and Nakamura (1956), Nakamura (1959, 1960, 1970, 1972, 1979), Nakamura et al. (1970), Tazawa (1974a, b, 2008c, 2014), Shen and Tazawa (1997, 2014), Afanasjeva and Tazawa (2007, 2010), Shiino and Suzuki (2007), Shiino (2009), Tazawa and

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⁽Manuscript received 4 January, 2016; accepted 12 February, 2016)



Fig. 1. Map showing the fossil localities KF11, KF13, KF21, KF22, KF39, KF46, KF64, KF67, KF84, KF90, KF96, KF121, KF128, KF217 and KF218 in the Kamiyasse-Imo area, South Kitakami Belt (using the topographical map "Shishiori" scale 1 : 25,000, published by the Geospatial Information Authority of Japan).

Araki (2013), Afanasjeva et al. (2015) and Tazawa and Kaneko (2016). However, systematic studies on the brachiopod species of the Kamiyasse–Imo fauna are not sufficiently complete.

One of the most controversial topic in geohistory of the Japanese Islands is the Palaeozoic geography and biogeography of Proto-Japan (including the South Kitakami, Hida Gaien and Kurosegawa belts). On the Permian geography and biogeography, Tazawa (1991, 1993, 2000, 2002, 2004, 2007, 2014) have been emphasized the importance of the Permian mixed Boreal–Tethyan brachiopod faunas from South Kitakami; which indicate the middle Permian palaeoposition of South Kitakami near North China (Sino–Korea). In contrast, Ehiro (1997, 2001, 2015; Ehiro et al., 2005) and Isozaki (1996; Isozaki et al., 2010a, b, 2011; Isozaki and Kase, 2014) asserted that South Kitakami was located in the equatorial region of Tethys near South China (Yangtze) in the middle Permian based on the occurrence of the Tethyan-type corals (Kato, 1990; Kawamura and Machiyama, 1995), molluscs (Nakazawa, 1991; Isozaki and Kase, 2014) and cephalopods (Ehiro, 1997, 2010, 2015; Ehiro et al., 2005; Ehiro and Misaki, 2005).

The present paper describes brachiopods of 10 species in 10 genera from the lower part of the Kamiyasse Formation (Wordian) of the Kamiyasse-Imo area, and discusses the age



Fig. 2. Generalized columnar section of the middle Permian of the Kamiyasse-Imo area, South Kitakami Belt, showing the fossil horizons KF11, KF13, KF21, KF22, KF39, KF46, KF64, KF67, KF84, KF90, KF96, KF121, KF128, KF217 and KF218 (modified and adapted from Tazawa and Kaneko 2016)

and palaeobiogeography of the brachiopod fauna (Kamiyasse-Imo fauna). The brachiopod specimens described herein were collected by Koji Nakamura, Tomoharu Ikeda and the present author; and they are now registered and housed in the Department of Geology, Faculty of Science, Niigata University, Niigata (with prefix NU-B) and the Hokkaido University Museum, Sapporo (with prefix UHR).

Stratigraphy

The stratigraphy of Permian rocks in the Kamiyasse-Imo area has been studied by Shiida (1940), Kambe and Shimazu (1961), Tazawa (1973, 1976) and Misaki and Ehiro (2004). According to Misaki and Ehiro (2004), the middle Permian (Guadalupian) of this area is

subdivided into two formations, the lower, Hosoo Formation and the upper, Kamiyasse Formation (Fig. 2). The Hosoo Formation (400–500 m thick) consists mainly of shale with subordinate sandstone, limestone and conglomerate; and the Kamiyasse Formation (150–250 m thick) consists mainly of sandstone with subordinate limestone, shale and conglomerate. The brachiopod specimens described in this paper were collected from greenish grey fine-grained sandstone and dark grey argillaceous limestone of the lower part of the Kamiyasse Formation at the following fifteen localities in the Kamiyasse-Imo area (see Figs. 1, 2).

- KF11: Upper Shigejisawa Valley (38°58′59″N, 141°30′31″E), dark grey argillaceous limestone of the lower part of the Kamiyasse Formation, with *Waagenoconcha irginae*.
- KF13: Upper Shigejisawa Valley (38°59′11″N, 141°31′22″E), dark grey argillaceous limestone of the lower part of the Kamiyasse Formation, with *Leptodus nobilis*.
- KF21: Upper Shigejisawa Valley (38°59′04″N, 141°31′22″E), greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, with Globiella tschernyschewi and Grandaurispina kozlowskiana.
- KF22: Upper Shigejisawa Valley (38°59′06″N, 141°31′35″E), greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, with *Grandaurispina kozlowskiana*.
- KF39: Upper Chayazawa Valley (38°58′35″N, 141°31′10″E), greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, with *Waagenoconcha irginae* and *Urushtenoidea crenulata*.
- KF46: Upper Shigejisawa Valley (38° 59' 11"N, 141° 31' 39"E), greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, with *Grandaurispina kozlowskiana*.
- KF64: Upper Minamizawa Valley (38°59′26″N, 141°31′04″E), greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, with *Vediproductus punctatiformis*.
- KF67: Upper Shigejisawa Valley (38°59′02″N, 141°31′39″E), dark grey argillaceous limestone of the lower part of the Kamiyasse Formation, with *Leptodus nobilis*.
- KF84: Upper Minamizawa Valley (38°59′26″N, 141°31′04″E), dark grey argillaceous limestone of the lower part of the Kamiyasse Formation, with *Leptodus nobilis*.
- KF90: Upper Shigejisawa Valley (38°59′14″N, 141°31′23″E), greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, with *Urushtenoidea crenulata*.
- KF96: Upper Minamizawa Valley (38°59′28″N, 141°31′08″E), greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, with *Tyloplecta yangtzeensis*.
- KF121: Upper Imosawa Valley (38°59′55″N, 141°31′18″E), greenish grey fine-grained

sandstone of the lower part of the Kamiyasse Formation, with *Tyloplecta* yangtzeensis.

- KF128: Upper Toyazawa Valley (38° 59′ 15″ N, 141° 31′ 53″ E), dark grey argillaceous limestone of the lower part of the Kamiyasse Formation, with *Leptodus nobilis*.
- KF217: Upper Imosawa Valley (38° 59′ 55″N, 141° 31′ 14″E), greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, with Transennatia gratiosa, Tyloplecta yangtzeensis, Vediproductus punctatiformis, Urushtenoidea crenulata, Leptodus nobilis and Alispiriferella lita.
- KF218: Upper Imosawa Valley (38° 59′ 55″ N, 141° 31′ 16″ E), dark grey argillaceous limestone of the lower part of the Kamiyasse Formation, with *Transennatia gratiosa*, *Tyloplecta yangtzeensis*, *Vediproductus punctatiformis*, *Urushtenoidea crenulata*, *Grandaurispina kozlowskiana*, *Leptodus nobilis* and *Cryptospirifer omeishanensis*.

The Kamiyasse-Imo fauna

The brachiopod fauna described herein includes the following 10 species in 10 genera: *Transennatia gratiosa* (Waagen, 1884), *Tyloplecta yangtzeensis* (Chao, 1927), *Vediproductus punctatiformis* (Chao, 1927), *Waagenoconcha irginae* (Stuckenberg, 1898), *Urushtenoidea crenulata* (Ding in Yang et al., 1962), *Globiella tschernyschewi* (Netschajew, 1911), *Grandaurispina kozlowskiana* (Fredericks, 1925), *Leptodus nobilis* (Waagen, 1883), *Cryptospirifer omeishanensis* Huang, 1933 and *Alispiriferella lita* (Fredericks, 1924). The stratigraphic and geographic distributions of the brachiopod species of the Kamiyasse-Imo fauna are summaraized in Fig. 3 and Fig. 4, respectively.



Fig. 3. Stratigraphic distribution of brachiopod species of the Kamiyasse-Imo fauna.

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1. Age

Of the brachiopods listed above, *Transennatia gratiosa, Tyloplecta yangzeensis* and *Alispiriferella lita* are known from the Wordian-Changhsingian, *Vediproductus punctatiformis* and *Waagenoconcha irginae* are known from the Asselian-Capitanian, *Urushtenoidea crenulata* is known from the Kungurian-Wuchiapingian and *Leptodus nobilis* is known from the Kungurian-Changhsingian. On the other hand, *Globiella tschernyschewi, Grandaurispina kozlowskiana* and *Cryptospirifer omeishanensis* are restricted to the Wordian. In summary, the age of the Kamiyasse-Imo fauna is assigned to the Wordian.

The age determination is consistent with Ehiro and Misaki (2005) and Tazawa (2014); both of them assigned the age of the lower part of the Kamiyasse Formation in the Kamiyasse–Imo area to the Wordian based on ammonoids and brachiopods, respectively.

2. Palaeobiogeography

The Kamiyasse-Imo fauna includes the Boreal (anti-tropical) elements Waagenoconcha irginae, Globiella tschernyschewi, Grandaurispina kozlowskiana and Alispiriferella lita, which are distributed in the Boreal Realm (Spitsbergen and northern Russia) and the Boreal-Tethyan transitional zone (central to eastern Russia, Mongolia, northern to northeastern China, South Kitakami Belt, Hida Gaien Belt and Mizukoshi, western extension of the Hida Gaien Belt). This fauna includes also the Tethyan (tropical) elements Transennatia gratiosa, Tyloplecta yangtzeensis, Vediproductus punctatiformis, Urushtenoidea crenulata, Leptodus nobilis and Cryptospirifer omeishanensis, which are distributed in the Tethyan Realm (eastern to southern China excluding Yunnan, Vietnam, Thailand, Iran, Armenia and Greece), and both the Boreal-Tethyan transitional Zone (Hungary, Balkan States, northwestern to northestern China, eastern Russia, South Kitakami Belt, Hida Gaien Belt, Mizukoshi, Maizuru and Akiyoshi) and the Gondwanan-Tethyan transitional zone (Yunnan, Tibet, Malaysia, Timor, Nepal and Pakistan). Therefore, the Kamiyasse-Imo fauna is a mixed Boreal-Tethyan fauna, dominated by the Tethyan elements. It is noteworthy that the Kamiyasse-Imo fauna has some affinities with the middle Permian (Wordian) faunas of northwestern to northeastern China, eastern Russia and central Japan, particularly South Primorye, eastern Russia and the Hida Gaien Belt, central Japan. The faunas of eastern China and central-southern China somewhat like to the Kamiyasse-Imo fauna, but they quite differ from the latter by completely lacking the Boreal elements.

The palaeobiogeographical data for the Kamiyasse-Imo fauna suggest that during the Wordian South Kitakami together with Hida Gaien was part of continental shelf developed along the eastern margin of North China in the mid-latitudes of the Northern Hemisphare, and located within the Sino-Mongolian-Japanese Province (Shi and Tazawa, 2001; Shi, 2006; Shen et al., 2009) [=Inner Mongolian-Japanese Transitional Zone (Tazawa, 1991, 1998)] which occupied area between the Boreal and Tethyan realms in East Asia.

Systematic descriptions

Order Productida Sarytcheva and Sokolskaya, 1959 Suborder Productidina Waagen, 1883 Superfamily Marginiferoidea Stehli, 1954 Family Marginiferidae Stehli, 1954 Subfamily Marginiferinae Stehli, 1954 Genus *Transennatia* Waterhouse, 1975

Type species.—Productus gratiosus Waagen, 1884.

Transennatia gratiosa (Waagen, 1884) Figs. 5.1-5.5

- Productus gratiosus Waagen, 1884, p. 691, pl. 72, figs. 3–7; Diener, 1897, p. 23, pl. 3, figs. 3–7;
 Mansuy, 1913, p. 115, pl. 13, fig. 1; Colani, 1919, p. 10, pl. 1, fig. 2; Chao, 1927, p. 44, pl. 4, figs. 6–10; Chi-Thuan, 1962, p. 491, pl. 2, figs. 5–7.
- Productus (Dictyoclostus) gratiosus Waagen: Huang, 1933, p. 88, pl. 11, fig. 14; Hayasaka, 1960, p. 49, pl. 1, fig. 8.
- Marginifera gratiosa (Waagen): Reed, 1944, p. 98, pl. 19, figs. 6, 7.
- *Dictyoclostus gratiosus* (Waagen): Zhang and Ching (Jin), 1961, p. 411, pl. 4, figs. 12–18; Wang et al., 1964, p. 291, pl. 45, figs. 14–19; Leman, 1994, pl. 1, figs. 11–13.
- *Gratiosina gratiosa* (Waagen): Grant, 1976, pl. 33, figs. 19–26; Licharew and Kotlyar, 1978, pl. 12, figs. 5, 6; pl. 20, fig. 1; Minato et al., 1979, pl. 61, figs. 11–13.
- Asioproductus gratiosus (Waagen): Yang et al., 1977, p. 350, pl. 140, fig. 5; Feng and Jiang, 1978, p. 254, pl. 90, figs. 1, 2; Tong, 1978, p. 228, pl. 80, fig. 7; Lee et al., 1980, p. 373, pl. 164, fig. 14; pl. 166, figs. 5, 6.
- Gratiosina sp. Minato et al., 1979, pl. 61, fig. 14.
- Dictyoclostus minor Lee and Gu in Lee et al., 1980, p. 372, pl. 166, figs. 1-4.
- *Transennatia gratiosus* (Waagen): Wang et al., 1982, p. 214, pl. 92, figs. 6–8; pl. 102, figs. 4–9; Liu et al., 1982, p. 185, pl. 132, fig. 9; Ding and Qi, 1983, p. 280, pl. 95, fig. 14; Zeng et al., 1995, pl. 5, figs. 14, 15.
- Transennatia gratiosa (Waagen): Yang, 1984, p. 219, pl. 33, fig. 7; Jin, 1985, pl. 4, figs. 33, 34, 45, 46; Tazawa and Matsumoto, 1998, p. 6, pl. 1, figs. 4–8; Tazawa et al., 2000, p. 7, pl. 1, figs. 3–5; Tazawa, 2001, p. 289, figs. 6.1–6.7; Tazawa and Ibaraki, 2001, p. 7, pl. 1, figs. 1–3; Shen et al., 2002, p. 676, figs. 4.27–4.31; Tazawa, 2002, fig. 10.2; Chen et al., 2005, p. 354, figs. 10E–10H, 11; Tazawa, 2008a, p. 26, fig. 4.1; Tazawa, 2008b, p. 43, figs. 6.6, 6.7; Shen and Zhang, 2008, figs. 4.20–4.22; Shen and Clapham, 2009, p. 718, pl. 1, figs. 13–22; Shen and





Fig. 5. 1–5, *Transennatia gratiosa* (Waagen); 1, internal mould of ventral valve, NU-B1736; 2a, 2b, 2c, 2d, ventral, anterior, posterior and lateral views of internal mould of ventral valve, NU-B1735; 3a, 3b, dorsal and lateral views of external mould of dorsal valve, NU-B1737; 4, external mould of dorsal valve, UHR12126; 5a, 5b, 5c, 5d, ventral, anterior, posterior and lateral views of internal mould of ventral valve, UHR30097; 6, *Tyloplecta yangtzeensis* (Chao); 6a, 6b, external mould and external latex cast of dorsal valve, NU-B1839. Scale bars represent 1 cm.

Shi, 2009, p. 157, figs. 3K–3O; Tazawa et al., 2014, p. 378, figs. 2.2, 2.3; Tazawa, 2015, p. 65, figs. 6.2, 6.3.

Material.—Eight specimens from localities KF217 and KF218: (1) internal moulds of four ventral valves, NU-B1735, 1736, 1738, UHR30097; (2) external moulds of four dorsal valves, NU-B1737, 1739, 1740, UHR12126.

J. Tazawa

Description.—Shell small in size for genus, transversely subquadrate in outline, with greatest width at hinge; length 15 mm, width 21 mm in the largest dorsal valve specimen (UHR12126). Ventral valve strongly and unevenly convex in lateral profile, most convex at umbonal region, strongly geniculated at anterior margin of visceral disc, and followed by a long trail; umbo small, slightly incurved; ears small, pointed; sulcus narrow and deep; lateral slopes steep. Dorsal valve nearly flat in visceral disc, geniculated at anterior margin of visceral disc, and followed by a short trail; fold narrow and low. External surface of ventral valve reticulate on visceral disc and costate on trail; costae converging into sulcus anteriorly, having a density of 7–8 per 5 mm at about midlength; spines or spine bases not preserved. External ornament of dorsal valve similar to that of the opposite valve. Ventral interior with elongate diductor scars on highly raised platform and large flabellate diductor scars. Dorsal interior with a short median septum and a pair of elongate smooth adductor scars. Other internal structures not preserved.

Remarks.—These specimens are referred to *Transennatia gratiosa* (Waagen, 1884), from the Wargal and Chhidru formations of the Salt Range, Pakistan, on the basis of their smallsized, strongly concavo-convex shells with reticulate ornament on the disks of both valves, although the Kitakami specimens are smaller than the type specimens from the Salt Range. *Transennatia insculpta* (Grant, 1976, p. 135, pl. 32, figs. 1–37; pl. 33, figs. 1–6), from the Rat Buri Limestone of Ko Muk, southern Thailand, differs from *T. gratiosa* in the smaller size and in having more extended ears.

Distribution.—Wordian-Changhsingian: northwestern China (Shaanxi), northeastern China (Heilongjiang and Jilin), eastern Russia (South Primorye), northeastern Japan (Setamai, Kamiyasse-Imo, Kesennuma, Ogatsu and Takakurayama in the South Kitakami Belt), central Japan (Moribu and Oguradani in the Hida Gaien Belt and Hitachi), southwestern Japan (Mizukoshi in central Kyushu), eastern China (Anhui, Zhejiang and Jiangxi), central-southern China (Hubei, Hunan, Guangdong and Guangxi), southwestern China (Guizhou, Sichuan and Yunnan), Vietnam, Cambodia (Sisophon), Greece (Hydra Island), Tibet (Xizang), Malaysia, Nepal (Kumaon Himalayas) and Pakistan (Salt Range).

Superfamily Productoidea Gray, 1840 Family Buxtoniidae Muir-Wood and Cooper, 1960 Subfamily Tyloplectinae Termier and Termier, 1970 Genus *Tyloplecta* Muir-Wood and Cooper, 1960

Type species.—Productus scabriculus mut. nankingensis Frech, 1911.

Tyloplecta yangtzeensis (Chao, 1927) Figs. 5.6, 6.1–6.3 Productus semireticulatus Martin: Kayser, 1883, p. 181, pl. 25, figs. 1-4.

Productus costatus Sowerby: Kayser, 1883, p. 182, pl. 25, figs. 5-7.

Productus sumatrensis Roemer: Fliegel, 1901, p. 128, pl. 6, fig. 1.

Productus sumatrensis var. palliata Frech, 1911, p. 126, 153, pl. 27, fig. 8.

Productus sumatrensis var. *palliata* Kayser em. Fliegel: Hayasaka, 1922b, p. 81, pl. 4, figs. 7–9; pl. 5, fig. 6.

Productus yangtzeensis Chao, 1927, p. 50, pl. 5, figs. 1–3; pl. 8, fig. 9; Simić, 1933, p. 31, 92, pl. 1, figs. 11–14.

Productus (Dictyoclostus) yangtzeensis Chao: Huang, 1932, p. 26, pl. 1, figs. 18-21.

Dictyoclostus yangtzeensis (Chao): Ramovs, 1958, p. 506, pl. 3, fig. 1.

Tyloplecta yangtzeensis (Chao): Schréter, 1963, p. 124, pl. 6, figs. 1–7; Yanagida, 1964, p. 3, pl. 1, figs. 1, 3, text-fig. 2; Ting, 1965, p. 268, pl. 3, figs. 1, 2; Sarytcheva, 1965, pl. 37, fig. 1; Fantini Sestini and Glaus, 1966, p. 909, pl. 64, figs. 1, 4; pl. 65, fig. 1; Pitakpaivan et al., 1969, p. 10, pl. 17, figs. 13–15; Termier and Termier, 1970, p. 458, pl. 31, fig. 4; Yang et al., 1977, p. 361, pl. 143, fig. 4; Feng and Jiang, 1978, p. 258, pl. 92, figs. 5–8; Licharew and Kotlyar, 1978, p. 12, figs. 11, 12; pl. 19, figs. 8, 9; Tong, 1978, p. 230, pl. 81, fig. 4; Zhan, 1979, p. 88, pl. 6, figs. 20–22; Nakamura et al., 1981, p. 44, pl. 1, figs. 1–3; pl. 3, figs. 1, 2; Liu et al., 1982, p. 186, pl. 133, figs. 4, 5; Wang et al., 1982, p. 212, pl. 89, figs. 5, 6; pl. 92, figs. 10, 11; Ding and Qi, 1983, p. 286, pl. 98, fig. 4; Liao, 1987, p. 104, pl. 5, figs. 23, 24; Liang, 1990, p. 192, pl. 33, figs. 1–9; Zhu, 1990, p. 70, pl. 13, figs. 1–9; pl. 14, fig. 28; Zeng et al., 1995, pl. 7, figs. 2, 3, 7; He et al., 2008, p. 815, figs. 3.14, 3.15; Shen and Zhang, 2008, figs. 5.1, 5.2; Shen and Shi, 2009, p. 159, figs. 4A–4H.

Tyloplecta sino-indicus (Frech): Tazawa, 1976, pl. 2, fig. 13.

Tyloplecta yangtzeensis (Chao): Liao, 1980, pl. 4, figs. 21, 22.

Tyloplecta cf. yangtzeensis (Chao): Tazawa and Ibaraki, 2001, p. 8, pl. 1, fig. 5.

Tyloplecta sp. Tazawa, 2002, fig. 10.6.

Material.—Seven specimens from localities KF96, KF121 and KF217: (1) internal mould of a conjoined shell, with external mould of the dorsal valve, NU-B1835; (2) external cast of a ventral valve, NU-B1836; (3) external mould of a ventral valve, NU-B1837; (4) internal mould of a ventral valve, NU-B1838; (5) external moulds of three dorsal valves, NU-B1839–1841.

Description.—Shell large in size for genus, subquadrate to subglobose in outline, with greatest width at just anterior to hinge line; length 55 mm, width 66 mm in the largest specimen (NU-B1837). Ventral valve highly inflated in both lateral and anterior profiles; umbo large, strongly incurved and slightly overhanging hinge line; ears large, triangular and slightly convex; cardinal extremities rounded; sulcus broad and shallow; lateral slopes steep. Dorsal valve gently concave in visceral disc, moderately geniculated and followed by short trail; fold very low or absent. External surface of ventral valve ornamented by



Fig. 6. 1–3, *Tyloplecta yangtzeensis* (Chao); 1, external latex cast of ventral valve, NU-B1837; 2, external mould of dorsal valve, NU-B1841; 3a, 3b, 3c, 3d, ventral and dorsal views of internal mould of conjoined shell, and internal cast and external mould of dorsal valve, NU-B1835. Scale bars represent 1 cm.

numerous costae with very fine capillae, concentric rugae, growth lines and spines; costae coarse, rounded but narrow-topped, often bifurcated near anterior margin, and numbering 4–5 in 10 mm at about midlength; rugae developed on posterior half of valve; growth lines numerous and very fine over valve; spine bases occurring in a row near hinge margin, and on nodes of visceral disc. External ornament of dorsal valve similar to that of ventral valve, but spines or spine bases absent. Interior of dorsal valve with a large trilobate cardinal process on broad shaft; lateral ridges downward laterally; median septum long and thin, extending to about midlength of valve, becoming prominent and elevated anteriorly; brachial ridges prominent; anterior adductor scars elongate, smooth and elevated, but posterior adductor scars large, flattened and dendritic.

Remarks.—These specimens are referred to *Tyloplecta yangtzeensis* (Chao, 1927), from the Lungtan Formation of Zhejiang, eastern China, by their size, shape and external ornament of both ventral and dorsal valves. *Tyloplecta sinoindica* (Frech, 1911, p. 162, pl. 22, figs. 1, 2), from the Lungtan Formation of Jiangsu, eastern China, is distinguished from *T. yangtzeensis* by its more elongate and strongly inflated ventral valve and the trapezoidal dorsal valve. *Tyloplecta nankingensis* (Frech, 1911, p. 163, pl. 22, fig. 3), from the Lungtan Formation of Jiangsu, differs from the present species by its much smaller size and the more strongly convex ventral valve.

Distribution.—Wordian-Changhsingian: Hungary, Balkan States (Serbia and Slovenia), northwestern China (Qinghai), northern China (Shanxi), eastern Russia (South Primorye), northeastern Japan (Kamiyasse-Imo in the South Kitakami Belt), eastern China (Anhui, Zhejiang, Fujian and Jiangxi), central-southern China (Hubei, Hunan, Guangdong and Guangxi), southwestern China (Guizhou and Sichuan), Iran, Armenia and central Thailand.

> Superfamily Echinoconchoidea Stehli, 1954 Family Echinoconchidae Stehli, 1954 Subfamily Juresaniinae Muir-Wood and Cooper, 1960 Genus *Vediproductus* Sarytcheva, 1965

Type species.—Vediproductus vediensis Sarytcheva, 1965.

Vediproductus punctatiformis (Chao, 1927) Figs. 7.1–7.5

Echinoconchus punctatiformis Chao, 1927, p. 72, pl. 6, figs. 9–12; Zhan and Lee, 1962, p. 477, pl. 2, fig. 9.
Echinoconchus cf. fasciatus (Kutorga): Minato et al., 1979, pl. 65, figs. 5–7.

Sentholonenius el juscialius (Ratorgaj, Milliato et al., 1979, pl. 00, 11gs. 0 7.

Vediproductus punctatiformis (Chao): Wang et al., 1982, p. 208, pl. 80, figs. 10, 11; pl. 84, fig. 4;



Ding and Qi, 1983, p. 282, pl. 96, fig. 3; Wang, 1984, p. 190, pl. 76, fig. 7; Chang, 1987, p. 759, pl. 2, fig. 4; Liang, 1990, p. 187, pl. 27, fig. 5; Shiino, 2009, p. 255, figs. 4A–4H.

Material.—Fourteen specimens from localities KF64, KF217 and KF218: (1) external and internal moulds of two conjoined shells, NU-B1660, 1661; (2) internal moulds of two conjoined shells, with external moulds of the dorsal valves, NU-B1662, 1663; (3) external and internal moulds of a ventral valve, NU-B1664; (4) internal moulds of six ventral valves, NU-B1666, 1667, UHR12022, 12472, 12612, 12641; (5) external moulds of three dorsal valves, NU-B1665, 1668, UHR17083.

Description.—Shell medium in size for genus, elongate oval in outline, with greatest width at slightly anterior to midlength; length 34 mm, width 26 mm in the best preserved specimen (NU-B1660). Ventral valve strongly and unevenly convex in lateral profile, most convex at umbonal region; umbo small, incurved and followed by narrow, strongly convex umbonal slope; ears small; sulcus originating slightly anterior to beak, narrow and moderately deep; lateral slopes steep. Dorsal valve gently concave, geniculated at anterior margin of visceral disc, and followed by a short trail; fold narrow and low. External surface of ventral valve ornamented with numerous regular concentric bands with rows of spine bases on each front; bands with narrow, steep anterior slope and broad, flat posterior slope, numbering 3-4 in 10 mm at about midlength; spine bases consisting of larger elongate spine bases and more numerous smaller spine bases. External surface of dorsal valve ornamented with regular concentric bands bearing numerous spine bases on each front; bands with narrow steep anterior slope and broad concave posterior slope, numbering 6-7 in 10 mm at about midlength. Interior of ventral valve not well preserved and obscure. Dorsal interior with dorsally recurving cardinal process, with deep median sinus and a thin median septum, extending to about midlength of valve; diductor scars large, flabellate and smooth; adductor scars small, elongate and dendritic.

Remarks.—These specimens are referred to *Vediproductus punctatiformis* (Chao, 1927), from the Ksiaokiang Limestone of Jiangxi, eastern China, in size, shape and external ornament of the shells, especially the elongate oval and strongly convex ventral valve and numerous regular spinose bands on both of the ventral and dorsal valves. The type species,

[←] Fig.7. 1-5, Vediproductus punctatiformis (Chao); 1a, 1b, 1c, 1d, ventral, anterior, posterior and lateral views of internal mould of ventral valve, UHR12472; 2a, 2b, external latex cast and internal mould of ventral valve, NU-B1660; 3a, 3b, 3c, 3d, ventral, anterior, posterior and lateral views of internal mould of ventral valve, NU-B1664; 4a, 4b, 4c, ventral and dorsal views of internal mould of conjoined shell, and external mould of dorsal valve, NU-B1662; 5a, 5b, 5c, ventral and dorsal views of internal mould of conjoined shell, and external mould of dorsal valve, NU-B1662; 6a, 5b, 5c, ventral and dorsal views of internal mould of conjoined shell, and external mould of dorsal valve, NU-B1663; 6-11, Waagenoconcha irginae (Stuckenberg), 6a, 6b, ventral and dorsal views of internal mould of conjoined shell, UHR19816; 7, internal mould of ventral valve, UHR19815; 8, internal mould of ventral valve, NU-B1659; 9a, 9b, ventral and dorsal views of internal mould of conjoined shell, UHR19817; 10a, 10b, ventral and dorsal views of internal mould of conjoined shell, UHR19814. Scale bars represent 1 cm.

Vediproductus vediensis Sarytcheva (1965, p. 221, pl. 35, figs. 1–3, text-fig. 33) from the Gnishik Horizon (Roadian) of Transcaucasus, differs from *V. punctatiformis* in the less convex and wider ventral valve and broader concentric bands on the both valves.

Distribution.—Asselian-Capitanian: northwestern China (Xinjiang and Gansu), northeastern Japan (South Kitakami Belt), eastern China (Anhui, Zhejiang and Jiangxi) and central southern China (Hubei).

> Family Waagenoconchidae Muir-Wood and Cooper, 1960 Subfamily Waagenoconchinae Muir-Wood and Cooper, 1960 Genus *Waagenoconcha* Chao, 1927

Type species.—Productus humboldti d'Orbigny, 1842.

Waagenoconcha irginae (Stuckenberg, 1898) Figs. 7.6–7.11

- *Productus irginae* Stuckenberg, 1898, p. 220, pl. 2, fig. 16; Tschernyschew, 1902, p. 273, 618, pl. 30, figs. 3, 4; pl. 52, figs. 1–4; Miloradovich, 1935, p. 67, 133, pl. 5, figs. 1, 2.
- Productus cf. humboldti irginae Stuckenberg: Fredericks, 1925, p. 19, pl. 4, fig. 117.
- Waagenoconcha humboldti var. irginae (Stuckenberg). Solomina, 1960, p. 31, pl. 2, figs. 1-4.
- Waagenoconcha irginae (Stuckenberg): Muir-Wood and Cooper, 1960, pl. 89, figs. 15, 16;
 Gobbett, 1963, p. 76, pl. 5, fig. 7; pl. 6, figs. 1–5; Zavodowsky and Stepanov, 1970, p. 89, pl. 3,
 figs. 3, 4; Ifanova, 1972, p. 103, pl. 3, figs. 14–16; Lee and Gu, 1976, p. 252, pl. 155, figs. 3, 4;
 pl. 170, fig. 3; Kalashnikov, 1986, pl. 118, figs. 2, 3; Kalashnikov, 1993, p. 70, pl. 36, figs. 3–5.
- Waagenoconcha imperfecta Prendergast: Tazawa, 1974b, p. 127, pl. 1, figs. 4–6; pl. 2, figs. 2–7; pl. 3, figs. 1–3; pl. 4, figs. 1–4, 7 (excluding pl. 2, fig. 6; pl. 3, fig. 2); Tazawa, 1976, pl. 2, fig. 6; Minato et al., 1979, pl. 65, figs. 1, 2; Manankov, 1991, p. 112, pl. 23, figs. 4–7; Tazawa. 2002, figs. 10.12; Tazawa, 2007, fig. 4.12.
- Waagenoconcha sp. Tazawa and Ibaraki, 2001, p. 9, pl. 1, fig. 4.
- Waagenoconcha cf. imperfecta Prendergast: Tazawa, 2001, p. 293, fig. 7.24.

Material.—Seven specimens from localities KF11 and KF39: (1) external and internal moulds of a conjoined shell, UHR19813; (2) internal moulds of two conjoined shells, with external moulds of the dorsal valves, UHR19816, 19817; (3) external and internal moulds of a ventral valve, UHR19812; (4) internal moulds of two ventral valves, NU-B1659, UHR19815; (5) external and internal moulds of a dorsal valve, UHR19814.

Description.—Shell medium to large in size for genus, equidimensional to slightly longer subrectangular in outline, with greatest width at about midlength; length 47 mm, width 40

mm in the largest specimen (UHR19813); length 10 mm, width 12 mm in the smallest specimen (UHR19816). Ventral valve moderately convex in lateral profile, most convex at umbo, not geniculated; ears small; sulcus narrow and moderately deep, commencing at umbo and extending to anterior margin; lateral slopes steep. Dorsal valve nearly flat on visceral disc, strongly geniculated, and followed by short trail; fold narrow and low on anterior half of valve. External surface of ventral valve ornamented with several irregular concentric rugae and numerous spine bases; spine bases fine, elongate, quincunxially arranged, and smaller in size anteriorly, numbering 8-9 in 5 mm width at midlength. External ornament of dorsal valve same as that of opposite valve, although spine bases being finer in dorsal valve. Ventral interior with large, longitudinally striated diductor scars and small, elongate dendritic adductor scars; coarse irregular pustules occurring around anterior margin. Dorsal interior with moderately large, trifid cardinal process bearing a groove on ventral face; median septum thin and long, extending to half or more length of valve; lateral ridges short and straight; adductor scars large and dendritic in anterior ones and small, elongate and smooth in posterior ones; numerous pustules becoming coarser anteriorly.

Remarks.—The specimens available are referred to *Waagenoconcha irginae* (Stuckenberg, 1898), redescribed and refigured by Tschernyschew (1902, p. 273, 618, pl. 30, figs. 3, 4; pl. 52, figs. 1–4) from the lower Permian (*Cora–Schwagerina* horizons) of Ufa, central Russia, in size, shape and external ornament of both valves, especially, fine quincunxially arranged spine bases becoming finer anteriorly. Tazawa (1974b) described most of the Kitakami specimens as *Waagenoconcha imperfecta* Prendergast, 1935. But the Australian species differs from the present species in its much larger size (see Archbold, 1993, p. 20, figs. 11–13) and in having finer spine bases on the ventral valve. The type species, *Waagenoconcha humboldti* (d'Orbigny, 1842), is distinguished from *W. irginae* by the coarser spine bases on the ventral valve.

Distribution.—Asselian-Capitanian: Spitsbergen, northern Russia (Kanin Peninsula, Timan, Pechora Basin, northern Urals and Kolyma), central Russia (southern Urals), southern Mongolia, northern China (Inner Mongolia), eastern Russia (South Primorye), northeastern Japan (Setamai and Kamiyasse-Imo in the South Kitakami Belt) and central Japan (Moribu in the Hida Gaien Belt).

> Superfamily Aulostegoidea Muir-Wood and Cooper, 1960 Family Echinostegidae Muir-Wood and Cooper, 1960 Subfamily Chonosteginae Muir-Wood and Cooper, 1960 Genus *Urushtenoidea* Jin and Hu, 1978

> > Type species.—Urushtenia chaoi Jin, 1963.

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Fig. 8. 1–4, *Urushtenoidea crenulata* (Ding in Yang et al., 1962); 1a, 1b, 1c, 1d, external mould and external latex cast of ventral valve, and external mould of dorsal valve, UHR30386; 2a, 2b, external mould and external latex cast of dorsal valve, NU-B2150; 3a, 3b, ventral and dorsal views of internal mould of conjoined shell, NU-B2146; 4a, 4b, 4c, 4d, ventral, anterior and dorsal views of internal mould of conjoined shell, NU-B2148. Scale bars represent 1 cm.

Urushtenoidea crenulata (Ding in Yang et al., 1962) Figs. 8.1–8.4

Eomarginifera crenulata Ding in Yang et al., 1962, p. 85, pl. 37, figs. 6-8.

- *Urushtenia crenulata* (Ding): Jin, 1963, p. 20, 29, pl. 1, figs. 17–24; pl. 2, figs. 9, 10, 18–20, text-fig. 5; Jin et al., 1974, p. 309, pl. 162, figs. 1–3; Yang et al., 1977, p. 335, pl. 136, fig. 11; Tong, 1978, p. 218, pl. 78, fig. 17; Yang and Gao, 1996, pl. 34, figs. 7, 8.
- Urushtenoidea crenulata (Ding): Nakamura, 1979, p. 228, pl. 1, figs. 5–9; pl. 3, figs. 1, 2; Yang, 1984, p. 213, pl. 31, fig. 19; Jin, 1985, pl. 6, fig. 41; Tazawa, 2001, p. 296, figs. 7.1–7.9; Shen et al., 2003, p. 1131, figs. 4.11–4.13; Tazawa, 2008b, p. 50, figs. 7.15, 7.16; Shen and Shi, 2009, p. 155, figs. 3B–3I.

- *Urushtenoidea maceus* (Jin): Nakamura, 1979, p. 227, pl. 1, figs. 1–4; pl. 2, figs. 1–3; Minato et al., 1979, pl. 65, figs. 8–11; Tazawa, 2002, fig. 10.8.
- *Uncisteges crenulata* (Ding): Liu et al., 1982, p. 178, pl. 129, fig. 1; Zhu, 1990, p. 74, pl. 14, figs. 4–14; pl. 17, fig. 12.

Material.—Eleven specimens from localities KF39, KF90, KF217 and KF218: (1) external moulds of both ventral and dorsal valves, UHR30386; (2) internal moulds of two conjoined shells, with external moulds of the dorsal valves, NU-B2142, 2143; (3) internal moulds of five conjoined shells, NU-B2144–2148; (4) internal mould of a ventral valve, NU-B2149; (5) external moulds of two dorsal valves, NU-B2150, 2151.

Description.—Shell medium in size for genus, transversely subquadrate in outline, with greatest width at about midlength; length about 17 mm, width about 25 mm in the largest specimen (NU-B2148). Ventral valve strongly and unevenly convex in lateral profile, nearly flat in visceral disc, strongly geniculated and followed by a long trail; umbo small, incurved; ears small; sulcus broad and shallow. Dorsal valve nearly flat in visceral disc, geniculated and followed by a short trail. External surface of ventral valve ornamented with numerous costae on trail, numbering 6 in 5 mm at mid of trail; several concentric lamellae, prolongated into tubular spines on anterior half of trail. External surface of dorsal valve ornamented with numerous costae and concentric rugae on visceral disc, and costae with spines on trail. Ventral interior with small, narrow, elongate adductor scars on raised platform and large, flabellate diductor scars lying on valve floor. Dorsal interior with robust trilobate cardinal process; median septum occurring at anterior ends of adductor scars and extending to two-thirds of valve length; adducor scars small, tear-drop shaped and highly raised on platform; brachial ridges prominent on both sides of valve anteriorly.

Remarks.—These specimens are referred to *Urushtenoidea crenulata* (Ding in Yang et al., 1962), from the Maokouan of Qinghai, northwestern China, in size, shape and external ornament of both valves, especially the relatively fine costae (6–7 in 5 mm) on the ventral trail. *Urushtenoidea maceus* Jin (1963, p. 19, pl. 2, figs. 1–6), from the Chihsian–Maokouan of eastern China (Jiangsu, Anhui and Zhejiang) and central-southern China (Hubei), differs from *U. crenulata* in having finer costae (8–9 in 5 mm) on the ventral valve. *Urushtenoidea chaoi* Jin (1963, p. 15, 28, pl. 1, figs. 1–4, 9–12; pl. 2, figs. 7, 8, 13–17), from the upper Chihsian–lower Maokouan of Jiangxi and Anhui, eastern China, is readily distinguished from the present species in having coarser costae (3–4 in 5 mm) on the ventral valve.

Distribution.—Kungurian-Wuchiapingian: northwestern China (Qinghai and Gansu), northeastern Japan (Kamiyasse-Imo, Matukawa in the South Kitakami Belt), central Japan (Moribu in the Hida Gaien Belt), southwestern Japan (Mizukoshi in Kyushu Island), eastern China (Jiangsu and Fujian), central-southern China (Hubei, Hunan, Guangdong and Guangxi), southwestern China (Sichuan), Laos, Cambodia and Tibet (Xizang). Superfamily Linoproductoidea Stehli, 1954 Family Linoproductidae Stehli, 1954 Subfamily Linoproductinae Stehli, 1954 Genus *Globiella* Muir-Wood and Cooper, 1960

Type species.—Productus hemispharium Kutorga, 1844.

Globiella tschernyschewi (Netschajew, 1911) Fig. 9.1

Productus tschernyschewi Netschajew, 1911, p. 31, 141, pl. 1, figs. 5, 7; pl. 2, figs. 5-11, 16.

Stepanoviella tschernyschewi (Netschajew): Grigorjewa, 1962, p. 45, pl. 10, figs. 1–3; pl. 13, fig. 5; pl. 14, fig. 3.

Globiella tschernyschewi (Netschajew): Grigorjewa et al. in Sarytcheva, 1977, p. 164, pl. 27, figs. 10, 11.

Material.—One specimen from locality KF21, external and internal moulds of a ventral valve, NU-B1977.

Description.—Shell small in size for genus, equidimensional to slightly transverse, hemispherical in outline, with greatest width at hinge; length 17 mm, width 22 mm. Ventral valve strongly and unevenly convex in lateral profile, most convex in umbonal region and flattened anteriorly; umbo small, ears small, slightly convex and not clearly demarcated from visceral region; lateral flanks steep; no sulcus. External surface of ventral valve ornamented with numerous capillae and four strong irregular rugae on whole valve; capillae numbering 16–17 in 5 mm at about midlength; a row of spines along hinge. Internal structures of ventral valve not clearly preserved and obscure.

Remarks.—This specimen is referred to *Globiella tschernyschewi* (Netschajew, 1911), from the Kazanian beds of the Pinega River, northern Russia, by its small, slightly transverse and hemisphaerical ventral valve ornamented with numerous capillae and strong, irregular concentric rugae. The type species, *Globiella hemisphaerium* (Kutorga, 1844), redescribed by Grigorjewa (1962, p. 42, pl. 9, figs. 1–9; pl. 13, figs. 6–9; text-figs. 3, 5, 14, 15) from the Kazanian beds of the Pinega River and the Kama River regions, northern Russia, is distinguished from *G. tschernyschewi* by its longer ventral valve.

Distribution.—Wordian: northern Russia (Pinega River) and northeastern Japan (Kamiyasse-Imo in the South Kitakami Belt).

Family Kansuellidae Muir-Wood and Cooper, 1960 Subfamily Paucispinauriinae Waterhouse, 1986



Fig. 9. 1, *Globiella tschernyschewi* (Netschajew); 1a, 1b, internal mould and external latex cast of ventral valve, NU-B1977; 2-5, *Grandaurispina kozlowskiana* (Fredericks), 2a, 2b, 2c, internal mould and external mould of dorsal valve, NU-B2001; 3, external mould of dorsal valve, NU-B2002, 4a, 4b, external latex cast and external mould of ventral valve, NU-B1997; 5a, 5b, external latex cast and external mould of ventral valve, NU-B2006. Scale bars represent 1 cm.

Genus Grandaurispina Muir-Wood and Cooper, 1960

Type species.-Grandaurispina kingorum Muir-Wood and Cooper, 1960.

Grandaurispina kozlowskiana (Fredericks, 1925) Figs. 9.2–9.5 *Productus villiersi kozlowskianus* Fredericks, 1925, p. 18, pl. 1, figs. 36–40; pl. 2, figs. 86, 87; Hayasaka, 1925, p. 96, pl. 5, figs. 10, 11.

Cancrinella villiersi kozlowskiana (Fredericks): Hayasaka and Minato, 1956, p. 144, pl. 23, fig. 5. *Cancrinella cancriniformis spinosa* Hayasaka and Minato, 1956, p. 144, pl. 23, fig. 4.

Cancrinella spinosa Hayasaka and Minato: Minato et al., 1979, pl. 62, figs. 5-8, 11; Tazawa, 1976, pl. 2, fig. 5; Tazawa, 2002, fig. 10.3.

Cancrinella kozlowskiana (Fredericks): Minato et al., 1979, pl. 62, figs. 9, 10.

Cancrinella truncata (Chao): Lee et al., 1980, p. 380, pl. 165, figs. 13, 14, 24; Gu, 1992, p. 237, pl. 68, figs. 18, 20.

Cancrinella sp. Tazawa and Ibaraki, 2001, p. 11, pl. 1, fig. 6.

Cancrinella cf. spinosa Hayasaka and Minato: Tazawa, 2001, p. 295, fig. 6.17.

Material.—Fifteen specimens from localities KF21, KF22, KF46 and KF218: (1) external and internal moulds of seven ventral valves, NU-B1997–2000, 2003–2005; (2) external mould of a ventral valve, NU-B2006; (3) internal moulds of three ventral valves, NU-B2007–2009; (4) external and internal moulds of two dorsal valves, NU-B2001, 2002; (5) external moulds of two dorsal valves, NU-B2010, 2011.

Description.—Shell small in size for genus, slightly elongate subquadrate in outline, with greatest width at midlength; length 23 mm, width 22 mm in the largest specimen (NU-B2006). Ventral valve strongly and unevenly convex in lateral profile, most convex in umbonal region; umbo small, incurved; ears small; hinge narrower than greatest width; lateral slopes steep; sulcus absent. Dorsal valve nearly flat on visceral disc, strongly geniculated and followed by a short trail; fold absent. External surface of ventral valve ornamented with numerous, quincunxially arranged, elongate spine bases on venter and dense strong spine bases on ears and adjacent lateral slopes; moreover, numerous capillae and some weak rugae on venter. Dorsal valve ornamented with numerous dimples corresponding to spine bases of opposite valve and numerous fine capillae and prominent concentric rugae on visceral disc. Internal structures of both valves not clearly preserved except for long, thin median septum extending to midlength of valve.

Remarks.—Part of the present specimens were figured by Minato et al. (1979) and Tazawa (1976, 2002) as *Cancrinella spinosa* Hayasaka and Minato, 1956 or *Cancrinella kozlowskiana* (Fredericks, 1925). But the specimens, from the Kamiyasse-Imo area, are referred to *Grandaurispina kozlowskiana* (Fredericks, 1925), originally described from the Chandalaz Formation of South Primorye, eastern Russia, on account of their small size, and in having numerous spine bases on the ventral valve. *Grandaurispina bella* Cooper and Grant (1975, p. 1162, pl. 442, figs. 1–38), from the Word Formation of West Texas, is also a small-sized *Grandaurispina* with numerous spine bases on the ventral valve, *Grandaurispina kozlowskiana* (*Fredericks from G. kozlowskiana* in its more rounded outline. The type species, *Grandaurispina kingorum*

Muir-Wood and Cooper (1960, p. 306, pl. 121, figs. 1–13), from the Word Formation of West Texas, differs from the present species in its larger size and in having more distant spine bases on the ventral valve.

Distribution.—Wordian: northern China (Inner Mongolia), northeastern China (Jilin), eastern Russia (South Primorye), northeastern Japan (Setamai, Kamiyasse–Imo and Iwaizaki in the South Kitakami Belt) and central Japan (Moribu in the Hida Gaien Belt).

Suborder Lyttoniidina Williams, Harper and Grant, 2000 Superfamily Lyttonioidea Waagen, 1883 Family Lyttoniidae Waagen, 1883 Subfamily Lyttoniinae Waagen, 1883 Genus *Leptodus* Kayser, 1883

Type species.—Leptodus richthofeni Kayser, 1883.

Leptodus nobilis (Waagen, 1883) Figs. 10.1–10.5, 11.5–11.7

Lyttonia nobilis Waagen, 1883, p. 398, pl. 29, figs. 1–3; pl. 30, figs. 1, 2, 5, 6, 8, 10, 11; Noetling, 1904, p. 112, text-figs. 4–7; Noetling, 1905, p. 140, pl. 17, figs. 1, 2; pl. 18, figs. 1–11, text-fig. 2; Mansuy, 1913, p. 123, pl. 13, fig. 10; Mansuy, 1914, p. 32, pl. 6, fig. 7; pl. 7, fig. 1; Albrecht, 1924, p. 289, fig. 1; Huang, 1932, p. 89, pl. 7, figs. 9, 10; pl. 8, figs. 8, 9; pl. 9, figs. 1–8, text-figs. 8–11.

Lyttonia sp. Yabe, 1900, p. 2, text-figs. 1, 2.

Oldhamina (Lyttonia) richthofeni var. *nobilis* Waagen: Fredericks, 1916, p. 76, pl. 4, fig. 2, text-fig. 22.

Lyttonia richthofeni Kayser: Hayasaka, 1917, p. 43, pl. 18, figs. 1–8; Hayasaka, 1922a, p. 62, pl. 11, figs. 1–6; Hayasaka, 1922b, p. 103, pl. 4, figs. 12, 13; Mashiko, 1934, p. 182, text-fig.

Lyttonia (Leptodus) richthofeni Kayser: Hamlet, 1928, p. 31, pl. 6, figs. 1-4.

Lyttonia richthofeni forma *nobilis* Waagen: Licharew, 1932, p. 69, 96, pl. 2, figs. 13, 14; pl. 5, figs. 1–4, 6, text-fig. 3.

Lyttonia cf. nobilis Waagen: Huang, 1936, p. 493, pl. 1, fig. 5.

Leptodus nobilis (Waagen): Termier and Termier, 1960, p. 241, text-pl. 3, figs. 1–10; Chi-Thuan, 1961, p. 274, pl. 1, fig. 1; Ding in Yang et al., 1962, p. 90, pl. 37, fig. 4; Schréter, 1963, p. 107, pl. 3, figs. 5–8; Cooper and Grant, 1974, pl. 191, figs. 8, 9; Grant, 1976, pl. 43, figs. 18, 19; Lee and Gu, 1976, p. 267, pl. 162, figs. 1, 2; Tazawa, 1976, pl. 2, fig. 8; Yang et al., 1977, p. 371, pl. 147, fig. 5; Feng and Jiang, 1978, p. 269, pl. 100, fig. 2; Licharew and Kotlyar, 1978, pl. 14, figs. 13–15; Jin et al., 1979, p. 82, pl. 23, fig. 15; Minato et al., 1979, pl. 66, figs. 1,



Fig. 10. 1–5, *Leptodus nobilis* (Waagen); 1, internal mould of ventral valve, NU-B1691; 2, internal mould of ventral valve, NU-B1701; 3a, 3b, internal mould and internal latex cast of ventral valve, NU-B1681, 4, internal mould of ventral valve, NU-B1693; 5, internal mould of ventral valve, UHR12111. Scale bars represent 1 cm.

4, 5; Zhan, 1979, p. 93, pl. 9, fig. 12; Lee et al., 1980, p. 389, pl. 172, figs. 15, 16; Liao, 1980, pl. 6, figs. 42, 43; Wang et al., 1982, p. 229, pl. 95, fig. 20; Gu and Zhu, 1985, pl. 1, figs. 31, 33, 34; Liao and Meng, 1986, p. 81, pl. 2, figs. 24, 25; Sremac, 1986, p. 30, pl. 10, figs. 1, 2; Liang, 1990, p. 225, pl. 40, figs. 1, 5; Leman, 1994, pl. 1, figs. 3, 4; Zeng et al., 1995, pl. 11, fig. 3; Tazawa et al., 1998, p. 241, figs. 2.1, 2.2, 4; Tazawa and Matsumoto, 1998, p. 7, pl. 2, figs. 7–12; Kato et al., 1999, p. 47, fig. 4; Tazawa, 2001, p. 297, figs. 7.13–7.16; Tazawa and Ibaraki, 2001, p. 11, pl. 1, figs. 7–10; Shen et al., 2002, p. 678, fig. 5.28; Tazawa, 2002, fig. 10.14; Tazawa, 2003, p. 31, figs. 4.1, 4.2; Wang and Zhang, 2003, p. 118, pl. 22, figs. 13–18; Tazawa, 2009, p. 71, fig. 4.7.

Gubleria armenica Sarytcheva, 1964, p. 68, pl. 8, figs. 1–3; Sarytcheva, 1965, p. 39, figs. 9, 10. *Gubleria* sp. Licharew and Kotlyar, 1978, pl. 15, figs. 5, 6.

Leptodus ivanovi Fredericks: Minato et al., 1979, pl. 66, fig. 3.

Leptodus sp. Minato et al., 1979, pl. 66, fig. 2.

Leptodus elongatus Ching and Hu: Wang et al., 1982, p. 229, pl. 91, figs. 16, 17; pl. 93, fig. 4.

- Gubleria sp. Zhu, 1990, p. 80, pl. 16, fig. 24.
- Leptodus sp. Yanagida et al., 1993, p. 5, pl. 1, figs. 8, 9.
- Leptodus sp. Yanagida, 1996, fig. 2.14.
- Leptodus sp. Tazawa, 1999, p. 5, pl. 1, fig. 1; Tazawa et al., 1999, fig. 2.1.
- Gubleria sp. Sone et al., 2001, p. 185, figs. 6.9-6.12.
- Leptodus sp. Shen and Zhang, 2008, fig. 5.4.

Material.—Fifty specimens from localities KF13, KF67, KF84, KF128, KF217 and KF218, (1) internal mould of a ventral valve, with external and internal moulds of the dorsal valve (internal plate), UHR12111; (2) external and internal moulds of a ventral valve, NU-B1681; (3) external moulds of two ventral valves, NU-B1682, 1683; (4) internal moulds of forty-six ventral valves, NU-B1684–1694, 1696–1704, 1706–1726, UHR11450, 12109, 12110, 12114, 12117.

Description.—Shell medium to large in size for genus, elongate subtrigonal to transversely oval in outline, scoop-shaped, with greatest width near anterior margin; length 89 mm, width 83 mm in the largest specimen (NU-B1693), length 36 mm, width 34 mm in an average-sized specimen (NU-B1691). Ventral valve almost flat to slightly convex in both lateral and anterior profiles; external surface of valve bumpy reflecting internal plates, and ornamented with numerous fine growth lines. Ventral interior with regularly and symmetrically arranged lateral septa on both sides of median septum; median septum strong, extending for valve length, mostly continuous but rarely having rough incisions; lateral septa broad, solid (solidiseptate), nearly straight to slightly arched toward anterior, numbering 21–22 on each side of median septum in adult specimen.

Remarks.—These specimens are referred to *Leptodus nobilis* (Waagen, 1883), from the Wargal and Chhidru formations of the Salt Range, by their flat ventral valve with numerous,

regularly and symmetrically disposed broad and solid lateral septa on both sides of median septum. *Leptodus richthofeni* Kayser (1883 p. 161, pl. 21, figs. 9–11), from the upper Permian of Loping, Jiangxi Province, eastern China, and refigured by Cooper and Grant (1974, pl. 191, figs. 11–15) on the lectotype, is readily distinguished from *L. nobilis* by its more highly convex ventral valve, sharp lateral septa and wider interseptal spaces.

Distribution.—Kungurian-Changhsingian; Hungary, Balkan States (Serbia and Croatia), northwestern China (Qinghai), northern China (Inner Mongolia), northeastern China (Heilongjiang and Jilin), eastern Russia (South Primorye), northeastern Japan (Setamai, Kamiyasse-Imo, Matsukawa, Ogatsu and Ichinoseki in the South Kitakami Belt), central Japan (Moribu and Oguradani in the Hida Gaien Belt, and Akasaka in the Mino Belt), southwestern Japan (Yakuno and Yachiyo in the Maizuru Belt, and Tsunemori in the Akiyoshi Belt), eastern China (Zhejiang, Fujian and Jiangxi), central-southern China (Hubei, Hunan, Guangdong and Guangxi), southwestern China (Guizhou, Sichuan and Yunnan), Cambodia, Armenia (Transcaucasia), Malaysia, Timor and Pakistan (Salt Range and Khisor Range).

> Order Athyridida Boucot, Johnson and Staton, 1964 Suborder Athyrididina Boucot, Johnson and Staton, 1964 Superfamily Athyridoidea Davidson, 1881 Family Athyrididae Davidson, 1881 Subfamily Lochengiinae Ching (Jin) and Yang in Yang et al., 1977 Genus *Cryptospirier* Grabau, 1931

Type species.—Cryptospirifer omeishanensis Huang, 1933.

Cryptospirifer omeishanensis Huang, 1933 Figs. 11.2–11.4

Cryptospirifer omeishanensis Huang, 1933, p. 44, pl. 6, fig. 4; pl. 8, fig. 1; Wang et al., 1964, p. 512, pl. 95, figs. 4, 7; Jin et al., 1974, p. 310, pl. 163, fig. 17; Yang et al., 1977, p. 413, pl. 163, fig. 5; Tong, 1978, p. 253, pl. 89, fig. 1; Wang, 1984, p. 220, pl. 88, fig. 12; Shi and Shen, 2001, p. 250, pl. 3, figs. 1–7, text-figs. 4–6.

Cryptospirifer sp. Minato et al., 1979, pl. 67, fig. 9.

Cryptospirifer iranica Nakamura and Golshani 1981, p. 72. pl. 2, fig. 1 only.

Cryptospirifer sp. Hu, 1983, pl. 1, figs. 1-3.

Material.—Three specimens from locality KF218, three ventral valves, NU-B2013–2015. *Remarks.*—These specimens are represented by imperfect abraded ventral valves, but



Fig. 11. 1, Alispiriferella lita (Fredericks): 1a, 1b, ventral and dorsal views of internal mould of conjoined shell, NU-B2016; 2-4, Cryptospirifer omeishanensis Huang; 2, ventral valve, NU-B2014; 3, slightly abraded ventral valve, NU-B2015; 4, ventral valve, NU-B2013; 5-7, Leptodus nobilis (Waagen), 5, internal mould of ventral valve, NU-B1722; 6, internal mould of ventral valve, NU-B1697; 7a, 7b, internal latex cast and internal mould of ventral valve, UHR12117. Scale bars represent 1 cm.

they can be referred to *Cryptospirifer omeishanensis* Huang, 1933, from the Maokou Formation of Omeishan, Sichuan Province, southwestern China, on account of their large size (length about 66 mm, width more than 100 mm in the largest specimen, NU-B2015), transversely subelliptical outline, and gently convex, smooth ventral valves. Part of the specimens, described by Nakamura and Golshani (1981, p. 72, pl. 2, fig. 1) as *Cryptospirifer iranica* Nakamura and Golshani, 1981, from the middle Permian (equivalent to Gnishik Formation) of Abadeh, central Iran, may be conspecific with the present species. Other two *Cryptospirifer* species from the Maokou Formation of Sichuan, *C. shawanensis* Jin, Liao and Fang (1974, p. 310, pl. 163, figs. 14–16) and *C. orbicularis* Tong (1978, p. 253, pl. 89, fig. 3), are readily distinguished from *C. omeishanensis* by the smaller size and slightly elongate outline.

Distribution.—Wordian: northeastern Japan (Kamiyasse–Imo in the South Kitakami Belt), eastern China (Jiangxi), central-southern China (Hubei), southwestern China (Sichuan and Yunnan) and central Iran (Abadeh).

Order Spiriferida Waagen, 1883 Suborder Spiriferidina Waagen, 1883 Superfamily Spiriferoidea King, 1846 Family Spiriferellidae Waterhouse, 1968 Genus *Alispiriferella* Waterhouse and Waddington, 1982

Type species.—Spirifer (Spiriferella) keilhavii var. ordinaria Einor, 1939.

Alispiriferella lita (Fredericks, 1924) Fig. 11.1

Spiriferella saranae mut. lita Fredericks, 1924, p. 36, pl. 1, figs. 16–27, text-fig. 2.
Spirifer cf. saranae mut. lita Fredericks: Hayasaka, 1925, p. 98, pl. 5, fig. 14.
Spiriferella cf. saranae mut. lita Fredericks: Nonaka, 1944, p. 86, pl. 7, figs. 12–14.
Spiriferella keilhavii (von Buch): Yanagida, 1963, p. 72, pl. 9, figs. 4–9; pl. 10, figs. 1–7.
Timaniella harkeri Waterhouse: Licharew and Kotlyar, 1978, pl. 18, figs. 2, 3.
Spiriferella grandis Kotlyar in Licharew and Kotlyar, 1978, p. 73, pl. 18, figs. 7, 8.
Spiriferella lita (Fredericks): Tazawa, 1979, p. 28, pl. 4, figs. 12, 13; pl. 5, figs. 1–4, 6; Tazawa,

2001, p. 302, figs. 8.19–8.22; Tazawa and Chen, 2006, p. 336, fig. 6.4. Spiriferella cf. lita (Fredericks): Tazawa et al., 2000, p. 12, pl. 1, figs. 16, 17. Alispiriferella ordinaria (Einor): Tazawa, 2001, p. 302, fig. 8.14. Alispiriferella japonica Tazawa, 2001, p. 303, figs. 8.15–8.18. Alispiriferella neimongolensis Wang and Zhang, 2003, p. 154, pl. 46, figs. 9–18; pl. 50, figs. 5, 9.
35

Alispiriferella lita (Fredericks): Tazawa and Hasegawa, 2007, p. 9, figs. 5.3–5.11; Tazawa, 2008a, p. 41, figs. 6.6, 6.7; Tazawa, 2008b, p. 55, figs. 9.8–9.14; Tazawa, 2009, p. 74, figs. 5.4–5.9.

Material.—One specimen from locality KF217, internal mould of a conjoined shell, NU-B2016.

Remarks.—The material available is a single internal mould of conjoined shell, but it can be referred to *Alispiriferella lita* (Fredericks, 1924), from the middle Permian (Wordian) of South Primorye, eastern Russia, by its medium-sized, transverse-shaped shell (length about 26 mm, width about 47 mm), with strong, simple costae on both ventral and dorsal valves, and in having characteristic large muscles in the posterior of the ventral valve. The Kamiyasse-Imo specimen resembles well the shell of *Alispiriferella lita*, described by Tazawa (2008b) from the upper Permian Mizukoshi Formation of Mizukoshi, central Kyushu, southwestern Japan.

Distribution.—Wordian-Changhsingian: northern China (Inner Mongolia), northeastern China (Heilongjiang), eastern Russia (South Primorye), northeastern Japan (Kamiyasse-Imo, Matsukawa, Ogatsu and Takakurayama in the South Kitakami Belt), central Japan (Moribu in the Hida Gaien Belt) and southwestern Japan (Tsunemori in the Akiyoshi Belt and Mizukoshi in central Kyushu)

Acknowledgements

Sincere thanks are due to Koji Nakamura (Professor Emeritus of Hokkaido University, Sapporo) and Tomoharu Ikeda (Fuji City Office, Fuji) for providing part of the brachiopod specimens; Yousuke Ibaraki (Fossa Magna Museum, Itoigawa) for his help in drawing the figures; and Atsushi Matsuoka (Department of Geology, Niigata University, Niigata) and an anonymous reviewer for their helpful comments that improved the paper.

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J. Tazawa

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Early Carboniferous (Visean) brachiopods from the Hina Limestone, Okayama Prefecture, SW Japan, and their palaeobiogeographical implications

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Abstract

A brachiopod fauna consisting of 9 species in 8 genera is described from the lower part (*Endothyra* Zone) of the Hina Limestone, Okayama Prefecture, southwestern Japan. The Hina fauna includes the following species: *Leptagonia analoga, Dictyoclostus pinguis, Marginatia burlingtonensis, Marginatia* cf. *magna, Schizophoria resupinata, Cleiothyridina* sp., *Spirifer* cf. *liangchowensis, Grandispirifer* sp. and *Syringothyris* cf. *cuspidatus.* The Hina fauna has some affinities with the Early Carboniferous (Visean) brachiopod faunas of South Kitakami, Xinjiang, Kirgiz, Kazakhstan, Kuznetsk Basin, Urals and England. The palaeobiogeographical data suggest that the Akiyoshi-type reef-seamount complexes, including the Hina Limestone, were probably located at mid-latitudes of the Northern Hemisphere in the Panthalassa, near North China and Kazakhstan during Early Carboniferous (Visean).

Key words: Brachiopoda, Hina Limestone, palaeobiogeography, southwestern Japan, Visean.

Introduction

The Hina Limestone (named by Cho, 1939), distributed in the Hina area, Okayama Prefecture, southwestern Japan, is one of the Carboniferous-Permian exotic limestonebasalt blocks, being reef-seamount complexes origin, in the Akiyoshi Terrane (Kanmera et al., 1990). According to Tazawa (2009; Tazawa et al., 2009), the accretion site of the exotic

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Fig. 1. Map showing the fossil locality HN1 in the Kamishigi area (using the topographical map "Jito" scale 1:25,000 published by the Geospatial Information Authority of Japan).

limestone-basalt blocks was probably located at subduction zone developed along the eastern margin of North China (Sino-Korea), and close to the South Kitakami and Maizuru areas, during the middle to late Permian (Capitanian-Changhsingian). However, the depositional site in Early Carboniferous is unclear, although it was supposed that the Akiyoshi-type reef-seamount complexes were probably located at the mid-Panthalassa in the Northern Hemisphere on the basis of palaeomagnetic data (Fujiwara, 1967) and brachiopod palaeobiogeography (Tazawa et al., 2005).

The present study describes brachiopod species from the lower part (*Endothyra* Zone) of the Hina Limestone, and discusses age and palaeobiogeography of the fauna. The Hina fauna is important for understanding the depositional site of the Akiyoshi-type reef-seamount complexes. In this study, I. Nishikawa prepared the brachiopod specimens; and J. Tazawa and Y. Ibaraki studied the systematics of the brachiopods. The specimens described herein are registered and housed in the Fossa Magna Museum, Itoigawa, Japan with prefix FMM.

Stratigraphy and locality

The stratigraphy of the Palaeozoic rocks in the Hina area has been studied by Cho (1939), Kobayashi (1950), Nakano (1952), Yoshimura (1961), Hase and Yokoyama (1975), Sada et al. (1978) and Sano et al. (1987). According to Hase and Yokoyama (1975) and Sada et al. (1978), the Hina Limestone is a large basalt-limestone block (2 km×1 km, 300-450 m thick) consisting of basaltic pyroclastic rocks (about 100 m thick) and overlying massive limestone (200-350 m thick) of late Early Carboniferous (Visean) to early Late Carboniferous (Bashkirian) in age; and the limestone is subdivided into three zones, *Endothyra* Zone, *Eostaffella–Millerella* Zone and *Profusulinella* Zone, in ascending order.

The brachiopod specimens treated in the present study were collected from grey limestone of the lower part (*Endothyra* Zone) of the Hina Limestone, cropping out at locality HN1, a road-cutting at Kamishigi (about 1 km northwest of Hina), Yoshii-cho, Ihara City, Okayama Prefecture (Fig. 1).

The Hina fauna

The Hina fauna consists of the following 9 species in 8 genera: *Leptagonia analoga* (Phillips, 1836), *Dictyoclostus pinguis* (Muir-Wood, 1928), *Marginatia burlingtonensis* (Hall, 1858), *Marginatia* cf. *magna* Carter, 1968, *Schizophoria resupinata* (Martin, 1809), *Cleiothyridina* sp., *Spirifer* cf. *liangchowensis* Chao, 1929, *Grandispirifer* sp. and *Syringothyris* cf. *cuspidatus* (Sowerby, 1816). The stratigraphic and geographic distributions of the brachiopod species of the Hina fauna are summarized in Fig. 2 and Figs. 3, 4, respectively.



Fig. 2. Stratigraphic distribution of brachiopod species of the Hina fauna. Broken lines indicate those of the allied species.

				r		-			_	
Australia	45. E. Australia	+								
	A. W. Australia	+								
SW China	ueuun 7.54	+		+		+				
	nodziuD .24					+				
CS China	ixaneuD . 14	+								
	P. Guanedone	+								
T	isduH.95	+								
neael WS	idsovislA .85					+	Ι	+		
C. Japan	37. Kanto Mountains					+				
NE Japan	36. South Kitakami Belt	+		+		+				
N. China	35. Inner Mongolia					+				
NW China	34. Shaanxi					+				
	33. Gansu	+								
	32. Xinjiang	+				+			Ι	
	31. Kirgiz		+	+						
30. Uzbekistan						+				
	29. Kazakhstan	+		+		+				
C. Russia	28. Kuznetsk Basin	+		+		+				
	27. Urals	+		+		+				I
26. Iran		+								
ς5. Turkey		+		+						
w. Russia	24. Donetz Basin	+				+				
	23. Moscow Basin		+			+				-
	22. Algeria								Ι	
ning2.12						+				
20. Belgium		+				+				
18. Poland 19. Germany		+	+							
			+			+				
NK	17. N. Ireland	+								
	16. Isle of Man	+								
	i 5. Wales		+			+				
	14. England	+	+			+				1
sizzuA .V	13. Pechora Basin	+				+				
	I. Novaya Zemlya					+				
	II. Taimyr Peninsula				-	+				1
	10. Verkhoyansk Range	+				+				
Canada	9. Alberta	+		+						
	8. New Mexico	+								
ASU	7. Utah	+			_	_				
	6. Idaho				-	+				
	2. Oklahoma	+								
	4. Arkansas	L.		+	<u> </u>					
		+				_				
	BWOL .2	+		+	-					
	siouiiii .i	+		+						
		ŀ		•		_				
Region		aloga	pinguis	rlingtonensis	. magna	resupinata	r sp.	ngchowensis	· sp.	cf. cuspidatus
Species		Leptagonia an	Dictyoclostus 1	Marginatia bu	Marginatia cf.	Schizophoria r	Cleiothyridina	Spirifer cf. lia	Grandispirifer	Syringothyris



1. Age

Of the brachiopods listed above, *Leptagonia analoga* is known from the lower Tournaisian-upper Visean; *Dictyoclostus pinguis* is known from the upper Visean-Serpukhovian; *Marginatia burlingtonensis* is known from the upper Tournaisian-lower Visean; and *Schizophoria resupinata* is known from the upper Tournaisian-upper Visean.

In addition, *Marginatia* cf. *magna* resembles *Marginatia magna* Carter, 1968, from the Burlington Limestone (lower Osagean, correlated with the upper Tournaisian) of Missouri, USA; *Cleiothyridina* sp. resembles the shells, described by Yanagida (1962) as *Cleiothyridina royssii* (Léveillé, 1835) from the lower part (*Millerella* Zone, Serpukhovian) of the Akiyoshi Limestone, Akiyoshi, southwestern Japan; *Spirifer* cf. *liangchowensis* is conspecific with both *Spirifer* aff. *liangchowensis* Yanagida, 1962, from the Akiyoshi Limestone (*Millerella* Zone) of Akiyoshi and *Spirifer* aff. *besnossovae* Hase and Yokoyama, 1975, from the lower part (*Endothyra* Zone, upper Visean-Serpukhovian) of the Hina Limestone at Hina; the genus *Grandispirifer* occurs from the upper Tournaisian-upper Visean of Canada, Algeria, Kirgiz and northwestern China (Xinjiang); and *Syringothyris* cf. *cuspidatus* resembles *Syringothyris cuspidatus* (Sowerby, 1816), from the lower Visean-Serpukhovian of England and Russia (Taimyr Peninsula, Russian Platform and Urals).

In summary, the age of the Hina fauna is assigned to Visean, probably late Visean. This conclusion is slightly later than the age determination by Hase and Yokoyama (1975); in which they considered the age of the lower part (*Endothyra* Zone) of the Hina Limestone to early Visean on the basis of brachiopods, *Schizophoria* aff. *resupinata* (Martin), *Rugosochonetes* sp., *Avonia* sp., *Eomarginifera* sp., *Striatifera striata* (Fischer), *Neospirifer*? sp. and *Phricodothyris insolita* George, although the brachiopods were not described. Our conclusion is consistent with that of Tazawa et al. (1983), who considered that the age of the late Visean–Serpukhovian, based on brachiopods, *Rhipidomella* sp. and *Delepinea* cf. *sayamensis* Yanagida from the Omi Limestone, Omi, central Japan.

2. Palaeobiogeography

Among the 9 species of the Hina fauna, three species occur in UK (England), central Russia (Urals and Kuznetsk Basin), Kazakhstan, northeastern Japan (Hikoroichi in the South Kitakami Belt) and southwestern China (Yunnan); and two species with one closely allied species occur from Canada (Alberta), Kirgiz, northwestern China (Xinjiang) and southwestern Japan (Akiyoshi in the Akiyoshi Belt). It is noteworthy that only one species occurs from South China and Australia. In terms of palaeobiogeography, the Hina fauna has some affinities with the Early Carboniferous (Visean) brachiopod faunas of South Kitakami, Xinjiang, Kirgiz, Kazakhstan, Kuznetsk Basin, Urals and England, but differs from those of South China and Australia.



Solid circles indicate numbers of brachiopod species listed in the Hina fauna (allied species are counted 0.5; and station Fig. 4. Early Carboniferous (Visean) reconstruction map of the world (base map modified from Qiao and Shen, 2015). numbers are same as in Fig. 3).

Our results suggest that the Akiyoshi-type reef-seamount complexes, including the Hina Limestone, were probably located at mid-latitudes of the Northern Hemisphere in the Panthalassa, near North China and Kazakhstan during Early Carboniferous (Visean). This conclusion is in agreement with that of Tazawa et al. (2005); in which they emphasized that the occurrence of the brachiopod genus *Daviesiella* is restricted to the lower-upper Visean of central Japan (Omi in the Akiyoshi Terrane), northwestern China (Xinjiang), Kirgiz and UK (England and Wales).

Systematic descriptions

Order Strophomenida Öpik, 1934 Superfamily Strophomenoidea King, 1846 Family Pafinesquinidae Schuchert, 1893 Subfamily Leptaeninae Hall and Clarke, 1894 Genus *Leptagonia* M'Coy, 1844

Type species.—Producta analoga Phillips, 1836.

Leptagonia analoga (Phillips, 1836) Fig. 5.5

Producta analoga Phillips, 1836, p. 116, pl. 7, fig. 10.

- Strophomena rhomboidalis var. analoga Phillips: Davidson, 1861, p. 119, pl. 28, figs. 1–6, 9–13; Etheridge, 1872, p. 333, pl. 18, fig. 1.
- Leptaena analoga (Phillips): Weller, 1914, p. 49, pl. 2, figs. 1–10; Frech, 1916, p. 237, pl. 2, figs. 2, 3d; Girty, 1920, pl. 54, fig. 3; Tolmatchoff, 1924, p. 209, 569, pl. 13, fig. 8; Girty, 1927, pl. 22, figs. 6–8; Demanet, 1934, p. 61, pl. 5, figs. 1–14, text-figs. 1–14; Branson, 1938, p. 24, pl. 5, fig. 31; Minato, 1951, p. 361, pl. 3, fig. 1; Nelson, 1961, pl. 4, fig. 26; Sokolskaya in Sarytcheva et al., 1963, p. 80, pl. 4, figs. 9–14.

Leptaena rhomboidalis Wilckens: Sommer, 1909, p. 626, pl. 29, fig. 14.

Leptagonia cf. analoga (Phillips): Cvancara, 1958, p. 860, pl. 110, figs. 6-13, text-figs. 3, 4.

- *Leptaenella analoga* (Phillips): Yang, 1964, p. 61, pl. 1, fig. 5; Gretchischnikova, 1966, p. 94, pl. 1, figs. 19, 20; pl. 2, figs. 1–6; Abramov, 1970, p. 108, pl. 1, figs. 11, 12; Aisenverg and Poletaev in Aisenverg, 1971, pl. 60, figs. 2, 3; Nalivkin and Fotieva, 1973, p. 20, pl. 1, figs. 9–13.
- Leptagonia analoga (Phillips): Brunton, 1968, p. 29, pl. 3, figs. 26–31; pl. 4, figs. 1–9, text-figs.
 6–17; Gaetani, 1968, p. 688, pl. 47, fig. 3; Thomas, 1971, p. 30, pl. 18, figs. 1–8, text-fig. 11; Bublitschenko, 1971, p. 37, pl. 3, figs. 1–5; Brand, 1972, p. 59, pl. 8, figs. 1–6, text-figs. 1a, 3; Kalashnikov, 1974, p. 23, pl. 3, fig. 5; Litvinovich et al., 1975, p. 53, pl. 16, fig. 11;

Bublitschenko, 1976, p. 22, pl. 1, fig. 10; Yang et al., 1977, p. 316, pl. 131, fig. 2; Minato et al., 1979, pl. 15, fig. 2; Nalivkin, 1979, p. 18, pl. 3, figs. 1–3, 5, 6; Ding and Qi, 1983, p. 251, pl. 89, figs. 9, 10, 12; Zhang et al., 1983, p. 271, pl. 107, fig. 13; pl. 106, fig. 3; Tazawa et al., 1984, p. 350, pl. 67, figs. 2–4; Yang, 1984, p. 205, pl. 29, fig. 11; Xu and Yao, 1988, p. 274, pl. 67, figs. 4, 6–10; Carter, 1999, p. 96, figs. 1A–1E; Shi et al., 2005, p. 39, figs. 3A, 3E.

Leptagonia sp. Hase and Yokoyama, 1975, pl. 18, fig. 6.

Material.—One specimen, a ventral valve, FMM6187.

Description.—Shell small in size, transversely trapezoidal in outline, with greatest width at hinge; length 22 mm, width about 36 mm. Ventral valve slightly convex in umbonal region, flat to gently concave in mid to anterior portion of visceral disc, strongly geniculated, and followed by a short trail; marginal ridge around visceral disc prominent. External surface of ventral valve ornamented with numerous fine costellae and regular, slightly flexuous rugae; numbering 6–7 costellae in 2mm at about midlength, and 10 rugae in visceral disc. Interior of ventral valve not observed.

Remarks.—This specimen can be referred to *Leptagonia analoga* (Phillips, 1836), redescribed by Brunton (1968, p. 29, pl. 3, figs. 26–31; pl. 4, figs. 1–9, text-figs. 6–17) on the type specimens from the Visean of England and northern Ireland, in its flat to slightly concave ventral valve with prominent marginal ridge and produced cardinal extremities, and the external ornament consisting of numerous fine costellae and regular, slightly flexuous rugae. The Hina specimen, being smaller in size than the type specimens, may be a juvenile shell. *Leptagonia* sp. (Hase and Yokoyama, 1975, pl. 18, fig. 6), from the Hina Limestone (*Endothyra* Zone) at Hina, is deemed conspecific with *Leptagonia analoga* (Phillips).

Distribution.—Lower Carboniferous (lower Tournaisian-upper Visean): USA (Illinois, Iowa, Missouri, Oklahoma, Utah and New Mexico), Canada (Alberta), northern Russia (Verkhoyansk Range and Pechora Basin), UK (England, Isle of Man and northern Ireland), Germany, Belgium, western Russia (Donetz Basin), Turkey (Taurus Mountains), Iran (Elburz Range), central Russia (southern Urals and Kuznetsk Basin), Kazakhstan, northwestern China (Xinjiang and Gansu), northeastern Japan (South Kitakami Belt), southwestern Japan (Hina in the Akiyoshi Belt), central-southern China (Hubei, Guangdong and Guangxi), southwestern China (Yunnan), western Australia (Bonaparte Gulf Basin) and eastern Australia (Queensland and New South Wales).

> Order Productida Sarytcheva and Sokolskaya, 1959 Suborder Productidina Waagen, 1883 Superfamily Productoidea Gray, 1840 Family Dictyoclostidae Stehli, 1954

Subfamily Dictyoclostinae Stehli, 1954 Genus *Dictyoclostus* Muir-Wood, 1930

Type species.—Anomites semireticulatus Martin, 1809.

Dictyoclostus pinguis (Muir-Wood, 1928) Fig. 5.3

Productus pinguis Muir-Wood, 1928, p. 104, pl. 5, figs. 1-3; pl. 6, fig. 1, text-fig. 20.

Productus (Dictyoclostus) pinguis Muir-Wood: Paeckelmann, 1931, p. 278, pl. 34, fig. 2.

Dictyoclostus pinguis (Muir-Wood): Sarytcheva in Sarytcheva and Sokolskaya, 1952, p. 138, pl. 38, fig. 191; Galitzkaya, 1977, p. 96, pl. 30, figs. 3, 4; Zakowa, 1988, p. 52, pl. 4, figs. 2, 4, 5; pl. 5, figs. 1, 2.

Material.-One specimen, a ventral valve, FMM6188.

Description.—Shell large in size for genus, transversely subquadrate in outline; length about 53 mm, width more than 65 mm. Ventral valve strongly and unevenly convex in lateral profile, most convex in umbonal region, gently geniculated at anterior margin of visceral disc; sulcus broad and shallow; lateral slopes steep. External surface of ventral valve ornamented with numerous costae and few weak rugae; costae rounded, with narrower interspaces, and often bifurcated, numbering 8–9 in 10 mm near anterior margin of valve; concentric rugae few on posterior of lateral slopes. Internal structure of ventral valve not observed, except for large flabellate diductor scars.

Remarks.—This specimen is referred to *Dictyoclostus pinguis* (Muir-Wood, 1928, p. 104, pl. 5, figs. 1–3; pl. 6, fig. 1, text-fig. 20), originally described from the upper Visean of England and Wales, in the large size and the external ornament consisting of comparatively fine costae and few weak rugae on the ventral valve. The type species, *Dictyioclostus semireticulatus* (Martin, 1809), from the Visean of Derbyshire, England, is distinguished from *D. pinguis* by its smaller size and having coarser costae in the ventral valve.

Distribution.—Lower Carboniferous (upper Visean-Serpukhovian): UK (England and Wales), Poland, Germany, western Russia (Moscow Basin), Kirgiz (Tien Shan) and southwestern Japan (Hina in the Akiyoshi Belt).

Family Buxtoniidae Muir-Wood and Cooper, 1960Subfamily Marginatiinae Waterhouse, 2002Genus *Marginatia* Muir-Wood and Cooper, 1960

Type species.—Productus fernglensis Weller, 1909.



Productus flemingi var. burlingtonensis Hall, 1858, p. 598, pl. 12, fig. 3.

Productus burlingtonensis Hall: Weller, 1914, p. 104, pl. 9, figs. 1-10; Frech, 1916, p. 239, pl. 6,

fig. 1; Tolmatchoff, 1924, p. 237, 575, pl. 14, figs. 8–11; Girty, 1929, p. 85, pl. 9, figs. 20–24.

Productus (Productus) burlingtonensis Hall: Nalivkin, 1937, p. 66, pl. 7, figs. 7-11.

Productus sp. Minato, 1951, p. 366, pl. 1, fig. 4.

Productus (Dictyoclostus) burlingtonensis Hall: Simorin, 1956, p. 136, pl. 9, figs. 1-3.

Marginatia burlingtonensis (Hall): Sarytcheva in Sarytcheva et al., 1963, p. 191, pl. 28, figs. 5–8, text-figs. 81, 82; Grechishnikova, 1966, p. 116, pl. 8, figs. 11–13; Litvinovich et al., 1969, p. 213, pl. 35, figs. 2–4; Nalivkin and Fotieva, 1973, p. 39, pl. 8, fig. 1; Garanj et al., 1975, p. 166, pl. 66, fig. 7; Bublitschenko, 1976, p. 50, pl. 2, fig. 12; pl. 4, fig. 6; pl. 5, figs. 4–6; pl. 6, fig. 9; Galitzkaja, 1977, p. 83, pl. 22, figs. 6–10; Nalivkin, 1979, p. 94, pl. 32, figs. 1–10; pl. 34, figs. 3, 4; Jin, 1985, p. 77, pl. 1, figs. 20–22; Carter, 1987, p. 39, pl. 9, figs. 1–8; Shi et al., 2005, p. 44, figs. 5D, 5I–5K, 5M; Tazawa, 2006, p. 132, figs. 6.1–6.8.

Dictyoclostus sp. Hase and Yokoyama, 1975, pl. 18, fig. 1.

Marginatia sp. Tazawa, 1985, p. 459, figs. 2.3–2.7; Tazawa, 1989, p. 60, pl. 1, fig. 1; Tazawa, 2002, figs. 7.1, 7.2.

Material.- Three specimens, three ventral valves, FMM6195-6197.

Remarks.—The specimens at hand are three abraded ventral valves, in which the external ornamentation are obscure, except for costellae on the trail. However, these specimens can be referred to *Marginatia burlingtonensis* (Hall, 1858), originally described by Hall (1858, p. 598, pl. 12, fig. 3) from the Burlington Limestone of Iowa and Illinois, USA, in the medium-sized (length 34 mm, width 35 mm in the largest specimen, FMM6196), strongly convex ventral valve, with narrow, deep sulcus and long trail, and ornamented with numerous fine costellae, numbering 13–14 in 5 mm at mid of trail. *Dictoclostus* sp. (Hase and Yokoyama, 1975, pl. 18, fig. 1), from the Hina Limestone (*Eostaffella–Millerella* Zone) at Hina, is deemed conspecific with the present species. *Marginatia burlingtonensis* somewhat resembles the type species, *Marginatia ferunglensis* (Weller, 1909, p. 299, pl. 12, figs. 14–17), from the Fern Glen Formation of Missouri, USA, in size and shape of the ventral valve, but differs from the latter in having deeper sulcus and lacking fluting on the ventral trail.

⁻Fig. 5. 1, 2, Marginatia burlingtonensis (Hall); 1a, 1b, 1c, 1d, ventral, anterior, posterior and lateral views of ventral valve, FMM6196; 3, Dictyoclostus pinguis (Muir-Wood); 3a, 3b, ventral and anterior views of ventral valve, FMM6188; 4, Marginatia cf. magna Carter; 4a, 4b, 4c, 4d, ventral, anterior, posterior and lateral views of ventral valve, FMM6189; 5, Leptagonia analoga (Phillips); 5a, 5b, ventral view of ventral valve, FMM6187. Scale bars represent 1 cm.

Marginatia toriyamai Yanagida (1973a, p. 41, pl. 1, figs. 1–5; pl. 2, figs. 1–9, text-figs. 6–8), from the lowest part of the Akiyoshi Limestone in Akiyoshi, southwestern Japan, is readily distinguished from the present species by its smaller size and having shorter ventral trail. The subsequent species, *Marginatia* cf. *magna* Carter, 1968, is distinguished from the present species by its much larger size, and having thicker costae.

Distribution.—Lower Carboniferous (upper Tournaisian-lower Visean): USA (Illinois, Iowa and Arkansas), Canada (Alberta), Turkey (Taurus Mountains), central Russia (Urals and Kuznetsk Basin), Kazakhstan, Kirgiz, northeastern Japan (South Kitakami Belt), southwestern Japan (Hina in the Akiyoshi Belt) and southwestern China (Yunnan),

Marginatia cf. magna Carter, 1968 Fig. 5.4

Cf. Marginatia magna Carter, 1968, p. 1147, pl. 147, figs. 1-9.

Material.—One specimen, a ventral valve, FMM6189.

Description.—Shell large in size for genus, transversely subrectangular in outline, with greatest width at hinge; length 28 mm, width about 55 mm. Ventral valve strongly and unevenly convex in lateral profile, most convex at umbonal region, gently convex in visceral disc, strongly geniculated at anterior margin of visceral disc, and followed by a long, weakly fluted trail; sulcus broad and shallow; lateral slopes steep. External surface of trail ornamented with numerous costae and sporadically distributed spine bases, numbering 5–6 costae in 5 mm at about mid of trail; but external ornament of visceral disc abraded and not preserved.

Remarks.—This specimen most resembles *Marginatia magna* Carter, 1968, from the Burlington Limestone of Missouri, USA, in its large size and the long and slightly fluted trail on the ventral valve, but differs in having finer costellae. The type species, *Marginatia ferunglensis* (Weller, 1909), also has fluting ventral trail, but differs from the present species in its smaller size and the finer costae on the ventral valve.

Order Orthida Schuchert and Cooper, 1932 Suborder Dalmanellidina Moore, 1952 Superfmily Enteletoidea Waagen, 1884 Family Schizophoriidae Schuchert and Le Vene, 1929 Genus *Schizophoria* King, 1850

Type species.—Conchyliolithus (Anomites) resupinatus Martin, 1809.

Schizophoria resupinata (Martin, 1809) Figs. 6.1, 6.2

Conchiliolithus (Anomites) resupinatus Martin, 1809, pl. 49, figs. 13, 14. Orthis resupinata (Martin): Davidson, 1861, p. 130, pl. 29, figs. 1–4; pl. 30, figs. 1–5. Schizophoria resupinata (Martin): Yanishevsky, 1918, p. 19, pl. 1, figs. 4, 12; pl. 4, fig. 2; pl. 6,

fig. 16; Demanet, 1934, p. 45, pl. 3, figs. 1-5, text-fig. 9; Miloradovich, 1935, p. 6, pl. 1, figs. 11, 12; Bond, 1941, p. 289, pl. 21, figs. a-c, text-figs. 33, 34; Minato, 1952, p. 150, pl. 5, fig. 3; pl. 6, fig. 4; Sarytcheva in Sarytcheva and Sokolskaya, 1952, p. 29, pl. 2, fig. 12; Parkinson, 1954, p. 368, text-figs. 1, 2; Litvinovich, 1962, p. 178, pl. 1, fig. 2; Besnossova in Sarytcheva et al., 1963, p. 77, pl. 3, figs. 5-8, text-fig. 24; Ustritsky and Tschernjak, 1963, p. 69, pl. 1, figs. 13-16; Yang, 1964, p. 59, pl. 1, figs. 2, 3; Abramov, 1965, p. 35, pl. 2, fig. 3; Brunton, 1968, pl. 2, figs. 1-6; Pocock, 1968, p. 80, pl. 18, fig. 7, text-figs. 13-15; Besnossova et al., 1968, p. 53, pl. 1, figs. 11-13; Lazarev, 1969, pl. 10, figs. 1-5, text-figs. 1, 2; Litvinovich et al., 1969, p. 129, pl. 2, fig. 1; Abramov, 1970, p. 107, pl. 1, figs. 5-7; Aisenverg and Poletaev in Aisenverg, 1971, pl. 60, fig. 1; Nalivkin and Fotieva, 1973, p. 20, pl. 1, figs. 6-8; Yanagida, 1973b, p. 101, pl. 16, figs. 3–9; Kalashnikov, 1974, p. 22, pl. 3, figs. 1–3; Garanj et al., 1975, p. 155, pl. 62, fig. 2; Volgin and Kushnar, 1975, p. 23, pl. 1, figs. 3-5; Litvinovich et al., 1975, p. 52, pl. 16, fig. 7; Lazarev, 1976, pl. 2, figs. 3, 4; pl. 3, figs. 1-5, text-fig. 58; Lee and Gu, 1976, p. 229, pl. 131, figs. 7, 9-11; Martinez Chacon, 1979, p. 54, pl. 2, figs. 1-15; pl. 3, figs. 1-10, text-figs. 3-5; Minato et al., 1979, pl. 22, figs. 1, 2; Tazawa and Katayama, 1979, p. 169, pl. 11, figs. 8-14; Kalashnikov, 1980, p. 24, pl. 2, figs. 2, 3; Mori and Tazawa, 1980, text-fig. 3.3; Tazawa, 1981, p. 67, pl. 5, figs. 3-5; Tazawa et al., 1981, pl. 1, figs. 4-6; Ding and Qi, 1983, p. 245, pl. 88, fig. 7; Zhang et al., 1983, p. 265, pl. 107, figs. 1-3; Tazawa, 1984, p. 304, pl. 61, fig. 9; Abramov and Grigorjeva, 1986, p. 74, pl. 1, figs. 15–18; Yanai et al., 1988, pl. 1, figs. 9, 10; Zakowa, 1989, p. 103, pl. 1, figs. 1–5; pl. 2, figs. 1–5; pl. 3, figs. 1–4, text-figs. 2–10; Jiang, 1997, pl. 1, figs. 1, 2; Bassett and Bryant, 2006, p. 504, pl. 6, figs. 1-10; pl. 7, figs. 1-16, textfigs. 5–7; Butts, 2007, p. 55, figs. 5.3–5.10; Ibaraki et al., 2014, p. 73, figs. 4.1, 4.2.

Schellwienella izirii Minato, 1951, p. 363, pl. 5, fig. 3; Minato et al., 1979, pl. 19, fig. 3.

Schizophoria aff. resupinata (Martin): Yanagida, 1962, p. 122, pl. 21, figs. 4–13, text-fig. 22; Hase and Yokoyama, 1975, pl. 16, figs. 6, 7.

Schizophoria (Schizophoria) resupinata (Martin): Sun and Baliński, 2008, p. 521, figs. 27F-27L.

Material.—Five specimens: (1) a ventral valve, FMM6190; (2) three dorsal valves, FMM6191-6193; (2) external mould of a dorsal valve, FMM6194.

Description.—Shell large in size for genus, transversely subcircular in outline; hinge much shorter than greatest width at about midlength; length 48 mm, width about 60 mm in the largest specimen (FMM6190). Ventral valve gently convex in both lateral and anterior



profiles; umbo small, incurved; interarea narrow; sulcus broad and very shallow near anterior margin. Dorsal valve moderately convex in both lateral and anterior profiles; no fold. External surface of both valves ornamented with numerous fine costellae, numbering 8–9 in 5 mm at about midlength of ventral valve.

Remarks.—These specimens are referred to *Schizophoria resupinata* (Martin, 1809), redescribed by Pocock (1968, p. 80, pl. 18, fig. 7, text-figs. 13–15) from the upper Tournaisian to upper Visean of Belgium and Britain, in the large sized, wider subcircular and slightly convex ventral valve, and external ornamentation of numerous fine costellae. *Schizophoria* aff. *resupinata* (Martin, 1809), described by Yanagida (1962, p. 122, pl. 21, figs. 4–13, text-fig. 22) from the Akiyoshi Limestone (*Millerella* Zone) of Akiyoshi, southwestern Japan, and also figured by Hase and Yokoyama (1975, pl. 16, figs. 6, 7) from the Hina Limestone at Hina, is conspecific with the present species.

Distribution.—Lower Carboniferous (upper Tournaisian-upper Visean): USA (Idaho), northern Russia (Verkhoyansk Range, Taimyr Peninsula, Novaya Zemlya and Pechora Basin), UK (England and Wales), Poland, Belgium, Spain, western Russia (Moscow Basin and Donetz Basin), central Russia (southern Urals and Kuznetsk Basin), Kazakhstan, Uzbekistan (Fergana), northwestern China (Xinjiang and Shaanxi), northern China (Inner Mongolia), northeastern Japan (South Kitakami Belt), central Japan (Kanto Mountains), southwestern Japan (Hina and Akiyoshi in the Akiyoshi Belt) and southwestern China (Guizhou and Yunnan).

> Order Athyridida Boucot, Johnson and Staton, 1964 Suborder Athyrididina Boucot, Johnson and Staton, 1964 Superfamily Athyridoidea Davidson, 1881 Family Athyrididae Davidson, 1881 Subfamily Cleiothyridinae Alvarez, Rong and Boucot, 1998 Genus *Cleiothyridina* Buckman, 1906

Type species.—Atrypa pectinifera Sowerby, 1840.

Cleiothyridina sp. Figs. 6.5, 7

<sup>Fig. 6. 1, 2, Schizophoria resupinata (Martin); 1a, 1b, 1c, 1d, ventral, anterior, posterior and lateral views of ventral valve, FMM6190; 2a, 2b, 2c, 2d, dorsal, anterior, posterior and lateral views of dorsal valve, FMM6191;
3, Spirifer cf. liangchowensis Chao; 3a, 3b, ventral and posterior views of ventral valve, FMM6185; 4, Grandispirifer sp., dorsal view of dorsal valve, FMM6199; 5, Cleiothyridina sp., ventral view of ventral valve, FMM61200; 6, Syringothyris cf. cuspidatus (Sowerby); 6a, 6b, posterior and lateral views of ventral interarea, FMM6198. Scale bars represent 1 cm.</sup>

Material.—One specimen, a ventral valve, FMM6200.

Remarks.—This specimen is safely assigned to the genus *Cleiothyridina* by its mediumsized (length 28 mm, width 43 mm), transversely elliptical and moderately convex ventral valve with very shallow sulcus, and ornamented by slightly irregular concentric lamellae bearing numerous fine flattened spines. The Hina specimen somewhat resembles the shells, described by Yanagida (1962, p. 103, pl. 17, figs. 2–11, text-figs. 10–15) as *Cleiothyridina royssii* (Léveillé, 1835) from the Akiyoshi Limestone (*Millerella* Zone) of Akiyoshi, southwestern Japan, in its size and shape of the ventral valve. However, accurate comparison is difficult for the poorly preserved specimen.

> Order Spiriferida Waagen, 1883 Suborder Spiriferidina Waagen, 1883 Superfamily Spiriferoidea King, 1846 Family Spiriferidae King, 1846 Subfamily Spiriferinae King, 1846 Genus *Spirifer* Sowerby, 1816

Type species.—Conchyliolithus (Avonia) striatus Martin, 1793.

Spirifer cf. liangchowensis Chao, 1929 Fig. 6.3

Spirifer aff. *liangchowensis* Chao: Yanagida, 1962, p. 96, pl. 15, fig. 7, text-figs. 5, 6. *Spirifer* aff. *besnossovae* Abramov: Hase and Yokoyama, 1975, pl. 16, figs. 1–5.

Material.-Two specimens, two ventral valves, FMM6185, 6186.

Description.—Shell medium in size for genus, transversely subelliptical in outline, widest at about midlength; length about 40 mm, width about 66 mm in the better preserved specimen (FMM6185). Ventral valve moderately convex in lateral profile, most convex at umbonal region; sulcus broad and shallow, not clearly demarcated from lateral slopes. External surface of ventral valve ornamented with numerous simple rounded costae and few irregular, weak concentric rugae; costellae often bifurcated in anterior portion, numbering 7–8 in 10 mm at about midlength.

Remarks.—The specimens from Hina resembles *Spirifer liangchowensis* Chao (1929, p. 6, pl. 1, figs. 1–7, text-fig. 1), from the Chouniugou Formation of Gansu, northwestern China, in size, shape and external ornament of the ventral valve. Both of *Spirifer* aff. *liangchowensis* Chao, 1929, described by Yanagida (1962, p. 96, pl. 15, fig. 7, text-figs. 5, 6) from the Akiyochi Limestone (*Millerella* Zone) at the Uzura Quarry, Akiyoshi, southwestern Japan and *Spirifer*

aff. *besnossovae* Abramov, 1965, figured by Hase and Yokoyama (1975, pl. 16, figs. 1–5) from the Hina Limestone (*Endothyra* Zone) at Hina, are deemed conspecific with the present species. *Spirifer besnossovae* Abramov (1965, p. 50, pl. 6, figs. 1–4; pl. 7, fig. 1), from the lower Visean of Sette Daban, southern Verkhoyansk Range, northeastern Russia differs from the present species by its much larger size.



Fig. 7. Microornament of *Cleiothyridina* sp., enlarged external surface of ventral valve (FMM6200, fig. 6.5), showing concentric lamella bearing numerous flattened spines.

Genus Grandispirifer Yang, 1959

Type species.—Grandispirifer mylkensis Yang, 1959.

Grandispirifer sp. Fig. 6.4

Material.-One specimen, a dorsal valve, FMM6199.

Remarks.—This specimen is safely assigned to the genus *Grandispirifer* by its large, strongly transverse dorsal valve (length about 55 mm, width more than 68 mm, probably about 100 mm) with alate cardinal extremities and ornamented by numerous costae on both fold and lateral slopes. The stratigraphic range of *Grandispirifer* is considered to be the

upper Tournaisian-upper Visean (Yang, 1959; Legrand-Blain, 1986). The Hina species is close to the type species, *Grandispirifer mylkensis* Yang (1959), originally described by Yang (1959, p. 118, pl. 1, figs. 1, 2; pl. 2, figs. 1–3), from the lower Visean of Mt. Borochoro, Xinjiang, northwestern China, in size and shape of the dorsal valve, but differs in having finer costae (numbering 6–7 in 5 mm at mid of lateral slopes).

Order Spiriferinida Ivanova, 1972 Suborder Spiriferinidina Ivanova, 1972 Superfamily Syringothyridoidea Fredericks, 1926 Family Syringothyrididae Fredericks, 1926 Genus *Syringothyris* Winchell, 1863

Type species.—Syringothyris typa Winchell, 1863.

Syringothyris cf. cuspidatus (Sowerby, 1816) Fig. 6.6

Syringothyris sp. Hase and Yokoyama, 1975, pl. 17, fig. 1.

Material.—One specimen, a fragment (posterior portion) of ventral valve, FMM6198.

Remarks.—This specimen is safely assigned to the genus *Syringothyris* by its large, triangular, high and flattened interarea (width 74 mm, height 42 mm) and a distinct syrinx in the ventral valve. The Hina specimen is identical with *Syringothyris* sp., figured by Hase and Yokoyama (1975, pl. 17, fig. 1) from the Hina Limestone (*Endothyra* Zone) at Hina, in size and shape of the ventral interarea. The Hina species, both the present specimen and the Hase and Yokoyama's specimen, resembles *Syringothyris cuspidatus* (Sowerby, 1816), redescribed by Muir-Wood (1951, p. 112, pl. 4, fig. 1) from the upper Visean of Derbyshire, England, in size and shape of the ventral valve, especially, in having high, triangular ventral interarea; the latter is known also from the lower (?) Visean-Serphkovian of Russia (Taimyr Peninsula, Russian Platform and western Urals) (Dedok and Tschernjak, 1960; Garanj et al., 1975). *Syringothyris altaica* Tolmatchoff (1924, p. 162, 555, pl. 8, figs. 9–11; pl. 9, fig. 1), from the upper Tournaisian of the Kuznetsk Basin, central Russia, is also a large-sized *Syringothyris*, with a high, flat ventral interarea. However, accurate comparison is difficult for the poorly preserved specimen.

Acknowledgements

We sincerely thank Shuji Niko (Department of Environmental Studies, Hiroshima University, Hiroshima) for providing information about the stratigraphy of the Hina Limestone; Naotomo Kaneko (AIST, Geological Survey of Japan, Tsukuba) for photography of microornament of a brachiopod specimen. We also thank Atsushi Matsuoka (Department of Geology, Niigata University, Niigata) and an anonymous reviewer for their critical review of the manuscript by which this paper is greatly improved.

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SEM morphological study of clam shrimp *Ganestheria* (spinicaudatan) from Upper Cretaceous of Jiangxi, southeastern China

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Abstract

Morphological re-examination of the specimen of *Ganestheria longnanensis* Bi and Xie from the Upper Cretaceous Zhoutian Formation in Chenglong Village, Longnan County, Jiangxi Province, southeastern China under a scanning electron microscope (SEM) revealed morphological features on the carapace that had not been recognized previously: widely spaced radial lirae on growth bands intercalate large-sized polygonal reticulation, within which small-sized reticulation also occurs.

Key words: fossil clam shrimp, taxonomy, Upper Cretaceous, Zhoutian Formation, China.

Introduction

Bi and Xie (in Chen and Shen, 1982) described the clam shrimp (spinicaudatan) *Ganestheria* from the Ganzhou Formation, which was uplifted to the Ganzhou Group by the Jiangxi Geological Survey in 1994, and containing two formations, i.e. the lower Maodian Formation and the upper Zhoutian Formation. The Zhoutian Formation is composed mainly of variegated siltstone and claystone, intercalated with thin-bedded sandstone, gypsum, salt and conglomerate. The holotype specimen of the type species *Ganestheria longnanensis* Bi and Xie was collected from the Zhoutian Formation in Chenglong Village, Longnan County, Jiangxi Province of southeastern China. Then later *Ganestheria* became an index genus to correlate the Zhoutian Formation with the upper Huizhou Formation in Shexian County of

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Anhui Province because of the occurrence of the genus in both sequences. In this paper a re-examination of a specimen of *Ganestheira longnanensis* under an SEM revealed important morphological features not previously seen, as recorded below.

Material and methods

The studied specimen is deposited in the collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPCAS). It is an external mould of a left valve, and was originally collected from the Upper Cretaceous Zhoutian Formation in Chenglong Village, Longnan County, Jiangxi Province.

Most of the previous studies on the palaeontology of fossil clam shrimps have used a light microscope. This means that some potential characters of taxonomic value were difficult to see clearly (Li, 2004; Li and Batten 2004, 2005; Li et al., 2004, 2006, 2007a, b, 2009, 2010, 2014, 2015; Li and Matsuoka, 2013). Here the authors have relied on examination of the specimen using a LEO 1530 VP SEM and a Zeiss V20 Stereomicroscope.

Systematic palaeontology

Class: Branchiopoda Latreille, 1817 Subclass: Phyllopoda Preuss, 1951 Order: Diplostraca Gerstaecker, 1866 Suborder: Spinicaudata Linder, 1945 Superfamily: Lioestheriacea Raymond, 1946 Family: Sinoestheriidea Chen and Shen, 1982 Genus *Ganestheria* Bi and Xie, in Chen and Shen, 1982, emend.

1982 Ganestheria Bi and Xie gen. nov., in Chen and Shen, p. 41.
1985 Ganestheria Bi and Xie (in Chen and Shen, 1982), Chen and Shen, p. 81.
2014 Ganestheria Bi and Xie (in Chen and Shen, 1982), emend., Chen and Shen, p. 445.

Type species. Ganestheria longnanensis Bi and Xie, in Chen and Shen, 1982

Occurrence. Upper Cretaceous Zhoutian Formation, Longnan County, Jiangxi Province; Upper Cretaceous Huizhou Formation, Shexian County, Anhui Province, China.

Emended diagnosis. Carapace very large, elliptical in outline; dorsal margin ridge-like and markedly serrated, with spinous apophyses; umbo located between the anterior and median points of the dorsal margin; growth lines stout and convex, posterodorsal part slightly



Fig. 1. 1-5, *Ganestheria longnanensis* Bi and Xie, in Chen and Shen, 1982, emend., all, except Fig. 1.1 (a light microscope image), are SEM images of an external mould of a left valve from the Upper Cretaceous Zhoutian Formation, Longnan County, Jiangxi Province. 1, NIGPCAS 160162. 2, large-sized reticulation intercalated between widely spaced radial lirae on growth band in the postero-dorsal part of the carapace. 3, secondary small-sized reticulation occurs within the large-sized polygonal reticulation. 4, irregular radial lirae on growth bands in the middle part of the specimen. 5, widely spaced regular radial lirae on growth bands in the antero-ventral part of the specimen.
recurved, with a row of rounded nodes; growth band broad, flattened and few in number, ornamented with widely spaced and regular radial lirae, large-sized polygonal reticulation occurs between radial lirae, secondary small-sized reticulation also occurs within the large-sized reticulation.

Discussion. Ganestheria was originally described with radial lirae ornamentation only (Bi and Xie in Chen and Shen, 1982). Chen and Shen (2014) described another specimen and recognized that it has markedly serrated ridge-like dorsal margin with spinous apophyses. Now through an SEM re-examination, we have revealed that reticulation occurs between the widely spaced radial lirae.

Ganestheria longnanensis Bi and Xie, in Chen and Shen, 1982, emend.

Fig. 1.

1982 Ganestheria longnanensis Bi and Xie gen. and sp. nov., Chen and Shen, p. 42, pl. 3, fig. 2.
2014 Ganestheria longnanensis Bi and Xie in Chen and Shen, 1982, emend., Chen and Shen, p. 449, pl. 1, figs. 6–8.

Material. External mould of a left valve, NIGPCAS 160162, Chenglong, Longnan County, Jiangxi Province, southeastern China.

Emended diagnosis. As the genus.

Description. Carapace very large, elliptical in outline, 22.9 mm long, 11.1 mm high; dorsal margin long and straight, ridge-like and markedly serrated, with spinous apophyses; umbo loacated between the anterior and median points of dorsal margin; anterior height less than the posterior, the greatest height near the median part of the carapace; growth lines stout and convex, slightly recurved at postero-dorsal margin, with a distinct row of rounded nodes, more than 14 in number; growth band broad and flattened, widely spaced radial lirae intercalate large-sized polygonal reticulation, within which small-sized reticulation also occurs.

Discussion. Another species of *Ganestheria* has been described from the Upper Cretaceous Huizhou Formation in Anhui Province, i.e. *G. shexianensis* (Zhang, in Zhang et al., 1976) Chen and Shen, 1982. Although it is very similar in outline with *G. longnanensis*, the rounded nodes on growth lines are not visible because of the poor preservation. It is only possible to make a detailed comparison when better preserved specimens are recovered in the future.

Acknowledgements

This study was supported by the Major Basic Research Projects of the Ministry of Science and Technology, China (National 973 Project 2012CB822004), National Natural Science Foundation of China (41172010, 41572006, 91514302). We are grateful to Mr. P. Fang for his help in taking some SEM images, and we are thankful to Dr. T. Kurihara for his constructive comments on the manuscript.

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Nestoria sikeshuensis (spinicaudatan), a new clam shrimp species from the Tugulu Group in Junggar Basin, northwestern China

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Abstract

A new species, *Nestoria sikeshuensis* Teng and Li sp. nov., is described from the core of the bore hole Ai2 in the Junggar Basin, northwestern China. These specimens were collected from the Lower Cretaceous Tugulu Group. In Xinjiang, only three species and two undeterminated species of *Nestoria* have been reported in the literature before.

Key words: Clam shrimp, Nestoria, Tugulu Group, Lower Cretaceous, Junggar Basin.

Introduction

In the original description of the clam shrimp genus *Nestoria*, growth bands are only ornamented by large reticulation (Krasinetz, 1963; Zhang et al., 1976; Chen and Wei, 1985). However, some workers (Wang, 1976; Wang, 1981; Wang et al., 1984; Niu, 2008; Wang, 2013) believe that, there are a few transitional growth bands near antero-ventral region, postero-ventral region or ventral region with reticulate and radial lirae sculptures, in spite of large reticulation is the primary sculpture pattern on growth bands, after the examination of specimens of *Nestoria* from the Dabeigou Formation in Inner Mongolia, northern Hebei, and contemporaneous horizons.

Nestoria krasinetzi (Novojilov, 1958) Krasinetz, 1963, the type species, was recovered in

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Fig. 1. Sketch map of the Junggar Basin, showing locality of the bore hole Ai2 (after Yang et al., 2015).

the Lower Cretaceous of Russia. While most *Nestoria* bearing strata in China were assigned to the Upper Jurassic (Zhang et al., 1976; Wang, 1976; Wu, 1983; Wang et al., 1984; Niu, 2008). In Xinjiang, only a few species of this genus had been reported (Chen and Wei, 1985; Wang, 2013). They are *Nestoria* sp. 1, *N.* sp. 2, *N. jungarensis* Wang, 2013, *N. shawanensis* Wang, 2013, and *N. donggouensis* Wang, 2013. All of them are recovered in the Lower Cretaceous Qingshuihe Formation at Ziniquanzi, Shihezi City. Here a new species, *Nestoria sikeshuensis* Teng and Li, is described from the bore hole Ai2 of the Tugulu Group in the southwestern Junggar Basin.

Material and method

The specimens are deposited in the collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPCAS). They were collected from the Lower Cretaceous Tugulu Group, the drilling core of the bore hole Ai2 (Fig. 1), at the depth of 2849.65-2853.35 m, in the Sikeshu Depression of the Junggar Basin, Xinjiang Uygur Autonomous Region, China (Chen, 1988; Eberth et al., 2001; Deng et al., 2015; Li and Matsuoka, 2015; Yang et al., 2015).

Specimens are examined by a LEO 1530 VP Scanning Electron Microscope (SEM) and a Zeiss V20 Stereomicroscope.

Systematic palaeontology

Class: Branchiopoda Latreille, 1817 Subclass: Phyllopoda Preuss, 1951 Order: Diplostraca Gerstaecker, 1866 Suborder: Spinicaudata Linder, 1945 Superfamily: Eosestherioidea Zhang and Chen in Zhang et al., 1976 Family: Nestoriidae Shen and Chen, 1984 Genus *Nestoria* Krasinetz, 1963

1963 Nestoria Krasinetz gen. nov., p. 43–45.
1976 Nestoria Krasinetz; Zhang et al., p. 147.
1976 Nestoria Krasinetz; Wang, p. 49.
1981 Nestoria Krasinetz; Wang, p. 107.
1983 Nestoria Krasinetz; Wu, p. 193.
1984 Nestoria Krasinetz; Shen and Chen, p. 316.
1984 Nestoria Krasinetz; Wang et al., p. 97.
1985 Nestoria Krasinetz; Chen and Wei, p. 132–133.
1985 Nestoria Krasinetz; Niu, p. 338.
2013 Nestoria Krasinetz; Wang, p. 960–963.

Type species. Nestoria krasinetzi (Novojilov, 1958) Krasinetz, 1963

Occurrence. Lower Cretaceous, Chita region, Trans-Baikal, Russia; Barremian-lower Aptian Jianchang Formation, eastern Inner Mongolia Autonomous Region, northeastern China; Hauterivian Dabeigou Formation, northern Hebei Province, northeastern China; Upper Jurassic, western Liaoning Province, northeastern China; Lower Cretaceous Qingshuihe Formation, Shihezi, Xinjiang Uygur Autonomous Region, northwestern China; Lower Cretaceous Tugulu Group of the bore hole Ai2, Sikeshu Depression, Junggar Basin, Xinjiang Uygur Autonomous Region, northwestern China.



Diagnosis. Carapace valve moderate or relatively large in size, elliptical to subcircular in outline; growth lines stout and convex; growth bands broad, flattened and relatively few in number, ornamented with large polygonal reticulum; mesh irregularly polygonal; mesh wall thin, mesh base shallow and flattened, diameter of mesh being around 0.1 mm; growth bands near antero-ventral region, postero-ventral region or ventral region ornamented by medium reticulation, and change to radial lirae gradually.

Nestoria sikeshuensis Teng and Li sp. nov.

Fig. 2.

Etymology. The figured clam shrimp specimens are from a drilling core sample of the bore hole Ai2, located in the Sikeshu Depression.

Type material. Holotype, NIGPCAS 163720, paratypes, NIGPCAS 163716-19, 21.

Dimensions. In order: Specimen no., number of growth lines, length of carapace (mm), height of carapace (mm), ratio of height/length: NIGPCAS 163716, 14, 11.7, 8.0, 0.68; NIGPCAS 163717, >12, 9.4, 6.1, 0.65; NIGPCAS 163718, >12, 5.2, 3.5, 0.67; NIGPCAS 163719, >10, 10.2, 6.8, 0.67; NIGPCAS 163720, >13, >4.1, 4.0, <0.98; NIGPCAS 163721, >13, >10.8, 8.3, <0.77.

Type locality and horizon. At the depth of 2849.65–2853.35 m, from the bore hole Ai2, locality at Sikeshu Depression, Junggar Basin, Xinjiang Uygur Autonomous Region, northwestern China; Lower Cretaceous Tugulu Group.

Diagnosis. Carapace valve moderate in size, oval in outline; umbo narrow and small; growth lines approximately 14 in total, stout and convex, ornamented with small reticulation; growth bands ornamented by medium polygonal reticulation; a few transitional growth bands near antero-ventral region, postero-ventral region or ventral region with reticulate and radial lirae sculptures.

Description. Carapace valve moderate in size, oval in outline; dorsal margin straight, umbo

⁻ Fig. 2. Nestoria sikeshuensis. A is a light microscope photograph, B-H are SEM images. A, NIGPCAS 163720, holotype, a left valve. B, NIGPCAS 163721, a right valve. C, shallow and medium reticulation on growth bands near the posterior margin of the carapace. D, growth bands near ventral region with reticulate and radial lirae sculptures. E, growth band near the umbo ornamented with medium reticulation, and showing the short spine on the polygon side. F, growth bands near postero-ventral region with reticulate and radial lirae sculptures. G, stout and convex growth line, ornamented with very shallow and minute reticulation. H, growth bands near ventral region ornamented with reticulation and radial lirae.

narrow and small, located in anterior part of the dorsal margin; growth lines stout and convex, around 14 in total, ornamented with very shallow and minute reticulation (Fig. 2G), mesh irregularly pentagonal or hexagonal, diameter of mesh being 0.006–0.008 mm; growth bands narrow in dorsal part, wider in the middle part, and narrow again near the ventral part; growth bands ornamented by shallow and medium reticulation (Fig. 2B, C, D, G); mesh irregularly pentagonal or hexagonal, and the middle of the side with a short spine (Fig. 2E); mesh wall thin, mesh base shallow, diameter of mesh being 0.03–0.06 mm; growth bands near antero-ventral region, postero-ventral region or ventral region, some reticulation gradually change to radial lirae, the distance between adjacent lirae is about 0.03–0.04 mm (Fig. 2D, F, H).

Discussion. Wang (2013) described three species of Nestoria from the Lower Cretaceous Qingshuihe Formation of Ziniquanzi, Shihezi City of Xinjiang. The medium reticulation sculpture on growth bands separates N. sikeshuensis from species of Yanjiestheria and many species of Nestoria (Zhang et al., 1976; Wang, 1976; Wang, 1981; Wu, 1983; Wang et al., 1984; Li et al., 2007; Niu, 2008; Wang, 2013). It is easily distinguished from the other three species of Nestoria known from the Junggar Basin. Both N. shawanensis and N. donggouensis with a relatively large umbo, the umbo of N. sikeshuensis is narrow and small; while N. jungarensis is of an elliptical outline, adjacent lirae are at a distance of 0.03 mm. N. sikeshuensis is oval in outline, and the distance between adjacent lirae is about 0.03–0.04 mm.

Acknowledgements

We are thankful to Dr. T. Sasaki of the University of Tokyo for his constructive comments on the manuscript. This study was supported by the Major Basic Research Projects of the Ministry of Science and Technology, China (National 973 Project 2012CB822004), National Natural Science Foundation of China (41172010, 41572006, 91514302), China University of Geosciences (Wuhan) Students' Innovation and Entrepreneurship Training Program (No. 201610491103 to Y. Zhang) and Chinese Academy of Sciences' Students Innovation and Entrepreneurship Training Program (No. Y521070001 to Y. Zhang).

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Construction of recirculating flow tank with water pumps: insight into experimental palaeontology

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Abstract

A flow tank with a circulatory pump system was constructed using water pumps connected with polyvinyl chloride pipes and suction hoses. The flow tank was 180 cm in length, 20 cm in width and 20 cm in height. The flow rate in the water tank was monitored by a clump-on flowmeter, and its relevant velocity was calculated by using simple particle-tracing velocimetry. For the visualisation of the stream, a sheet laser light and small ion-exchange particle resins were used. The present recirculating experimental system realised a steady flow condition at a velocity of 7.8 cm/s or 13.0 cm/s at 5 cm from the bottom. Using the spiriferide brachiopod *Paraspirifer bownockeri* model, the present experiments reproduced the hydrodynamic properties for generating gyrating flows as observed in previous studies and found a velocity gradient and a gyrating axis position for gyrating.

Key words: flume experiment, pump, experimental palaeontology, biomechanics.

Introduction

Biomechanical approaches to fossil organisms are crucial for understanding the adaptive ability and functionality that have never been observed in extant terrestrial and marine environments (Clarkson, 1975; Rayfield, 2007; Fujiwara and Hutchinson, 2012). Supplying the fossil morphology with quantitative facts, researchers could compare the results in a comprehensive way and examine how biological phenotypes have evolved in terms of biomechanical aspects within variable, extrinsic conditions. Of these approaches, experimental methods typically require a "custom-made" system for each method, unlike

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computational simulations. One may constitute a unique experimental system corresponding to the relevant condition such as body size, ambient scale and surrounding medium.

In contrast to terrestrial organisms in a gravitational environment, aquatic organisms are influenced by the viscous medium rather than by gravity. The difference in ambient conditions occasionally results in the evolution of a hydrodynamic shape to utilise fluids for biological performance (Shiino and Kuwazuru, 2010, 2011a; Shiino and Suzuki, 2011, 2015; Shiino et al., 2012, 2014; Shiino and Angiolini, 2014). Fossil skeletal invertebrates such as trilobites and brachiopods have also been re-examined in light of biomechanical and hydrodynamic aspects, but these examinations still do not provide enough information to discuss those evolutionary scenarios in a quantitative manner. The problem begins with the construction of a custom-ordered experimental system on a scale appropriate to the organism; in turn, difficulty arises when considering the physical and biological viewpoints.

As a preliminary step in understanding the hydrodynamic properties of fossil organisms, we constructed a simple recirculating water tank system for application to a few centimetres of fossilised skeletal organisms. Using the present system and a shell spiriferide brachiopod model, we examined the validity and repeatability compared with results from previous experiments.

Experimental procedure

A recirculating water tank system with a sheet laser light was constructed in the present study to institute a simple particle tracing method. A steady recirculating flow was generated by magnetic pumps. Using the experimental system, we examined flow behaviours around a shell model of the spiriferide brachiopod *Paraspirifer*, the hydrodynamic property that has been well demonstrated in previous studies (Shiino et al., 2009; Shiino, 2010; Shiino and Kuwazuru, 2010, 2011b).

1. Construction of flow tank

The water tank was 180 cm in length, 20 cm in width, and 20 cm in depth and consisted of two water pumps, JM-25H (Koshin Ltd., Japan) and SL-75N (Elepon E.C.A.P. Corporation, Japan) (Figs. 1, 2). One of the 20 cm side walls was hollowed out by a holing saw to function as a drain outlet. The outlet was directly connected via polyvinyl chloride pipes and suction hoses to the water intake of the pumps. The water from the spouts of the pumps was supplied from suction hoses on the upstream side of the water tank. A punching plate with hundreds of 5 mm holes was implemented at the upstream side of the water tank as a strainer function. The flume experiments began after filling the tank with fresh water. The water depth was maintained at a height of 15 cm throughout the experiments. The stream velocity was controlled by the combination of two pumps. Because the JM-25H water pump



Fig. 1. Photograph of recirculating flow tank for flume experiments.



Fig. 2. Schematic illustrations of recirculating water tank with a flowmeter.

was not stable, we adopted two types of stream velocities, as follows: a slower velocity using the SL-75N and a higher velocity using both pumps. The experimental domain was set around the upstream area, 60 cm distant from the strainer plate.

A flowmeter FD-Q50C (Keyence Corporation, Japan) was clamped on the polyvinyl chloride pipe to monitor the total flow rate inside the water tank. The flowmeter analysed the average volume every 5 seconds, in litres per minute, L/min. Prior to the flume experiments using the model, the stream velocity was calculated by tracing the small particles of air bubbles.

2. Flow visualisations

Ion-exchange resin DIAION HP20 (Mitsubishi Chemical, Japan), which contains mediumgrained particles, was used to visualise the flows inside the water tank. Each particle was $500 \,\mu$ m in average diameter, with a specific gravity of 1.02 g/cm³. Because the ion-exchange resins were originally not water soluble, we first reduced surface groups to alcohols for dispersion into the water solution. The water solution of the ion-exchange resins was injected into the water tank using a syringe. The visualised flows were filmed by a Power Shot SX digital camera (Canon, Japan). Adjusting the settings on the digital camera, we adopted hi-vision 60 frames per second with 1920×1080 pixels.

For the examination of the selected section within an upstream-downstream transect, we adopted a sheet laser light, which consists of a 200 mW laser light module with a wavelength of 405 nm and a cylindrical lens. The sheet laser induced fluorescence of the ion-exchange resins. The stream direction and velocity were measured by tracing the small particles of the ion-exchange resins and air bubbles moving with the fluids.

3. Evaluation of stream condition

For application to experimental palaeontology, an understanding of the flow conditions in the recirculating flow tank is needed. As a preliminarily step, we examined stream direction and velocity within the upstream-downstream transect of median and lateral regions. To measure the stream direction and velocity, the experimental movie was translated into sequential images that filmed the luminescent particles of ion-exchange resins. The sequential images, each of which was captured every 0.05 s, were reconstructed by ImageJ image analysis software (National Institutes of Health, USA). The coordinate data from each particle was taken by a measurement function in ImageJ. Based on the coordinates of the same two particles in neighbouring images, stream direction and velocity were calculated.

Using the present experimental system, the flow patterns around the shell model of the Devonian spiriferide brachiopod *Paraspirifer bownockeri* (Stewart) were demonstrated for comparison with previous studies from our group. According to the hydrodynamic studies of spiriferides, the shell form has a role to generate spiral flows inside, enabling efficient small food particle sieving (Shiino et al., 2009; Shiino, 2010; Shiino and Kuwazuru, 2010). Identifying the function of the spiriferide shell could reveal the validity and repeatability of this experimental system. The same *Paraspirifer* model already used in Shiino et al. (2009) was attached to the bottom of the water tank with adhesive cure tape. The model was oriented with the dorsal valve facing upstream, and the flow pattern was analysed. Vector representations of the stream were drawn in Microsoft Excel (Microsoft, USA) and were composed on the first image of the sequential images.

Results and discussion

1. Stream velocity

The flowmeter showed 85.5 L/min (1425 cm³/s) with the SL-75N pump in operation and 145 L/min (2417 cm³/s) with two pumps in operation (Table 1). These numerical values did not change throughout the experiments. Based on the numerical values, average flow velocities in the water tank were 4.8 cm/s and 8.1 cm/s (Table 1: Expected velocity). Using the equivalent diameter d_{eq} of the water tank, calculated as $d_{eq} = 4dw / (2d + w)$, where d represents the depth of water and w represents the width of the water tank, the Reynolds numbers $Re = d_{eq}u / v$ (equivalent diameter d_{eq} , stream velocity u and kinematic viscosity v) were approximated to be 11520 and 19440 for the velocities of 4.8 cm/s and 8.1 cm/s, respectively. For values larger than Re = 2000, it would be expected that both stream conditions were between steady and turbulent flows.

Table 1. Velocity conditions of the present recirculating flow tank.

Pump operation	Flow rate [L/min]	Expected velocity [cm/s]	Average velocity of stable interval [cm/s]
SL-75N	85.5	4.8	7.8
SL-75N+JM-25H	145	8.1	13.0



Fig. 3. Velocity distributions of median and lateral planes in the experimental area for two stream velocity conditions. **A.** Velocity distributions. Grey tones indicate stable intervals of velocities under the conditions of lower and higher stream velocities. **B.** Selected photograph of 0.05 s of a camera shutter opening showing the case of a median plane under the condition of a higher stream velocity. The photograph indicates that the stream was steady with no turbulent vortices.

Figure 3 shows the velocity gradient along the bottom to the top of the flow tank in median and lateral planes under the conditions of the two stream velocities. The lateral plane was set 3 cm distant from the side wall of the water tank. The local velocities of the experimental area, which were calculated by tracing the particles, differed throughout the space of the water tank (Fig. 3). Generally, the velocities were lower around the bottom level, and those of the lateral plane were also lower than the median plane (Fig. 3). Such a velocity gradient would be the result of wall friction from the water tank. In the case of the lower stream velocity, the interval between 3 to 14 cm distant from the bottom was comparatively a stable velocity condition with a maximum of velocity, a stable interval of velocity was narrower as observed in the increase from the lower level to 5 cm above the bottom. The average velocity of this interval was 13.0 cm/s (Fig. 3; Table 1: Average velocity).

In the case of laminar flow through a pipe, it is known that the maximum velocity at the axis of pipe is twice larger than the net average velocity (Vogel, 1994). The velocity decreases close to the wall, finally reaching zero on the wall. In the present flow tank, the maximum stream velocities in all the experimental conditions were around twice the average velocities expected from the flow rate that seems to be a laminar flow. However, there is no dominant disparity of velocities between those of the median and lateral planes, suggesting the development of a turbulent boundary layer. Such an intermediate nature may be attributed to the transition conditions between the laminar and turbulent flows as estimated by the Reynolds number.

2. Comparison with previous studies

Figure 4 shows the vector representations of flows along the median plane view and its composite image at maximum intensity. The length of each vector indicates the velocity, and black circles are the initial luminescent points of the ion-exchange resins. The internal flows had gyrating movements with a left-to-right axis direction, as shown in our previous studies (Fig. 4; Shiino et al., 2009; Shiino, 2010; Shiino and Kuwazuru, 2010). The velocities of the gyrating flows moving downward along the inner surface of the ventral valve were considerably higher than those moving upward along the dorsal valve (Fig. 4A). The centre of the gyrating axis was a lateral gape located slightly above the bottom (Fig. 4B, C).

The difference in gyrating velocities within the shell model may be attributed to the shell function to generate passive flows. Based on previous studies from our group, the spiriferide sulcus, a major depression along the midline of the shell, functions to obtain a higher pressure around the sulcus gape (Shiino and Kuwazuru, 2010). This pressurisation results in the inflow through the sulcus gape and the outflows through the right and left lateral gapes (Shiino et al., 2009). Consequently, a flow velocity immediately after the inflow



Fig. 4. Flow behaviours for the shell model of spiriferide brachiopod *Paraspirifer bownockeri*. A. Vector representations of flows inside the model. The vectors realised a vortex movement and its velocity gradient inside the model. B. Composite image of maximum brightness. Sequential images of 10 s were merged into one image to extract the brightest pixel. C. Schematic illustration of B. Drawing the luminescent particles allowed visualisation of the gyrating motion of flows inside the model. The gyrating axis was on the projection of the lateral gape slightly above the bottom.

through the sulcus gape was higher than any of the others. The present results indicate that our experimental system determined the velocity gradient of the gyrating flows, as has been demonstrated previously by the computational fluid dynamics simulation.

3. Future perspectives of the present recirculating system and its application

The present study reconstructed the recirculating flow tank with mechanical water pumps. This flume experimental system could realise a steady flow condition with a stream velocity of 7.8 cm/s or 13.0 cm/s, 5 cm distant from the bottom. Although the present recirculating flow tank demonstrated only two types of stream velocities at this time, in the future, it can be improved to install additional pumps and voltage regulators. The present experimental system could be applicable for understanding the hydrodynamic properties of skeletal organisms with small to moderate sizes less than 10 cm such as brachiopods.

There still remain problems on the visualisations of flows. As is clear from the results shown in Fig. 4, the refractive index of the model inhibited the ability to obtain a clear image; the ion-exchange resin particles seem to be fogged by halation or refraction. In addition, the air-water interface of the flow tank refracted the sheet laser light, and thus, the luminescence of visualised particles was not stable. Further improvements of model construction and laser lighting conditions may provide a rigorous experimental method to find quantitative biomechanical features in fossilised aquatic organisms.

Acknowledgements

We gratefully acknowledge Hiroshi Kurita for helpful support of experimental facilities. We thank Hayato Ueta, Atsushi Matsuoka, Toshiyuki Kurihara and Isao Niikawa for their thorough discussions. This study was financially supported in part by the Uchida Energy Science Promotion Foundation, by the Sasakawa Scientific Research Grant from the Japan Science Society and by the JSPS KAKENHI Grant Numbers 25630047 and 26400503.

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Early Carboniferous (Visean) brachiopods from the Taishaku Limestone in the Wada area, Hiroshima Prefecture, southwest Japan

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Abstract

An Early Carboniferous brachiopod fauna consisting of three species, *Dictyoclostus* sp. (Productidina), *Finospirifer* sp. (Spiriferidina) and *Syringothyris* sp. (Spiriferinidina), is described from a tuffaceous limestone in the upper part of the Dangyokei Formation (the lowest formation of the Taishaku Limestone) in the Wada area, Jinsekikogen-cho, Jinsekigun, Hiroshima Prefecture, southwest Japan. The Wada fauna is assigned a (probably late) Visean age. This is the first report of Early Carboniferous brachiopods from the Taishaku Limestone.

Key words: brachiopod, Dangyokei Formation, Early Carboniferous, Taishaku Limestone, Visean, Wada area.

Introduction

The Taishaku Limestone, distributed on the Taishaku Plateau, northeastern Hiroshima Prefecture, southwest Japan, is one of the Carboniferous-Permian limestone-basalt blocks in a Permian accretionary complex of the Akiyoshi Terrane (Kanmera et al., 1990). The limestone is stratigraphically subdivided into three formations (in ascending order): the Dangyokei Formation, the Eimyoji Formation and the Uyamano Formation. According to Hase et al. (1974), the Dangyokei Formation (150 m thick) consists of Lower Carboniferous basaltic rocks with thin limestone layers, the Eimyoji Formation (150 m thick) consists of Lower-Upper Carboniferous limestone, and the Uyamano Formation (400-500 m thick)

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⁽Manuscript received 12 February, 2015; accepted 19 March, 2016)



Fig. 1. Map showing the fossil locality (WD1) in the Wada area, using the topographic map "Fukunaga" scale 1:25,000, published by the Geospatial Information Authority of Japan.

consists of lower-middle Permian limestone.

The palaeontology of the Taishaku Limestone has been investigated in numerous studies, starting with the work of Yoshino (1937), and also including studies by Hanzawa (1941), Minato (1951, 1955), Yokoyama (1957, 1960), Endo (1957), Konishi (1960) and Akagi (1971). However, the lithostratigraphy and biostratigraphy of the limestone are relatively poorly documented, as compared with similar studies on the Akiyoshi and Omi limestones of the Akiyoshi Terrane. Recently, Ehiro et al. (2013) described the ammonoid *Dombarites taishakuensis* Ehiro from the upper part of the Dangyokei Formation in the Wada area, and based on this occurrence assigned the upper part of the formation to the Serpukhovian.

The present study describes several species of small brachiopod fauna from the Dangyokei Formation (newly named as the Wada fauna), and discusses the age of the fauna. The brachiopod specimens were collected by the second author (I. Nishikawa) from purple to greenish-grey tuffaceous limestone in the upper part of the Dangyokei Formation at locality WD1 (34° 48′ 58″ N, 133° 14′ 14″ E) in the Wada area, Jinsekikogen-cho, Jinseki-gun, Hiroshima Prefecture, southwest Japan (Fig. 1), which is the same locality as that examined by Ehiro et al. (2013). The specimens are registered and housed in the Fossa Magna

Museum in Itoigawa, Niigata Prefecture, central Japan, with the prefix FMM. This is the first report of Early Carboniferous brachiopods from the Taishaku Limestone.

Age of the Wada fauna

The Wada fauna comprises the following three species: *Dictyoclostus* sp., *Finospirifer* sp. and *Syringothyris* sp. Among these, *Dictyoclostus* sp. resembles *Dictyoclostus* sp. reported by Hase and Yokoyama (1975) from the *Eostaffella–Millerella* Zone (upper Visean) of the Hina Limestone, Okayama Prefecture, southwest Japan. *Finospirifer* sp. may be a new species, although the species somewhat resembles *Finospirifer shaoyangensis* (Ozaki, 1939), described by Ozaki (1939) from the upper Tournaisian of Hunan, central-southern China. *Syringothyris* sp. resembles *Syringothyris* cf. *cuspidata* (Martin), described by Ibaraki et al. (2014) from the *Eostaffella–Millerella* Zone (upper Visean) of the Koyama Limestone, Okayama Prefecture, southwest Japan. The occurrence of *Dictyoclostus* sp. and *Syringothyris* sp. suggests the Wada fauna is of Visean age, probably late Visean.

Our conclusion regarding the age of the newly described fauna is largely in agreement with previous studies on the age of the upper part of the Dangyokei Formation. Okimura (1966) and Sada (1975) considered the age to be late Visean-Serpukhovian, based on smaller foraminifers and fusulinids, and Ehiro et al. (2013) considered the age to be early Serpukhovian, based on the presence of the ammonid species *Dombarites taishakuensis*. Further investigations of the fossil fauna of the Dangyokei Formation are needed to confirm the age and composition of the faunas in the formation.

Systematic descriptions

Order Productida Sarytcheva and Sokolskaya, 1959 Suborder Productidina Waagen, 1883 Superfamily Productoidea Gray, 1840 Family Dictyoclostidae Stehli, 1954 Subfamily Dictyoclostinae Stehli, 1954 Genus *Dictyoclostus* Muir-Wood, 1930

Type species.—Anomites semireticulatus Martin, 1809.

Dictyoclostus sp. Figs. 2.1–2.3

Material.-Four ventral valves, FMM5273-5275.



Fig. 2. Dictyoclostus sp.; 1, ventral valve, FMM5273; 2a, 2b, 2c, 2d, ventral, anterior, posterior and lateral views of ventral valve, FMM5274; 3a, 3b, 3c, ventral, anterior and lateral views of ventral valve, FMM5276.

Description.—Shell medium in size for genus, transversely rounded-quadrate in outline, with greatest width at hinge; length about 40 mm, width about 56 mm in the best preserved ventral valve specimen (FMM5273). Ventral valve strongly and unevenly convex in lateral profile, most convex at umbonal region, roundly geniculated, and followed by a long trail; umbo massive; ears small, slightly convex; sulcus narrow and shallow, originating at about mid of visceral disc; lateral slopes steep. External surface of ventral valve ornamented with numerous fine costae and rugae on visceral disc, and costae only on trail; numbering 8–9 costae and 3 rugae in 5 mm at about midlength; spines or spine bases absent.

Remarks.—The Wada species resembles *Dictyoclostus* sp., figured by Hase and Yokoyama (1975, pl. 18, fig. 1), from the *Eostaffella–Millerella* Zone (upper Visean) of the Hina Limestone in the Hina area, Okayama Prefecture, southwest Japan, in size, shape and

external ornament of the ventral valve. But specific identification is difficult owing to the lack of a description of the Hina specimens.

The type species, *Dictyoclostus semireticulatus* (Martin, 1809), redescribed and refigured by Muir-Wood (1928, p. 93, pl. 4, figs. 1, 2; text-fig. 19), from the Visean of England and Ireland, is clearly distinguished from the present species by its much larger size, larger ears, and coarser costae on the ventral valve.

Dictyoclostus multispiniferus (Muir-Wood, 1928, p. 121, pl. 7, fig. 6; pl. 8, figs. 1, 2; text-fig. 23), from the Tournaisian and Visean of England and Ireland, is similar to the Wada species in size and shape of the shell, but differs in having coarser costae and numerous spine bases over the visceral disc of the ventral valve.

Order Spiriferida Waagen, 1883 Suborder Spiriferidina Waagen, 1883 Superfamily Spifireroidea King, 1846 Family Spiriferidae King, 1846 Subfamily Prospirinae Carter, 1974 Genus *Finospirifer* Yin, 1981

Type species.—Finospirifer taoyangensis Yin, 1981.

Finospirifer sp. Fig. 3.3

Material.-One specimen: a conjoined valve, FMM5280.

Description.—Shell small in size for genus, transversely subtrianglar in outline, with greatest width at slightly anterior to hinge line; length 22 mm, width 30 mm. Ventral valve moderately and unevenly convex in lateral profile, most convex at umbonal region; umbo small; interarea low and slightly shorter than hinge line; cardinal extremities produced; sulcus narrow and deep, with a strong median costa. Dorsal valve with a narrow and high fold, developed in anterior margin. External surface of both ventral and dorsal valves ornamented with numerous simple strong costae and numerous fine growth lines; costae numbering 7–8 in each lateral flank of ventral valve.

Remarks.—This specimen is safely assigned to the genus *Finospirifer*, based on its strongly transverse, alate outline, low interarea, and sulcus with a disproportionately strong median costa. The Wada species, which may be a new species, most closely resembles *Finospirifer shaoyangensis* (Ozaki, 1939), originally described as *Spirifer shaoyangensis* by Ozaki (1939, p. 257, pl. 41, fig. 1), from the upper Tournaisian of Hunan, central-southern China in general shape, but differs from the later in its smaller size and more acute cardinal



Fig. 3. 1, 2, *Syringothyris* sp.; 1, dorsal valve, FMM5277; 2a, 2b, ventral and posterior views of ventral valve, FMM5278; 3, *Finospirifer* sp.; 3a, 3b, 3c, 3d, 3e, ventral, dorsal, anterior, posterior views and a part of enlarged ventral view of conjoined valves, FMM5280.

extremities. The type species, *Finospirifer taoyangensis* Yin, 1981, from the Mengongao Formation (upper Tournaisian) of Hunan, central-southern China, differs from the present species in having finer and more numerous costae and a higher interarea.

Order Spiriferinida Ivanova, 1972 Suborder Spiriferinidina Ivanova, 1972 Superfamily Syringothyridoidea Fredericks, 1926 Family Syringothyrididae Fredericks, 1926 Subfamily Syringothyridinae Fredericks, 1926 Genus *Syringothyris* Winchell, 1863

Type species.—Syringothyris typa Winchell, 1863.

Syringothyris sp. Figs. 3.1, 3.2

Material.—Three specimens: (1) a ventral valve, FMM5277; (2) two dorsal valves, FMM5278, 5279.

Description.—Shell large in size for genus, transversely subelliptical in outline; length about 58 mm, width more than 73 mm in the best preserved dorsal valve specimen, FMM5277. Ventral valve subpyramidal; umbo small; cardinal extremities are not observable because of its ill preservation; interarea high, about 40 mm height in the single ventral valve specimen (FMM 5279), nearly flat, with triangular delthyrium, delthyrial angle 40°. External surface of dorsal valve ornamented with numerous simple coarse costae; numbering 5–6 in 10 mm at about midlength.

Remarks.—The materials from Wada are safely assigned to the genus *Syringothyris*, based on the large transverse shell, high and nearly flat ventral interarea and in having numerous simple coarse costae on lateral flanks of the dorsal valve. The Wada species somewhat resembles *Syringothyris* cf. *cuspidata* (Martin), described by Ibaraki et al. (2014, p. 74, figs. 4.4, 4.5), from the lower part of the Koyama Limestone (upper Visean), Oga, Okayama Prefecture, southwest Japan in having high ventral interarea and a number of costae on the dorsal valve. But accurate comparisons are difficult due to the poor preservation of the Wada specimens.

Acknowledgements

We sincerely thank Yuta Siino and Atsushi Matsuoka of the Department of Geology, Niigata University, Niigata for their critical reading of the manuscript. Thanks are also due to Shuji Niko of the Department of Environmental Studies, Hiroshima University, Hiroshima for providing bibliographic information on the Taishaku Limestone.

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Report of the 12th symposium on Mesozoic Terrestrial Ecosystems, August 16–20, 2015, Shenyang, China

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Abstract

The 12th symposium on Mesozoic Terrestrial Ecosystems (MTE-12) was held in the historical city of Shenyang, northeast China in August 16-20, 2015. A total of 150 participants from 18 countries including Australia, Austria, Belgium, France, Germany, India, Japan, Korea, Malaysia, Mongolia, New Zealand, Nigeria, Pakistan, Philippines, Russia, UK, USA, and China joined the symposium. The 3rd Workshop of the UNESCO-IUGS International Geoscience Programme was held accompanied with the MTE-12. The scientific sessions were held on August 16-18 at the Liaoning Mansion Hotel, Shenyang, which included 4 plenary lectures, 89 oral presentations, and 37 poster presentations. A proceeding issue will be published in the geoscience journal of Global Geology. About 70 participants attended the field excursion in western Liaoning Province. During the two-day field excursion, we visited Early Cretaceous "Jehol Biota" in Beipiao City (Sihetun Village and Huangbanjigou Village), Jurassic "Yanliao Biota" in Daxishan Village, the Bird Fossil National Geopark of Chaoyang, and the Paleontological Museum of Jizangtang. The symposium is co-organized by Shenyang Normal University, Paleontological Museum of Liaoning, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China University of Geosciences (Beijing), and Jilin University.

Key words: MTE-12, IGCP608, Shenyang, western Liaoning, Jehol Biota, Yanliao Biota.

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Introduction

The Symposium on Mesozoic Terrestrial Ecosystems (MTE) is a successful and continuous international symposium which has been held in many countries over 30 years. The purpose of the symposium on MTE is to promote the exchange of ideas about the evolution of life in terrestrial environments during the 190 million years of the Mesozoic. The symposium has contributed to figure out the Mesozoic terrestrial ecosystem in diverse aspects. The first Symposium on MTE was held in Paris, in September, 1978. The 12th Symposium followed the highly successful 11th symposium on MTE held in 2012 in Kwangju, Korea.

The 12th symposium on MTE was held in historical city of Shenyang, northeast China in August 16–20, 2015. The symposium is co-organized by Shenyang Normal University, Paleontological Museum of Liaoning (PMOL), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS), China University of Geosciences (Beijing), and Jilin University. The chairman of the MTE-12 is SUN, G. who is the Director of PMOL and the Vice-President of the Palaeontological Society of China.

This symposium focused on a series of scientific sessions and symposia to display new research progress relating to the Mesozoic terrestrial ecosystems. In the meantime, the 3rd Workshop of the UNESCO-IUGS International Geoscience Programme was held accompanied with the MTE-12. A total of 150 participants from 18 countries including Australia, Austria, Belgium, France, Germany, India, Japan, Korea, Malaysia, Mongolia, New Zealand, Nigeria, Pakistan, Philippines, Russia, UK, USA, and China joined the symposium. The symposium included three-day scientific sessions and two-day field excursion. During the scientific sessions, researchers presented their achievements either in oral or in poster presentations. Besides, the presenters obtained useful comments through the discussion. During the field excursion, participants visited to western Liaoning Province, including Beipiao (the sites of *Sinosauripteryx prima* and the earliest known angiosperm *Archaefructus liaoningensis*), Jianchang (the site of the oldest known feathered dinosaur *Achiornis huxleyi*), famous museums, and geopark in Liaoning.

This report introduces the organization of the symposium, the scientific sessions, and the excursion in western Liaoning Province.

Organization of the symposium

The symposium was sponsored and carried out by the following committees.

Sponsors:

National Natural Science Foundation of China (NSFC)

Palaeontological Society of China (PSC)

International Geoscience Program of UNESCO-IUGS (IGCP)

China Fossil Protection Foundation (CFPF)

General Office of National Paleontological Expert Committee

Organized by:

Shenyang Normal University (SNU)

Paleontological Museum of Liaoning (PMOL)

Nanjing Institute of Geology and Palaeontology, CAS (NIGPAS)

China University of Geosciences, Beijing (CUG, Beijing)

Jilin University (JU)

Co-organized by :

Fossil Protection Bureau of Liaoning Province, China

Key Lab for Evolution of Past Life in NE Asia, Ministry of Land & Resources, China Key Lab for Evolution of Past Life & Environment in NE Asia, Ministry of Education, China Key Lab of Palaeontology Evolution & Palaeoenvironmental Change of Liaoning, China Base of Introducing Talents of Discipline to Universities on Evolution of Past Life (Proj. 111, China)

Honorable Chairmen:

LI Tingdong, Academician CAS, Chinese Academy of Geosciences, Beijing ZHOU Zhonghe, Academician CAS, Institute of Vertebrate Paleontology and Paleoanthropology WANG Chengshan, Academician CAS, China University of Geosciences, Beijing CHAI Yucheng, Vice Director, Earth Science Division, NSFC, Beijing YANG Qun, Director, NIGPAS, President of PSC, Nanjing

LIN Qun, President of SNU, Shenyang

Chairman:

SUN Ge, Director of PMOL; Vice-President of PSC

Scientific sessions

The scientific sessions were held on August 16–18 at the Liaoning Mansion Hotel, Shenyang. These scientific sessions included 4 plenary lectures, 89 oral presentations, and 37 poster presentations. A proceeding issue will be published in the geoscience journal Global Geology.

Most of the participants registered in the Liaoning Mansion Hotel in the evening of 15 August. After registration, they received the Programme, the Abstract (Fig. 1), a notebook, a pen, a T-shirt, a handbag, and some brochures about the PMOL. The T-shirt is well designed with the picture of emblem of the MTE-12.



Fig. 1. Photo of the Programme (left) and the Abstracts (right) of the 12th Symposium on Mesozoic Terrestrial Ecosystems.



Fig. 2. Opening ceremony in the hall of Liaoning Mansion Hotel.

The scientific sessions are introduced as follows:

1. Opening ceremony

In the morning of 16 August, the opening ceremony (Fig. 2) was held in a big hall (first floor) of the Liaoning Mansion Hotel. The symposium started with an opening address by Sun, G. (Chairman of MTE-12) and two welcome addresses by Lin, Q. (President of Shenyang Normal University) and Ma, Y. (Vice-Director of Bureau of Land & Resources, Liaoning, Shenyang). They expressed their warmly welcome for all the participants and presented best wishes for the future research. Then followed five invited speeches by Li, T. D. (Academician, Chinese Academy of Sciences, Chinese Academy of Geological Sciences), Dilcher, D. L. (Academician, US, Indiana University, Bloomington), Kirillova, G. (Institute of



Fig. 3. Group photograph after the opening ceremony.

Tectonics & Geophysics, Russian Academy of Sciences, Russia), Martin, T. (University of Bonn, Germany), and Ando, H. (Leader of IGCP608, Ibaraki University, Japan). Four plenary lectures were presented by Zhou, Z. H. (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences), Dilcher, D. L. (Indiana University, USA) & Sun, G. (Shenyang Normal University, China), Wan, X. Q. & Wang, C. S. (China University of Geosciences, Beijing, China), and Spicer, R. A. (Open University, UK). A group photograph (Fig. 3) was taken at the garden of the Liaoning Mansion Hotel after the opening ceremony.

2. Oral and poster presentations

The oral presentations started from the afternoon of 16 August till the noon of 18 August. The MTE-12 arranged 9 scientific sessions: M-1 Biodiversity of the Mesozoic terrestrial ecosystems, M-2 Mesozoic geology and environmental changes, M-3 Mesozoic tectonics and sedimentary mineral resources, M-4 Evolution of dinosaurs and origin of birds, M-5 Mesozoic plants and their diversity, M-6 Mesozoic climatic and environmental changes, M-7 Cretaceous ecosystem in Asia and Pacific (Workshop of IGCP608), M-8 Vertebrate keyfaunas of the Mesozoic, and M-9 Mesozoic fossil footprints. According to the close connection, M-3 was integrated into M-2. M-4 and M-8 gathered together with the topic of Mesozoic evolution of vertebrates and origin of aves. The 89 oral presentations included in 7 sessions mentioned above (including 18 keynote lectures, separately 7 in M-1; 14 in M-2, 3; 16 in M-4, 8; 20 in M-5; 5 in M-6; 4 in M-7, and 10 in M-9) were given in 3 meeting rooms in the 7th floor of the Liaoning Mansion Hotel (Fig. 4). The schedule for each meeting room was shown in the Programme and a paper pasted on the front door of the meeting room. Researchers can attend freely as they like. There were about 10-40 participants in each session (Fig. 4A). Keynote was 30 minutes (including discussion part) and the normal speech was 15 minutes. Every half a day, there was a 30-minute tea break during the oral presentation for the participants to enjoy fruits, cakes, and some drinks. During these breaks, researchers discussed and talked with each other friendly. A total of 37 posters



Fig. 4. Scientific sessions in Liaoning Mansion Hotel. **A.** Oral presentation in session M-5 Mesozoic Plants and Their Diversity; **B.** Poster corner in the hall of the 7th floor of the hotel; **C.** The best oral presentation award to Yoshino, K.; **D.** The best oral presentation award to Li, X.; **E.** Participants from Niigata University, Yoshino, K., Sakai, Y., Matsuoka, A. and Li, X. from left to right; **F.** Yoshino, K. during the oral presentation; **H.** Business meeting of the IGCP608.

were presented in the hall outside of the meeting rooms in the afternoon of 17 August (Fig. 4B).

During the symposium, it was decided that the MTE-13 would be held in Bonn, Germany in 2018. Nine best oral presentation awards and seven best poster presentation awards were given to students from Russia, Korea, Belgium, Japan, Malaysia, and China. Yoshino, K. and Li, X. received the best oral presentation awards (Figs. 4C, 4D).

Matsuoka, A. and 3 graduate students (Yoshino, K., Sakai, Y. and Li, X.) from Niigata University, Japan participated in the MTE-12 (Fig. 4E). Yoshino, K. and Sakai, Y. attended the M-5 session and gave oral presentations. The titles were as follows: Palynoflora during the Campanian/Maastrichtian boundary interval in Songliao Basin, NE China (by Yoshino, Fig. 4F); New late Early Cretaceous fossil plants from the Tetori Group in central Japan and their paleaoclimatic implications (by Sakai, Fig. 4G). Matsuoka, A. and Li, X. gave presentations in the M-2, 3 session. The titles were as follows: Jurassic-Cretaceous boundary sequences in Japan and their implication for biochronological correlation (by Matsuoka); Method of observing microfossil-bearing clasts in the neritic-terrestrial conglomerate: advantages, significance and applications (by Li).

3. The accompanied IGCP608 workshop

The IGCP608 (2013–2017) is an international symposium supported by International Geoscience Programme (IGCP) of UNESCO (United Nations Educational, Scientific and Cultural Organization) and IUGS (the International Union of Geological Sciences). It focuses on Cretaceous ecosystems and their responses to paleoenvironmnetal changes in Asia and the western Pacific. The IGCP608 has been promoting communication at the level of geoscience among various Asian countries, including some countries outside of Asia. IGCP608 Project Leaders are Ando, H. (Department of Earth Sciences, Ibaraki University, Japan), Wan, X. Q. (School of Geosciences and Resources, China University of Geosciences, China), Cheong, D. (Department of Geology, College of Natural Sciences, Kangwon National University, Korea), and Bajpai, S. (Birbal Sahni Institute of Palaeobotany, Lucknow, India). The 3rd International Meeting of IGCP608 was held jointly with the MTE-12. It was held as a special session (M-7) (Fig. 4H) in the morning of 18 August. Four oral presentations including 2 keynotes by Ando, H. and Wan, X. Q. were given. Other presentations involved in IGCP608 were separated into other sessions based on their topics.

The 4th IGCP608 was decided to be held in Trofimuk Institute of Petroleum Geology, Nobosibirsk, Russia in 2016 during the symposium.

4. The visit to the Paleontological Museum of Liaoning

In the afternoon of 18 August, all the participants of the scientific sessions visited the Paleontological Museum of Liaoning (PMOL) (Fig. 5A). The PMOL, the largest



Fig. 5. Visit to the Paleontological Museum of Liaoning (PMOL). **A.** Front view of the PMOL; **B.** Group photograph of some participants in the Hall of Dinosaurs; **C.** Sun, G. gave introductions for the participants; **D.** Workshop which produces models of dinosaur.

paleontological museum in China, was approved by Liaoning Provincial Government and was co-constructed by Department of Land and Resources of Liaoning Province (DLRL) and Shenyang Normal University (SNU) since 2006. The "Jehol Biota", "Yanliao Biota", early birds, early angiosperms, and ancient human beings in Liaoning are exhibited in the 8 halls of the museum. A group photograph was taken in the Hall of Dinosaurs (Fig. 5B). The chairman of the MTE-12, Sun, G., gave a specific introduction to the museum and its scientific research (Fig. 5C). The PMOL is located in SNU. In SNU, there is also a workshop to produce the models of dinosaurs (Fig. 5D). After two-hour visit, delegates attended the business conference in the PMOL.

5. Performance

In the evening of 16 August, a performance was held in the hall of the Liaoning Mansion Hotel. Peking Opera Drama "The Goddess Chang's Fly to the Moon" performed by Xiao, D. (Chief of Mei Lanfang's Art Research Institute, SNU). The drama was Master Mei Lanfang's performance lost for a century. The Chinese Instruments Quintet "Jasmine Fragrant" and "Guests from Afar, Please Stay" were happy and smooth melodies with nationalistic style (Fig. 6A). Traditional Peking Opera "Pass the Four Gates" was a famous story about a war



Fig. 6. Performance in the evening of 16 August. A. Chinese Instruments Quintet; B. Traditional Peking Opera; C. Researchers went to the stage to express their appreciate for actors; D. Participants enjoyed the performance.

in the Song Dynasty (Fig. 6B). Peking Opera Dance "The King of Qin Ordered Soldiers for War" and Solo Dance "A Touch of Red" were also very impressive. The performance displayed the deep roots and huge charm of Chinese traditional culture. Participants enjoyed and gave high compliments (Figs. 6C, 6D). The performance was organized by Shenyang Normal University and Paleontological Museum of Liaoning.

Field excursion in western Liaoning Province

After the scientific session in the Liaoning Mansion Hotel, 78 participants (54 foreigners) joined a two-day field excursion in western Liaoning Province (Fig. 7). In this excursion, they visited Early Cretaceous "Jehol Biota" in Beipiao City (Sihetun Village and Huangbanjigou Village), Jurassic "Yanliao Biota" in Daxishan Village, the Bird Fossil National Geopark of Chaoyang, and Paleontological Museum of Jizangtang.

The organizers provided famous local sausage, duck's eggs, fruit, and bread as two-day lunch for the participants because of the tight schedule. The organizers also provided hummers for the field excursion. The field excursion will be introduced according to the stops.



Fig. 7. Field excursion in western Liaoning Province. A. Group photograph at the Jizantang Fossil Museum; B. Outcrop that has yielded *Sinosauropteryx prima*; C. China Sihetun Paleontological Museum; D. Outcrop that has produced *Archaefructus liaoningensis*; E. Fossil Excavation Site in the Liaoning Chaoyang Bird Fossil National Geopark; F. Petrified Wood Forest; G. Jizantang Fossil Museum; H. Outcrop that has included *Anchiornis huxleyi*; I. Outcrop that has contained *A.huxleyi*. It is stratigraphically above outcrop of H. (H, I: Strata are exposed below white broken line).
1. The first day

Two tour buses headed for western Liaoning Province in the morning of 19 August. After 5-hour drive, the participants arrived at Sihetun Village in Beipiao City which is a state-level natural protection area. The participants observed the Yixian Formation which has yielded Early Cretaceous "Jehol Biota" including feathered dinosaur *Sinosauropteryx prima*. Firstly, the participants observed and collected samples from the outcrop composed of lacustrine sediments (Fig. 7B). They consist mainly of whitish gray tuffaceous mudstone. Conchostracan and insect fossils are abundant in the outcrop. Then, the participants moved to the China Sihetun Paleontological Museum (Fig. 7C). This museum is built to protect and display dinosaur and bird fossil-bearing horizons. In addition, plant, arthropod, fish, amphibian, reptile, dinosaur, pterosauria, and bird fossils obtained in western Liaoning Province were in the exhibition rooms. After one-hour stay, the participants moved toward the next site.

The second stop was an outcrop of the Yixian Formation in Huanbanjigou Village (Fig. 7D). This site is very famous for the discovery of the earliest angiosperm *Archaefructus liaoningensis*. The lithological feature is similar to the first outcrop. Unfortunately, we met with heavy rain at this stop. Therefore, most of us just observed the outcrop without trying to find fossils.

After the outdoor activity, the participants arrived at the Bird Fossil National Geopark of Liaoning Chaoyang which was built for spreading scientific knowledge. In this time, we visited the Fossil Excavation Site which keeps the vertebrate-bearing horizons (Fig. 7E) and the Petrified Wood Forest that exhibits many silicified woods (Fig. 7F). After visiting these sites, the participants visited the Paleontological Museum of Chaoyang located in the geopark.

In the evening, we moved to the Jizantang Fossil Museum (Figs. 7A, 7G). This museum has not only exhibition rooms but also workshop to produce craft products with silicified wood. In the museum, the staff provided fish fossil bearing rocks. Visitors could experience the interest of finding fossils in the park of the museum instead of in the field. Participants also enjoyed this activity and brought back the fish fossils they found.

After the first day's excursion, the participants stayed at the Fusidun International Hotel. In suppertime, government leader of Chaoyang City and Sun, G. expressed their welcome and appreciation to the participants on the stage of the dining room.

2. The Second Day

In the morning of 20 August, the participants left for Jianchang County. After 3 hourdrive, we arrived at Daxishan Village within the county. The participants observed the middle Jurassic Tiaojishan Formation. This formation yielded the earliest feathered dinosaur *Anchiornis huxleyi*. Normally, most part of the Tiaojishan Formation was covered by surface soil and recent plants. Outcrops were dug out by local citizens before this field excursion (Figs. 7H, 7I). As a result, the participants could observe the Tiaojishan Formation successively. This formation is composed of lacustrine sediments. They consist of mudstone, arkose sandstone, greywacke, and tuff. The section is subdivided into 29 lithostratigraphic units. *Anchiornis huxleyi* appeared in the lower unit composed of blackish gray mudstone with yellow tuff (Fig. 7H) and the upper unit that consists of grayish green sandy mudstones and tuffaceous fine-grained sandstones (Fig. 7I).

This field excursion was planned and guided by Sun, G. (Shenyang Normal University/ Paleontological Museum of Liaoning), Wang, Y. D. (Nanjing Institute of Geology and Palaeontology), Wan, X. Q. (China University of Geosciences (Beijing)), and Zhang, H. G. (Shenyang Normal University/Paleontological Museum of Liaoning). During the two-day field excursion, we observed a variety of fossils of the Cretaceous "Jehol Biota" and Jurassic "Yanliao Biota". Also, we noticed the effort from the government to protect the heritage of the Earth and display to the public at the meantime.

Acknowledgements

We sincerely express our thanks to all the organizers of the MTE-12 and IGCP608 for organizing this successful international symposium. We thank the researchers who gave us important comments and advice during the symposium. Careful reading by Dr. Zhang Yiyi of China University of Geosciences, Beijing helped us to improve the manuscript. We would like to thank the Graduate School of Science and Technology, Niigata University for supporting the Double Degree Program to Yoshino, K. and Sakai, Y. and the International Office, Niigata University for providing the traveling fund to Li, X.

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CONTENTS

Shuji NIKO, Yousuke IBARAKI and Jun-ichi TAZAWA
Devonian tabulate corals from pebbles in Mesozoic conglomerate, Kotaki,
Niigata Prefecture, central Japan
Part 3: Heliolitida 1–6
Jun-ichi TAZAWA
Middle Permian (Wordian) mixed Boreal–Tethyan brachiopod fauna from
Kamiyasse–Imo, South Kitakami Belt, Japan
Jun-ichi TAZAWA, Yousuke IBARAKI and Isao NISHIKAWA
Early Carboniferous (Visean) brachiopods from the Hina Limestone, Okayama
Prefecture, SW Japan, and their palaeobiogeographical implications $\ldots \ldots 45-68$
Gang LI, Xiao TENG and Atsushi MATSUOKA
SEM morphological study of clam shrimp <i>Ganestheria</i> (spinicaudatan)
from Upper Cretaceous of Jiangxi, southeastern China
Xiao TENG, Ji'nan XIAO, Yanzhen ZHANG, Atsushi MATSUOKA and Gang LI
Nestoria sikeshuensis (spinicaudatan), a new clam shrimp species from
the Tugulu Group in Junggar Basin, northwestern China 75–81
Takafumi TSUCHIDA and Yuta SHIINO
Construction of recirculating flow tank with water pumps:
insight into experimental palaeontology
Yousuke IBARAKI, Isao NISHIKAWA and Jun-ichi TAZAWA
Early Carboniferous (Visean) brachiopods from the Taishaku Limestone
in the Wada area, Hiroshima Prefecture, southwest Japan
Report
Xin LI, Kohei YOSHINO, Yusuke SAKAI and Atsushi MATSUOKA
Report of the 12th symposium on Mesozoic Terrestrial Ecosystems,

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