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

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## 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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**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





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

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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.

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*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.

Echinoconchus ci. Jascianas (Kutorga). Miniato et al., 1979, pl. 00, ligs. 5-7.

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,

<sup>←</sup> 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, textfig. 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.

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*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)

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