Middle Permian (Wordian) Mixed Boreal—Tethyan Brachiopod Fauna from Matsukawa, South Kitakami Belt, Japan

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

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Abstract. A middle Permian (Wordian) brachiopod fauna, consisting of 19 species in 18 genera, is described from the lower part of the Kamiyasse Formation in Matsukawa, South Kitakami Belt, northeastern Japan. The Matsukawa fauna is a mixed Boreal–Tethyan brachiopod fauna that shows strong affinities with the middle Permian (Wordian–Capitanian) brachiopod faunas of central Japan (Hida Gaien Belt), eastern Russia (South Primorye), northeastern China (Heilongjiang), northern China (Inner Mongolia) and northwestern China (Xinjiang). The palaeobiogeographical data suggest that Proto-Japan, including South Kitakami, was part of a continental shelf along the northern and eastern margins of North China, located in the mid-latitudes of the Northern Hemisphere during the middle Permian (Wordian).

Key words: Brachiopoda, Matsukawa, middle Permian, mixed Boreal–Tethyan fauna, South Kitakami Belt

Introduction

Matsukawa, located in Kesennuma City, Miyagi Prefecture, South Kitakami Belt, northeastern Japan (Figure 1), is a classic locality for Permian marine invertebrate fossils. In the first study of the locality, Wakimizu (1892) reported on occurrences of fossil corals, bryozoans, brachiopods and crinoids. Then, in the first study on the Palaeozoic brachiopods in Japan, Yabe (1900) described the brachiopod species *Lyttonia* sp. (= *Leptodus nobilis*) from Matsukawa. Later, 16 Permian brachiopod species were described by Hayasaka (1917, 1922a, 1925, 1963), Tazawa (1979, 1999b) and Tazawa and Araki (1984a, 1984b, 1999, 2013). However, systematic and palaeobiogeographic studies on the brachiopods of the Matsukawa fauna remain insufficient and incomplete.

During the past three decades, middle Permian mixed brachiopod faunas containing both Boreal and Tethyan elements have been recognized in Japan (South Kitakami and Hida Gaien belts), eastern Russia (South Primorye), northeastern China (Jilin and Heilongjiang), northern China (Inner Mongolia) and northwestern China (Xinjiang) (Tazawa, 1987, 1991, 1998, 2001a, 2003, 2007; Nakamura and Tazawa, 1990; Shi *et al*., 1995, 2002; Shi and Zhan, 1996; Shi and Tazawa, 2001; Shi, 2006; Tazawa and Chen, 2006; Kotlyar *et al*., 2007; Shen *et al*., 2009). Palaeobiogeographically, the regions cited above are included in a province (transitional zone) between the Boreal and Tethyan realms, located in the region of North China (Sino-Korea) in the Northern Hemisphere; i.e., the Sino-Mongolian–Japanese Province of Shi and Tazawa (2001) [= the Inner Mongolian–Japanese Transition Zone of Tazawa (1991), or the Northern Transitional Zone of Shi *et al*. (1995)]. The Permian brachiopod fauna of Matsukawa has also been assigned to the Sino-Mongolian–Japanese Province based on the presence of both Boreal (*Costatumulus*, *Yakovlevia* and *Alispiriferella*) and Tethyan (*Neorichthofenia*, *Leptodus* and *Paralyttonia*) genera (Yabe, 1900; Tazawa, 1979, 2003; Tazawa and Araki, 1984a, 1984b).

The present paper describes brachiopod species from the middle Permian of Matsukawa, and discusses the age and palaeobiogeography of the fauna, based on the collections of K. Nakamura, H. Koizumi and the present authors, which were collected during the period of 1960–2000s. The fossils described herein are registered and housed in the Department of Geology, Niigata University, Niigata (NU-B prefix); the Tohoku University Museum, Sendai (IGPS prefix); the Hokkaido University Museum, Sapporo (UHR prefix); and the Kesennuma Board of Education (tentatively placed in the Old Tsukitate Junior High School) in Kesennuma (KCG prefix).

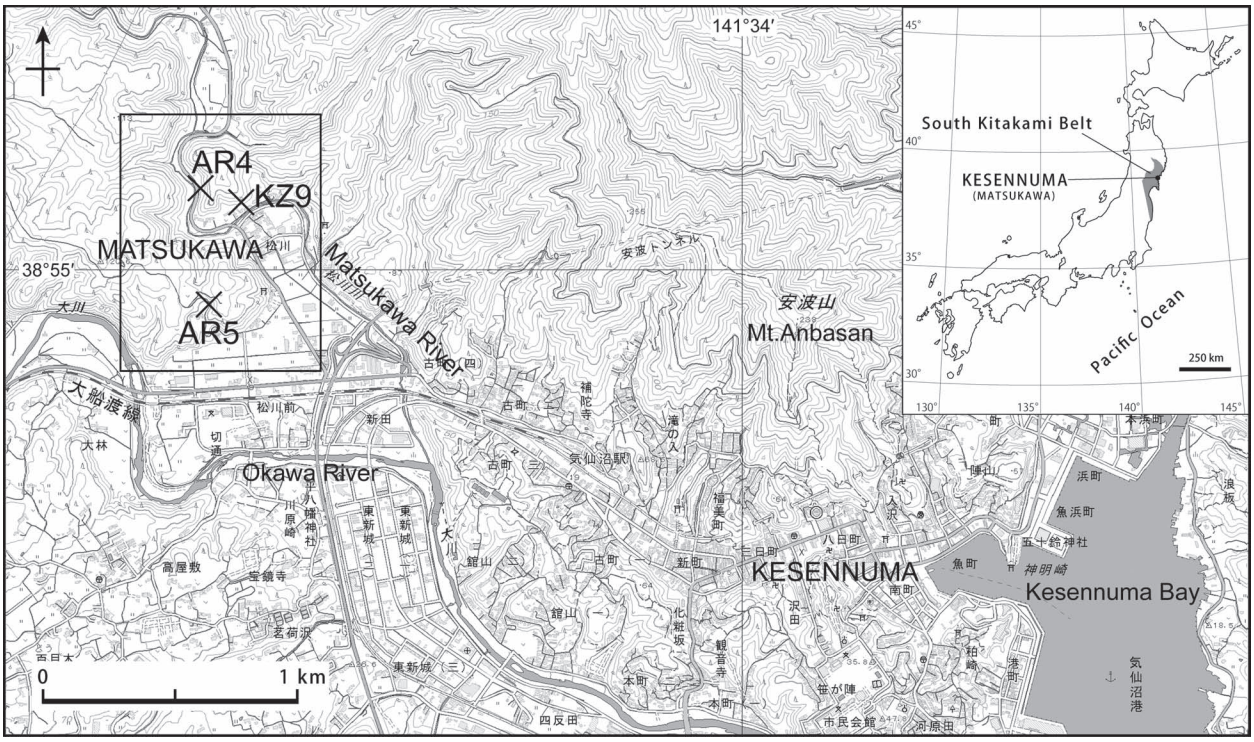

Figure 1. Map showing the Matsukawa area, enclosed by solid line, and fossil localities AR4, AR5 and KZ9 (using the topographic map of GSI).

Stratigraphy

The stratigraphy of the Permian rocks in the Matsukawa area has been studied by Shiida (1940), Kambe and Shimazu (1961) and Tazawa (1975, 1976). According to Tazawa (1975, 1976) and unpublished data by the present author (J. Tazawa), the Permian of the Matsukawa area is represented by the lower part of the Kamiyasse Formation, which consists mainly of sandstone and shale with thin argillaceous limestone layers; the formation has a total thickness of 215 m (Figure 2), is distributed over an area of approximately 300 m (E–W) × 850 m (N–S), and exhibits a NE–SW strike and a dip of 50°–70° to the WNW. The fusulinid *Monodiexodina* sp., probably *Monodiexodina sutchanica* (Dutkevich), commonly occurs in sandstone and argillaceous limestone beds in the Matsukawa area. Brachiopods were collected from three localities, AR4 (Anabuchi), AR5 (Kiritoshi) and KZ9 (Omotematsukawa). The topographic and stratigraphic locations, and fossil contents of the fossil localities are as follows:

AR4 (Anabuchi): Cliff along the Matsukawa River (38°55′12″N, 141°32′32″E) exposing dark grey argillaceous limestone of the lower part of the Kamiyasse Formation, and containing the fusulinid species *Monodiexodina* sp. and ten brachiopod species (*Hexiproductus echidniformis*, *Urushtenoidea crenulata*, *Permundaria tenuistriata*, *Yakovlevia mammata*, *Neorichthofenia mabutii*, *Leptodus nobilis*, *Paralyttonia kesennumensis*, *Martinia* sp., *Alispiriferella lita* and *Licharewina arakii*).

AR5 (Kiritoshi): Road cutting (38°54′55″N, 141°32′33″E) exposing greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, and containing six brachiopod species [*Capillomesolobus heritschi*, *Dyoros* (*Dyoros*) sp., *Linoproductus hayasakai*, *Costatumulus cancriniformis*, *Yakovlevia kaluzinensis* and *Alispiriferella lita*].

KZ9 (Omotematsukawa): Sandstone quarry (38°55′09″N, 141°32′39″E) exposing greenish grey fine-grained sandstone of the lower part of the Kamiyasse Formation, and containing five brachiopod species (*Transennatia gratiosa*, *Hexiproductus echidnigormis*, *Urushtenoidea crenuata*, *Scacchinella gigantea* and *Keyserlingina* sp).

Matsukawa fauna

The brachiopod fauna described herein includes the following 19 species in 18 genera: *Capillomesolobus heritschi* Pečar, 1986, *Dyoros* (*Dyoros*) sp., *Transennatia grati-*

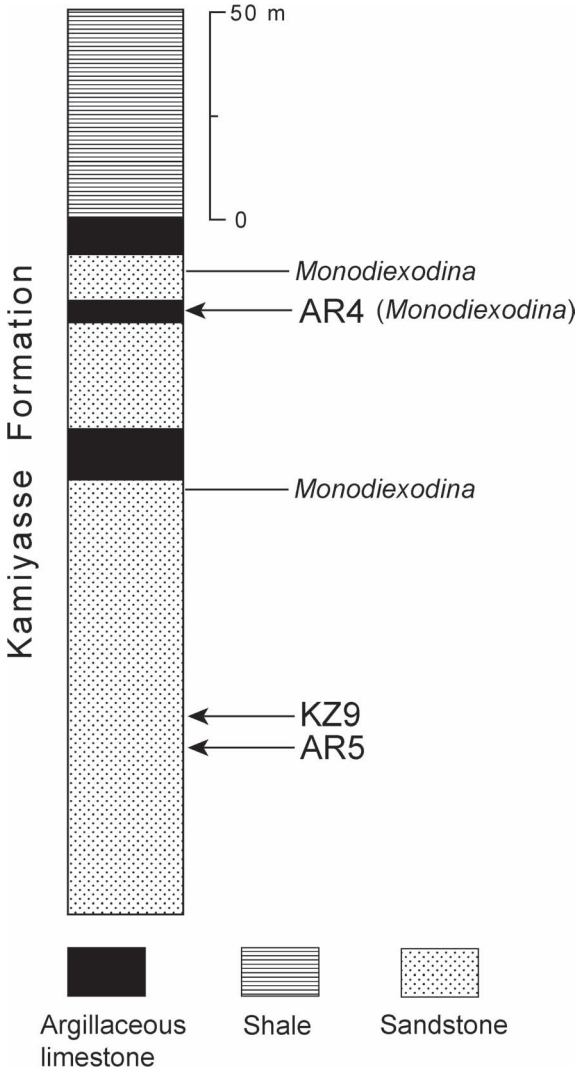

Figure 2. Generalized columnar section of the lower part of the Kamiyasse Formation in the Matsukawa area, showing the fossil horizons of *Monodiexodina* and localities AR4, AR5 and KZ9.

osa (Waagen, 1884), *Hexiproductus echidniformis* (Chao, 1925), *Urushtenoidea crenulata* (Ding in Yang *et al*., 1962), *Scacchinella gigantea* Schellwien, 1900, *Linoproductus hayasakai* Tazawa, 1979, *Costatumulus cancriniformis* (Tschernyschew, 1889), *Permundaria tenuistriata* Tazawa, 1974, *Yakovlevia mammata* (Keyserling, 1846), *Yakovlevia kaluzinensis* Fredericks, 1925, *Neorichthofenia mabutii* (Tazawa and Araki, 1984b), *Leptodus nobilis* (Waagen, 1883), *Keyserlingina* sp., *Paralyttonia kesennumensis* Tazawa and Araki, 1984a, *Martinia* sp., *Alispiriferella lita* (Fredericks, 1924), *Licharewina arakii* (Hayasaka, 1963) and *Dielasma* sp.

Species \ Stage	Permian								
	Asselian	Sakmarian	Artinskian	Kungurian	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian
Capillomesolobus heritschi									
Transennatia gratiosa									
Hexiproductus echidniformis									
Urushtenoidea crenulata									
Scacchinella gigantea									
Linoproductus hayasakai									
Costatumulus cancriniformis									
Permundaria tenuistriata									
Yakovlevia mammata									
Yakovlevia kaluzinensis									
Neorichthofenia mabutii									
Leptodus nobilis									
Paralyttonia kesennumensis									
Alispiriferella lita									
Licharewina arakii									

Figure 3. Stratigraphic distribution of brachiopod species of the Matsukawa fauna, excluding the four uncertain species [*Dyoros* (*Dyoros*) sp., *Keyserlingina* sp., *Martinia* sp. and *Dielasma* sp].

Age

The stratigraphic distribution of the brachiopod species of the Matsukawa fauna, excluding the four uncertain species, *Dyoros* (*Dyoros*) sp., *Keyserlingina* sp., *Martinia* sp. and *Dielasma* sp., are summarized in Figure 3.

Of the brachiopods listed above, *Capillomesolobus heritschi* is known from the Sakmarian–Wordian, and *Hexiproductus echidniformis* and *Costatumulus cancriniformis* are known from the Asselian–Wordian. In contrast, *Transennatia gratiosa*, *Neorichthofenia mabutii*, and *Alispiriferella lita* are known from the Wordian–Changhsingian. *Linoproductus hayasakai*, *Permundaria tenuistriata*, *Paralyttonia kesennumensis* and *Licharewina arakii* are restricted to the Wordian. The other species, *Urushtenoidea crenulata* and *Yakovlevia kaluzinensis* are known from the Kungurian–Wuchiapingian, *Leptodus nobilis* is known from the Kungurian–Changhsingian, and *Scacchinella gigantea* and *Yakovlevia mammata* are long-ranging species known from the Kasimovian–Capitanian. In summary, the age of the Matsukawa fauna is assigned to the Wordian. This conclusion is supported by the occurrence of the Wordian–Capitanian fusulinid *Monodiexodina* [probably *M. sutchanica* (Dutkevich)] in three horizons in the lower Kamiyasse Formation of Matsukawa (see Figure 2).

Region / Species	Japan							N. USA	N. Canada		N. Russia						C. Russia					NW China					N. China		
	1. South Kitakami B.	2. Hitachi	3. Hida Gaien Belt	4. Mizukoshi	5. Maizuru Belt	6. Akiyoshi Belt	7. Mino Belt	8. Alaska	9. Devon Island	10. Spitsbergen	11. Timan	12. Pechora Basin	13. N. Urals	14. Taimyr Peninsula	15. Verkhoyansk	16. Kolyma-Omolon	17. S. Urals	18. Hungary	19. Balkan States	20. Uzbekistan	21. S. Mongolia	22. Xinjiang	23. Qinghai	24. Gansu	25. Ningxia	26. Shaanxi	27. Inner Mongolia	28. Shanxi	29. Hebei
Capillomesolobus heritschi	+																		+										
Transennatia gratiosa	+	+	+	+																						+			
Hexiproductus echidniformis	+																			+		+		+	+		+	+	+
Urushtenoidea crenulata	+		+	+																			+	+					
Scacchinella gigantea	+																+		+	+									
Linoproductus hayasakai	+																												
Costatumulus cancriniformis	+										+	+	+	+	+	+					+							+	
Permundaria tenuistriata	+																												
Yakovlevia mammata	+							+	+	+	+	+			+							+					+		
Yakovlevia kaluzinensis	+		+	+																	+								
Neorichthofenia mabutii	+																												
Leptodus nobilis	+		+		+	+	+											+	+				+				+		
Paralyttonia kesennumensis	+																												
Alispiriferella lita	+		+	+		+																					+		
Licharewina arakii	+																												

Region / Species	NE China			E. Russia	E. China						CS China				SW China														
	30. Heilongjiang	31. Jilin	32. Liaoning	33. South Primorye	34. Shandong	35. Jiangsu	36. Anhui	37. Zhejiang	38. Fujian	39. Jiangxi	40. Hubei	41. Hunan	42. Guangdong	43. Guangxi	44. Guizhou	45. Sichuan	46. Yunnan	47. Vietnam	48. Laos	49. Cambodia	50. Armenia	51. Greece	52. Tibet (Xizang)	53. Malaysia	54. Timor	55. Nepal	56. Pakistan (Salt Range)	57. India (Kashmir)
Capillomesolobus heritschi																												
Transennatia gratiosa	+	+		+			+	+		+	+	+	+	+	+	+	+	+		+		+	+	+		+	+	+
Hexiproductus echidniformis			+		+																							
Urushtenoidea crenulata						+			+		+	+	+	+		+			+	+			+					
Scacchinella gigantea																												
Linoproductus hayasakai																												
Costatumulus cancriniformis				+																								
Permundaria tenuistriata																												
Yakovlevia mammata	+			+																								
Yakovlevia kaluzinensis				+																								
Neorichthofenia mabutii																+												
Leptodus nobilis	+	+		+				+	+	+	+	+	+	+	+	+	+			+	+			+	+		+	
Paralyttonia kesennumensis																												
Alispiriferella lita	+			+																								
Licharewina arakii																												

Figure 4. Geographic distribution of brachiopod species of the Matsukawa fauna, excluding the four uncertain species [*Dyoros* (*Dyoros*) sp., *Keyserlingina* sp., *Martinia* sp. and *Dielasma* sp].

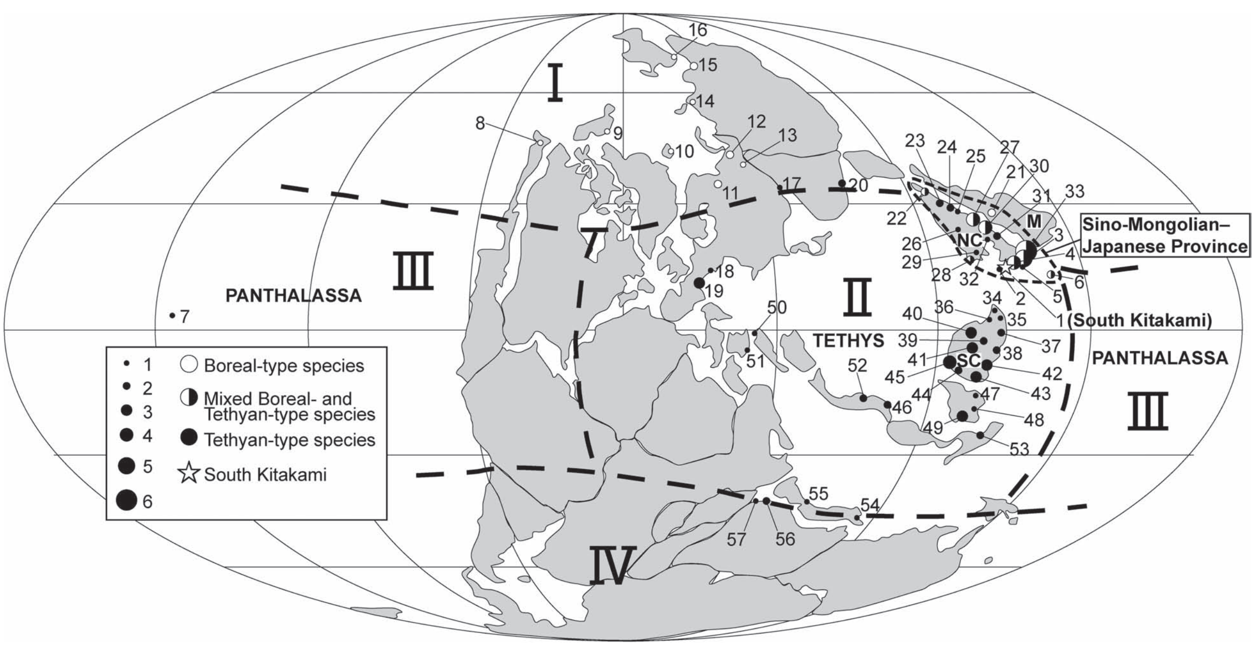

Figure 5. Middle Permian (Wordian) reconstruction map of the world (adapted from Scotese, 2004), showing the geographic distribution of brachiopod species of the Matsukawa fauna excluding the four uncertain species [*Dyoros* (*Dyoros*) sp., *Keyserlingina* sp., *Martinia* sp. and *Dielasma* sp]. Location numbers are same in Figure 4, and the numbers appended to the circles in the legend indicate the species numbers. M: Mongolia, NC: North China, SC: South China, I: Boreal Realm, II: Tethyan Realm, III: Panthalassan Realm, IV: Gondwanan Realm.

Palaeobiogeography

The geographic distribution of the brachiopod species of the Matsukawa fauna, excluding the four uncertain species, *Dyoros* (*Dyoros*) sp., *Keyserlingina* sp., *Martinia* sp. and *Dielasma* sp., are summarized in Figures 4 and 5.

The Matsukawa fauna includes the Boreal (antitropical) elements *Dyoros* (*Dyoros*) sp., *Costatumulus cancriniformis*, *Yakovlevia mammata*, *Y. kaluzinensis* and *Alispiriferella lita*, and also the Tethyan (tropical) elements *Transennatia gratiosa*, *Hexiproductus echidniformis*, *Urushtenoidea crenulata*, *Permundaria tenuistriata*, *Neorichthofenia mabutii*, *Leptodus nobilis*, *Keyserlingina* sp., *Paralyttonia kesennumensis* and *Licharewina ara-*

kii. Consequently, the fauna is a mixed Boreal–Tethyan fauna, with the Tethyan elements predominating.

Notably, mixed Boreal–Tethyan faunas are also known from southwestern Japan (Maizuru and Akiyoshi belts and Mizukoshi, which is the southwestern extension of the Hida Gaien Belt), central Japan (Hida Gaien Belt and Hitachi, which is the southern extension of the South Kitakami Belt), eastern Russia (South Primorye), northeastern China (Heilongjiang), northern China (Inner Mongolia) and northwestern China (Xinjiang). In terms of its specific composition, the Matsukawa fauna most closely resembles the middle Permian brachiopod fauna of South Primorye, eastern Russia, as the following six species are common to both faunas: *Transennatia gratiosa*, *Costatumulus cancriniformis*, *Yakovlevia mammata*, *Y. kaluzinensis*, *Leptodus nobilis* and *Alispiriferella lita*. On the other hand, the middle Permian brachiopod faunas of South China (Yangtze) are clearly distinguished from the Matsukawa fauna by the absence of Boreal elements.

The palaeobiogeographical data suggest that Proto-Japan, including South Kitakami, was part of a continental shelf along the northern and eastern margins of North China, located in mid-latitude regions of the Northern Hemisphere during the middle Permian (Wordian), as stated by Tazawa (1993, 2000, 2004).

Systematic descriptions

Order Productida Sarytcheva and Sokolskaya, 1959
Suborder Chonetidina Muir-Wood, 1955
Superfamily Chonetoidea Bronn, 1862
Family Rugosochonetidae Muir-Wood, 1962
Subfamily Capillomesolobinae Pečar, 1986
Genus ***Capillomesolobus*** Pečar, 1986

Type species.—*Capillomesolobus karavankensis* Pečar, 1986.

Capillomesolobus heritschi Pečar, 1986

Figure 6.1

Chonetes sinuosa Schellwien, 1900, p. 38, pl. 9, figs. 17, 18.
Chonetes sp. Heritsch, 1938, p. 103, pl. 7, figs. 6, 7.
Mesolobus mesolobus (Norwood and Pratten). Nakamura, 1959, p. 205, pl. 2, figs. 2, 3; Minato *et al*., 1979, pl. 46, fig. 11.
Mesolobus sp. Tazawa, 1979, p. 25, pl. 4, fig. 2.
Capillomesolobus heritschi Pečar, 1986, p. 28, pl. 3, figs. 1–9, text-fig. 11; Tazawa and Nakamura, 2015, p. 159, figs. 4.1–4.3.

Material.—One specimen from locality AR5, external and internal moulds of a ventral valve, IGPS96237.

Remarks.—This specimen was previously described by Tazawa (1979) as *Mesolobus* sp. The Matsukawa specimen can be referred to *Capillomesolobus heritschi* Pečar (1986, p. 28, pl. 3, figs. 1–9, text-fig. 11), from the Trogkofel Limestone of the Karavanke Mountains, Slovenia, in its small size (length about 10 mm, width about 12 mm), deep ventral sulcus with median lobe, and numerous capillae (numbering 13–14 in 2 mm at mid-length) on the external surface of the ventral valve. Comparison with the other species of *Capillomesolobus* has been discussed by Tazawa and Nakamura (2015, p. 161).

Distribution.—Sakmarian–Wordian: Balkan States (Slovenia) and northeastern Japan (South Kitakami Belt).

Subfamily Svalbardiinae Archbold, 1982
Genus *Dyoros* Stehli, 1954
Subgenus ***Dyoros* (*Dyoros*)** Stehli, 1954

Type species.—*Chonetes consanguineous* Girty, 1929.

***Dyoros* (*Dyoros*)** sp.

Figure 6.2

Neochonetes sp. Tazawa, 1979, p. 25, pl. 4, fig. 1.

Material.—One specimen from locality AR5, internal mould of a ventral valve, IGPS96238.

Remarks.—This specimen is assigned to the subgenus *Dyoros* (*Dyoros*) by its large, transverse ventral valve (length 13 mm, width 25 mm), with large, angular ears, deep sulcus and short median septum. The Matsukawa species somewhat resembles *Dyoros* (*Dyoros*) sp., described by Tazawa (2008a, p. 23, figs. 3.18, 3.19) from the Takakurayama Formation of the Takakurayama area, South Kitakami Belt (Abukuma Mountains), northeastern Japan. Accurate comparison is, however, difficult because of poor preservation of the present material.

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)

Figure 6.3

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; Diener, 1915, p. 70, pl. 7, fig. 4; 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.

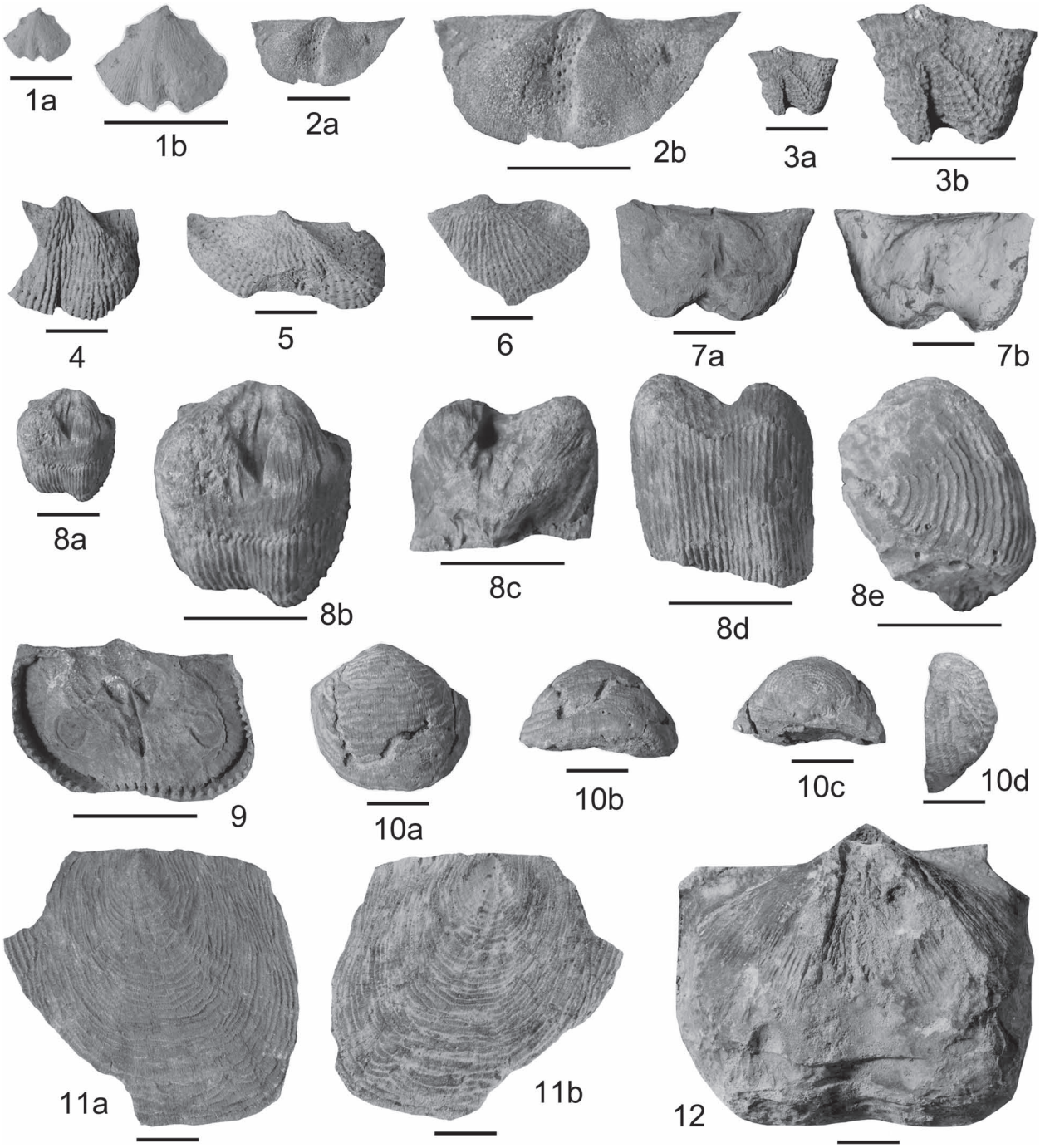

Figure 6. **1,** *Capillomesolobus heritschi* Pečar; 1a, b, external latex cast of ventral valve, IGPS96237; **2,** *Dyoros* (*Dyoros*) sp.; 2a, b, internal mould of ventral valve, IGPS96238; **3,** *Transennatia gratiosa* (Waagen); 3a, b, external mould of dorsal valve, IGPS17099; **4–6,** *Hexiproductus echidniformis* (Chao); 4, internal mould of ventral valve, KCG050; 5, external mould of dorsal valve, KCG051; 6, external mould of dorsal valve, KCG053; **7,** *Yakovlevia mammata* (Keyserling); 7a, b, internal mould and internal latex cast of ventral valve, KCG015; **8, 9,** *Urushtenoidea crenulata* (Ding); 8a–e, ventral, posterior, anterior and lateral views of internal mould of ventral valve, UHR30387; 9, internal mould of dorsal valve, UHR17068; **10,** *Costatumulus cancriniformis* (Tschernyschew); 10a–d, ventral, anterior, posterior and lateral views of internal mould of ventral valve, IGPS96217; **11,** *Permundaria tenuistriata* Tazawa; 11a, b, external mould and external latex cast of dorsal valve, KCG014; **12,** *Yakovlevia kaluzinensis* Fredericks, internal mould of ventral valve, KCG008. Scale bars represent 1 cm.

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.
Asioproductus bellus Chan (Zhan), 1979, p. 85, pl. 6, figs. 7–13; pl. 9, figs. 8–10, text-fig. 18.
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, 2001b, 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, fig. 10E–H, 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 Shi, 2009, p. 157, fig. 3K–O; Tazawa *et al*., 2014, p. 378, figs. 2.2, 2.3; Tazawa, 2015, p. 65, figs. 6.2, 6.3.

Material.—Two specimens from locality KZ9: (1) external mould of a ventral valve, UHR17098; and (2) external mould of a dorsal valve, UHR17099.

Remarks.—The specimens from Matsukawa are poorly preserved, but they can be referred to *Transennatia gratiosa* (Waagen, 1884, p. 691, pl. 72, figs. 3–7), from the Wargal and Chhidru formations of the Salt Range, Pakistan, on the basis of their small size (length 12 mm, width 16 mm in the dorsal valve specimen, UHR17099), large triangular ears, strongly geniculated dorsal valve with nearly flat visceral disc and moderately long trail, and sharply reticulate ornament on visceral discs of both ventral and dorsal valves, although the Matsukawa specimens are smaller in size than the Pakistani specimens. *Dictyoclostus minor* Lee and Gu (in Lee *et al*., 1980), from the Miaoling Formation of Jilin, northeastern China, is probably a junior synonym of *Transennatia gratiosa*.

Distribution.—Wordian–Changhsingian: northwestern China (Shaanxi), northeastern China (Heilongjiang and Jilin), eastern Russia (South Primorye), northeastern Japan (South Kitakami Belt), central Japan (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), Tibet (Xizang), Vietnam, Cambodia, Malaysia, Nepal (Kumaon Himalayas), Pakistan (Salt Range), India (Kashmir) and Greece.

Family Paucispiniferidae Muir-Wood and Cooper, 1960
Subfamily Paucispiniferinae Muir-Wood and Cooper, 1960
Genus ***Hexiproductus*** Shi, Chen and Tong, 2008

Type species.—*Productus echidniformis* Chao, 1925.

Hexiproductus echidniformis (Chao, 1925)

Figures 6.4–6.6

Productus echidniformis Grabau emend. Chao, 1925, p. 239, pl. 2, figs. 7–9.
Avonia echidniformis (Grabau emend. Chao). Chao, 1927, p. 120, pl. 14, figs. 17–27; Chao, 1928, p. 55, pl. 6, fig. 7; Ozaki, 1931, p. 108, pl. 10, figs. 6–9; Nakamura, 1959, p. 201, pl. 1, figs. 2–8; Volgin, 1960, p. 47, pl. 4, fig. 4; Sergunkova and Zhizhilo, 1975, p. 60, pl. 9, fig. 7; Lee and Gu, 1976, p. 240, pl. 141, fig. 1; Minato *et al*., 1979, pl. 46, figs. 15–17; Lee *et al*., 1980, p. 350, pl. 145, fig. 25; Lee and Duan, 1985, p. 227, pl. 66, figs. 16–21; Zhan and Wu, 1987, p. 203, pl. 47, figs. 23–25; He *et al*., 1995, pl. 56, figs. 51, 52, 61–64; Wang, 1995, pl. 1, fig. 4; Wang and Yang, 1998, p. 67, pl. 3, figs. 21–25.
Productus (*Avonia*) *echidniformis* Grabau and Chao. Licharew, 1939, p. 86, pl. 17, figs. 9, 10.
Avonia sp. Minato *et al*., 1979, pl. 46, figs. 13, 14.
"*Avonia*" *echidniformis* (Grabau emend. Chao). Zhang *et al*., 1983, p. 286, pl. 131, fig. 1.
"*Avonia*"? *echidniformis* (Grabau emend. Chao). Chen and Shi, 2002, p. 299, fig. 4J.
Breileenia echidniformis (Grabau in Chao). Chen and Shi, 2006, p. 137, pl. 1, figs. 13, 14; text-fig. 10.
Hexiproductus echidniformis (Grabau in Chao). Shi *et al*., 2008, p. 290, figs. 6A–6D.
Hexiproductus echidniformis (Chao). Tazawa and Nakamura, 2015, p. 161, figs. 4.4–4.10.

Material.—Four specimens from localities AR4 and KZ9: (1) internal mould of a ventral valve, KCG050; and (2) external moulds of three dorsal valves, KCG051–053.

Description.—Shell medium in size for genus, transversely subrectangular in outline, hinge slightly shorter than greatest width at midlength; length about 17 mm, width about 35 mm in the largest dorsal valve specimen (KCG052). Ventral valve strongly and unevenly convex in lateral profile, most convex in umbonal region, gently convex visceral disc; umbo small, incurved and overhanging hingeline a little; ears small, not clearly demarcated from visceral region; sulcus shallow on visceral region. Dorsal valve moderately concave, with deeply concave umbonal region and nearly flat visceral disc, roundly geniculated, and followed by a short trail; fold absent. External surface of ventral valve ornamented with strong costae and irregular fine concentric rugae; costae bearing numerous elongate spine bases. External ornament of dorsal valve similar to that of ventral valve, but no spine

bases. Internal structures of ventral valve not clearly preserved and obscure.

Remarks.—These specimens can be referred to *Hexiproductus echidniformis* (Chao, 1925), originally described from the upper Carboniferous–lower Permian of Gansu, northwestern China and Shanxi, northern China, in shape and external ornament of both valves. The Matsukawa specimens most resemble the shells described by Tazawa and Nakamura (2015) as *Hexiproductus echidniformis* (Chao, 1925) from the lower part of the Hosoo Formation of Nakadaira, South Kitakami Belt, in size, outline and external ornament of both the ventral and dorsal valves.

Distribution.—Kasimovian–Wordian: Uzbekistan (Fergana), northwestern China (Xinjiang, Gansu and Ningxia), northern China (Inner Mongolia, Shanxi and Hebei), northeastern China (Liaoning), northeastern Japan (South Kitakami Belt) and eastern China (Shandong).

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.

Urushtenoidea crenulata (Ding in Yang *et al*., 1962)

Figures 6.8, 6.9

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, 2001b, 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, fig. 3B–I.
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.—Three specimens from localities AR4 and KZ9: (1) internal moulds of two ventral valves, UHR30387, 30388; and (2) internal mould of a dorsal valve, UHR17068.

Remarks.—These specimens can be referred to *Urushtenoidea crenulata* (Ding in Yang *et al*., 1962), from the Maokouan of Qinghai, northwestern China, in their small, transversely subquadrate shell (length about 15 mm, width about 21 mm in the largest dorsal valve specimen, UHR17068), numerous fine costae (6–7 in 5 mm) on the ventral trail, and internal structures of the dorsal valve consisting of long median septum, small and highly raised adductor scars, and prominent brachial ridges. *Urushtenoidea maceus* Jin (1963, p. 19, pl. 2, figs. 1–6), from the Chihsian and Maokouan of eastern China (Jiangsu, Anhui and Zhejiang) and central-southern China (Hubei), differs from *U. crenulata* in having finer costae 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 on the ventral valve.

Distribution.—Kungurian–Wuchiapingian: northwestern China (Qinghai and Gansu), northeastern Japan (South Kitakami Belt), central Japan (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), Tibet (Xizan), Laos and Cambodia.

Family Scacchinellidae Licharew, 1928
Subfamily Scacchinellinae Licharew, 1928
Genus ***Scacchinella*** Gemmellaro, 1891

Type species.—*Scacchinella variabilis* Gemmellaro, 1891.

Scacchinella gigantea Schellwien, 1900

Figures 7.8, 7.9

Scacchinella gigantea Schellwien, 1900, p. 35, pl. 4, figs. 1–3; pl. 5, figs. 1–8, text-figs. 5, 6, 8; Heritsch, 1938, p. 101, pl. 5, figs. 1, 2, 9; Licharew, 1939, p. 96, pl. 23, fig. 2; Ramovs, 1965, p. 357, pl. 13, figs. 3–6; Tazawa and Araki, 1999, p. 453, figs. 2.1–2.4.

Material.—Five specimens from locality KZ9: (1) external mould of a ventral valve, NU-B197; and (2) internal moulds of four ventral valves, NU-B198–201.

Remarks.—These specimens were described by Tazawa and Araki (1999) as *Scacchinella gigantea* Schellwien, 1900. The Matsukawa specimens are strongly deformed and imperfect, but they can be referred to *Scacchinella gigantea* Schellwien (1900, p. 35, pl. 4, figs. 1–3; pl. 5, figs. 1–8, text-figs. 5, 6, 8), from the Trogkofel Formation of the Carnic Alps, by the medium to large, transversely subelliptical ventral valve with a broad and very shallow depression in the middle of the anterior side of the valve. *Scacchinella exasperata* Cooper and Grant (1975, p. 921, pl. 271, figs. 14–24; pl. 273, figs. 26–28), from the lower Wolfcampian of West Texas, differs from *S. gigantea* in the more rounded cylindrical outline and in having a broader ventral interarea. *Scacchinella titan* Cooper and Grant (1975, p. 923, pl. 270, figs. 12–16; pl. 272, figs.

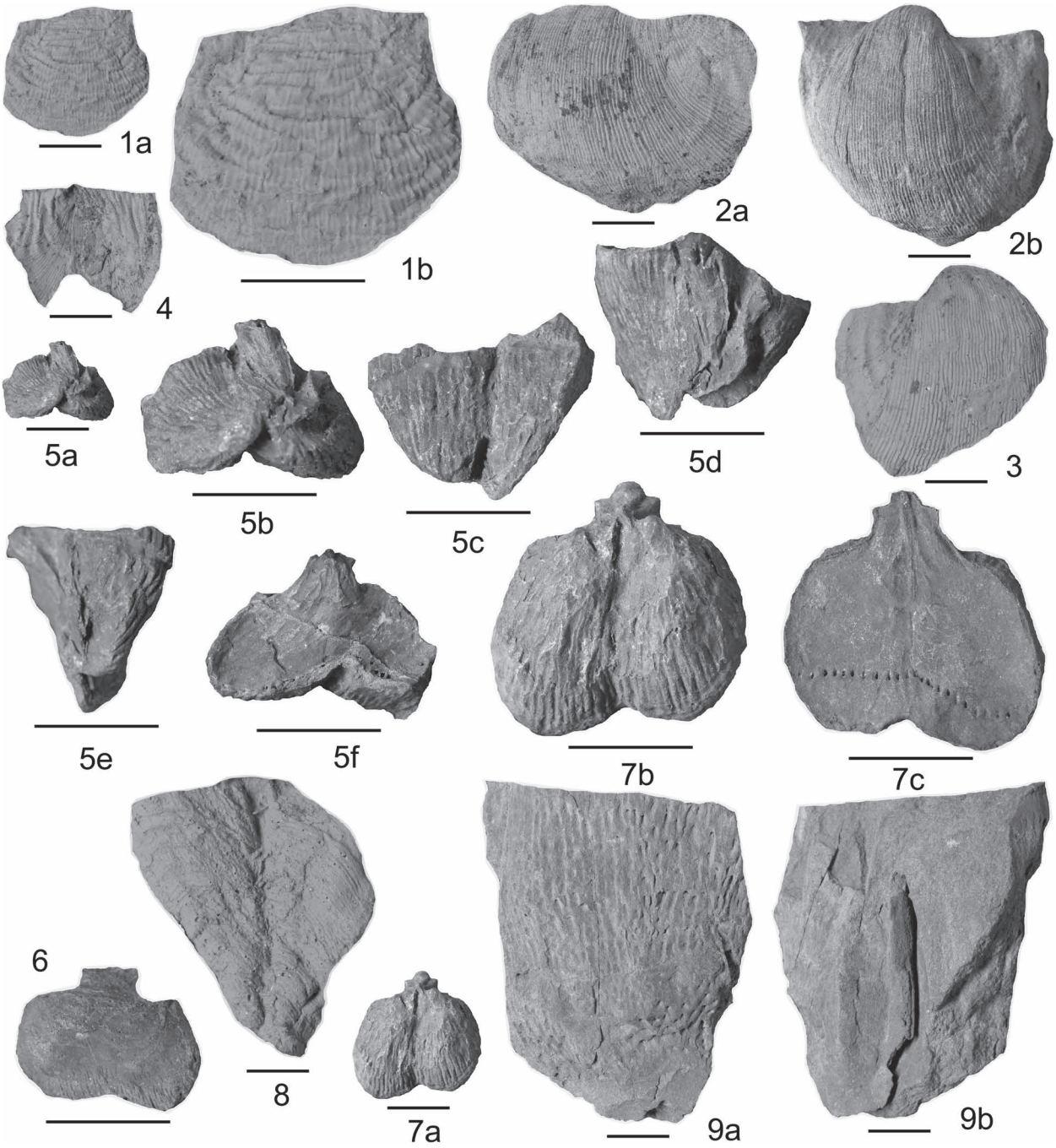

Figure 7. **1,** *Costatumulus cancriniformis* (Tschernyschew); 1a, b, external latex cast of ventral valve, IGPS96218; **2–4,** *Linoproductus hayasakai* Tazawa; 2a, b, external latex cast and internal mould of ventral valve, IGPS96239 (holotype); 3, external latex cast of ventral valve, IGPS96241; 4, external latex cast of dorsal valve, IGPS96249; **5–7,** *Neorichthofenia mabutii* (Tazawa and Araki); 5a–f, ventral, anterior, posterior and lateral views of internal mould of ventral valve, and internal mould of dorsal valve, IGPS98870 (holotype); 6, external mould of dorsal valve, IGPS98877; 7a–c, ventral view of internal mould of ventral valve, and internal mould of dorsal valve, IGPS98872; **8, 9,** *Scacchinella gigantea* Schellwien; 8, anterior view of external latex cast of ventral valve, NU-B197; 9a, b, anterior and posterior views of internal mould of ventral valve, NU-B198. Scale bars represent 1 cm.

1–6; pl. 273, figs. 1–25; pl. 274, figs. 1–6; pl. 275, figs. 1–4; pl. 276, figs. 1–3; pl. 277, figs. 1–4; pl. 278, figs. 1–19; pl. 279, figs. 1–9; pl. 280, figs. 1–8; pl. 281, figs. 1–18; pl. 282, figs. 1–19; pl. 283, figs. 1–22; pl. 284, figs. 16–30), from the upper Wolfcampian of West Texas, differs from the present species in the larger dimensions, more rounded, nearly circular anterior profile and much broader ventral interarea.

Distribution.—Asselian–Capitanian: Balkan States (Slovenia), central Russia (southern Urals), Uzbekistan (Fergana) and northeastern Japan (South Kitakami Belt).

Superfamily Linoproductoidea Stehli, 1954
Family Linoproductidae Stehli, 1954
Subfamily Linoproductinae Stehli, 1954
Genus ***Linoproductus*** Chao, 1927

Type species.—*Productus cora* d'Orbigny, 1842.

Linoproductus hayasakai Tazawa, 1979

Figures 7.2–7.4

Productus cora d'Orbigny. Hayasaka, 1925, p. 94, pl. 5, figs. 7–9.
Linoproductus cora (d'Orbigny). Hayasaka and Minato, 1956, p. 145, pl. 23, figs. 9, 10; Tazawa, 1976, pl. 2, fig. 11; Minato *et al*., 1979, pl. 62, figs. 1, 2; Tazawa and Ibaraki, 2001, p. 10, pl. 1, figs. 11–13; pl. 2, figs. 1–8.
Linoproductus sp. Minato *et al.*, 1979, pl. 62, figs. 3, 4.
Linoproductus hayasakai Tazawa, 1979, p. 26, pl. 4, figs. 5–11.

Material.—Eleven specimens from locality AR5: (1) external and internal moulds of four ventral valves, IGPS96239 (holotype), IGPS96240–96242; (2) external mould of a ventral valve, IGPS96243; (3) internal moulds of five ventral valves, IGPS96244–96248; and (4) external mould of one dorsal valve, IGPS96249.

Description.—Shell medium in size for genus, equidimensional subquadrate in outline, with greatest width at hinge; length 41 mm, width 42 mm in the holotype (IGPS96243). Ventral valve moderately convex in lateral profile, most convex at umbonal slope, not geniculated; umbo massive, strongly incurved and overhanging hingeline a little; ears large, flattened, extremities blunt, angular; sulcus absent; lateral slopes steep. Dorsal valve moderately concave, with deeply concave umbonal region, nearly flat visceral disc, strongly geniculated and followed by a short trail; fold absent. External surface of ventral valve ornamented with numerous regular costellae on whole valve, and concentric rugae on ears; costellae intercalated and bifurcated anteriorly, numbering 15–18 in 10 mm at midlength of valve; no spines or spine bases. External ornament of dorsal valve similar to those of ventral valve, but concentric rugae stronger and developed on both ears and visceral disc; no spines or spine bases. Internal structures of both valves not well preserved.

Remarks.—These specimens were described by Tazawa (1979) as a new species, *Linoproductus hayasakai*, which is characterized by its medium size, fine costellae and no spines on the ventral valve. The type species, *Linoproductus cora* (d'Orbigny, 1842), redescribed by Tschernyschew (1902, p. 279, 621, pl. 33, figs. 2, 3; pl. 35, fig. 1; pl. 54, figs. 1–5, text-figs. 69–71), from the lower Permian of Timan, northern Russia, differs from *L. hayasakai* in its larger size and in having coarser costellae and sporadically distributed spines on the ventral valve. *Linoproductus kaseti* Grant (1976, p. 154, pl. 41, figs. 8–28), from the Rat Buri Limestone of Phangnga, southern Thailand, is also a medium-sized *Linoproductus* species, but the Thailand species differs from the present species in its elongate outline and in having coarser costellae and some spines on the ventral valve.

Distribution.—Wordian: northeastern Japan (South Kitakami Belt).

Genus ***Costatumulus*** Waterhouse in Waterhouse and Briggs, 1986

Type species.—*Auriculispina tumida* Waterhouse in Waterhouse, Briggs and Parfrey, 1983.

Costatumulus cancriniformis (Tschernyschew, 1889)

Figures 6.10, 7.1

Productus cancriniformis Tschernyschew, 1889, p. 283, 373, pl. 7, figs. 32, 33; Tschernyschew, 1902, p. 292, 629, pl. 52, figs. 5, 6; Fredericks, 1925, p. 27, pl. 4, figs. 115, 116.
Cancrinella cancriniformis (Tschernyschew). Kaschirzew, 1959, p. 39, pl. 15, figs. 4, 5; Solomina, 1960, p. 49, pl. 8, figs. 3–7; Ustritsky and Tschernjak, 1963, p. 84, pl. 13, figs. 6–8; pl. 14, figs. 1–5; Abramov, 1970, p. 124, pl. 5, figs. 9–12; Solomina, 1970, p. 85, pl. 5, fig. 9; Zavodowsky and Stepanov, 1970, p. 101, pl. 24, fig. 8; pl. 27, fig. 10; pl. 35, figs. 4–7; Grigorjeva *et al*., 1977, p. 134, pl. 20, fig. 1; Tazawa, 1979, p. 27, pl. 4, figs. 3, 4; Lee and Duan, 1985, p. 239, pl. 75, figs. 2–5; Pavlova and Lazarev in Tatarinov *et al*., 1991, p. 114, pl. 26, figs. 5, 6, 8, 14; Kalashnikov, 1993, p. 81, pl. 33, fig. 10.
Costatumulus cancriniformis (Tschernyschew). Shen *et al*., 2000, p. 743.

Material.—Two specimens from locality AR5, external and internal moulds of two ventral valves, IGPS96217, 96218.

Description.—Shell medium in size for genus, subcircular in outline, with greatest width at midlength; length 24 mm, width 26 mm in the better preserved specimen (IGPS96217). Ventral valve strongly convex in both lateral and anterior profiles; umbo small, strongly incurved; ears small; sulcus absent. External surface of ventral valve

ornamented with numerous fine costellae, quincuncially arranged elongate spine bases and numerous, somewhat undulated concentric rugae; numbering 12–13 costellae and 4 rugae in 5 mm at about midlength of valve.

Remarks.—These specimens are referred to *Costatumulus cancriniformis* (Tschernyschew, 1889, p. 283, 373, pl. 7, figs. 32, 33), from the lower Permian (Artinskian) of the northern Urals, by the strongly inflated ventral valve, ornamented with numerous undulated concentric rugae. *Costatumulus tazawai* Shen, Archbold, Shi and Chen (2000, p. 743, figs. 12.1–12.8, 12.11–12.14), from the Selong Group (Wuchiapingian) of Xizang (Tibet), differs from *C. cancriniformis* in having more numerous, finer costellae on the ventral valve. The type species, *Costatumulus tumida* (Waterhouse in Waterhouse *et al*., 1983, p. 133, pl. 3, figs. 2–4, 6, 7), from the Tiverton Formation of the Bowen Basin, Queensland, eastern Australia, is readily distinguished from the present species in having less strong concentric rugae on the ventral valve.

Distribution.—Moscovian–Wordian; northern Russia (Timan, Pechora Basin, northern Urals, Taimyr Peninsula, Verkhoyansk Range and Kolyma–Omolon), southern Mongolia, northern China (Shanxi), eastern Russia (South Primorye) and northeastern Japan (South Kitakami Belt).

Family Kansuellidae Muir-Wood and Cooper, 1960
Subfamily Auriculispininae Waterhouse in Waterhouse and Briggs, 1986
Genus ***Permundaria*** Nakamura, Kato and Choi, 1970

Type species.—*Permundaria asiatica* Nakamura, Kato and Choi, 1970.

Permundaria tenuistriata Tazawa, 1974

Figure 6.11

Permundaria tenuistriata Tazawa, 1974, p. 317, pl. 43, figs. 1, 2.

Material.—One specimen from locality AR4, external mould of a dorsal valve, KCG014.

Remarks.—The material available is lacking the ventral valve, but it can be referred to *Permundaria tenuistriata* Tazawa, 1974, from the lower part of the Kamiyasse Formation of the Kamiyasse–Imo area, South Kitakami Belt, northeastern Japan, on account of its large (length 45 mm, width about 50 mm), semicircular and almost flat dorsal valve, ornamented by numerous regular concentric rugae and numerous capillae (11–12 capillae in 2 mm at about midlength). *Permundaria asiatica* Nakamura, Kato and Choi (1970, p. 296, pl. 2, figs. 1, 2), from the lower part of the Kanokura Formation of the Setamai area, South Kitakami Belt and from the middle Permian (Capitanian) of Sisophon, western Cambodia, is distinguished from *P. tenuistriata* in having coarser capillae (6–8 in 3 mm at 10 mm from umbo) on the ventral valve.

Distribution.—Wordian: northeastern Japan (South Kitakami Belt).

Family Yakovleviidae Waterhouse, 1975
Genus ***Yakovlevia*** Fredericks, 1925

Type species.—*Yakovlevia kaluzinensis* Fredericks, 1925.

Yakovlevia mammata (Keyserling, 1846)

Figure 6.7

Productus mammatus Keyserling, 1846, p. 206, pl. 4, fig. 5; de Koninck, 1847, p. 49, pl. 7, fig. 4; Tschernyschew, 1902, p. 295, pl. 35, figs. 4–6; Keidel, 1906, p. 367, pl. 12, fig. 5.
Linoproductus? *mammatus* (Keyserling). Chao, 1927, p. 146, pl. 15, figs. 10–14.
Productus (*Linoproductus*?) *mammatus* Keyserling. Grabau, 1931, p. 288, pl. 29, figs. 10–14.
Productus (*Thomasina*) *mammatus* Keyserling. Stepanov, 1937, p. 127, 177, pl. 2, figs. 5–7.
Muirwoodia mammata (Keyserling). Muir-Wood and Cooper, 1960, pl. 120, figs. 9–11; Harker in Harker and Thorsteinsson, 1960, p. 58, pl. 16, figs. 1–5; Gobbett, 1963, p. 112, pl. 13, figs. 23–28; Lee and Gu, 1976, p. 263, pl. 159, figs. 7–9; pl. 163, fig. 2; pl. 164, figs. 3, 4; pl. 170, figs. 6, 7; Licharew and Kotlyar, 1978, pl. 14, figs. 3–5; Liu and Waterhouse, 1985, p. 17, pl. 4, figs. 4–6; Nakamura *et al*., 1992, pl. 1, fig. 4; Kalashnikov, 1993, p. 63, pl. 19, figs. 1–3.
Yakovlevia mammatus (Keyserling). Kotlyar, 1961, text-figs. 4–6.
Yakovlevia mammata (Keyserling). Brabb and Grant, 1971, p. 16, pl. 1, figs. 9–12, 33–36; Ifanova, 1972, p. 121, pl. 7, figs. 4, 5; Kalashnikov, 1986, pl. 121, figs. 5, 6; Malkowski, 1988, p. 40, pl. 5, fig. 6; Zhang, 1990, pl. 2, figs. 4, 7, 9; Tazawa, 1999b, p. 90, figs. 3.1–3.5; Wang and Zhang, 2003, p. 85, pl. 6, figs. 1–8; pl. 7, figs. 1–10; Klets, 2005, pl. 11, figs. 1–7.
Yakovlevia paramammata Lee and Gu in Lee *et al*., 1980, p. 382, pl. 171, figs. 4, 15.
Muirwoodia sp. Tazawa, 1987, fig. 1.6.

Material.—One specimen from locality AR4, internal mould of a ventral valve, KCG015.

Remarks.—The single ventral valve specimen from Matsukawa is safely assigned to the genus *Yakovlevia* by the flattened, transversely subtrapezoidal ventral valve, with large diductor scars which are striated and encircled by a strong ridge posterolaterally. This specimen is referred to *Yakovlevia mammata* (Keyserling, 1846), from the lower Permian (Sakmarian?) of the Pechora Basin, northern Russia, in its small size (length 19 mm, width 33 mm), and in having large, acute ears and a narrow, moderately deep sulcus on the trail. *Yakovlevia greenlandica* (Dunbar, 1955, p. 103, pl. 16, figs. 1–17), from the Guadalupian of eastern Greenland, is also a small-sized *Yakovlevia* species, but the Greenlandic species is distinguished from *Y. mammata* by its less transverse outline.

Yakovlevia mammatiformis (Fredericks, 1926, p. 87, pl. 3, figs. 4–6), from the lower Permian (Artinskian) of the Pechora Basin, northern Russia, is clearly distinguished from the present species by its larger size and more transverse outline.

Distribution.—Kasimovian–Capitanian: northern USA (Alaska), northern Canada (Devon Island), Spitsbergen, northern Russia (Timan, Pechora Basin and Verkhoyansk Range), northwestern China (Xinjiang), northern China (Inner Mongolia), northeastern China (Heilongjiang), eastern Russia (South Primorye) and northeastern Japan (South Kitakami Belt).

Yakovlevia kaluzinensis Fredericks, 1925

Figure 6.12

Chonetes (*Yakovlevia*) *kaluzinensis* Fredericks, 1925, p. 7, pl. 2, figs. 64–66.

Yakovlevia kaluzinensis Fredericks. Kotlyar, 1961, text-figs. 1–3; Licharew and Kotlyar, 1978, pl. 14, figs. 1, 2; Manankov, 1998, pl. 8, figs. 18, 19; Tazawa, 1999b, p. 90, figs. 3.7–3.15; Tazawa, 2001b, p. 291, figs. 6.20–6.25; Tazawa, 2008b, p. 49, fig. 7.14; Tazawa and Araki, 2013, p. 5, fig. 2.2.

Material.—One specimen from locality AR5, internal mould of a ventral valve, KCG008.

Remarks.—This specimen was described by Tazawa and Araki (2013) as *Yakovlevia kaluzinensis* Fredericks, 1925, originally described by Fredericks (1925, p. 7, pl. 2, figs. 64–66) from the Chandalaz Formation of the Vladivostok area, South Primorye, eastern Russia. *Yakovlevia impressa* (Toula, 1875, p. 236, pl. 5, fig. 11), from the middle Permian of Spitsbergen, differs from *Y. kaluzinensis* in having larger and more prominent ears. The preceding species, *Yakovlevia mammata* (Keyserling, 1846), is distinguished from the present species by its much smaller size and the larger and more acute ears.

Distribution.—Kungurian–Wuchiapingian?: southern Mongolia, eastern Russia (South Primorye), northeastern Japan (South Kitakami Belt), central Japan (Hida Gaien Belt) and southwestern Japan (Mizukoshi in central Kyushu).

Superfamily Richthofenioidea Cooper and Grant, 1975
Family Hercosiidae Cooper and Grant, 1975
Genus ***Neorichthofenia*** Shen, He and Zhu, 1992

Type species.—*Richthofenia mabutii* Tazawa and Araki, 1984b.

Neorichthofenia mabutii (Tazawa and Araki, 1984b)

Figures 7.5–7.7

Richthofenia mabutii Tazawa and Araki, 1984b, p. 3, pl. 1, figs. 1–7.

Neorichthofenia mabutii (Tazawa and Araki). Shen *et al*., 1992, p. 180, pl. 3, figs. 13–22.

Material.—Eight specimens from locality AR4: (1) internal moulds of five conjoined shells, IGPS98870 (holotype), 98871–98874; (2) internal moulds of two ventral valves, IGPS98875. 98876; and (3) external mould of a dorsal valve, IGPS98877.

Description.—Shell medium in size for genus, highly conical in shape; hinge shorter than greatest width at about midlength; length about 12 mm, width about 19 mm, height about 15 mm in the holotype (IGPS98870); length 13 mm, width 14 mm in the sole dorsal valve specimen (IGPS98877). External features of ventral valve unknown. Dorsal valve semicircular in outline, almost flat and slightly concave in both lateral and anterior profiles; hinge short and straight; posterior projection (neck) long and slender. External surface of dorsal valve ornamented with 5 concentric rugae and numerous fine pustules on visceral disc, and numerous fine prostrate spines on front of valve. Internally, ventral valve being a deep conical cavity, with a broad low median ridge anteriorly and an elongate trigonal median hollow posteriorly; median ridge developed on anterior half or more; median hollow corresponding to interarea and pseudodeltidium of ventral valve; internal surface of ventral cavity covered by numerous fine irregular radial ribs and some strong concentric rugae near commissure. Dorsal interior with a weak median septum, a bilobed cardinal process bearing a long shaft, and a pair of dendritic adductor scars; endospines occurring in a row at one-third length from anterior margin of valve.

Remarks.—The specimens from Matsukawa were described by Tazawa and Araki (1984b) as a new species, *Richthofenia mabutii*. Subsequently Shen *et al.* (1992) proposed the genus *Neorichthofenia* with the Matsukawa species as type species. *Neorichthofenia* is characterized by having a median ridge in the ventral valve. No other species have been assigned to the genus.

Distribution.—Wordian–Changhsingian: northeastern Japan (South Kitakami Belt) and southwestern China (Sichuan).

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)

Figures 8.1, 8.2

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, 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, 2001b, 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 in Ruzhentsev and 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, 1999a, 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.—Three specimens from locality AR4, internal moulds of three ventral valves, KCG016–018.

Description.—Shell small in size for genus, elongate subtrigonal to transversely oval in outline, scoop-shaped, with greatest width near anterior margin; length 30 mm, width 26 mm in an elongate specimen (KCG017), length 14 mm, width 28 mm in a transverse specimen (KCG018). Ventral interior with regularly and symmetrically arranged lateral ridges on both sides of median ridge; median ridge strong, extending for valve length; lateral ridges broad, solid (solidiseptate), nearly straight to slightly arched toward anterior, numbering 13 on each side of median septum in the elongate specimen (KCG017).

Remarks.—These specimens are referred to *Leptodus nobilis* (Waagen, 1883), originally described 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 ridges on both sides of the median ridge. The Matsukawa specimens, being smaller than the type specimens of the Salt Range, may be young shells. *Leptodus richthofeni* Kayser, 1883, originally described by 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. nobil*is by its more highly convex ventral valve and the sharp lateral ridges with wider interspaces.

Distribution.—Kungurian–Changhsingian: Hungary, Balkan States (Croatia and Serbia), Armenia (Transcaucasia), northwestern China (Qinghai), northern China (Inner Mongolia), northeastern China (Heilongjiang and Jilin), eastern Russia (South Primorye), northeastern Japan (South Kitakami Belt), central Japan (Hida Gaien and Mino belts), southwestern Japan (Maizuru and Akiyoshi belts), eastern China (Zhejiang, Fujian and Jiangxi), central-southern China (Hubei, Hunan, Guangdong and Guangxi), southwestern China (Guizhou, Sichuan and Yunnan), Cambodia, Malaysia, Timor and Pakistan (Salt and Khisor ranges).

Genus ***Keyserlingina*** Tschernyschew, 1902

Type species.—*Keyserlingina schellwieni* Tschernyschew, 1902.

Keyserlingina sp.

Figure 8.3

Material.—One specimen from locality KZ9, internal mould of a ventral valve, KCG019.

Description.—Ventral internal plate small in size (length 10 mm, width 8 mm), nearly flat, elongate subcircular in outline, and marked with numerous fine pustules; median ridge long and broad, not well preserved in anterior parts; lateral ridges symmetrically arranged and slightly inclined towards front, numbering 2 on each side of median ridge.

Remarks.—The specimen from Matsukawa is safely assigned to the genus *Keyserlingina* on the basis of its small, nearly flat internal plate, with a broad median ridge and symmetrically arranged, broad and deeply grooved

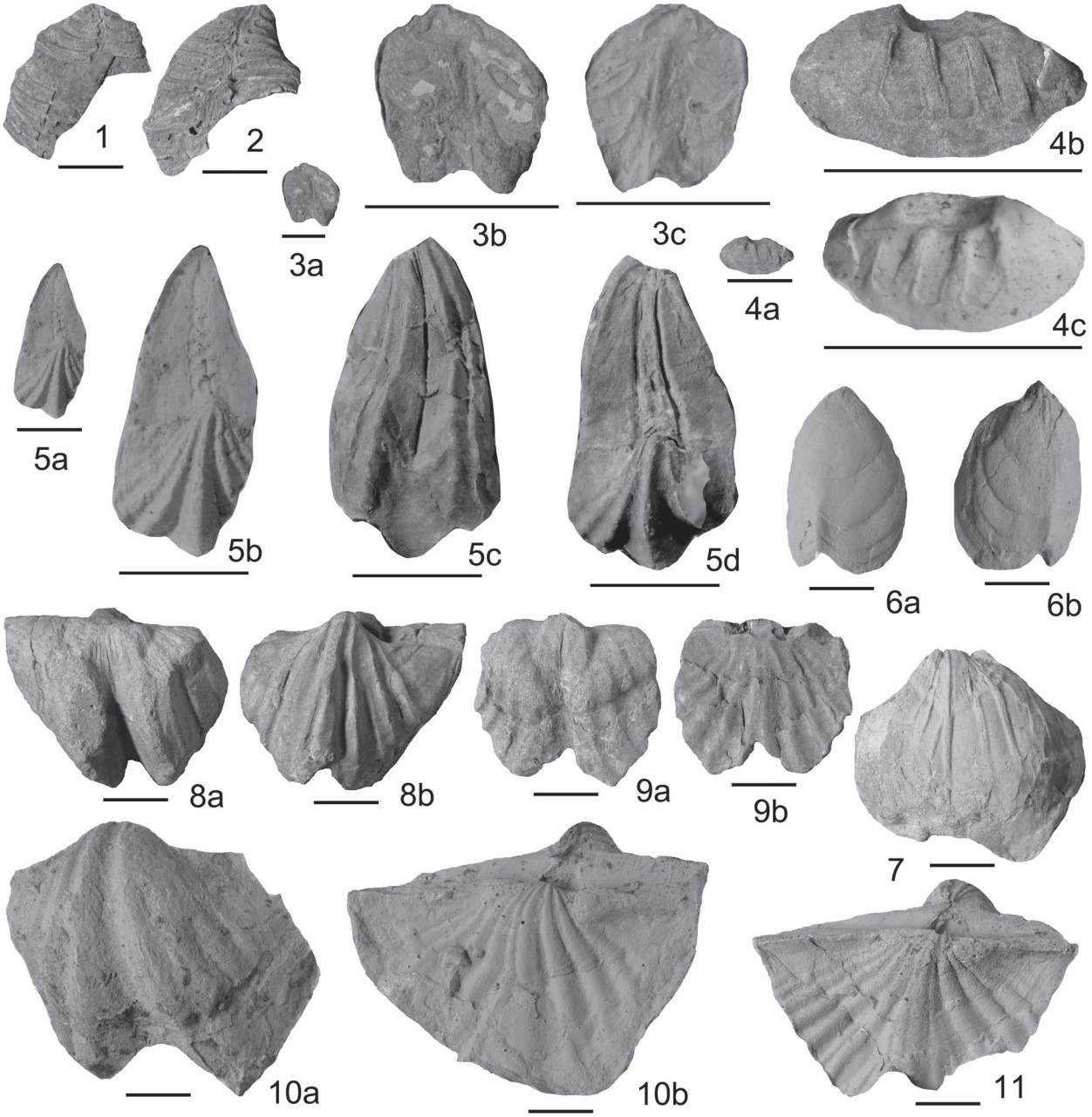

Figure 8. **1, 2,** *Leptodus nobilis* (Waagen); 1, internal mould of ventral valve, KCG016; 2, internal mould of ventral valve, KCG017; **3,** *Keyserlingina* sp., 3a–c, internal mould and internal latex cast of ventral valve, KCG019; **4,** *Paralyttonia kesennumensis* Tazawa and Araki; 4a–c, internal mould and internal latex cast of dorsal valve, IGCP98393; **5,** *Licharewina arakii* (Hayasaka); 5a–d, dorsal view of external latex cast, and ventral and dorsal views of internal mould of conjoined shell, KCG004; **6,** *Dielasma* sp.; 6a, b, external latex cast and internal mould of dorsal valve, IGPS96236; **7,** *Martinia* sp., internal mould of ventral valve, NU-B2012; **8–11,** *Alispiriferella lita* (Fredericks); 8a, b, ventral and dorsal views of internal mould of conjoined shell, KCG020; 9a, b, ventral and dorsal views of conjoined shell, KCG021; 10a, b, external latex casts of ventral and dorsal valves, IGPS96219; 11, external latex cast of dorsal valve, IGPS96220. Scale bars represent 1 cm.

lateral ridges. The Matsukawa species resembles *Keyserlingina filicis* (Keyserling, 1853), redescribed by Tschernyschew (1902, p. 56, 474, pl. 42, figs. 16, 17) from the lower Permian *Schwagerina* Limestone of the Urals, in having lateral ridges slightly inclined towards the anterior. An accurate comparison is difficult for this poorly preserved specimen.

Family Rigbyellidae Williams, Harper and Grant, 2000
Genus ***Paralyttonia*** Wanner in Wanner and Sieverts, 1935

Type species.—*Paralyttonia permica* Wanner in Wanner and Sieverts, 1935.

Paralyttonia kesennumensis Tazawa and Araki, 1984a

Figure 8.4

Paralyttonia kesennumensis Tazawa and Araki, 1984a, p. 122, figs. 2.1, 2.2.

Material.—Two specimens from locality AR4, internal moulds of two ventral valves, IGPS98393, 98394.

Remarks.—This species was described by Tazawa and Araki (1984a) based on the holotype from the lower part of the Kamiyasse Formation at Takayashiki (about 1.6 km south from locality AR4) and the paratypes from both Takayashiki and Matsukawa (locality AR4). Until now the following four species have been assigned to the genus *Paralyttonia*: *P. permica* Wanner in Wanner and Sieverts, 1935, *P. transiens* Wanner in Wanner and Sieverts, 1935, *P. tenax* Grant, 1976 and *P. kesennumensis* Tazawa and Araki, 1984a. The Kitakami species is most like *Paralyttonia tenax* Grant (1976, p. 168, pl. 44, figs. 4–36; pl. 45, figs. 32–42, text-fig. 15), from the Rat Buri Limestone of Ko Muk, southern Thailand, but it differs from the Thailand species in its smaller size and in having longer and more regular septa.

Distribution.—Wordian: northeastern Japan (South Kitakami Belt).

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Martinioidea Waagen, 1883
Family Martiniidae Waagen, 1883
Subfamily Martiniinae Waagen, 1883
Genus ***Martinia*** M'Coy, 1844

Type species.—*Spirifer glaber* Sowerby, 1820.

Martinia sp.

Figure 8.7

Material.—One specimen from locality AR4, internal mould of a ventral valve, NU-B2012.

Remarks.—This specimen is safely assigned to the genus *Martinia* by its medium-sized (length about 35 mm, width about 38 mm), subcircular-shaped and moderately convex ventral valve and several conspicuous radial vascular markings on the internal surface of the ventral valve. An accurate comparison is difficult for this poorly preserved specimen.

Superfamily Spiriferoidea King, 1846
Family Spiriferellidae Waterhouse, 1968
Genus ***Alispiriferella*** Waterhouse and Waddington, 1982

Type species.—*Spirifer* (*Spiriferella*) *keilhavii* var. *ordinaria* Einor in Licharew and Einor, 1939.

Alispiriferella lita (Fredericks, 1924)

Figures 8.8–8.11

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.
Alispirifer aff. *laminosus transversa* Maxwell. Yanagisawa, 1967, p. 90, pl. 2, fig. 3.
Cancellospirifer? *maxwelli* Campbell. Yanagisawa, 1967, p. 92, pl. 3, fig. 16.
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, 2001b, p. 302, figs. 8.19–8.22; Tazawa and Chen, 2006, p. 336, fig. 6.4.
Alispiriferella sp. Yanagida, 1996, figs. 2.2, 2.4.
Spiriferella cf. *lita* (Fredericks). Tazawa *et al*., 2000, p. 12, pl. 1, figs. 16, 17.
Alispiriferella ordinaria (Einor). Tazawa, 2001b, p. 302, fig. 8.14.
Alispiriferella japonica Tazawa, 2001b, 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; Tazawa and Chen, 2006, p. 336, fig. 6.3.
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.—Nineteen specimens from localities AR4 and AR5: (1) external and internal moulds of a conjoined shell, IGPS96219: (2) internal mould of a conjoined shell, with external mould of the ventral valve, IGPS96221; (3) internal mould of a conjoined shell, with external mould of the dorsal valve, IGPS96220; (4) internal moulds of two conjoined shells, KCG020, 021; (5) external and internal moulds of three ventral valves, IGPS96222–96224; (6) internal moulds of three ventral valves, IGPS96225–96227; (7) external and internal moulds of three dorsal valves, IGPS96228–96230; (8) external mould of a dorsal valve, IGPS96231; and (9) internal moulds of four dorsal valves, IGPS96232–96235.

Remarks.—Most of the specimens from Matsukawa were previously described by Tazawa (1979) as *Spirifer-*

ella lita (Fredericks, 1924). Two newly added specimens, numbered KCG020 and KCG021, are also referred to *Alispiriferella lita* (Fredericks, 1924), from the middle Permian (Wordian) of South Primorye, eastern Russia, by their large transverse shells and deep ventral sulcus with smooth V-shaped bottom and strong simple costae on the ventral valve. The type species, *Alispiriferella ordinaria* (Einor in Licharew and Einor, 1939, p. 140, 217, pl. 23, figs. 6, 7; pl. 24, fig. 1), from the lower Permian of Novaya Zemlya, northern Russia, differs from *A. lita* by the smaller and less transverse shell with ventral sulcus bearing two prominent sulcal costae. *Alispiriferella keilhavii* (von Buch), redescribed by Dunbar (1955, p. 199, pl. 25, figs. 1–9; pl. 26, figs. 1–11; pl. 27, figs. 1–44), from the middle Permian of Greenland, differs from the present species in having weakly fasciculate costae on both valves.

Distribution.—Wordian–Changhsingian: northern China (Inner Mongolia), northeastern China (Heilongjiang), eastern Russia (South Primorye), northeastern Japan (South Kitakami Belt), central Japan (Hida Gaien Belt) and southwestern Japan (Akiyoshi Belt and Mizukoshi in central Kyushu).

Order Spiriferinida Ivanova, 1972
Suborder Cyrtinidina Carter and Johnson, 1994
Superfamily Cyrtinoidea Fredericks, 1911
Family Cyrtinidae Fredericks, 1911
Genus ***Licharewina*** Kotlyar, Zakharov and Polubotko, 2004

Type species.—*Licharewina praetriassica* Kotlyar, Zakharov and Polubotko, 2004.

Licharewina arakii (Hayasaka, 1963)

Figure 8.5

Geyerella arakii Hayasaka, 1963, p. 481, figs. 2, 3.
Licharewina arakii (Hayasaka). Tazawa and Araki, 2013, p. 9, figs. 3.1, 3.2.

Material.—One specimen from locality AR4, internal mould of a conjoined shell, with external mould of the dorsal valve and interarea of the ventral valve, KCG004.

Remarks.—This specimen was first described by Hayasaka (1963) as *Geyerella arakii* Hayasaka, 1963. Then, Tazawa and Araki (2013) redescribed the specimen as *Licharewina arakii* (Hayasaka, 1963). This species is characterized by its large size and the highly pyramidal ventral valve. *Licharewina josephinae* (Gemmellaro, 1899), redescribed by Shen and Clapham (2009, p. 732, pl. 6, figs. 1–15) from the Episkopi Formation (Wuchiapingian) of Hydra Island, Greece, differs from *L. arakii* in its smaller size and less pyramidal outline. The type species, *Licharewina praetriassica* Kotlyar, Zakharov and Polubotko (2004, p. 522, figs. 6.13–6.20), from the upper Permian (Changhsingian) of the Caucasus Mountains, is readily distinguished from the present species by its much smaller size.

Distribution.—Wordian: northeastern Japan (South Kitakami Belt).

Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Dielasmatoidea Schuchert, 1913
Family Dielasmatidae Schuchert, 1913
Subfamily Dielasmatinae Schuchert, 1913
Genus ***Dielasma*** King, 1859

Type species.—*Terebratulites elongatus* Schlotheim, 1816.

Dielasma sp.

Figure 8.6

Dielasma sp. Tazawa, 1979, p. 30, pl. 5, fig. 5.

Material.—One specimen from locality AR5, external and internal moulds of a dorsal valve, IGPS96236.

Remarks.—This specimen was described by Tazawa (1979) as *Dielasma* sp. The Matsukawa species is large in size for the genus (length 29 mm, width 20 mm in the dorsal valve, IGPS96236), and characterized by the presence of a sharp fold on the anterior portion of the dorsal valve. This species is most like *Dielasma plica* (Kutorga, 1842), redescribed by Diener (1903, p. 44, pl. 2, fig. 2) from the middle Permian (Capitanian) of Chitichun No. 1, southern Tibet, in having a dorsal fold. An accurate comparison, however, is difficult for this poorly preserved specimen.

Distribution.—Wordian: northeastern Japan (South Kitakami Belt).

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