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Early Asselian (earliest Permian) ammonoids from the Taishaku Limestone, Akiyoshi Belt, Southwest Japan: an Asselian ammonoid fauna of the Mid-Panthalassan Realm

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Abstract. An early Asselian ammonoid fauna comprising nine species belonging to nine genera (*Agathiceras*, *Neoglaphyrites*, *Somoholites*, *Shumardites*, *Vidrioceras*, *Almites*, *Eoasianites*?, *Boesites* and *Metapronorites*) and one indeterminable Adrianitidae is described from the Uyamanoro Formation of the Taishaku Limestone at Miharanoro in the Akiyoshi Belt (late Permian accretionary belt), Southwest Japan. The fauna includes four new species: *Shumardites umbilicatus*, *Vidrioceras ellipticum*, *Almites hayasakai* and *Boesites biconcavus*. The age of the fauna is determined to be early Asselian based on the fusulinoidean biostratigraphy. In addition to the previously known late Asselian taxa, the number of Taishaku Asselian ammonoid genera is now ten genera. This is the only known Asselian ammonoid fauna from the mid-Panthalassa Ocean. The ammonoid faunal composition of this region, the Mid-Panthalassa Realm, is closely related to those of Paleotethyan (Pamirs and South China), Uralian and American (eastern Panthalassa) realms.

Key words: Asselian, mid-Panthalassa, paleobiogeography, Permian ammonoid, Taishaku Limestone

Introduction

Early Permian (Cisuralian) ammonoids have been widely known from various areas in the world. Their main distribution areas were divided into five realms having their own biogeographic characteristics (Leonova, 1999, 2011): the Arctic (Arctic Canada, Alaska and Arctic Russia), Uralian (Urals), Paleotethyan (Pamirs, South China, Timor, etc.), Australian (western Australia) and American (Texas, New Mexico, Oklahoma and Kansas). These realms occupied the continental shelves of the Pangea continent or small continents located within the Tethys/Panthalassa border. Outside these realms, there was an extensively wide area between the American Realm (eastern Panthalassa) and the Paleotethyan Realm, i.e. mid-Panthalassa region, during the late Paleozoic. This region is significant for determining the faunal connection between the Paleotethyan and American realms, but only a few Cisuralian ammonoid-bearing strata originated in mid-Panthalassa have been known from the Akiyoshi Limestone and the Taishaku Limestone in the Akiyoshi Belt of Southwest Japan (Figure 1a). These two large limestone bodies, with other limestones in the Akiyoshi Belt such as the Omi, Atetsu, Nakamura, Koyama, Hina and Hiraodai limestones, are included in the late Permian accretionary complexes. Sano and Kanmera (1988) and Sano *et al*. (2000) considered that these units were deposited in the open-ocean realm of the low-latitude Panthalassa Ocean as seamount limestones, ranging in age from Early Carboniferous to Middle Permian, and were accreted to the eastern margin of the Paleo-Asian continent during the Middle to Late Permian.

The Cisuralian ammonoids hitherto known from the Akiyoshi Belt are: seven late Asselian genera, *Agathiceras*, *Neoglaphyrites*, *Emilites*, *Somoholites*, *Marathonites*, *Eoasianites* and *Metapronorites*, from the Taishaku Limestone in Hiroshima Prefecture (Ehiro *et al*., 2014), and two Artinskian genera, *Paraperrinites* and *Stacheoceras*, from the Akiyoshi Limestone in Yamaguchi Prefecture (Nishida *et al*., 2002). Isao Nishikawa collected the late Asselian ammonoids of the Taishaku Limestone above from the late 1950s to the early 1960s from the limestone of the lower part of the Uyamanoro Formation (the *Pseudoschwagerina miharanoensis* Zone) at a locality in Miharanoro, Tojo Town, Shobara City.

In 1986 and 1987, one of the authors (T. O.) collected

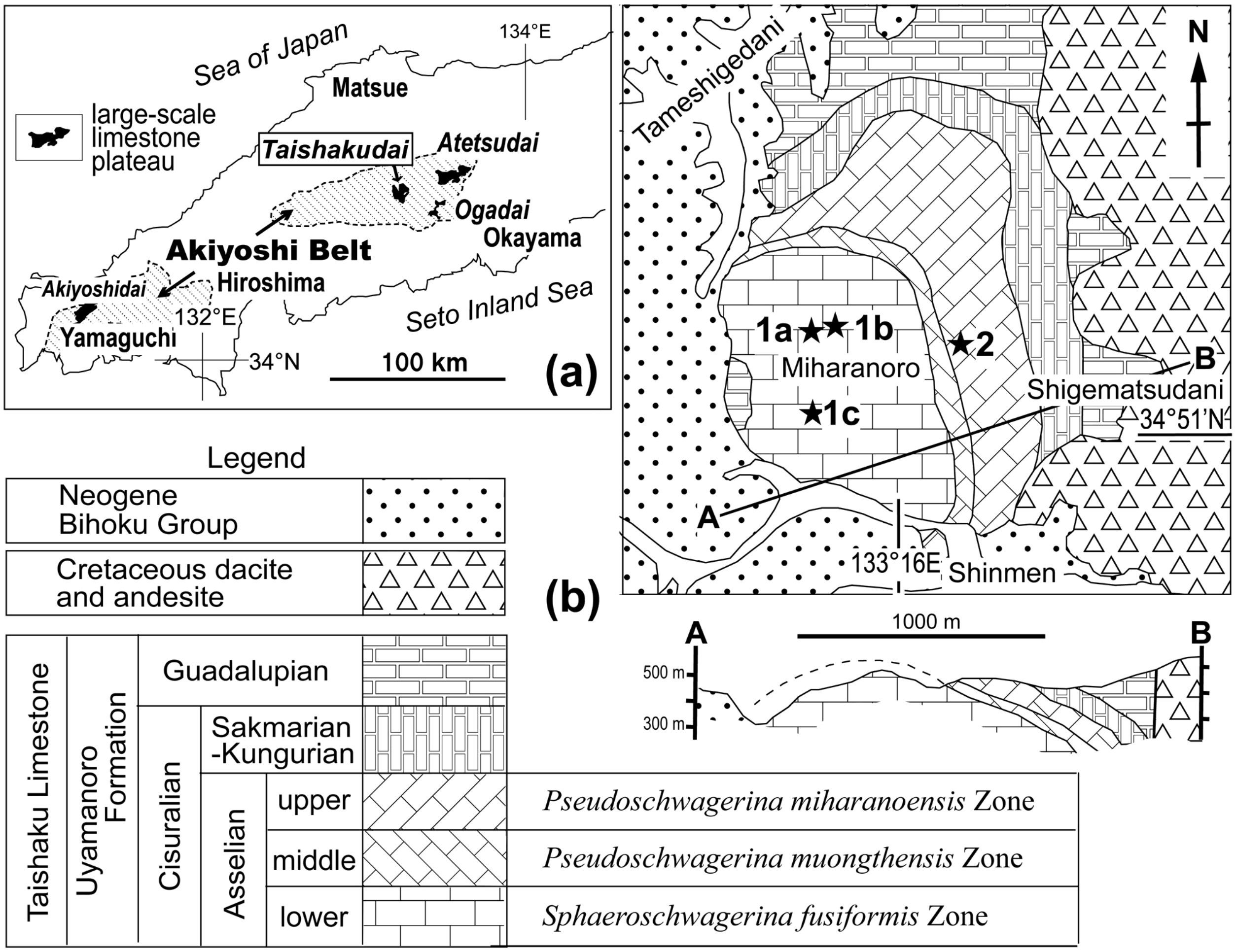

Figure 1. Index map of the Taishakudai area (a), and geologic map and cross section of the Miharanoro area (b), Akiyoshi Belt, Southwest Japan. Stars (1a, 1b, 1c and 2) are ammonoid localities of the Uyamanoro Formation.

a number of well-preserved ammonoid fossils, in association with gastropods, pelecypods, non-ammonoid cephalopods, crinoids, brachiopods and corals, from weathered surfaces of lapiés exposed during the construction of golf courses made in 1986 and 1987 in the southern part of Miharanoro. The fossil horizon is the lower part of the Uyamanoro Formation (the *Sphaeroschwagerina fusiformis* Zone: lower Asselian). This paper describes these early Asselian ammonoids from Miharanoro and discusses the paleobiogeographic significance of the Miharanoro Asselian ammonoid fauna.

Geologic setting of the ammonoid locality

The Taishaku Limestone (Group), which is exposed in northeastern Hiroshima Prefecture (Figure 1a), comprises the Carboniferous Dangyokei and Eimyoji formations, and the Permian Uyamano Formation, in ascending order (Hase and Okimura, 1971; Hase *et al*., 1974). Sada (1973) renamed the Uyamano Formation as the Uyamanoro Formation, since the geographic name of the type locality of the formation is “Uyamanoro”, not “Uyamano”. The ages of the formations of the Taishaku Limestone were determined primarily based on their foraminiferal fauna (e.g. Akagi, 1958; Sada, 1967, 1969, 1972, 2014; Sada and Yokoyama, 1970; Sada *et al*., 1984; Ueno and Mizuno, 1993). Ammonoid fossils are restricted to the Uyamanoro Formation in the Taishaku Limestone. In addition to the above-mentioned Asselian ones from the Uyamanoro Formation, only one Serpukhovian (upper Mississippian) species, *Dombarites taishakuensis* Ehiro, Nishikawa and Nishikawa (2013) has been described from the Dangyokei Formation.

The ammonoid specimens described here were collected from the limestone of the lower part of the Uyamanoro Formation distributed in the southern part of

Miharanoro, Tojo-cho, on the eastern end of Shobara City, Hiroshima Prefecture (Figure 1b). In order to determine the geologic age of the ammonoid-bearing limestone, restudy of the fusulinoidean biostratigraphy of the lower part of the Uyamanoro Formation (Asselian limestone) was made by T. O. based on a number of limestone samples and thin-sections of limestone collected during fossil sampling. This study revealed three fusulinoidean zones in the Asselian Stage, namely the *Sphaeroschwagerina fusiformis* Zone (lower Asselian), *Pseudoschwagerina muongthensis* Zone (middle Asselian) and *Pseudoschwagerina miharanoensis* Zone (upper Asselian) (Figure 1b). The Carboniferous/Permian boundary is not determined in this area, as the upper Carboniferous limestone is not exposed at the surface in Miharanoro.

The Asselian limestones in Miharanoro form the core part of a dome structure (Figure 1b). The *Sphaeroschwagerina fusiformis* Zone faunule occurs in grey poorly sorted biosparudite in a channel-like depression between marked carbonate mounds dominated by *Palaeoaplysina*, and is composed of *Triticites* sp. (abundant in occurrence), *Sphaeroschwagerina fusiformis* (Krotow) (common), *Daixina* sp. (common) and *Ozawainella* sp. The *Pseudoschwagerina muongthensis* Zone faunule consists of *Pseudoschwagerina muongthensis* (Deprat) (abundant), *Sphaeroschwagerina pavlovi* (Rauser-Chernousova) (common), *Paraschwagerina* sp. (common) and *Daixina* sp. (common). The *Pseudoschwagerina miharanoensis* Zone faunule occurs in white to gray biomicrite and composed mainly of zonal species with association of *Daixina* sp. and *Pseudofusulina* sp. The representative fusulinoidean species from the Asselian limestone of the Uyamanoro Formation are shown in Figure 2.

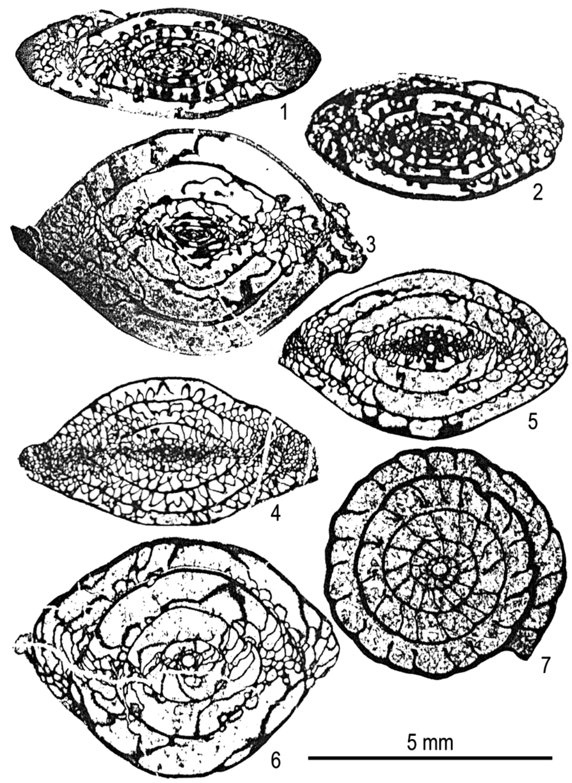

Figure 2. Asselian representative fusulinoideans from the Uyamanoro Formation of the Taishaku Limestone. **1**, *Daixina* sp.; **2**, *Triticites* sp.; **3**, *Sphaeroschwagerina fusiformis* (Krotow) (*Sphaeroschwagerina fusiformis* Zone); **4**, *Paraschwagerina* sp.; **5**, *Pseudoschwagerina muongthensis* (Deprat) (*Pseudoschwagerina muongthensis* Zone); **6**, **7**, *Pseudoschwagerina miharanoensis* Akagi (*Pseudoschwagerina miharanoensis* Zone).

These three Asselian fusulinoidean zones, *S. fusiformis* Zone (early Asselian), *P. muongthensis* Zone (middle Asselian) and *P. miharanoensis* Zone (late Asselian) of the Uyamanoro Formation at Miharanoro are confidently correlative with the same named fusulinoidean zones of the Akiyoshi Limestone, namely *S. fusiformis* Zone (AK31), *P. muongthensis* Zone (AK32) and *P. miharanoensis* Zone (AK33) (Ozawa and Kobayashi, 1990; Ozawa *et al*., 1991), respectively, and also with *S. fusiformis* Zone, *Sphaeroschwagerina pavlovi*-*P. muongthensis* Zone + "*Alpinoschwagerina*" cf. *saigusai* Zone, and *Schwagerina globulus japonicas*-*P. miharanoensis* Zone of the Nagatoan Stage of the Akiyoshi Limestone (Watanabe, 1991), respectively.

Present ammonoid localities (Localities 1a, 1b and 1c of Figure 1b) are all in the *Sphaeroschwagerina fusiformis* Zone (lower Asselian), and *Sphaeroschwagerina fusiformis* occurs commonly from biosparitic limestone of the Locality 1a. The previously reported ammonoid locality (Ehiro *et al*., 2014; Locality 2 of Figure 1b) belongs to the *Pseudoschwagerina miharanoensis* Zone (upper Asselian). The limestones of the *S. fusiformis* Zone in Miharanoro also yield four orthocerids, *Michelinoceras*? sp., *Bogoslovskya miharanoroensis* Niko and Ozawa, *Geisonocerina*? sp. and *Lopingoceras hayasakai* Niko and Ozawa, two nautiloids, *Parachouteauoceras bingoense* Niko and Ozawa and *P.*? sp., and a bactritid, *Bactrites* sp. (Niko and Ozawa, 1997). The *P. miharanoensis* Zone limestone yields two orthocerids, *Michelinoceras hasei* Niko *et al*. and *B. miharanoroensis* Niko and Ozawa, and a bactritid, *Aktastioceras nishikawai* Niko, Nishida and Hamada (Niko *et al*., 1993, 2015).

Materials

Ammonoid specimens described here were all collected from the lower part of the Uyamanoro Formation (*Sphaeroschwagerina fusiformis* Zone) at Miharanoro. Over 120 ammonoid specimens are at hand. However, many specimens are so small and/or poorly preserved that 56 specimens are used in the description. The unused specimens include questionable *Agathiceras* (four specimens), *Almites* (15 specimens) and *Boesites* (five specimens). All specimens, including unnumbered ones, are kept in the Tohoku University Museum (Institution abbreviation: IGPS = Institute of Geology and Paleontology, Tohoku University, Sendai).

Voucher specimens of fusulinoidean zonal indeces of the lower to upper Asselian of the Uyamanoro Formation are also housed in the Tohoku University Museum. These comprise the following six species:

Sphaeroschwagerina fusiformis Zone: *S. fusiformis* (Krotow), IGPS coll. cat. no. 112385; "*Triticites*" sp. (ancestral species of *Nagatoella orientis* (Ozawa)), IGPS coll. cat. no. 112386.

Pseudoschwagerina muongthensis Zone: *P. muongthensis* (Deprat), IGPS coll. cat. no. 112387; *Paraschwagerina* sp., IGPS coll. cat. no. 112388; *Daixina* sp., IGPS coll. cat. no. 112389.

Pseudoschwagerina miharanoensis Zone: *P. miharanoensis* Akagi, IGPS coll. cat. no. 112390.

Table 1. Dimensions (in mm) and ratios of *Agathiceras* sp. from the Uyamanoro Formation. α: the angular position adapical from the preserved end.

Catalog no.	α	*D*	*H* (*H*/*D*)	*W* (*W*/*D*)	*UD* (*UD*/*D*)
IGPS 112269	0°	*ca*. 23.0	12.7 (0.55)	*ca*. 16.5 (0.72)	–
	180°	*ca*. 15.5	*ca*. 9.0 (0.58)	13.5 (0.87)	–
IGPS 112271	0°	16.4	9.5 (0.58)	9.5 (0.58)	–
IGPS 112272	0°	16.4	9.1 (0.55)	9.7 (0.59)	–
IGPS 112273	0°	*ca*. 17.0	*ca*. 8.0 (0.47)	*ca*. 9.5 (0.56)	–
	180°	*ca*. 13.0	16.2 (0.48)	8.4 (0.65)	–
IGPS 112274	0°	11.0	5.5 (0.50)	8.0 (0.73)	1.4 (0.13)
IGPS 112276	0°	10.2	5.2 (0.51)	7.3 (0.72)	–

Systematic description

Morphological terminology of the ammonoid conch basically follows Korn (2010) and the classification of taxonomic ranks higher than genus follows Furnish *et al*. (2009). The following abbreviations are used in the descriptions: *D* = shell diameter, *H* = height of whorl, *W* = width of whorl, *UD* = diameter of umbilicus.

Order Goniatitida Hyatt, 1884
Superfamily Agathiceratoidea von Arthaber, 1911
Family Agathiceratidae von Arthaber, 1911
Genus ***Agathiceras*** Gemmellaro, 1887

Type species.—*Agathiceras suessi* Gemmellaro, 1887.

Agathiceras spp.

Figures 3.1–3.7

Material examined.—Fourteen specimens: IGPS coll. cat. nos. 112269–112282.

Descriptive remarks.—Small specimens, the largest one attains 23 mm in diameter, are examined. They are thickly discoidal to thinly pachyconic, involute and weakly compressed to weakly depressed. The venter is rounded without remarkable ventral shoulders. The flanks are broadly convex and converge to the venter. The maximum width is near the umbilical shoulder. The umbilicus is deep, and almost closed or very narrow, with rounded umbilical shoulder. There are prominent spiral lirae on the shell surface. No constrictions are observed. Suture line (internal) is only observed in a small specimen as moulds on the surface of the preceding whorl (*D* = 7 mm). It consists of a V-shaped dorsal lobe and a V-shaped lateral lobe (Figure 3.7). The second lateral saddle is gentle and wide.

Dimensions and ratios of shell are shown in Table 1. Specimens having rather large diameter (*D* ≥ 15 mm) include at least two types: one has pachyconic conch shape (*W*/*D* = 0.72–0.73: IGPS coll. cat. nos. 112269 and 112270) and the other has thickly discoidal shape (*W*/*D* = 0.56–0.58: IGPS coll. cat. nos. 112271–112273). Also in the discoidal one (Figure 4.4: IGPS coll. cat. no. 112273), inner volutions are thinly pachyconic (*W*/*D* = 0.65 at *D* = *ca*. 13.0). Other small specimens (*D* ≤ 11 mm: IGPS coll. cat. nos. 112274–112282) all have pachyconic shell form.

Based on the shell shape and shell ornamentation, it is highly probable that these Miharanoro specimens belong to the genus *Agathiceras* Gemmellaro, 1887. But the specific identification is difficult due to the poor state of preservation.

Superfamily Thalassoceratoidea Hyatt, 1900
Family Bisatoceratidae Miller and Furnish, in Miller, Furnish, and Schindewolf, 1957
Genus ***Neoglaphyrites*** Ruzhentsev, 1938

Type species.—*Glaphyrites* (*Neoglaphyrites*) *bashkiricus* Ruzhentsev, 1938.

Neoglaphyrites sp.

Figures 3.8–3.9

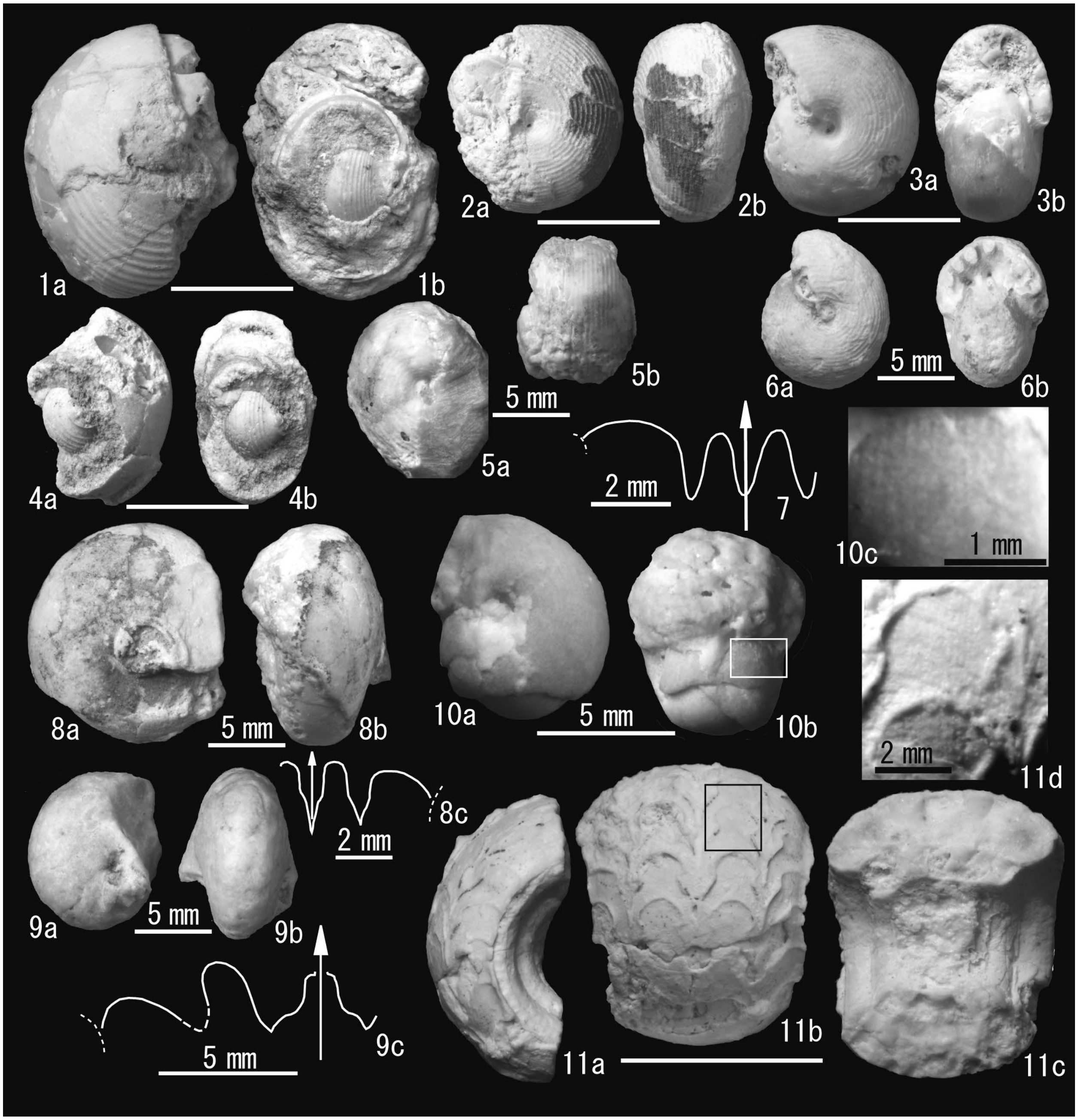

Figure 3. *Agathiceras*, *Neoglaphyrites*, Adrianitidae gen. and sp. indet. and *Somoholites* from the Uyamanoro Formation of the Taishaku Limestone. **1–7,** *Agathiceras* sp.; 1, IGPS coll. cat. no. 112269, lateral view (1a) and transversal section (1b); 2, IGPS coll. cat. no. 112271, lateral (2a) and ventral (2b) views; 3, IGPS coll. cat. no. 112272, lateral (3a) and ventral (3b) views; 4, IGPS coll. cat. no. 112273, lateral view (4a) and transversal section (4b); 5, IGPS coll. cat. no. 112274, lateral (5a) and ventral (5b) views; 6, IGPS coll. cat. no. 112275, lateral (6a) and ventral (6b) views; 7, IGPS coll. cat. no. 112276, internal suture line; **8, 9,** *Neoglaphyrites* sp.; 8, IGPS coll. cat. no. 112283, lateral (8a) and ventral (8b) views and internal suture line (8c); 9, IGPS coll. cat. no. 112284, lateral (9a) and ventral (9b) views and external suture line (9c); **10,** Adrianitidae gen. and sp. indet, IGPS coll. cat. no. 112285, lateral (10a) and ventral (10b) views, and enlarged photograph of the shell surface (10c: the position is shown by a frame in figure 10b); **11,** *Somoholites* sp., IGPS coll. cat. no. 112286, lateral (11a) and ventral (11b: moulds of the internal suture lines are on the preceding shell surface) views, transversal section (11c) and enlarged photograph of the shell surface (11d: the position is shown by a frame in figure 11b). Fine dotted arc line in the suture line drawing denotes the position of umbilical shoulder. Scale bars are 1 cm, unless otherwise stated.

Material examined.—Two specimens: IGPS coll. cat. nos. 112283 and 112284.

Descriptive remarks.—Two small specimens are at hand. The larger specimen (112283) attains a diameter of *ca*. 14 mm, and its corresponding height (*H*/*D*), width (*W*/*D*) and umbilical diameter (*UD*/*D*) are 8.0 (0.57), 9.4 (0.67) and *ca*. 3 mm (0.21) , respectively. Dimensions of the smaller specimen (112284) are D = 12.5, H = 6.6 (*H*/*D*: 0.53), W = 6.4 (*W*/*D*: 0.51) and UD = 1? (*UD*/*D*: 0.08?), respectively. The conch is thickly discoidal to thinly pachyconic, involute to subinvolute and weakly depressed. The flanks converge to the rounded venter, without remarkable ventral shoulders. The maximum width is near the umbilical shoulder. The umbilicus is very small with an angular or sharply rounded umbilical shoulder and steep wall. No visible ornamentation is observed on the shell surface.

The external suture, preserved in a smaller specimen (at a diameter of 12 mm) is characterized by a broad ventral lobe subdivided into two bluntly pointed asymmetrical prongs by a wide and moderately high (about two-thirds the height of the first lateral saddle) median saddle (Figure 3.9c). The widths of the prongs of the ventral lobe are slightly wider than the V-shaped first lateral lobe. The rounded, high first lateral saddle is inclined toward the umbilicus. The internal suture lines are observed in a larger specimen as moulds on the surface of the preceding whorl (D = 14 mm). The dorsal lobe is deep and lanceolated (Figure 3.8c). The first internal lateral lobe is also lanceolated.

Based on the shell morphology and the shape of the suture line, it is highly probable that the Miharanoro specimens belong to the genus *Neoglaphyrites* Ruzhentsev, 1938, but the specific identification is difficult due to their poor state of preservation.

Superfamily Adrianitoidea Schindewolf, 1931
Family Adrianitidae Schindewolf, 1931
Subfamily Adrianitinae Schindewolf, 1931

Adrianitidae gen. and sp. indet.

Figure 3.10

Material examined.—One specimen: IGPS coll. cat. no. 112285.

Descriptive remarks.—One small specimen is examined. The conch is thickly pachyconic, subinvolute and weakly depressed. The shell diameter at the preserved end is *ca*. 8 mm, and corresponding height (*H*/*D*), width (*W*/*D*) and umbilical diameter (*UD*/*D*) are about 4.5 (0.56), 6.2 (0.76) and 1.5 mm (0.19), respectively. The venter is broadly rounded without ventral shoulders. The flanks are rounded and the maximum shell width is at the center of the flank. The umbilicus is small with rounded umbilical shoulder. The shell surface is ornamented with fine spiral lirae and fine, more or less indistinct radial lirae (Figure 3.10c).

Based on the shell shape and shell ornamentation, the present species is thought to belong to some genera of the subfamily Adrianitinae, among which the genus *Crimites* Tumanskaya, 1937 is the most likely candidate. But the further consideration is difficult because the specimen is immature and no suture line is preserved.

Superfamily Shumarditoidea Plummer and Scott, 1937
Family Somoholitidae Ruzhentsev, 1938
Genus ***Somoholites*** Ruzhentsev, 1938

Type species.—*Gastrioceras beluensis* Haniel, 1915.

Somoholites sp.

Figure 3.11

Material examined.—One fragmental specimen: IGPS coll. cat. no. 112286.

Descriptive remarks.—A fragmental phragmocone, about 2/5 of two volutions, is at hand. The shell is pachyconic, subevolute and strongly depressed. The estimated diameter of the conch reaches 21 mm, and the corresponding height, width, and umbilical diameter are *ca*. 7 (*H*/*D* = 0.33), 16.5 (*W*/*D* = 0.76) and 9 mm (*UD*/*D* = 0.43), respectively. Fine longitudinal and transverse lirae are preserved on the shell surface (Figure 3.11d). The latter form a slight ventro-lateral sinus. A constriction parallel to the transverse lirae is observed. The internal sutures are preserved as moulds on the surface of the preceding whorl. It consists of deep lanceolate dorsal and lateral lobes, both having pouches on the upper sides (Figure 3.11b).

Based on the shell morphology and the shape of the internal suture line, it is highly probable that the Miharanoro specimen belongs to the genus *Somoholites* Ruzhentsev, 1938, but the specific identification is difficult due to the poor state of preservation.

Family Shumarditidae Plummer and Scott, 1937
Genus ***Shumardites*** Smith, 1903

Type species.—*Shumardites cuyleri* Plummer and Scott, 1937.

Shumardites umbilicatus sp. nov.

Figures 4.1–4.2

Etymology.—The specific epithet refers to the evolute shell shape of the species.

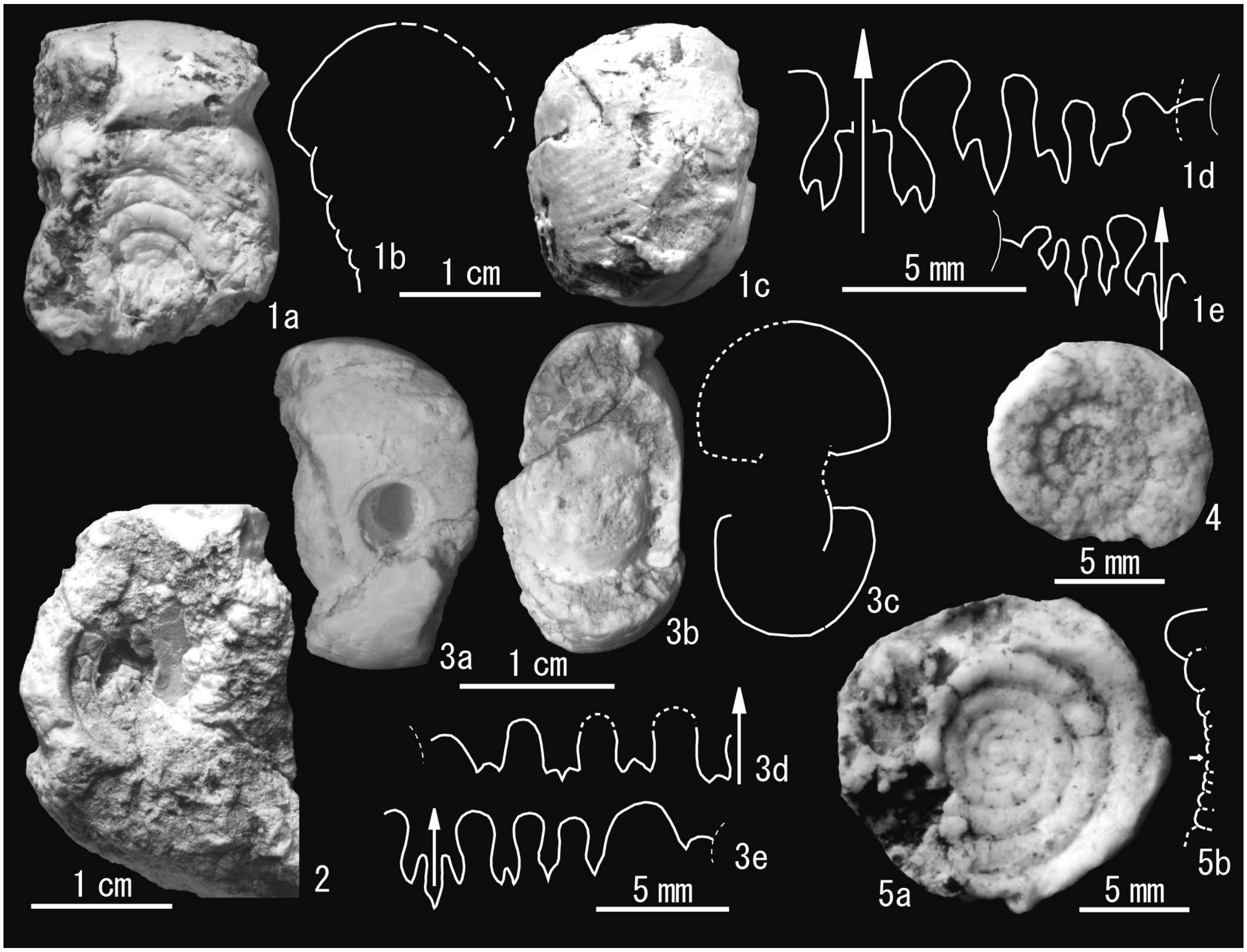

Figure 4. *Shumardites*, *Vidrioceras*, and *Eoasianites*? from the Uyamanoro Formation of the Taishaku Limestone. **1, 2,** *Shumardites umbilicatus* sp. nov.; 1, IGPS coll. cat. no. 112287 (holotype), lateral view (1a), cross section (1b), ventral view (1c) , and external (1d) and internal (1e) suture lines; 2, IGPS coll. cat. no. 112288 (paratype), lateral view; **3,** *Vidrioceras ellipticum* sp. nov., IGPS coll. cat. no. 112289 (holotype), lateral (3a) and ventral (3b) views, cross section (3c), and external (3d) and internal (3e) suture lines; **4, 5,** *Eoasianites*? sp.; 4, IGPS coll. cat. no. 112311, lateral view; 5, IGPS coll. cat. no. 112312, lateral view (5a) and cross section (5b). Fine dotted arc line and fine solid arc line in the suture line drawing denote the position of umbilical shoulder and umbilical margin, respectively.

Material examined.—Two specimens: IGPS coll. cat. no. 112287 (holotype) and IGPS coll. cat. no. 112288 (paratype).

Diagnosis.—A species of *Shumardites* with thinly discoidal, evolute shell. The dorsal prong of the internal lateral lobe is deep and lanceolated.

Description.—Two fragmental specimens, one of which is partly crushed, are examined. The holotype specimen (IGPS coll. cat. no. 112287) is a phragmocone, the diameter of which attains more than 30 mm. The conch is thinly discoidal and evolute, with weakly depressed shell. The venter is rounded without remarkable ventral shoulders. The umbilical wall is rounded by a rounded umbilical shoulder. The maximum width is at the umbilical shoulder. At the diameter of *ca*. 21.5 mm, the corresponding height, width and umbilical diameter are, *ca*. 7 (H/D = 0.33), 8–8.5 (W/D = 0.37–0.39) and *ca*. 11 mm (UD/D = 0.51), respectively. On the shell surface of the preserved last whorl, coarse straight transverse ribs run from the umbilical shoulder to the venter and across the venter without sinus (Figure 4.1c). The paratype specimen attains 25 mm in diameter. It is also thinly discoidal and evolute, with transverse ribs on the shell surface.

The suture is typical type of the genus *Shumardites*, but rather complex. The large ventral love significantly narrows upward. It is divided into two bifid prongs by a relatively wide and moderately high median saddle (about three-fifth the height of the first lateral saddle). The wide external lateral lobe is divided into three branches. The branches are all asymmetrically bifid. The ventral branch is larger and deeper than the central one, and the dorsal one is shallow and wide. The umbilical lobe is shallow and V-shaped. The internal sutures are preserved as moulds on the surface of the preceding whorl. The dorsal lobe is deep and trifid. The internal lateral lobe is wide and divided into three branches. The central branch of it is deepest and lanceolated. The dorsal prong is also lanceolated and deep with a small pouch on the dorsal side. The secondary saddle, which divides the dorsal and central branches, is higher than the saddle that divides the central and ventral branches.

Comparison.—Although the examined specimens are fragmental, *Shumardites umbilicatus* sp. nov. from Miharanoro is easily distinguished from other species of *Shumardites* by its thinly discoidal and evolute shell form. It is also unique by having a rather complex suture line characterized by a deep, lanceolate dorsal branch of the internal lateral lobe with high secondary saddle that divides it from the central one.

Superfamily Cycloloboidea Zittel, 1895
Family Vidrioceratidae Plummer and Scott, 1937
Genus ***Vidrioceras*** Böse, 1919

Type species.—*Vidrioceras uddeni* Böse, 1919.

Vidrioceras ellipticum sp. nov.

Figures 4.3a–4.3e

Etymology.—Named after its elliptical shell form.

Material examined.—One specimen: IGPS coll. cat. no. 112289 (holotype).

Diagnosis.—A species of *Vidrioceras* with thickly discoidal to thinly pachyconic, elliptical shell cross section.

Description.—A small fragmental phragmocone, partly displaced by a small oblique crack, is examined. The conch is thickly discoidal to thinly pachyconic, subinvolute and weakly depressed. The venter is broadly rounded without visible ventral shoulders. The flanks converge to the venter and the maximum shell width is near the umbilical shoulder. The umbilicus is deep, with steep umbilical wall and abruptly rounded umbilical shoulder. The shell surface seems to be smooth. The maximum diameter is *ca*. 21 mm, and its corresponding height (H/D), width (W/D) and umbilical diameter (UD/D) are *ca*. 9 (0.42), 13 (estimated) (0.62) and 3.5 mm (0.17), respectively.

The external suture is partly observed at the preserved end. The broad ventral lobe is subdivided into two symmetrically bifid prongs by a moderately high median saddle (Figure 4.3d). There are three lateral lobes. The first lateral lobe is symmetrically bifid, the second is trifid and the third is bifid. The depths of lateral lobes are nearly equal and slightly shallower than the ventral lobe. The external suture on the umbilical shoulder is not preserved. The internal sutures are preserved as moulds on the surface of the preceding whorl. The large and deep dorsal lobe is strongly trifid (Figure 4.3e). The prongs are lanceolated and the central one is deepest. There are four internal lateral lobes. The first three are deep and diminish slightly their depth toward the umbilicus. The first one is bifid, and the second and third are pointed. The fourth lobe, divided from the third by a wide rounded saddle, is small.

Comparison.—The single fragmental specimen is examined. But *Vidrioceras ellipticum* sp. nov. is clearly distinguished from other species of *Vidrioceras* by having a thickly discoidal to thinly pachyconic shell with a broadly rounded venter. The H/D ratio of the present species is 0.62, while those of the other species of *Vidrioceras* are larger than 0.8, except for that of *Vidrioceras timorense* (Haniel) (Schindewolf, 1931, p. 201: = *Popanoceras timorense* form. α Haniel, 1915, p. 93, text-fig. 25, pl. 51 (6), figs. 4 and 8) from the Artinskian of Timor and *Vidrioceras zacharovi* (Popov) (Popov, 1992, p. 56, text-fig. 1a, 1b; pl. 1, fig. 5, as *Hypershumardites*: = *Vidrioceras conlini* Miller and Downs: Zakharov, 1978, p. 52, text-fig. 1.9, 19a) from the upper Gzhelian of Uzbekistan. *V. timorense* has nearly the same ratio of H/D (*ca*. 0.62) as the present species, but is different in having an almost closed umbilicus. *V. zacharovi* also has nearly the same H/D ratio (0.60 at D = 45 mm), but at D = 20.9 (nearly the same size as the present new species) its H/D ratio is 0.86 and considerably larger than the new species. *V. wanneri* Schindewolf (Schindewolf, 1931, p. 201: = *Popanoceras tridens* form. α Haniel, 1915, p. 103, text-fig. 32, pl. 52 (7) fig. 3–4) from the Artinskian of Timor differs in having smaller ratio of H/D (*ca*. 0.51) and almost closed umbilicus.

Superfamily Marathonitoidea Ruzhentsev, 1938
Family Marathonitidae Ruzhentsev, 1938
Genus ***Almites*** Tumanskaya, 1941

Type species.—*Perrinites Brouweri* Smith, 1927.

Almites hayasakai sp. nov.

Figures 5.1–5.10

Marathonites cf. *jpsmithi* Bose: Ehiro, Nishikawa and Nishikawa, 2014, p. 58, figs. 5.1–5.4.

Etymology.—The specific epithet honors Ichiro Hayasaka who studied the Paleozoic ammonoids of Japan.

Material examined.—Twenty-one specimens: IGPS coll. cat. no. 112290 (holotype) and IGPS coll. cat. nos. 112291–112310 (paratypes).

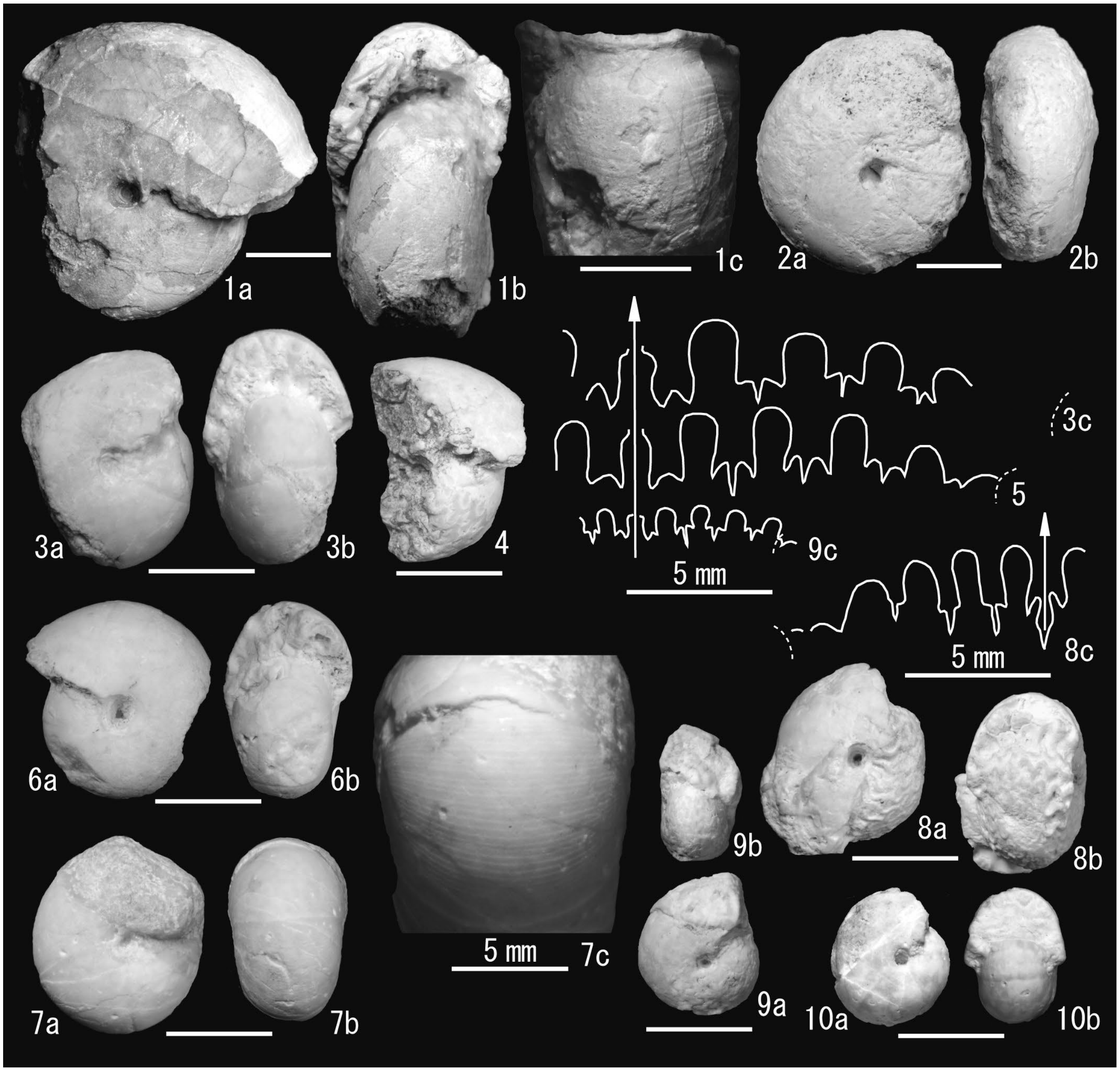

Figure 5. *Almites hayasakai* sp. nov. from the Uyamanoro Formation of the Taishaku Limestone. **1,** IGPS coll. cat. no. 112290 (holotype), lateral (1a) and ventral (1b) views, and close up of the ventral part (1c); **2,** IGPS coll. cat. no. 112291 (paratype), lateral (2a) and ventral (2b) views; **3,** IGPS coll. cat. no. 112292 (paratype), lateral (3a) and ventral (3b) views, and external suture line (3c); **4,** IGPS coll. cat. no. 112296 (paratype), lateral view; **5,** IGPS coll. cat. no. 111398 (as *Marathonites* cf. *jpsmithi*), external suture line; **6,** IGPS coll. cat. no. 112293 (paratype), lateral (6a) and ventral (6b) views; **7,** IGPS coll. cat. no. 112294 (paratype), lateral (7a) and ventral (7b) views, and close up of the ventral part (7c); **8,** IGPS coll. cat. no. 112295 (paratype), lateral (8a) and ventral (8b) views, and internal suture line (8c); **9,** IGPS coll. cat. no. 112297 (paratype), lateral (9a) and ventral (9b) views, and external suture line (9c); **10,** IGPS coll. cat. no. 112298 (paratype), lateral (10a) and ventral (10b) views. Fine dotted arc line in the suture line drawing denotes the position of umbilical shoulder. Scale bars are 1 cm, unless otherwise stated.

Diagnosis.—A species of *Almites* with small umbilicus and very wide ventral lobe.

Description.—The conch is thinly pachyconic in small specimens (*D* smaller than 25 mm) and thickly discoidal in larger ones (*D* larger than 25 mm). It is involute and weakly compressed to weakly depressed. The venter is rounded without remarkable ventral shoulders. The flanks converge toward the venter and the maximum shell width is near the umbilical shoulder. The umbilicus is small with steep umbilical wall and sharply rounded umbili-

Table 2. Dimensions (in mm) and ratios of *Almites hayasakai* sp. nov. from the Uyamanoro Formation. Measurements with asterisk are re-measured. For abbreviations, see Table 1.

Catalog no.	α	*D*	*H* (*H*/*D*)	*W* (*W*/*D*)	*UD* (*UD*/*D*)
IGPS 112290	90˚	35.1	19.1 (0.54)	*ca*. 19.5 (0.56)	2.4 (0.07)
IGPS 111399*	0˚	29.3	15.9 (0.54)	*ca*. 17.0 (0.58)	*ca*. 3.0 (0.10)
IGPS 112291	0˚	29.2	16.6 (0.57)	*ca*. 15.0 (0.51)	2.0 (0.07)
IGPS 112292	180˚	20.1	10.1 (0.50)	12.5 (0.62)	1.7 (0.09)
IGPS 112293	60˚	18.6	9.6 (0.52)	*ca*. 12.0 (0.65)	1.9 (0.10)
IGPS 112294	50˚	16.5	8.7 (0.53)	10.1 (0.61)	1.5? (0.09)
IGPS 112295	0˚	16.5	8.5 (0.52)	10.7 (0.65)	1.5? (0.09)
IGPS 112297	0˚	12.7	6.8 (0.54)	6.8 (0.54)	?
IGPS 112298	0˚	13.3	7.8 (0.59)	9.5 (0.71)	?
IGPS 112299	0˚	16.8	10.2 (0.61)	10.6 (0.63)	?
	90˚	14.7	7.1 (0.48)	9.4 (0.64)	?

cal shoulder. The diameter of the largest specimen attains 35 mm. The ratios *H*/*D*, *W*/*D* and *UD*/*D* are 0.48–0.61 (average 0.54, n = 11), 0.51–0.71 (average 0.61, n = 11) and 0.07–0.10 (average 0.09, n = 7), respectively (Table 2).

Shell surface is covered by slightly convex transverse lirae (Figure 5.1c, 5.7c), which extend from umbilical shoulder and across the venter without sinus. Four weak constrictions, parallel to the lirae, present on the inner mould of the shell.

The external suture consists of a ventral lobe and four lateral lobes. The ventral lobe is considerably wide (about 2.5 times wider than the first lateral lobe) and is divided into two bifid prongs by a high (about 3/4 height of the ventrolateral saddle) median saddle. The first to third lateral lobes have nearly the same width and their bases are all trifid distinctly. The fourth lateral lobe is shallow and bifid. The dorsal lobe is narrow, deep and trifid, and the central one of the prongs is deepest. The first to third internal lateral lobes are all trifid, although the division of the third is incomplete. The fourth and fifth? internal lateral lobes are simple.

Comparison.—*Marathonites* cf. *jpsmithi* Bose described by Ehiro *et al*. (2014, p. 58, figs. 5.1–5.4) collected from a slightly higher horizon in the Miharanoro locality has the same shell shape and external suture line, and is considered to be conspecific to the present species. *Almites hayasakai* sp. nov. is easily distinguished by the other species of *Almites* in having an extremely wide ventral lobe. As to the shell form, *Almites multisulcatus* Bogoslovskaya, 1978 from the Asselian of Pamirs (Bogoslovskaya, 1978, p. 56, pl. 5, figs. 1, 2) and South China (Zhou, 1987, p. 140, pl. 4, figs. 4, 5 as *Marathonites* sp.: Zhou, 2017, p. 65, figs. 40. 1–15, 41. 2–6) is somewhat similar to the present species, but differs in having a larger umbilicus (*UD*/*D* = 0.18–0.19) and more constrictions. *A. leveni* Leonova (Leonova in Leven *et al*., 1992, p. 159, pl. 32, fig. 7) from the Sakmarian of Pamirs has a *UD*/*D* ratio of 0.13 close to the present species, but the former species is less well preserved and precise comparison is difficult.

Superfamily Neoicoceratoidea Hyatt, 1900
Family Neoicoceratidae Hyatt, 1900
Genus ***Eoasianites*** Ruzhentsev, 1933

Type species.—*Eoasianites subhanieli* Ruzhentsev, 1933.

Eoasianites? sp.

Figures 4.4–4.5

Material examined.—Two specimens: IGPS coll. cat. nos. 112311 and 112312.

Descriptive remarks.—Two small fragmental specimens, 7.5 and 4.5 mm in diameter, are at hand. The conch is extremely discoidal, very evolute and weakly depressed to moderately depressed. At the shell diameter of about 7.5 mm, corresponding height (*H*/*D*), width (*W*/*D*) and umbilical diameter (*UD*/*D*) are about 1.5 (0.2), 2.2 (0.29) and 5.2 (0.69), respectively. At the preserved end, the venter seems to be slightly convex with rounded ventral shoulders (Figure 4.5b). The umbilical shoulder is broadly rounded with moderately inclined umbilical wall. No suture line is observed.

Based on the shell morphology the two specimens from Miharanoro are probably immature specimens of the genus *Eoasianites* Ruzhentsev, 1933, but there remains a question about the generic assignment due to the poor state of preservation.

Order Prolecanitida Miller and Furnish, 1954
Superfamily Prolecanitoidea Hyatt, 1884
Family Daraelitidae Chernov, 1907
Genus ***Boesites*** Miller and Furnish, 1940

Type species.—*Daraelites texanus* Böse, 1919.

Boesites biconcavus sp. nov.

Figures 6.1–6.8

Etymology.—Named after its biconcave shape of the first lateral lobe.

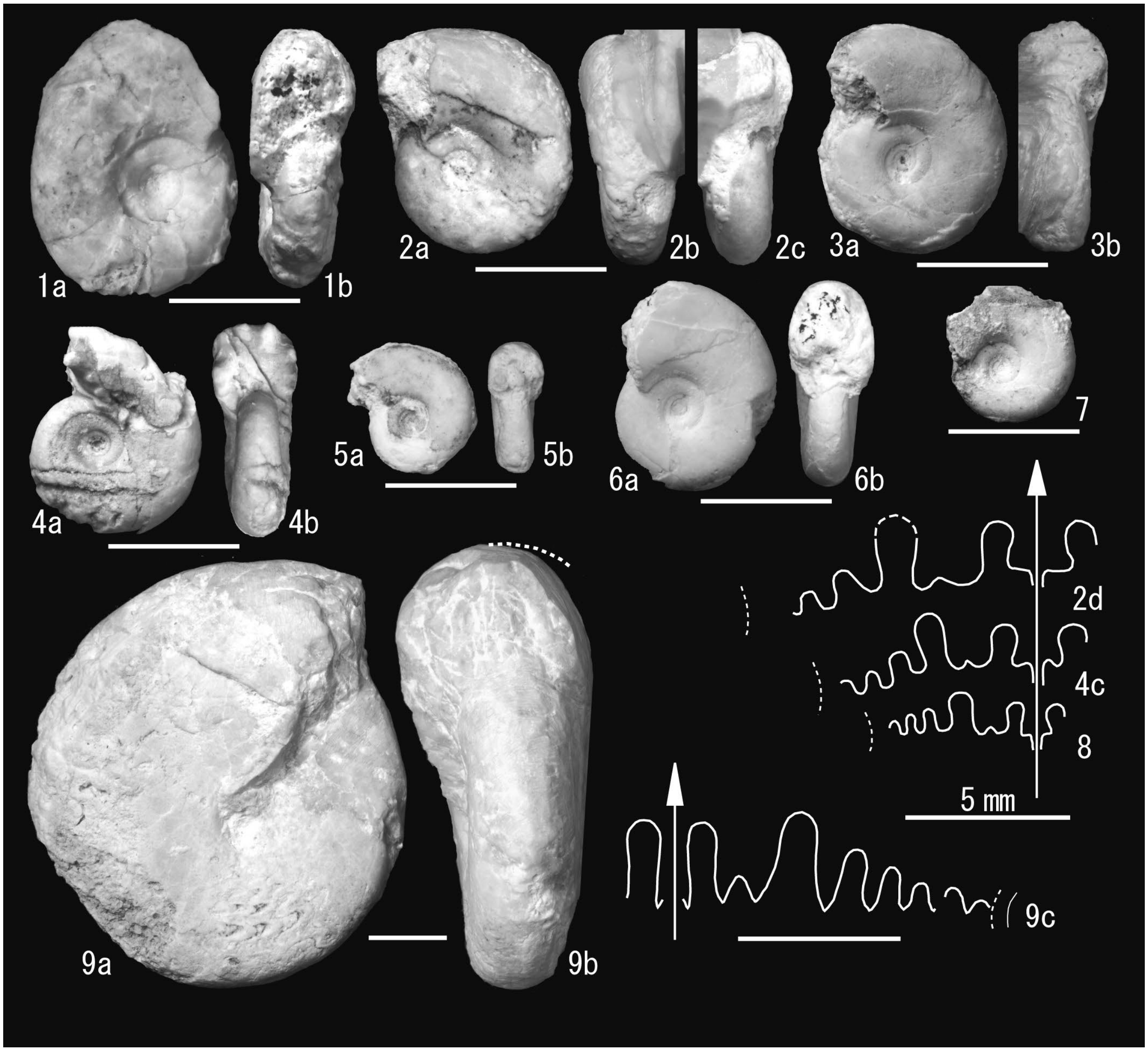

Figure 6. *Boesites* and *Metapronorites* from the Uyamanoro Formation of the Taishaku Limestone. **1**–**8,** *Boesites biconcavus* sp. nov.; 1, IGPS coll. cat. no. 112311 (paratype), lateral (1a) and ventral (1b) views; 2, IGPS coll. cat. no. 112314 (paratype), lateral (2a) and ventral (2b and 2c) views, and external suture line (2d); 3, IGPS coll. cat. no. 112315 (paratype), lateral (3a) and ventral (3b) views; 4, IGPS coll. cat. no. 112316 (holotype), lateral (4a) and ventral (4b) views, and external suture line (4c); 5, IGPS coll. cat. no. 112318 (paratype), lateral (5a) and ventral (5b) views; 6, IGPS coll. cat. no. 112317 (paratype), lateral (6a) and ventral (6b) views; 7, IGPS coll. cat. no. 112319 (paratype), lateral view; 8, IGPS coll. cat. no. 112321 (paratype), external suture line; **9,** *Metapronorites timorensis* (Haniel): IGPS coll. cat. no. 112324, lateral (9a) and ventral (9b) views, and external suture line (9c). Fine dotted arc line and fine solid arc line in the suture line drawing denote the position of umbilical shoulder and umbilical margin, respectively. Scale bars are 1 cm, unless otherwise stated.

Material examined.—Eleven specimens: IGPS coll. cat. no. 112316 (holotype) and IGPS coll. cat. nos. 112313–112315, 112317–112323 (paratypes).

Diagnosis.—A species of *Boesites* with thinly discoidal, subinvolute to subevolute, subelliptical shell cross-section. The base of the wide first lateral lobe is biconcave.

Description.—The conch is small and the largest specimen is 21.6 mm in diameter. It is thinly discoidal and subinvolute to subevolute, and its cross section is weakly compressed. The venter is rounded and the conch cross-section is elliptical. The flanks are subparallel, broadly convex, without remarkable ventral and umbilical shoulders. The maximum conch width is near the middle of the flank. The *H*/*D*, *W*/*D* and *UD*/*D* are 0.42–0.47 (aver-

Table 3. Dimensions (in mm) and ratios of *Boesites biconcavus* sp. nov. from the Uyamanoro Formation. For abbreviations, see Table 1.

Catalog no.	α	*D*	*H* (*H*/*D*)	*W* (*W*/*D*)	*UD* (*UD*/*D*)
IGPS 112313	0°	21.2	9.7 (0.46)	7.8 (0.37)	6.3 (0.29)
IGPS 112314	0°	18.4	7.8 (0.42)	*ca*. 7.5 (0.41)	4.8 (0.26)
IGPS 112315	0°	17.4	8.1 (0.47)	6.9 (0.40)	4.6 (0.26)
IGPS 112316	90°	13.3	6.1 (0.46)	5.5 (0.34)	3.9 (0.29)
IGPS 112317	0°	16.2	7.2 (0.44)	6.0 (0.37)	3.9 (0.24)
IGPS 112318	0°	10.4	4.5 (0.43)	4.0 (0.38)	2.8 (0.27)
IGPS 112319	90°	9.9	4.7 (0.47)	4.0 (0.40)	2.4 (0.24)
IGPS 112320	0°	8.5	3.8 (0.45)	3.3 (0.39)	2.3 (0.27)
IGPS 112321	60°	14.0	6.3 (0.45)	?	4.0 (0.29)
IGPS 112322	0°	10.2	4.3 (0.42)	3.6 (0.35)	2.7 (0.26)

age 0.45, n = 10), 0.35–0.41 (average 0.38, n = 9) and 0.24–0.29 (average 0.27, n = 10), respectively (Table 3). The shell surface is smooth and there are no constrictions.

The ventral lobe is trifid and slightly narrows upward. The central branch is narrow and deep, while the branches of both sides are shallow and rounded. Four lateral lobes are observed. The first lateral lobe is very wide and the width is the same as or slightly wider than the ventral one. Its depth is nearly the same as or somewhat shallower than those of the side branches of the ventral lobe. The base of the first lateral lobe, probably without denticulation, is biconcave, consisting of two circular arcs joining at a low, crest-like protrusion. The remaining lateral lobes, having rounded base, are small and become smaller toward the umbilicus. The umbilical margin of the external suture line is not preserved, and there should be one or two additional lobes. All saddles have rounded crests. The second lateral saddle is considerably high.

Comparison.—*Boesites biconcavus* sp. nov. is clearly distinguished from all other species of *Boesites* in having a unique biconcave base of the first lateral lobe. As for the shell morphology, *Boesites aktubensis* Bogoslovskaya and Popov (Bogoslovskaya and Popov, 1986, p. 125, text-fig. 16a, pl. 26, figs. 1, 2; Leonova in Bogoslovskaya *et al*., 1995, p. 295, figs. 4.3–4.6, 7.2) from the Asselian of Kazakhstan is similar to the present species, but has slightly smaller umbilicus (*UD*/*D* = 0.24). Another Asselian species *Boesites intercalaris* Ruzhentsev (Ruzhentsev, 1978, p. 39, pl. 3, fig. 1) from Pamir and South China (Zhou, 1987, p. 136, pl. 1, figs. 9, 10, pl. 2, figs. 1–10; Zhou, 2017, p. 21, figs. 10.7–10.12, 11.1–11.4) also somewhat resembles the present species, but the former differs from by having slightly smaller *W*/*D* and larger *UD*/*D* ratios.

Superfamily Medlicottitoidea Karpinskii, 1889
Family Pronoritidae Frech, 1901
Subfamily Pronoritinae Frech, 1901
Genus ***Metapronorites*** Librovich, 1938

Type species.—*Pronorites timorensis* Haniel, 1915.

Metapronorites timorensis (Haniel)

Figures 6.9a–6.9c

Pronorites uralensis var. *timorensis* Haniel, 1915, p. 25, pl. 46, figs. 1–5, text-fig. 2.
Pronorites timorensis Haniel. Smith, 1927, p. 13, pl. 10, figs. 1–15; Böhmers, 1936, p. 14, fig. 4.
Metapronorites timorensis (Haniel). Librovich, 1938, p. 82; Ruzhentsev, 1949, pl. 2, figs. 9–13, text-fig. 3; Nassichuk, 1975, text-fig. 22; Ruzhentsev, 1978, p. 40, pl. 3, figs. 2–3; Zhou, 1987, p. 134, pl. 2, figs. 1–8, pl. 2, figs. 11–12, text-fig. 2; Zhou, 2017, p. 22, figs. 12.1–12.18, 13.1–13.2.

Material examined.—One specimen: IGPS coll. cat. no. 112324.

Description.—A moderate-sized specimen consists of a phragmocone and living chamber. The right side of the conch is mostly missing. The living chamber occupies about a half of the last volution. The conch is thinly to thickly discoidal, involute and weakly depressed. The conch attains about 55 mm in diameter, and corresponding height, width (estimated) and umbilical diameter are, 28.5 (*H*/*D* = 0.52), 25 (*W*/*D* = 0.45) and *ca*. 8 mm (*UD*/*D* = 0.15), respectively. At the adoral end of the phragmocone (*D* = *ca*. 45 mm), the width is estimated to be *ca*. 15 mm and the conch is extremely to thinly discoidal (*W*/*D* = 0.33). The venter is rounded with rounded ventral shoulders. The flanks are subparallel on the living chamber and diverge to the umbilicus, and the maximum width is at about two-third of the umbilical shoulder. On the phragmocone, on the other hand, the flanks are nearly flat and parallel.

The suture consists of a deep and narrow, bifid ventral lobe and six lateral lobes. The bifid first lateral lobe is considerably wide and deep (slightly shallower than the ventral lobe). The second to sixth lateral lobes are narrow; their bases are pointed, and decrease in size toward the umbilicus. It seems that there are two additional lobes on the umbilical shoulder toward the umbilical wall.

Discussion.—Although the Taishaku specimen of *Metapronorites* is not well preserved and one side of the flanks is almost missing, its estimated shell shape and suture line are very similar to those of the type species *Metapronorites timorensis* (Haniel, 1915) known from the

Asselian–Artinskian of Timor, South China (Guangxi), South Urals (Kazakhstan) and Pamirs (Tajikistan). The living chamber of the present specimen has a somewhat wider conch (W/D = 0.45), but at the adoral end of the phragmocone the conch has nearly the same W/D ratio (0.33) as those of the Timor specimens (Haniel, 1915; Smith, 1927), South Urals and Pamir specimens (Ruzhentsev, 1949, 1978) and South China specimens (Zhou, 1987, 2017). Specimens of *M*. cf. *timorensis* collected near the present locality of Miharanoro, but from a slightly higher horizon (Ehiro *et al*., 2014), are small, but resemble the present specimen in their shapes of shell and suture line.

Discussion

Composition and age of the ammonoid fauna

The new ammonoid fauna from Miharanoro comprises *Agathiceras* sp., *Neoglaphyrites* sp., Adrianitidae gen. and sp. indet., *Somoholites* sp., *Shumardites umbilicatus* sp. nov., *Vidrioceras ellipticum* sp. nov., *Almites hayasakai* sp. nov., *Eoasianites*? sp. (Goniatitida), *Boesites biconcavus* sp. nov. and *Metapronorites timorensis* (Haniel) (Prolecanitida). They are collected from the *Sphaeroschwagerina fusiformis* fusulinoidean Zone, which occupies the lower part of the Asselian. A previously reported Miharanoro ammonoid fauna (Ehiro *et al*., 2014), collected from slightly higher horizon belongs to the *Pseudoschwagerina miharanoensis* Zone (late Asselian), consists of 8 species belonging to 7 genera: *Agathiceras* sp., *Neoglaphyrites discoidalis* Ehiro, Nishikawa and Nishikawa, *Emilites* cf. *prosperus* Ruzhentsev, *Somoholites miharanoroensis* Ehiro, Nishikawa and Nishikawa, *Almites hayasakai* sp. nov. (originally described as *Marathonites* cf. *jpsmithi* Böse), *Eoasianites* cf. *subhanieli* Ruzhentsev, *Metapronorites* cf. *timorensis* (Haniel) and *Metapronorites* sp. They belong to the order Goniatitida, except for *Metapronorites* (Prolecanitida). In this upper Asselian fauna *Agathiceras* and *Metapronorites* are dominant. On the other hand, the present lower Asselian ammonoid fauna differs from the previous one by the dominant *Almites* and *Boesites* specimens, by containing the genera *Shumardites* and *Vidrioceras*, and by lacking the genus *Emilites*.

Some discussion is needed concerning the age of the present ammonoid fauna, because the known stratigraphic distribution data (based on Korn and Ilg, 2007; Kullmann *et al*., 2007, and Furnish *et al*., 2009) of the genera is partly inconsistent with the age of the fusulinoidean fauna (early Asselian). Except for questionable *Eoasianites* and Adrianitidae gen. and sp. indet., the hitherto known ranges of the eight ammonoid genera are from the Bashkirian to Wordian, with an overlapped period, the Gzhelian, not Asselian (Figure 7). The most severe age control factor is the genus *Shumardites*, the known stratigraphic occurrence of which is restricted to the Kasimovian to Gzhelian. The Miharanoro species of *Shumardites* is, however, a new species and clearly distinguished from the Carboniferous species in shell shape. Moreover, its suture line, especially the internal one, is more advanced than those of previously known, suggesting the age of the new species is post Gzhelian. Another problem is the stratigraphic range of the genus *Vidrioceras*. Leonova (2018) contradicted Furnish *et al*. (2009), who considered the genus ranges from the Gzhelian to the Artinskian, and stressed that the genus *Vidrioceras* is the index of the uppermost Carboniferous. However, she did not show any evidence. As compared to the Artinskian *Vidrioceras* species, *V. timorense* (Haniel) and *V. wanneri* Schindewolf, with *V. ellipticum* sp. nov. in the systematic section, we follow Schindewolf (1931) and consider that these two Artinskian species belong to the genus *Vidrioceras*.

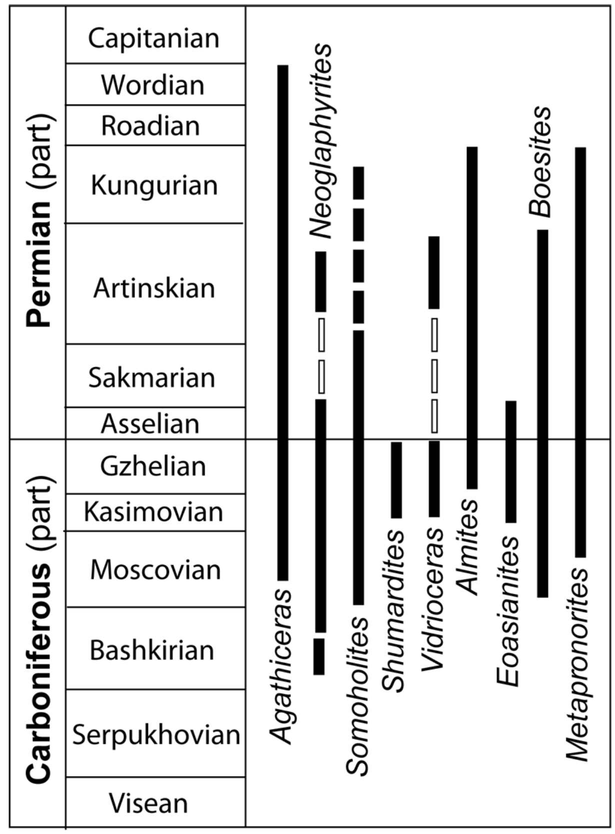

Figure 7. Conventionally known stratigraphic distribution of the ammonoid genera known from the Uyamanoro Formation (Taishaku Limestone) at Miharanoro.

The Miharanoro fauna includes *Metapronorites timorensis* (Haniel), the range of which is restricted in Early

Figure 8. Asselian paleomap showing the ammonoid realms of Leonova (1999) and new Mid-Panthalassan Realm (base map modified from Scotese, 2002).

Permian (Asselian to Artinskian). Miharanoro species of *Vidrioceras*, *Almites* and *Boesites* are new species. But *Vidrioceras ellipticum* sp. nov. from Miharanoro somewhat resembles in shell shape Artinskian *V*. *timorense* (Haniel) from Timor and Gzhelian *V*. *zacharovi* (Popov) from Uzbekistan. *Almites hayasakai* sp. nov. is somewhat similar to Asselian *A*. *multisulcatus* Bogoslovskaya from Pamirs and South China, and to Sakmarian *A. leveni* Leonova from the Pamirs. *Boesites biconcavus* sp. nov. has close similarities in its shell morphology to some Asselian species, such as *B*. *aktubensis* Bogoslovskaya and Popov from Kazakhstan, and *B*. *intercalaris* Ruzhentsev from the Pamirs and South China.

Therefore, the age of the present ammonoid fauna is certainly restricted to the Asselian, agreement with the fact that the ammonoids were collected from the early Asselian fusulinoidean *Sphaeroschwagerina fusiformis* Zone.

Paleobiogeography of the ammonoid fauna

In addition to the previously reported late Asselian taxa (Ehiro *et al*., 2014), the Asselian ammonoid fauna of the Uyamanoro Formation comprises ten ammonoid genera, except for indererminate Adrianitidae: *Agathiceras*, *Neoglaphyrites*, *Emilites*, *Somoholites*, *Shumardites*, *Vidrioceras*, *Almites*, *Eoasianites*, *Boesites* and *Metapronorites*. The Cisuralian ammonoid realms are divided into the Arctic (Arctic Canada-Alaska-Arctic Russia), Uralian (Urals), Paleotethyan (Pamirs, South China, Timor, etc.), Australian (western Australia) and American (Texas, New Mexico, Oklahoma and Kansas) realms (Leonova, 1999, 2011: Figure 8). The faunal relationships between the Taishaku Asselian ammonoid fauna and Asselian faunas in these Cisuralian ammonoid realms were examined mainly using stratigraphic and geographic distribution data of the late Paleozoic ammonoids (e.g. Korn and Ilg, 2007; Kullmann *et al*., 2007).

Genus *Agathiceras* is widely known from the Kasimovian to Wordian strata of the world and more than 35 species are described. Outside Taishaku, the Asselian *Agathiceras* has been known from Arctic Russia (*A*. *verkhoyanicum* Andrianov, 1985), South Urals (*A*. *uralicum* (Karpinskiy): e.g. Bogoslovskaya *et al*., 1995), Pamirs (*A*. *vulgatum* Ruzhentsev, 1978), South China (*A*. *sequaxilirae* Zhou, 2017), Timor (*A*. *sundaicum* Haniel, 1915) and Texas (*A*. *uralicum*: Wardlaw, 1996; Leonova, 2011).

Species of *Neoglaphyrites* are known from the Moscovian to Artinskian of Arctic Canada, South Urals, North China, Oklahoma, and Akiyoshi and North Kitakami belts (accretionary complexes of mid-Panthalassa origin) of Japan. The Asselian species are distributed in the South Urals (*N*. *bashkiricus* Ruzhentsev, 1938: *N*. *satrus* (Maximova, 1940: as *Bisatoceras satrum*)).

The genus *Emilites* has been described from the Kasimovian to Asselian of Arctic Canada, Uzbekistan-Pamirs, South China and North America. Of these, Asselian species are from Uzbekistan (*E*. *ruzhencevi* Popov: Zakharov, 1978 as *E*. *plummeri* Ruzhentsev), Pamirs (*E*. *prosperus* Ruzhentsev, 1978), South China (*E*. *globosum* Zhou, 2017) and New Mexico (?*Emilites* sp.: Leonova, 2011).

The genus *Somoholites*, distributed worldwide, ranges from the Moscovian to Artinskian (Kungurian?). The Asselian species of the genus are known from Arctic Russia (*Somoholites serus* Bogoslovskaia, 1997; *S*. *andrianovi* Kutygin, 1999; *S*. *sebyanicus* Kutygin, 1999), South Urals (*S. artus* Ruzhentsev, 1951), Pamirs (*Somoholites* sp.: Ruzhentsev, 1978) and Timor (*S. beluensis* (Haniel, 1915)).

As described in the preceding section, species of the genus *Shumardites* have been described from the Kasimovian to Gzhelian strata, and no *Shumardites* species has hitherto been known from the Permian. *Shumardites* species from the Gzhelian strata are known from the South Urals and Moscow basin (*S. confessus* Ruzhentsev, 1939; *S. librovichi* Ruzhentsev in Librovich, 1939; *S. aktubensis* Ruzhentsev, 1950) and Texas (*S. simondsi* Smith, 1903; *S. cuyleri* Plummer and Scott, 1937).

The species of the genus *Vidrioceras* have been described from the Kasimovian to Artinskian of the South Urals, Uzbekistan, Timor and Texas, but the Permian occurrence is restricted to the Artinskian of Timor (*V. timorense* (Haniel, 1915); *V. wanneri* Schindewolf, 1931).

The species of the genus *Almites* are mainly known from the Early Permian, except for *A. reverendus* (Bogoslovskaia and Popov, 1986) from the Gzhelian of Kazakhstan. Nine named species have been described from the Asselian to Kungurian strata. In those, Asselian species are *Almites multisulcatus* Bogoslovskaya from the Pamirs (Bogoslovskaya, 1978) and South China (Zhou, 1987, 2017), and *A. sellardsi* (Plummer and Scott, 1937) and *A.* cf. *sellardsi* (Wardlaw, 1996; Leonova, 2011) from Texas and New Mexico.

Eoasianites is distributed in the Kasimovian to Asselian of Arctic Canada, North America, South Urals, Pamirs and South China. From the Asselian strata, six species have been described from the South Urals (*E. subhanieli* Ruzhentsev, 1933; *E. hartmannae* Ruzhentsev, 1938; *E. trapezoidalis* Maximova, 1948), Pamirs (*E. grandis* Ruzhentsev, 1978; *E. stenus* Ruzhentsev, 1978), South China (*E. subhanieli*: Zhou, 2017), and New Mexico and Oklahoma (*Eoasianites* sp.: Wardlaw, 1996; Leonova, 2011).

The genus *Boesites* is widespread in the Upper Carboniferous and Lower Permian strata. Although more than 14 species are known from various regions of the world, the Asselian species are restricted to Kazakhstan (*Boesites aktubensis* Bogoslovskaya and Popov, 1986), Pamir (*B. intercalaris* Ruzhentsev, 1978), South China (*B. intercalaris*: Zhou, 1987, 2017) and Texas (*Boesites* sp.: Wardlaw, 1996; Leonova, 2011).

Species of the genus *Metapronorites* are widespread in the Upper Carboniferous and Lower Permian. More than nine named species and some indeterminable ones are known from Arctic Canada, Arctic Russia, Moscow Basin, South Urals, Austria, Carnic Alps, Pamirs, Guangxi, Timor and Texas. There are three Asselian species, *Metapronorites angustus* Andrianov, 1985 and *M. certus* Andrianov, 1985 from Arctic Russia, and *M. timorensis* (Haniel) from Timor (Haniel, 1915, as *Pronorites uralensis* var. *timorensis*), Pamirs (Ruzhentsev, 1978) and South China (Zhou, 1987, 2017).

The Taishaku Limestone was deposited on a seamount in the mid-Panthalassa Ocean during the late Paleozoic (Sano and Kanmera, 1988; Sano *et al*., 2000). Paleomagnetic study on the greenstone (basaltic lava and tuff) of the Akiyoshi Limestone, Taishaku Limestone and Koyama Limestone gave palaeolatitudes of 17.4°S–14.3°N for these limestones (Nishiyama, 1997). Paleobiogeographic reconstruction based on the Permian fusulinoideans revealed that huge limestone masses in the Akiyoshi Belt were in low latitudes in the mid-Panthalassa (Ozawa, 1987). These evidences indicate that the Asselian ammonoid fauna of the Uyamanoro Formation of the Taishaku Limestone is a representative of the tropical ammonoid fauna in the mid-Panthalassa Ocean, Mid-Panthalassan Realm (Figure 8). Thus, the Taishaku Limestone was situated at the intermediate position between the Paleotethyan region (Paleotethyan Realm) and eastern margin of the Panthalassa region (American Realm). As shown above, the Taishaku Asselian ammonoid fauna is, in its generic composition, most closely related to that of the Pamir region, followed by those of South China, South Urals and Texas-New Mexico. On the other hand, evidence of the Arctic realm and Timor do not seem to be of much consequence. Conclusively, it is considered that there were substantial faunal interactions among the Mid-Panthalassan, Paleotethyan (South China and Pamirs) and American realms in the late Paleozoic regarding the ammonoid migration and expansion.

Conclusions

1. The ammonoid fauna collected from the *Sphaeroschwagerina fusiformis* Zone of the Uyamanoro Formation (Taishaku Limestone) in the Akiyoshi Belt of Southwest Japan comprises *Agathiceras*, *Neoglaphyrites*, *Somoholites*, *Shumardites*, *Vidrioceras*, *Almites*, *Eoasianites*?, *Boesites*, *Metapronorites* and an indeterminate adrianitid. It is highly probable that the fauna is early Asselian in age, based on the generic and specific composition of ammonoids and associated fusulinoideans.

2. The Taishaku Limestone is considered to be deposited in the low-latitude Panthalassa Ocean, and, therefore, occupies a new ammonoid realm (the Mid-Panthalassa Realm), which was not previously known among early Permian ammonoid realms, such as the Arctic, Uralian, Paleotethyan, Australian and American realms.

3. The Taishaku Asselian ammonoid fauna comprises ten genera, in addition to those previously known. In generic composition, the Taishaku fauna is closely related

to those of the Paleotethyan (South China and Pamirs), the Uralian and the American realms.

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Author contributions

T.O. collected the material and is responsible for its geological setting. M.E. is responsible for its taxonomic aspects. All authors contributed to the writing of the paper.