

The late Pliensbachian (Early Jurassic) ammonoid *Amaltheus* in Japan: systematics and biostratigraphic and paleobiogeographic significance

Kentaro Nakada,¹  Michiharu Goto,¹ Christian Meister,² and Atsushi Matsuoka³

¹Fukui Prefectural Dinosaur Museum, 51–11 Terao, Muroko, Katsuyama, Fukui 911–8601, Japan <k-nakada@dinosaur.pref.fukui.jp>, <amaltheus0797@gmail.com>

²Department of Geology and Paleontology, Natural History Museum of the City of Geneva, 1 route de Malagnou, c.p. 6434, CH–1211, Geneva 6, Switzerland <Christian.Meister@ville-ge.ch>

³Department of Geology, Faculty of Science, Niigata University, Niigata 950–2181, Japan <amatsuoka@geo.sc.niigata-u.ac.jp>

Abstract.—The genus *Amaltheus*, one of the representative late Pliensbachian ammonoids, has biostratigraphic and paleobiogeographic significance in Japan. Four species, *Amaltheus stokesi* (Sowerby, 1818), *A. margaritatus* de Montfort, 1808, *A. repressus* Dagis, 1976, and *A. orientalis* new species, have been found in the Kuruma Group in central Japan; *A. stokesi* and *A. margaritatus* are also from the Toyora Group in southwest Japan. On the basis of taxonomic analysis of the genus *Amaltheus*, we distinguish two successive ammonoid biozones in the lower part of the Teradani Formation of the Kuruma Group: the *Amaltheus stokesi*–*Amaltheus repressus* and the *Amaltheus margaritatus* assemblage zones, in stratigraphic ascending order. This study also establishes the presence of the *Amaltheus stokesi* Assemblage Zone in the Higashinagano Formation of the Toyora Group. The *stokesi*–*repressus* and the *stokesi* assemblage zones correspond biostratigraphically to the *Amaltheus stokesi* Standard Subzone of the *margaritatus* Zone. The *margaritatus* Assemblage Zone is correlated with the *Amaltheus subnodosus* and *Amaltheus gibbosus* standard subzones. The Japanese early–middle late Pliensbachian ammonoid faunas are composed almost entirely of pan-Boreal and Arctic species of the genus *Amaltheus*. This faunal composition has an affinity with that of the Northeast Russian region, and thus suggests a strong paleobiogeographic relationship between East Asian and Northeast Russian faunas throughout this time interval.

UUID: <http://zoobank.org/5F08121F-1DAF-4B24-BCBE-B08F7101CF29>

Introduction

Late Pliensbachian–early Toarcian ammonoid assemblages have been recognized in Lower Jurassic epicontinental deposits exposed in central and southwest Japan as follows: the Kuruma Group (Sato, 1955; Kobayashi et al., 1957), the Higuchi Group (Hirano et al., 1978), and the Toyora Group (Matsumoto and Ono, 1947; Hirano, 1971, 1973a, b; Nakada and Matsuoka, 2009, 2011). They provide important biostratigraphic and paleobiogeographic data and, therefore, play a significant role in analyzing the paleoceanographic environment, such as ocean anoxic events, during this period. However, most of these ammonoid assemblages are composed primarily of species endemic to the East Asian region. These faunal compositions have previously prevented detailed biostratigraphic and paleobiogeographic correlation of Japanese assemblages with faunas outside Japan.

Amaltheus, typically characterized by having an involute whorl, irregular ribbing, and a crenulated keel, has been regarded as one of the most important of the late Pliensbachian ammonoid taxa because of its biostratigraphic and paleobiogeographic utility. During the late Pliensbachian, the typical ammonoid assemblages from high-latitude areas of the Northern Hemisphere, such as the northern Northwest European, northern North American Cordillera, Arctic islands of Canada, and Russian regions, are dominated by the Amaltheinae, including *Amaltheus*, *Amauroceras*, and

Pleuroceras. On the basis of this geographic distribution, the Amaltheinae has been designated as an index taxon of the late Pliensbachian Boreal Realm fauna (e.g., Dommergues, 1987; Smith et al., 2001). In addition, species belonging to the genus *Amaltheus* are the most significant late Pliensbachian biostratigraphic index taxa because the standard ammonoid zonation of this period established in the Northwest European province has been discussed in detail on the basis of the well-established phylogeny of the genus (Howarth, 1958; Dean et al., 1961; Meister, 1988; Bardin et al., 2017).

In Japan, *Amaltheus* has been collected from two areas: the Kuruma Group in central Japan and the Toyora Group in southwest Japan. Sato (1955) described two specimens from the Kuruma Group as *Amaltheus* sp. indet. One specimen of *Amaltheus* sp. cf. *A. stokesi* (Sowerby, 1818) was reported from the Toyora Group by Hirano (1971). The biostratigraphic and paleobiogeographic significance of this genus in Japan has been recognized in previous studies (Sato, 1955; Hirano, 1973b). *Amaltheus* has been used as the index fossil for the late Pliensbachian in the Kuruma and the Toyora groups (Sato, 1955; Hirano, 1973b). Sato (1956) suggested a Boreal influence on the Kuruma Group fauna on the basis of the occurrence of this genus. However, detailed biostratigraphic and paleobiogeographic analyses of these Japanese *Amaltheus* occurrences have not been developed as the small number of well-preserved specimens collected has precluded taxonomic discussions until recently.

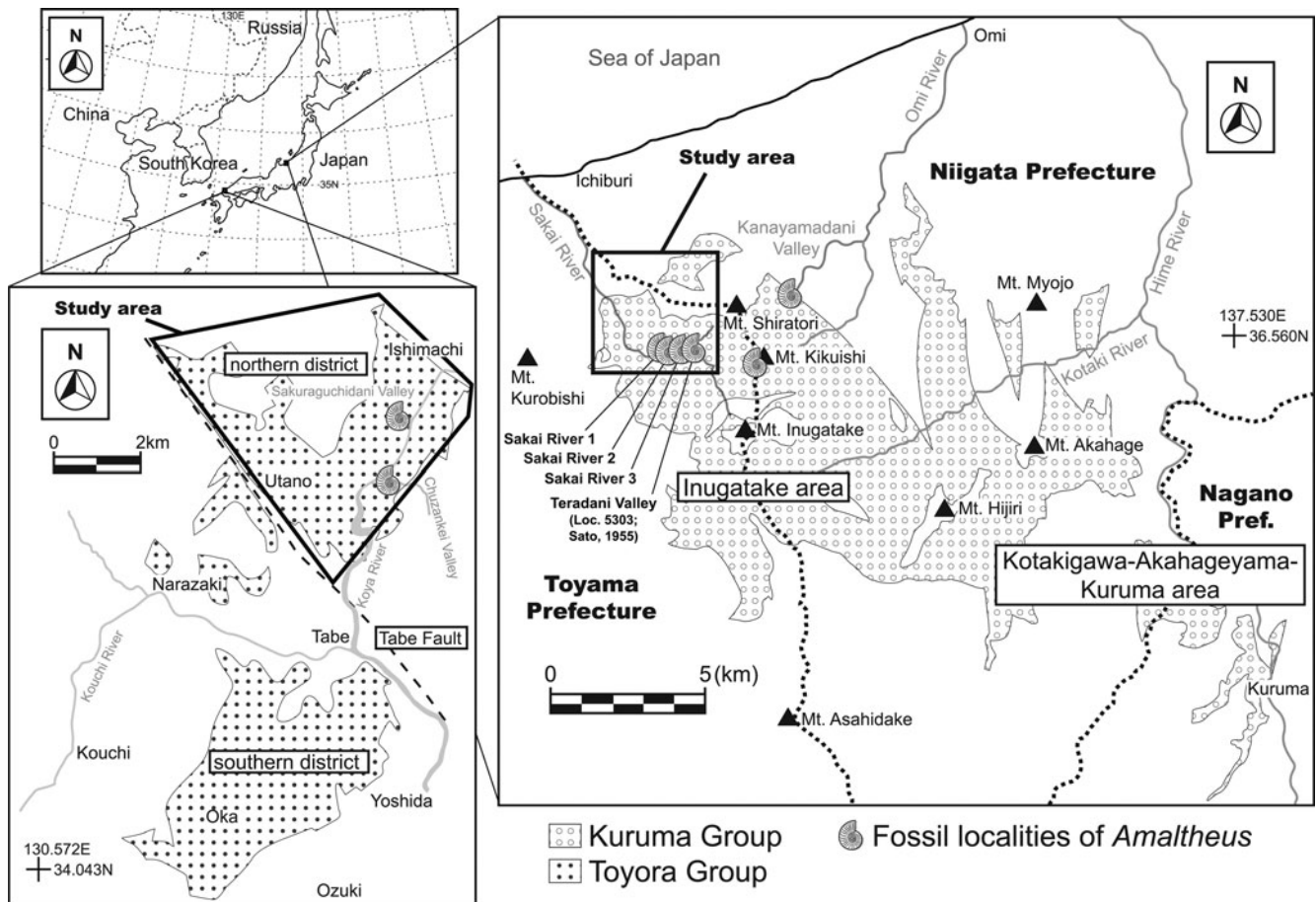


Figure 1. Locations of the Toyora and Kuruma groups with *Amaltheus* localities denoted by the ammonoid shape. The stratigraphies in the Sakai River 1, 2, and 3 localities are displayed in Figure 2; fossil locality numbers are shown in Table 1.

The aims of this study are to identify *Amaltheus* from Japan at the species level by utilizing 34 specimens and to discuss the biostratigraphic and paleobiogeographic significance of the four species identified, including a new endemic species. These materials involve every recognizable *Amaltheus* specimen in Japan, including all material described in previous studies.

Geological framework

As mentioned, *Amaltheus* specimens in this study were obtained from two areas: the Kuruma Group and the Toyora Group.

Kuruma Group.—This unit comprises Lower Jurassic continental shelf sediments and is widely exposed in the northeastern part of the circum-Hida terrane of eastern Toyama, western Niigata, and northern Nagano prefectures, central Japan (Fig. 1). This group's distribution is divided into the Inugatake and the Kotakigawa–Akahageyama–Kuruma areas because of the difficulty of their lithostratigraphic correlation (Takeuchi et al., 2017) (Fig. 1), and the former yields numerous Early Jurassic ammonoid fossils (Sato, 1955; Kobayashi et al., 1957). Most of the studied materials were obtained from the Inugatake area. Detailed localities are shown in Table 1.

The lithostratigraphy of the Kuruma Group has been separately analyzed for each area. In the Inugatake area, the group

was subdivided into seven formations by Kobayashi et al. (1957): the Jogodani, Kitamatadani, Negoya, Teradani, Shinatani, Otakidani, and Mizukamidani formations, in ascending order (Fig. 2). Later, Takizawa (1984) assigned the Mizukamidani Formation to the Tetori Group, which consists of epicontinental sediments of Early Cretaceous age. The Kuruma Group is composed mainly of sandstones, mudstones, and conglomerates with numerous fossils, including ammonoids, bivalves, gastropods, belemnites, crinoids, fish, turtles, and terrestrial plants and is characterized by alternation of marine and non-marine clastic sediments (Kobayashi et al., 1957; Kimura and Tsujii, 1980–1984; Hayami and Akahane, 1981; Goto, 1983, 1994; Kimura et al., 1988; Sonoda et al., 2015; Iba et al., 2015). Ammonoid fossils have been collected from the Teradani Formation (Sato, 1955), which is composed mainly of sandy siltstones, and the Otakidani Formation (Kobayashi et al., 1957), which is composed mainly of black mudstones with thin sandstone and conglomerate intercalations. On the basis of these ammonoid faunas, the Teradani Formation has been roughly correlated to the upper Pliensbachian, and the Otakidani Formation is thought to correspond to the upper Toarcian to Aalenian (Sato, 1955, 1992; Kobayashi et al., 1957). In addition, Takeuchi et al. (2017) reported that the U–Pb age of detrital zircon grains from four sandstone samples in the Jogodani and Kitamatadani formations in the Inugatake area were dated ca. 188–186 Ma and compared these data to Pliensbachian age.

Table 1. Occurrence and repository list of *Amaltheus* from Japan. All of the specimens included in this table are illustrated in Figures 4–7.

Species	Specimen no.	Locality	Horizon	Repository	
<i>Amaltheus stokesi</i> (Sowerby, 1818)	NU-MM0001	Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Niigata University	
	NU-MM0002	Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Niigata University	
	NU-MM0003	Sakai River 3, Kuruma Group (Inugatake area)	from floated rock	Niigata University	
	NU-MM0075	Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Niigata University	
	NMNS PM17559	Mt. Kikuishi, Kuruma Group (Inugatake area)	from floated rock	National Museum of Nature and Science	
	NMNS PM23447	Kanayamadani V., Kuruma G. (Inugatake area)	unknown	National Museum of Nature and Science	
	FMM3051-3	Mt. Kikuishi, Kuruma Group (Inugatake area)	from floated rock	Fossa Magna Museum	
	FMM3051-4	Mt. Kikuishi, Kuruma Group (Inugatake area)	from floated rock	Fossa Magna Museum	
	FMM3051-5	Mt. Kikuishi, Kuruma Group (Inugatake area)	from floated rock	Fossa Magna Museum	
	TOYA-Fo-2992	Mt. Kikuishi, Kuruma Group (Inugatake area)	unknown	Toyama Science Museum	
	<i>Amaltheus margaritatus</i> de Montfort, 1808	GK.G.11293	Chuzankei Valley, Toyora Group	unknown	Kyushu University
		NU-MM0005	Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Niigata University
		NU-MM0006	Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Niigata University
		NU-MM0007	Sakai River 3, Kuruma Group (Inugatake area)	from floated rock	Niigata University
NU-MM0011		Sakai River 4, Kuruma Group (Inugatake area)	SR0303	Niigata University	
NU-MM0076		Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Niigata University	
FMM2007		Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Fossa Magna Museum	
FMM2008		Sakai River 3, Kuruma Group (Inugatake area)	from floated rock	Fossa Magna Museum	
FMM2009		Kanayamadani V., Kuruma G. (Inugatake area)	from floated rock	Fossa Magna Museum	
FMM3051-2		Mt. Kikuishi, Kuruma Group (Inugatake area)	from floated rock	Fossa Magna Museum	
TOYA-Fo-3015		Sakai River 1, Kuruma Group (Inugatake area)	unknown	Toyama Science Museum	
MM2791		Teradani Valley, Kuruma G. (Inugatake area)	Loc. 5303 (Sato, 1955)	University Museum of the University of Tokyo	
MM2792		Teradani Valley, Kuruma G. (Inugatake area)	Loc. 5303 (Sato, 1955)	University Museum of the University of Tokyo	
NU-MM0077		Sakuraguchidani Valley, Toyora Group	SA36-1 (Nakada and Matsuoka, 2011)	Niigata University (rubber cast)	
NU-MM0078	Sakuraguchidani Valley, Toyora Group	SA36-1 (Nakada and Matsuoka, 2011)	Niigata University (rubber cast)		
<i>Amaltheus</i> sp. cf. <i>A. margaritatus</i> de Montfort, 1808	FMT0001	unknown, Toyora Group	unknown	Firefly Museum of Toyota Town	
	NU-MM0004	Sakai River 1, Kuruma Group (Inugatake area)	SR0101	Niigata University	
<i>Amaltheus repressus</i> Dagens, 1976	NU-MM0009	Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Niigata University	
	NU-MM0079	Sakai River 3, Kuruma Group (Inugatake area)	SR0301	Niigata University (rubber cast)	
<i>Amaltheus orientalis</i> n. sp.	TOYA-Fo-2974	Sakai River 2, Kuruma Group (Inugatake area)	SR0201	Toyama Science Museum	
	TOYA-Fo-2986	Sakai River 2, Kuruma Group (Inugatake area)	SR0201	Toyama Science Museum	
	NMNS PM23448	Teradani Valley, Kuruma G. (Inugatake area)	Loc. 5303 (Sato, 1955)	National Museum of Nature and Science	
	NU-MM0010	Sakai River 1, Kuruma Group (Inugatake area)	from floated rock	Niigata University	
<i>Amaltheus</i> sp. indet.	NU-MM0008	Sakai River 3, Kuruma Group (Inugatake area)	from floated rock	Niigata University	

Almost all the additional *Amaltheus* specimens in this study were obtained from the lowermost Teradani Formation exposed along the Sakai River, except for some specimens from Mt. Kikuishi, the Teradani Valley, and the Kanayamadani Valley (Fig. 2; Table 1).

Toyora Group.—This unit outcropping in the western part of Yamaguchi Prefecture, southwest Japan, consists of epicontinental sediments deposited during the Early and Middle Jurassic (Fig. 1). This group crops out separately in two regions, the northern and the southern districts (Hirano,

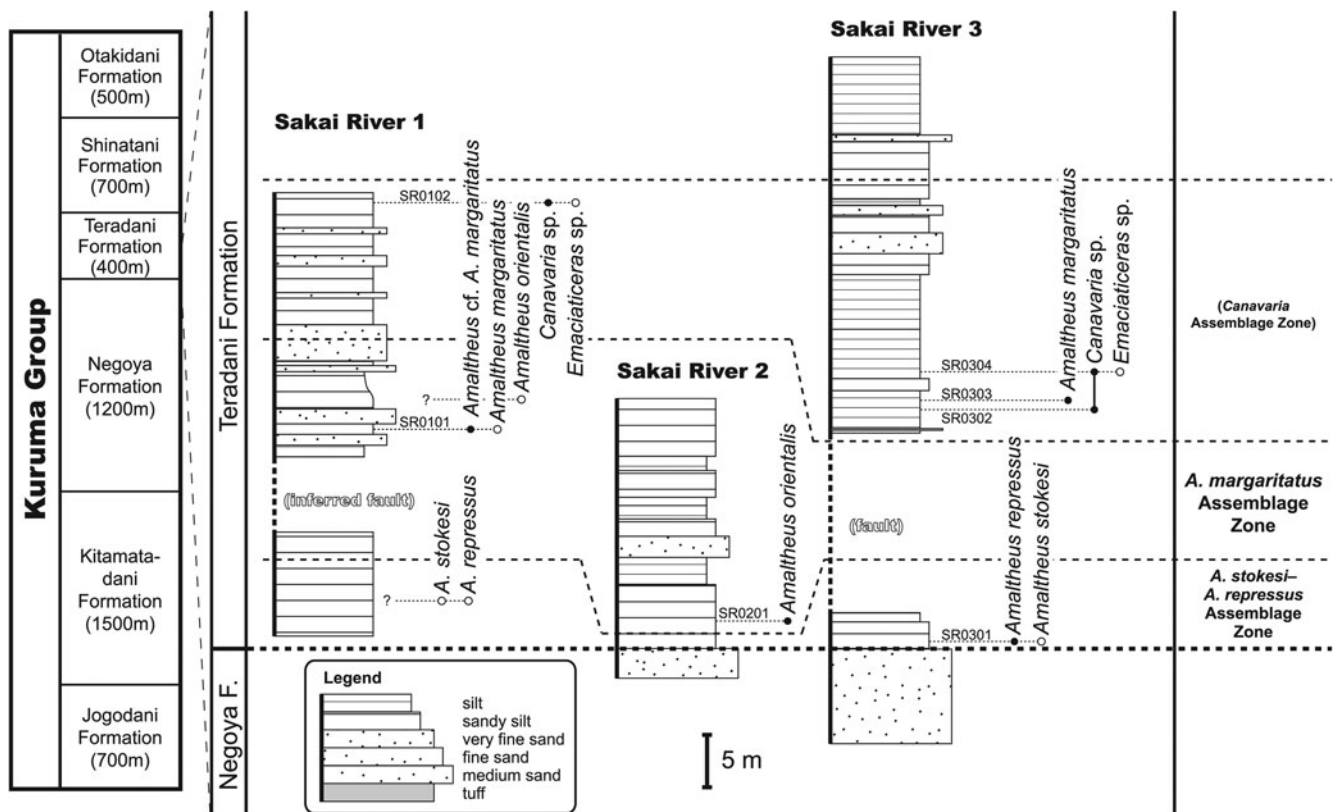


Figure 2. Columnar sections, biostratigraphic succession of ammonoids, and the biostratigraphic framework of the lowermost part of the Teradani Formation, Kuruma Group, exposed along the Sakai River. The horizon numbers beside the columnar sections correspond to the horizon numbers in Table 1. The lithostratigraphic division of the Kuruma Group with the thickness of each formation utilized in this figure follows Kumazaki and Kojima (1996).

1971) (Fig. 1). The northern district is characterized by abundant occurrences of ammonoids (Matsumoto and Ono, 1947; Hirano, 1971, 1973a, b; Nakada, 2008; Nakada and Matsuoka, 2009, 2011), including all the materials used in this study.

The Toyora Group is composed mainly of sandstones, mudstones, and conglomerates. It has been divided into three formations in ascending order: the Higashinagano, Nishinakayama, and Utano formations; each formation has been further subdivided into several members (Matsumoto and Ono, 1947; Hirano, 1971; Nakada and Matsuoka, 2011; Fig. 3). Ammonoid fossils are especially abundant in the Sakuraguchidani Mudstone Member, the lower part of the Nishinakayama Formation that is composed dominantly of black mudstone, and thus the ammonoid biostratigraphy has been analyzed frequently in this member (Matsumoto and Ono, 1947; Hirano, 1973b; Tanabe, 1991; Nakada and Matsuoka, 2009, 2011). Nakada and Matsuoka (2011) proposed four successive ammonoid zones: the *Canavaria japonica*, *Paltarpites paltus*, *Dactylioceras helianthoides*, and *Harpoceras inouyei* zones, in ascending order. Two additional *Amaltheus* specimens described in this study (NU-MM0077 and NU-MM0078) were obtained from the lowermost part of the Sakuraguchidani Mudstone Member, corresponding to the lowermost part of the *japonica* Zone, exposed along the Sakuraguchidani Valley (Figs. 1, 3; Table 1). An *Amaltheus* specimen described by Hirano (1971) was obtained from the lowermost part of the Kido Sandstone Member, which is composed mainly of bedded sandstones and sandy mudstones with thin coal beds, along the Chuzankei Valley (Fig. 3; Table 1).

Materials and methods

The abbreviations used throughout the descriptions are as follows: diameter, D; umbilical diameter, U; whorl height, Wh; ratio of umbilical diameter to diameter, U/D; and ratio of whorl height to diameter, Wh/D. All measurements are shown in Table 2. Almost all of the materials used in this analysis are flattened horizontal to bedding planes; the degree of compaction was almost similar in all specimens and thus shows poor preservation.

Repositories and institutional abbreviations.—The specimens described and illustrated in this study are deposited in the following institutions: Niigata University (NU-MM), the University Museum of the University of Tokyo (MM), Fossa Magna Museum in Itoigawa City (FMM), National Museum of Nature and Science (NMNS PM), Toyama Science Museum (TOYA-Fo), Kyushu University (GK.G.), and the Firefly Museum of Toyota Town in Shimonoseki City (FMT).

Systematic paleontology

Class Cephalopoda Cuvier, 1798
 Subclass Ammonoidea von Zittel, 1884
 Order Psiloceratida Housa, 1965
 (emended by Dommergues, 2002)
 Superfamily Eoderoceratoidea Neumayr, 1875

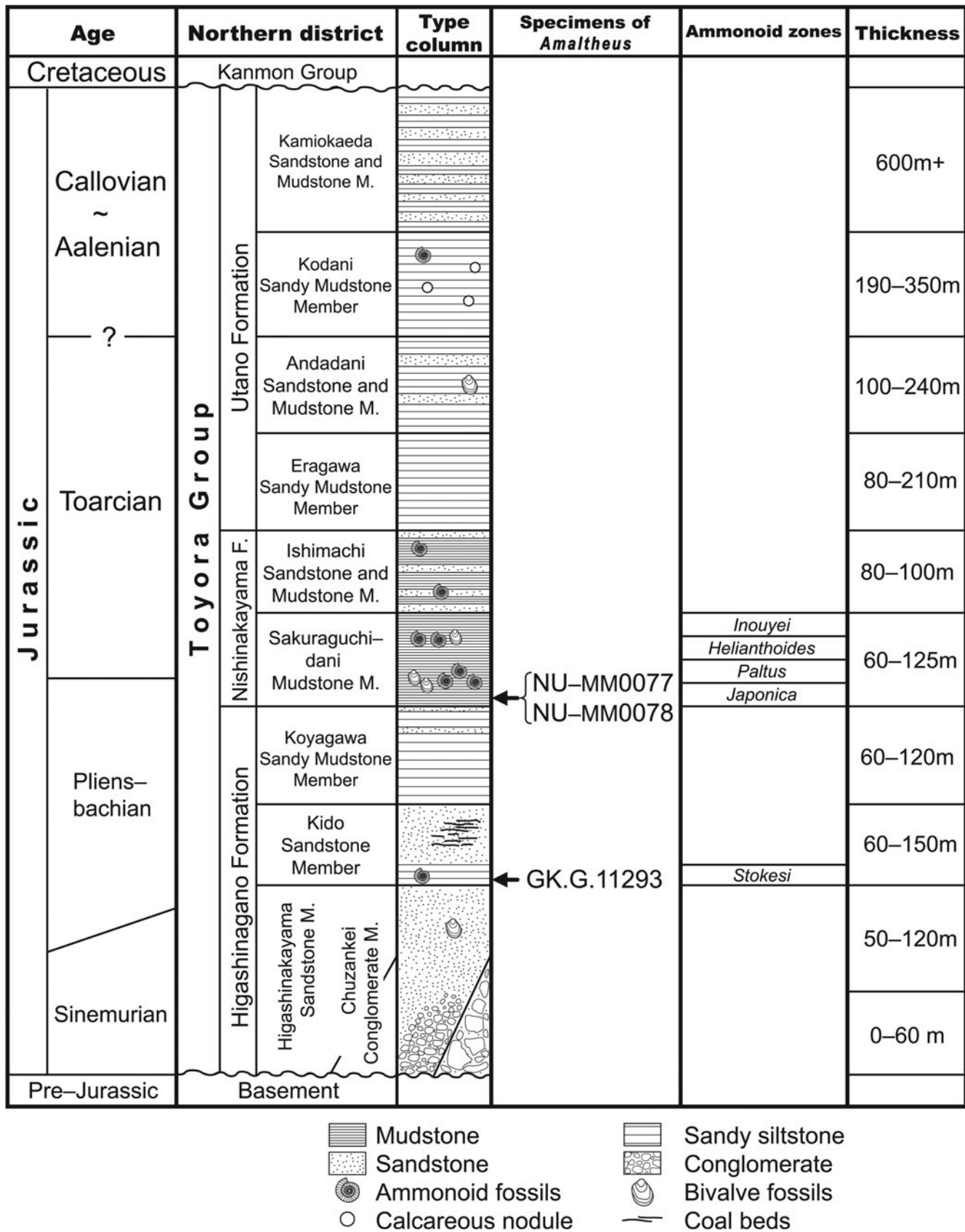


Figure 3. Generalized geological column of the Toyora Group in the study area after Nakada and Matsuoka (2011) with *Amaltheus*-bearing horizons and the zonal framework proposed by Nakada and Matsuoka (2011) and this study.

Table 2. Dimensions of the ammonoid specimens utilized in this taxonomic analysis (mm).

Species	Specimen no.	D	Wh	U	U/D	Wh/D
<i>Amaltheus stokesi</i> (Sowerby, 1818)	NU-MM0001	47.7	23.0	11.2	0.235	0.482
	NU-MM0075	29.2	14.2	6.0	0.206	0.486
	NU-MM0002	35.2	15.6	9.1	0.259	0.443
	GK.G.11293	41.4+	20.5	8.2	0.198	0.495
	NMNS PM17559	42.0	10.9	17.6	0.260	0.419
	NMNS PM23447	47.6	19.6	16.7	0.351	0.412
<i>Amaltheus margaritatus</i> de Montford, 1808	NU-MM0005	33.0	16.6	6.8	0.206	0.503
	NU-MM0006	24.7	11.0	5.5	0.223	0.445
	NU-MM0076	40.2	19.2	9.2	0.229	0.478
	FMM2007	41.3	18.1	11.2	0.271	0.438
	FMM2008	36.4	13.6	11.4	0.313	0.374
	MM2792	35.9	16.6	10.2	0.284	0.462
	MM2791	25.2	12.4	5.5	0.218	0.492
	NU-MM0077	33.5	17.4	10.7	0.319	0.519
	FMT0001	41.7	18.6	11.0	0.264	0.446
	NU-MM0079	27.1	12.4	6.8	0.251	0.458
<i>Amaltheus repressus</i> Dagus, 1976	TOYA-Fo-2974	56.3	23.3	22.6	0.401	0.414
	NU-MM0010	48.2	15.8	19.6	0.407	0.328

Family Liparoceratidae Hyatt, 1867
(emended by Dommergues and Meister, 1999)
Subfamily Amaltheinae Hyatt, 1867
Genus *Amaltheus* de Montford, 1808

Type species.—*Amaltheus margaritatus* de Montford, 1808.

Remarks.—The whorl section is compressed and subelliptical. Surface ornament is extremely varied; some species have smooth whorl flanks with sigmoidal ribs, and others are characterized by spiny or strong ribbing. Almost all species have a crenulated keel and a suboxycone coiling with moderately open umbilicus.

Amaltheus stokesi (Sowerby, 1818)
Figure 4

- 1818 *Ammonites stokesi* Sowerby, p. 205, pl. 190.
1955 *Amaltheus* cf. *A. nudus* (Quenstedt, 1858; Imlay, p. 87, pl. 10, fig. 5.
1958 *Amaltheus stokesi*; Howarth, p. 3, text-figs. 4–5, pl. 1, figs. 5, 7, 12–14, pl. 2, figs. 1, 3, 10, with synonymy.
1964 *Amaltheus stokesi*; Frebold, pl. 6, figs. 6, 13.
1967 *Amaltheus stokesi*; Frebold, Mountjoy, and Tempelman-Kluit, pl. 1, figs. 1, 7.
1971 *Amaltheus* cf. *A. stokesi*; Hirano, p. 101, pl. 17, fig. 11.
1974 *Amaltheus (Amaltheus) stokesi*; Repin, pl. 1, figs. 4–9.
1975 *Amaltheus stokesi*; Frebold, pl. 4, figs 3, 4.
1976 *Amaltheus (Proamaltheus) stokesi*; Dagus, p. 21, pl. 10, figs. 5–7.
1980 *Amaltheus stokesi*; Sey and Kalacheva, pl. 1, figs 4, 7, 8, 11, 13.
1988 *Amaltheus (Amaltheus) stokesi*; Krymholts, Mesezhnikov and Westermann, pl. 2, fig. 1.
1991 *Amaltheus stokesi*; Poulton, p. 18, pl. 8, figs. 2, 7, 8.
1992 *Amaltheus stokesi*; Westermann, pl. 3, fig. 11, pl. 5, fig. 9, pl. 6, fig. 4 (cf.).
1994 *Amaltheus* cf. *A. stokesi*; Pálffy and Hart, pl. 1, fig. 12.
1994 *Amaltheus stokesi*; Jakobs and Pálffy, pl. 1, fig. 9.

- 1996 *Amaltheus stokesi*; Smith and Tipper, pl. 19, fig. 1, pl. 20, fig. 3.
1997 *Amaltheus stokesi*; Johannson, Smith, and Gordey, pl. 2, fig. 13.
1998 *Amaltheus stokesi*; Géczy and Meister, p. 102, pl. 6, fig. 10.
2002 *Amaltheus stokesi*; Rakus and Guex, pl. 27, fig. 8.
2003 *Amaltheus stokesi*; Meister and Friebe, pl. 16, figs. 9, 14.
2004 *Amaltheus stokesi*; Schubert, pl. 1, fig. 1.
2005 *Amaltheus stokesi*; Callomon and Gradinaru, pl. 2, fig. 2.
2006 *Amaltheus stokesi*; Fauré, p. 43, fig. 8.
2006 *Amaltheus stokesi*; Topchishvili et al., pl. 11, fig. 4.
2007 *Amaltheus stokesi*; Rulleau, Guiffroy, and Dommergues, pl. 34, fig. 5, pl. 35, fig. 1.
2007 *Amaltheus stokesi*; Mouterde et al., p. 75, pl. 1, figs. 9, 14, with synonymy.
2016 *Amaltheus (Amaltheus) stokesi*; Repin, p. 37, figs 4, 5.
2016 *Amaltheus stokesi*; Nützel et al., p.3, fig. 2.

Type.—The holotype, OUM.J2248, was collected by J. Sowerby (1818) from Dorset.

Diagnosis (modified from Howarth, 1958).—Large oxycone with highly compressed elliptical whorl section. Ventral halves of the inside whorls are covered by the next outer whorls. The venter bears a barely developed keel with coarse crenulation. Each serration of crenulation is connected with ribs.

Occurrence.—*Amaltheus stokesi* is the index species at the base of the late Pliensbachian in Northwest Europe.

This taxon has been recognized in the Northwest European province, the northern Tethys margin (Southern Alps, Austroalpine units, Carpathians), the Caucasus (Georgia), East Asia (Japan), North American Cordillera (British Columbia and northern Alaska), Arctic Canada, and Russia (the Northeast, the Siberian Platform, and the Far East regions).

Description.—The whorls are moderately to extremely involute, with a high expansion rate; the umbilici are narrow. Detailed

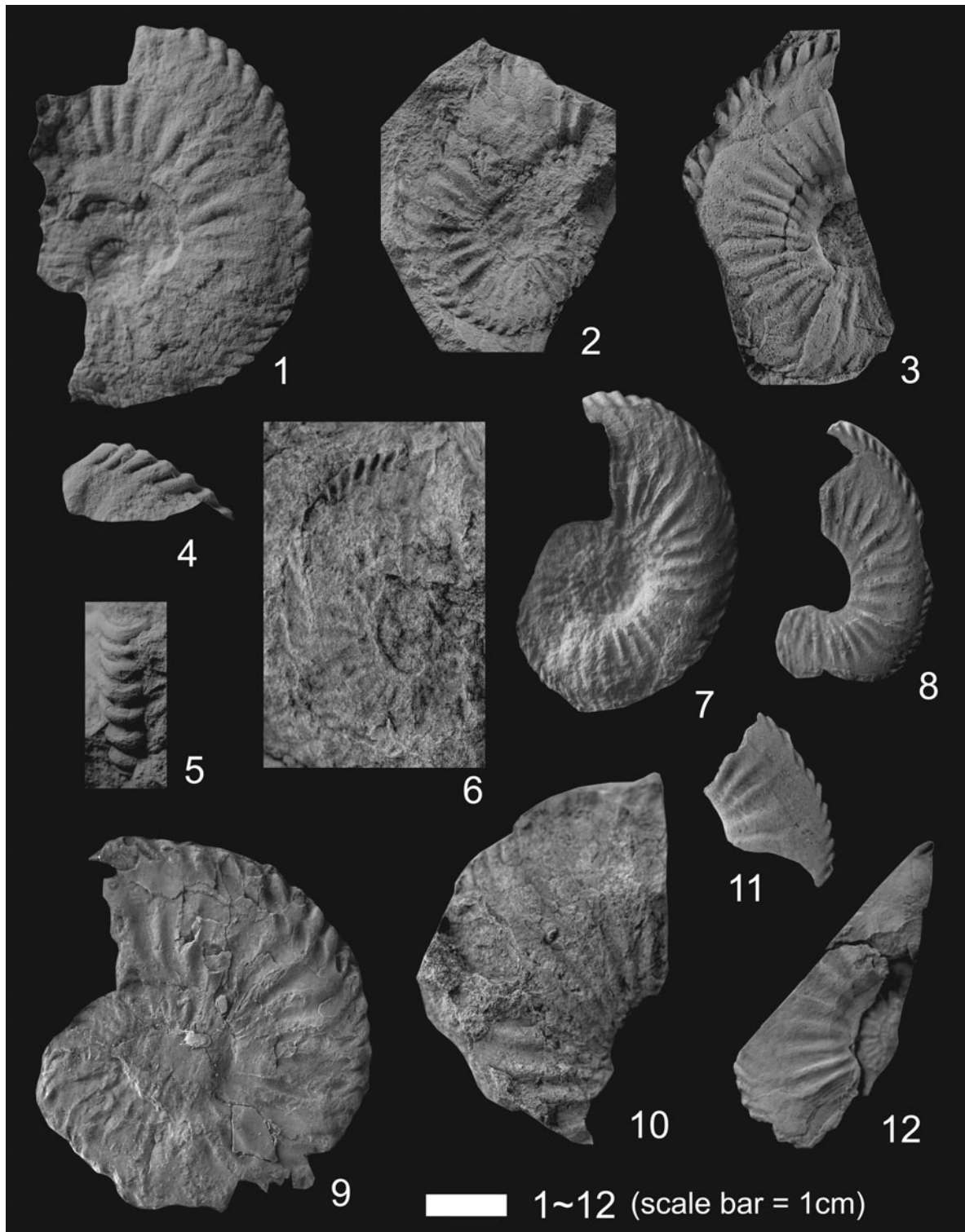


Figure 4. *Amaltheus stokesi* from Japan. The locality and the repository data are shown in Table 1. (1) NU-MM0001; (2) NU-MM0075; (3) GK.G.11293 (rubber cast); (4, 5) NU-MM0003: (4) lateral view; (5) ventral view; (6) NU-MM0002; (7) NMNS PM17559 (rubber cast); (8) FFM3051-4; (9) NMNS PM23447; (10) FMM3051-3; (11) TOYA-Fo-2992; (12) FMM3051-5.

characteristics of the whorl section are unknown because of compression. The venter bears a broad and elevated keel with coarse crenulations (NU-MM0003; Fig. 4.4). The radial and sometimes irregular ribs are stronger on the inner two-thirds of

the whorl flank and become slightly weak toward the venter. They are strongly projected forward in the ventrolateral part and pass on to the keel as a serration of the crenulation. Tubercles are not recognized on ribs.

Materials.—Ten specimens, NU-MM0001, NU-MM0075, NU-MM0002, NU-MM0003, NMNS PM17559, NMNS PM23447, FMM3051-3, FMM3051-4, FMM3051-5, and TOYA-Fo-2992, from the Teradani Formation, the Kuruma Group, and one specimen, GK.G.11293, from the Higashinagano Formation of the Toyora Group.

Remarks.—*Amaltheus stokesi* is distinguished from *Amaltheus margaritatus* de Montfort, 1808, one of the most typical species of this genus, mainly by the characteristics of the keel and the connecting pattern between the ribs and crenulations. *Amaltheus stokesi* has a rounded keel and is characterized by ribs that are connected to each serration of the crenulated keel; a typical example of this is seen in NU-MM0075 (Fig. 4.2). The keel of *Amaltheus margaritatus* is more developed, the crenulation becomes finer, and the ribbing seems a little weaker. Moreover, the ribs of *Amaltheus margaritatus* are not connected individually with each serration of the crenulation. In Japan, the morphological variability of *A. stokesi* is rather high. If the classic morphology of Sowerby's species is represented in Figure 4.1–4.7, 4.10–4.12, a specimen illustrated in Figure 4.8 develops a more derived morphology with a “*stokesi* habitus” in the inner whorls and a “*margaritatus* habitus” in the outer whorls with a more differentiated keel. This kind of ontogeny was already illustrated by Poulton (1991, pl. 8, fig. 5) and Frebald (1964, pl. 6, fig. 7). For this specimen, we use the terminology *A. stokesi* (Sowerby, 1818) transitional form to *A. margaritatus* de Montfort, 1808.

Amaltheus sensibilis Dagis, 1976 and *A. subbifurcus* Repin, 1968 were both collected from the Northeast Russian region (Repin, 1974, 2009, 2016; Dagis, 1976) and are distinguished from *A. stokesi* by the larger umbilicus and stronger projection of the ribs in the ventrolateral part.

A. stokesi is quite similar to *A. bifurcus* Howarth, 1958. However, *A. bifurcus* is characterized by coarse ribbing and an undeveloped keel (see Howarth, 1958, pl. 1, fig. 6). NMNS PM23447 (Fig. 4.9) still evokes the ancestral morphology of *A. bifurcus* with a coarser and stronger ribbing, but the whorl section is already more compressed and the inner-to-middle whorls seem to develop a finer and more flexuous ribbing than does the true *A. bifurcus*. Due to the preservation, we prefer to keep this specimen in the variability domain of *A. stokesi*.

Amaltheus margaritatus de Montfort, 1808
Figures 5, 6.1–6.6

- 1808 *Amaltheus margaritatus* de Montfort, p. 90, fig. 91.
1812 *Ammonites acutus* Sowerby, p. 51, pl. 17, fig. 1.
1845 *Ammonites sedgwickii* Buckman, p. 40 (nomen nudum).
1852 *Ammonites foliaceus* Giebel, p. 540.
1885 *Ammonites amaltheus nudus* Quenstedt, p. 321, pl. 41, figs. 1, 2.
1885 *Ammonites amaltheus compressus* Quenstedt, p. 327, pl. 41, fig. 17, pl. 42, fig. 8.
1955 *Amaltheus* sp. indet. Sato, p. 114, pl. 18, figs. 1, 2.
1958 *Amaltheus margaritatus*; Howarth, p. 13, text-fig. 8 (neotype), 9 (lectotype), pl. 3, figs. 4–6, with synonymy.

- 1964 *Amaltheus stokesi* (Sowerby, 1818); Frebald, pl. 6, fig. 7.
1974 *Amaltheus margaritatus*; Elmi, Atrops, and Mangold, pl. 1, fig. 1.
1976 *Amaltheus margaritatus*; Pourmotamed and Motamed, p. 106, fig. 3.
1980 *Amaltheus margaritatus*; Sey and Kalacheva, pl. 1, figs 5, 9, 10, 12.
1988 *Amaltheus margaritatus* form *margaritatus*; Meister, pl. 1, figs. 2–4, pl. 2, figs. 1–3, 5, 10, pl. 4, figs. 1, 3, 4.
1988 *Amaltheus (Amaltheus) margaritatus*; Krymholts, Mesezhnikov, and Westermann, pl. 2, fig. 5 only.
1991 *Amaltheus stokesi* (Sowerby, 1818); Poulton, p. 18, pl. 8, fig. 1.
1992 *Amaltheus (Amaltheus) margaritatus*; Westermann, pl. 17, fig. 6, except for fig. 3 (*A. (Amaltheus)* nov. sp. in Repin, 2009).
1996 *Amaltheus stokesi* (Sowerby, 1818); Smith and Tipper, pl. 19, fig. 1, pl. 20, fig. 3.
1997 *Amaltheus stokesi* (Sowerby, 1818); Johannson, Smith, and Gordey, pl. 2, fig. 12.
1998 *Amaltheus margaritatus*; Géczy and Meister, p. 103, with synonymy.
2002 *Amaltheus margaritatus*; Fauré, pl. 7, fig. 16.
2006 *Amaltheus margaritatus*; Topchishvili et al., pl. 11, figs. 1, 2.
2006 *Amaltheus margaritatus*; Fauré, p. 43, figs. 1, 3, 4.
2007 *Amaltheus margaritatus*; Rulleau, Guiffroy, and Dommergues, pl. 35, figs. 3–5.
2007 *Amaltheus margaritatus*; Mouterde et al., p. 76, pl. 2, figs. 1, 8, with synonymy.
2008 *Amaltheus margaritatus* form *margaritatus*; Dommergues et al., p. 293, pl. 10, fig. 4.
2008 *Amaltheus margaritatus*; Seyed-Emami et al., p. 244, 246, fig. 4T.
2013 *Amaltheus* aff. *margaritatus*; Bardin, Rouget, and Cecca, p. 321, fig. 4A, B, p. 323, fig. 5A, B, E, F, fig. 6F, G.
2017 *Amaltheus* gr. *margaritatus*; Dommergues and Meister, p. 302, fig. 175, with synonymy.
2018 *Amaltheus margaritatus*; van de Schootbrugge, Richoz, Pross, Luppold, Hunze, Wonik, Blau, Meister, van der Weijst, Suan, Fraguas, Fiebig, Herrle, Guex, Little, Wignall, Piittmann and Oschmann, 2018, p. 10, figs 27, 28, 34.
2019 *Amaltheus margaritatus*; Fauré and Teodori, pl. 23, fig. 8.

Type.—The neotype, BM.37039, designated by Howarth (1958), was obtained from Croisilles (France).

Diagnosis (modified from Howarth, 1958).—Large oxycone with a compressed triangular or elliptical whorl section. The venter bears a well-developed keel with fine crenulation, except for the large body chamber. Radial and sigmoidal ribs curve forward strongly in the ventrolateral part and are reduced to striae before reaching the keel.

Occurrence.—This species is the index taxon of the *Amaltheus margaritatus* Zone for the standard zonation. It ranges from the *Amaltheus subnodosus* Subzone of the *margaritatus* Zone to the *Pleuroceras apyrenum* Subzone of

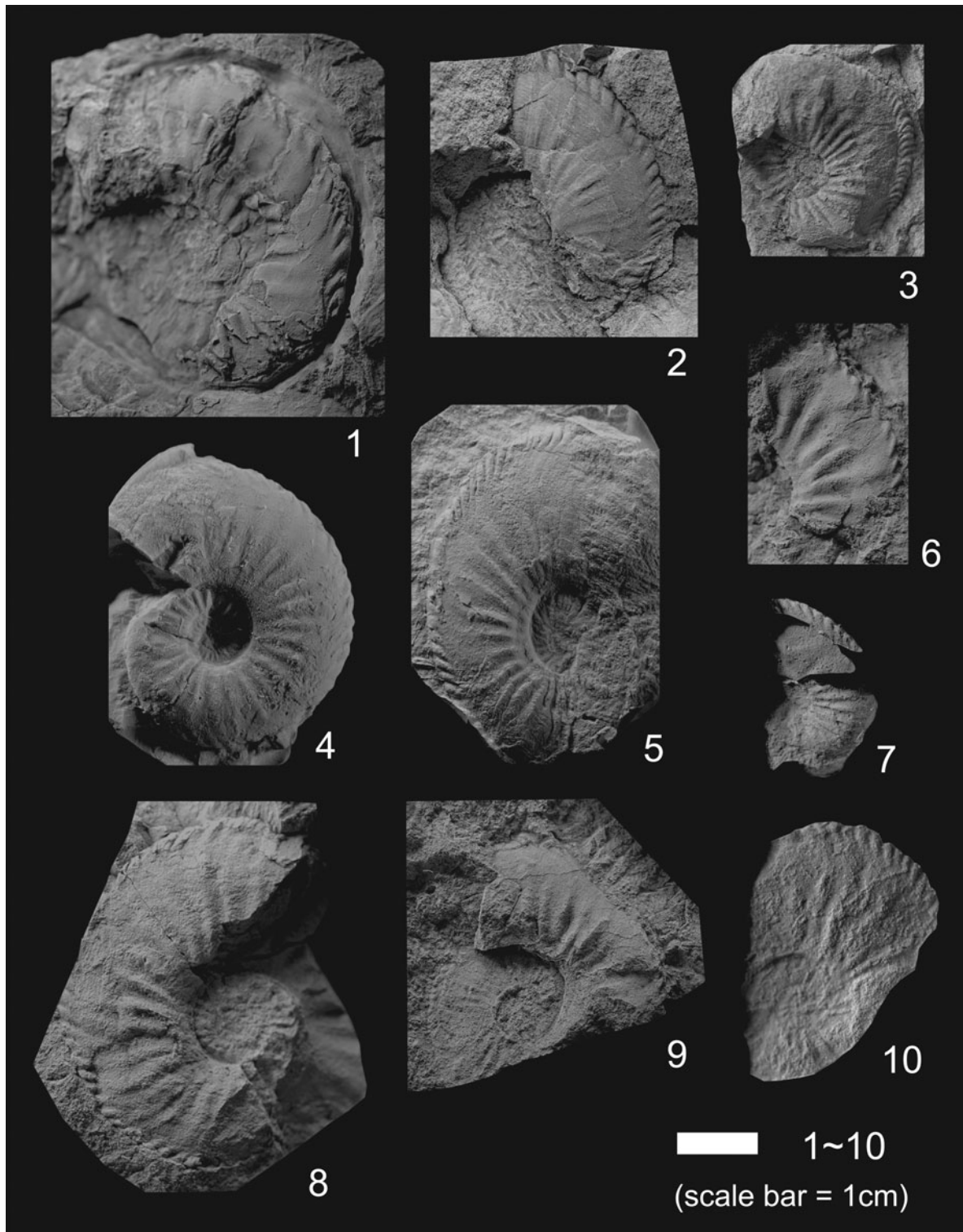


Figure 5. *Amaltheus margaritatus* from Japan. The locality and the repository data are shown in Table 1. (1) NU-MM0076. (2) NU-MM0005. (3) NU-MM0006. (4) MM2791 (rubber cast). (5) MM2792 (rubber cast). (6) FMM2009. (7) NU-MM0007. (8) FMM2007. (9) FMM2008. (10) FMM3051-2 (rubber cast).

the *Pleuroceras spinatum* Zone in the Northwest European zonation, late Pliensbachian.

Amaltheus margaritatus was distributed mainly in high-latitude areas of the Northern Hemisphere, approximating to the Boreal Realm in the late Pliensbachian, as follows. It has been documented from the Northwest European province, the

Caucasus (Georgia), West Asia (Alborz Province in Iran), East Asia (Japan), the North American Cordillera (British Columbia), and Russia (the northeast, the Siberian Platform, and the Far East regions). In addition, a few specimens of this species have been recognized in the Mediterranean province (Sicily in Italy, and Algeria and Morocco in North Africa).

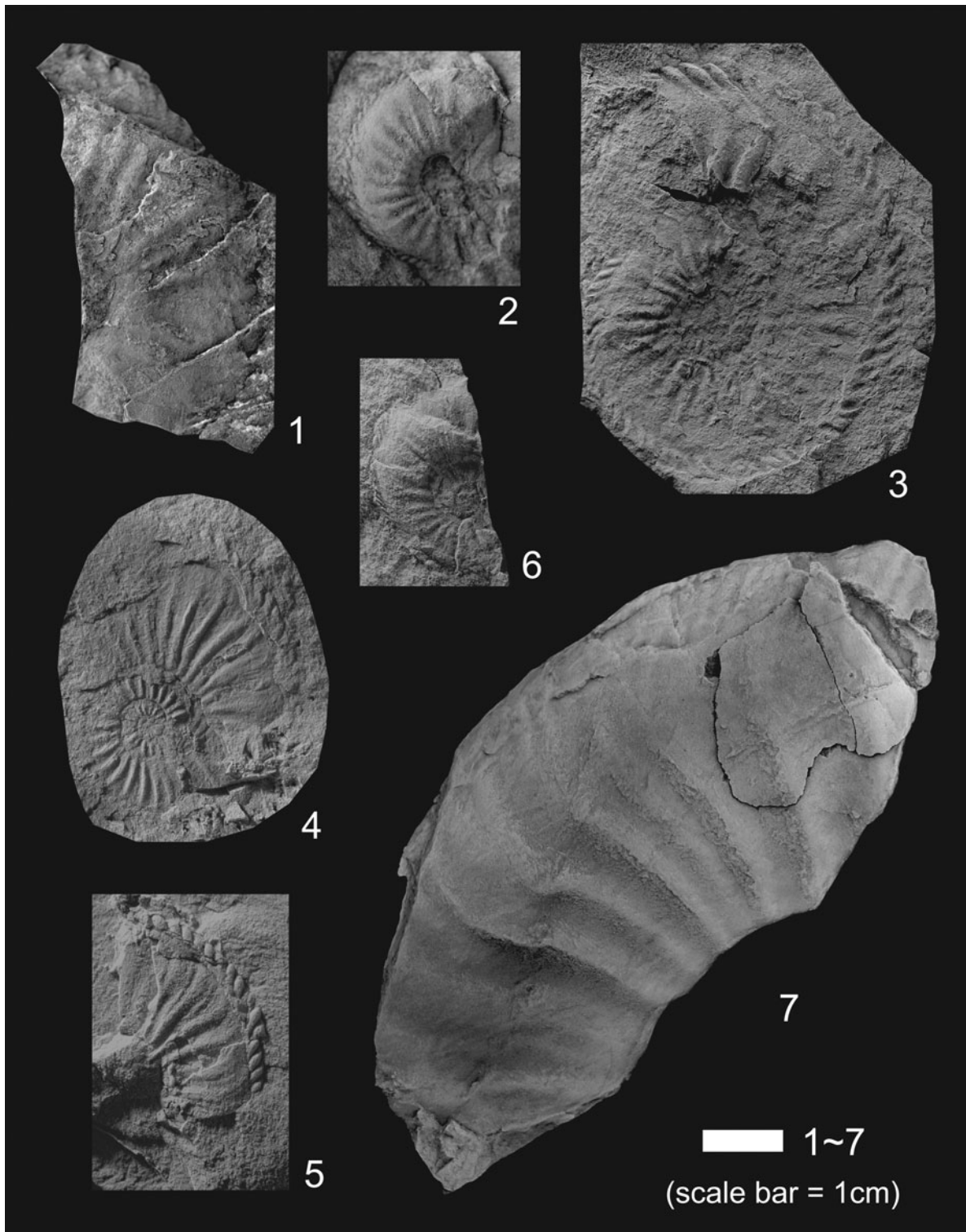


Figure 6. *Amaltheus* from Japan. The locality and the repository data are shown in Table 1. (1–5) *Amaltheus margaritatus*: (1) NU-MM0011; (2) TOTA-Fo-3015; (3) FMT0001; (4) NU-MM0077 (rubber cast); (5) NU-MM0078 (rubber cast). (6) *Amaltheus* sp. cf. *A. margaritatus*, NU-MM0004. (7) *Amaltheus* sp. indet., NU-MM0008.

Description.—The whorls are moderately involute and enlarge rapidly, and the umbilici are narrow. Detailed characteristics of the whorl section are unknown because of compression. The venter bears a well-developed and elevated keel with fine crenulation. The present species from Japan has characteristic

ribbing. On the inner whorl, the radial and slightly sigmoidal ribs starting from the umbilical edge are well developed in the middle of the flank and tend to disappear near the venter, but do not completely fade out. They are projected forward strongly in the upper part of the flank until the keel, but each serration of the

crenulated keel is not connected with the ribs. The ribs weaken and finally fade on the outer whorl. NU-MM0005 (Fig. 5.2) displays some longitudinal striae on the whorl's flank. Tubercles on the ribs are not visible in this species.

Materials.—Eleven specimens (NU-MM0005, NU-MM0006, NU-MM0076, NU-MM0007, FMM2007, FMM2008, FMM2009, FMM3051-2, MM2791 [IT5303-1a; Sato, 1955], MM2792 [IT5303-1; Sato, 1955], and TOTA-Fo-3015) from the Teradani Formation of the Kuruma Group and three specimens (NU-MM0077 [SA36-1-1; Nakada and Matsuoka, 2011], NU-MM0078 [SA36-1-2; Nakada and Matsuoka, 2011], and FMT0001) from the Nishinakayama Formation of the Toyora Group.

Remarks.—On the basis of recognizable characteristics of surface ornament and keel, all of the materials identified as the present species are similar to the *Amaltheus* from Europe (defined as *A. margaritatus* form *margaritatus* in Meister, 1988). The present species is distinguished from *A. stokesi* by characteristics of the ribbing and keel, as mentioned in the preceding.

The Japanese specimens of *Amaltheus margaritatus* are quite similar to those described by Dagens (1976, pl. 1–3) from the Northeast Russian region. However, the Northeast Russian specimens, especially those shown in Dagens (1976, pl. 2, fig. 2, pl. 3, fig. 1), have more evolute whorls and less-developed (thicker and round) keels. Thus, these specimens are excluded from the synonymy of *A. margaritatus* in this taxonomic analysis.

Amaltheus conspectus Dagens, 1976 is similar to the present species in terms of ribbing characteristics, but it differs in that it has quite involute coiling of the whorls (e.g., Dagens, 1976, pl. 12, figs. 4, 5) and connections between the serration of the crenulated keel and the ribs (Dagens, 1976, pl. 13, fig. 2).

Amaltheus margaritatus also has some affinities with *A. talrosei* Repin, 1968, which likely represents varieties of *A. margaritatus*. However, *A. talrosei* is distinguishable from the present species by the more evolute whorl and stronger projection of the ribs in the ventrolateral part (Dagens, 1976, pl. 7, fig. 1).

The specimens collected from the *japonica* Zone of the Nishinakayama Formation, Toyora Group (NU-MM0077, Fig. 6.4; NU-MM0078, Fig. 6.5), and some specimens from the Teradani Formation (e.g., NU-MM0076, Fig. 5.1; NU-MM0011, Fig. 6.1) are characterized by an elevated and individual keel with well-prorsiradiated serrations and the direct connection between some ribs and the serrations of the crenulated keel. These characteristics are limited to the specimens obtained from the *apyrenum* Subzone of the Northwest European province (e.g., Meister, 1988, pl. 4, fig. 3). The *japonica* Zone proposed by Nakada and Matsuoka (2011) in the Toyora Group was correlated with the *apyrenum* Standard Subzone on the basis of the occurrence of some specimens of *Amaltheus margaritatus* exhibiting these morphological characters.

A specimen obtained from the Kuruma Group, NU-MM0004 (Fig. 6.6), has some affinities with the present species—for example, the relatively fine serration of the crenulated keel. However, this specimen is small with inadequate preservation of ventrolateral surface ornament. In this description, the specimen is treated as *Amaltheus* cf. *A. margaritatus*.

A specimen derived from the Teradani Formation, Kuruma Group, NU-MM0008 (Fig. 6.7; Table 1) is similar to the present species in terms of ribbing characteristics, but lacks a venter and an inner whorl. Thus, this specimen is described as *Amaltheus* sp. indet. in this study.

Amaltheus repressus Dagens, 1976

Figure 7.7, 7.8

1976 *Amaltheus* (*Proamaltheus*) *repressus* Dagens, p. 24, pl. 11, figs. 1–5.

Type.—The holotype, no. 517–50, from Omolon Massif, Northeast Russia, was illustrated by Dagens (1976, pl. 11, fig. 2).

Diagnosis (modified from Dagens, 1976).—The whorls are slightly involute. The flat whorl flanks have strong ribs that are radial along the dorsal part and curve forward in the ventrolateral part. This species characteristically exhibits a large number of constrictions. The venter bears a slightly developed keel with crenulations independent of ribs.

Occurrence.—*Amaltheus repressus* co-occurs with *A. stokesi* in the Northeast Russian region, and thus the range of *A. repressus* is correlated with the *Amaltheus stokesi* Standard Subzone of the *margaritatus* Standard Zone, earliest late Pliensbachian (Dagens, 1976).

The present species was distributed in the Northeast Russian region and East Asia (Japan).

Description.—The whorls are moderately involute and expand rapidly; thus, the umbilicus is relatively narrow (Fig. 8). Details of the whorl section are unknown. The venter bears a weak and crenulated keel, and the crenulations are very fine and prorsiradiated. However, surface ornaments on the whorl flank are generally weak. The present species is characterized by the presence of constrictions. On the early whorl of specimen NU-MM0079 (Fig. 7.7), the radial and irregular ribs starting from the umbilical edge are well developed in the inner half of the whorl and weaken rapidly toward the venter. They project strongly forward in the ventrolateral part and are connected to the keel. A slightly sigmoidal constriction is developed on the whorl flank, and it also projects strongly onto the ventrolateral part. In the outer whorls on specimen NU-MM0009 (Fig. 7.8), the ribs become very weak, and two constrictions per 45° of a whorl are developed near the aperture.

Materials.—Two specimens, NU-MM0009 and NU-MM0079, from the Teradani Formation, Kuruma Group.

Remarks.—In previous studies, characteristic Russian species of *Amaltheus* were recognized outside Russia only in the North American Cordillera. Imlay (1955) and Smith et al. (2001) described a Russian species, *A. viligaensis* (Tuchkov, 1954), from Alaska. The occurrence of the present species is the first recorded occurrence of the Russian *Amaltheus* outside of Russia.

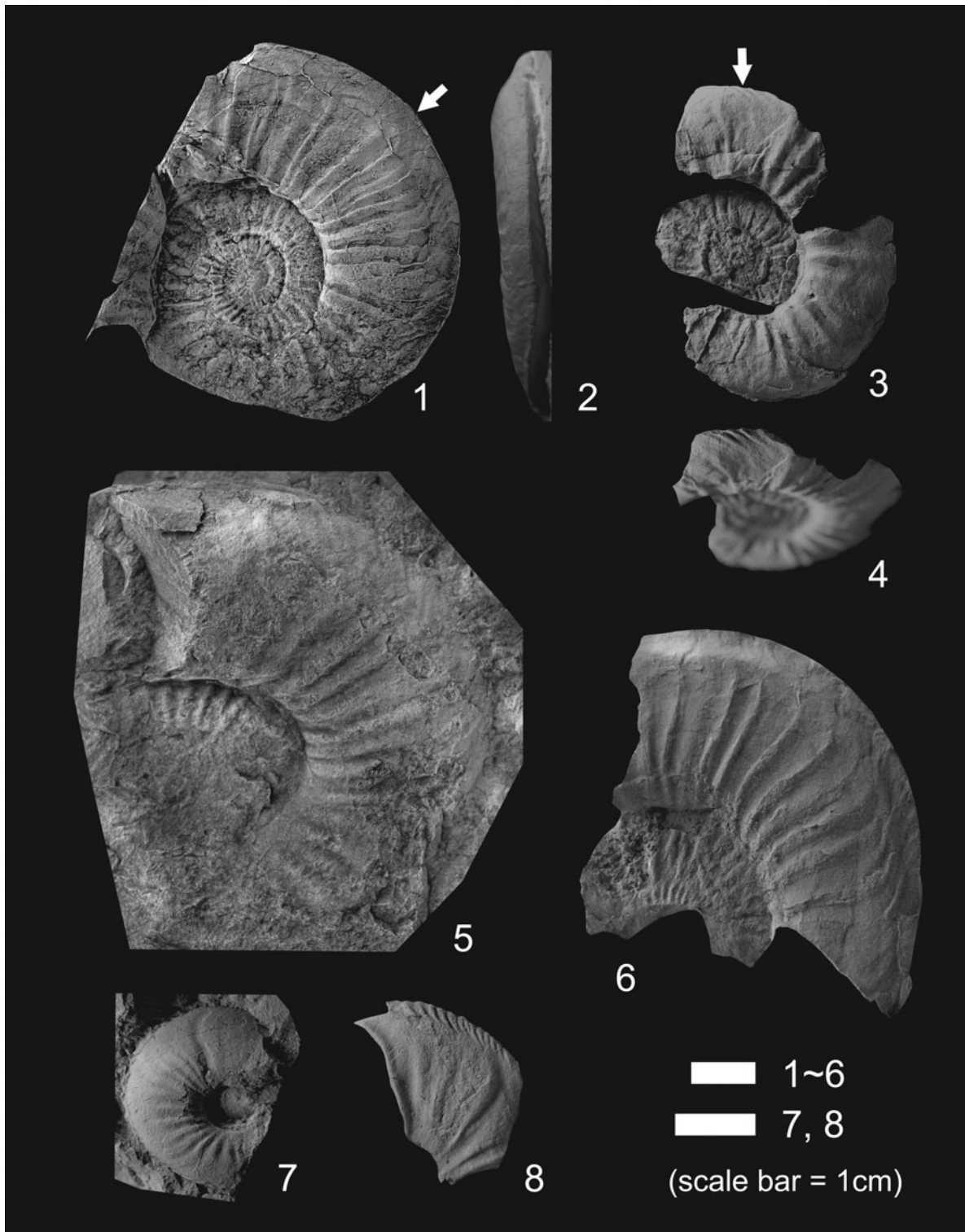


Figure 7. *Amaltheus* from Japan. The locality and the repository data are shown in Table 1. (1–6) *Amaltheus orientalis* n. sp.: (1, 2) TOYA-Fo-2974: (1) lateral view; (2) ventral view of gypsum cast photographed from the direction of the arrow of (1); (3, 4) NU-MM0010: (3) lateral view; (4) ventral view photographed from the direction of the arrow of (3); (5) TOYA-Fo-2986; (6) NMNS PM23448. (7, 8) *Amaltheus repressus*: (7) NU-MM0079 (rubber cast); (8) NU-MM0009.

The present species is similar to *Amaltheus margaritatus* and *A. conspectus* in surface ornament (e.g., the slightly sigmoidal, irregular, and weak ribbing and the strongly prorsiradiate crenulation of the keel). However, the former is distinguished from the latter by the presence of constrictions.

Amaltheus orientalis new species

Figure 7.1–7.6

Type.—The holotype, TOYA-Fo-2974, and two paratypes, TOYA-Fo-2986 and NU-MM0010, were collected from the

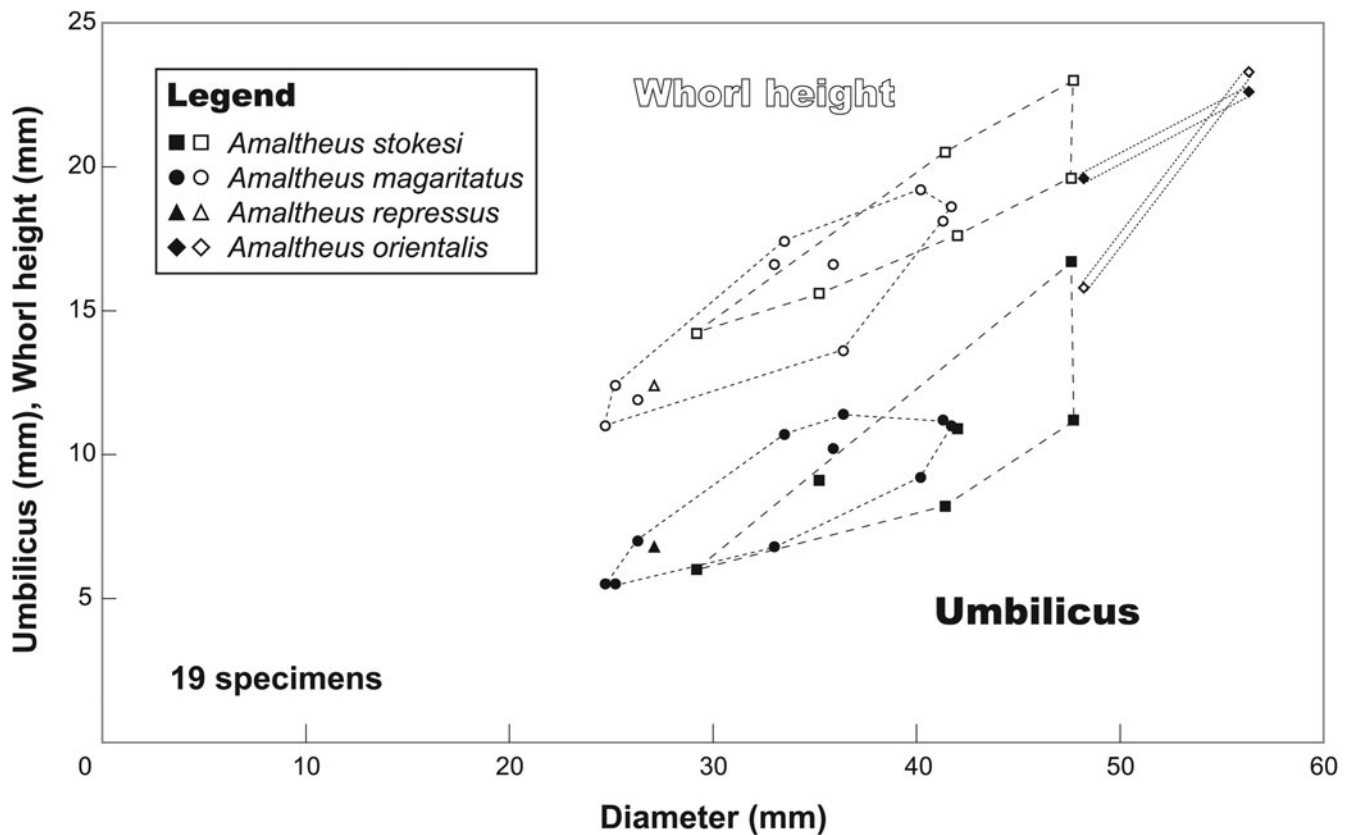


Figure 8. Variation in whorl height and umbilical width of *Amaltheus* specimens from Japan.

fossil localities Sakai River 2 and 3 (Fig. 2; Table 1). Another paratype, NMNS PM23448, is from Loc. 5303 (shown in Sato, 1955) along the Teradani Valley.

Diagnosis.—The whorls are moderately evolute. The whorl flanks have quite irregular, rigid (strong and rather tense), and generally radial ribs that are characterized by a strong projection in the ventrolateral portion. The ribs are irregular with some intercalations. The venter bears a not developed (thick and round) keel with coarse crenulations.

Occurrence.—The detailed biostratigraphic distribution of the present endemic species is difficult to discuss because no index taxa have been obtained from the Sakai River 2 section (Fig. 2). However, NMNS PM23448 (Fig. 7.6) co-occurs with *Amaltheus margaritatus* (MM2791, Fig. 5.4; MM2792, Fig. 5.5) and *Canavaria* sp. ex gr. *geyeriana* (Haas, 1913) from Loc. 5303 (Sato, 1955) along the Teradani Valley (Fig. 1). On the basis of the biostratigraphic range of these latter two taxa (e.g., Howarth, 1958; Repin, 1968; Dagens, 1976; Meister, 1988), the range of the present species seems to be comparable to the *subnodosus* Standard Subzone of the *margaritatus* Standard Zone to the *spinatum* Standard Zone, equal to the *margaritatus* and the *Canavaria* assemblage zones of the Kuruma Group (see Figs. 2, 9).

The present species is found only in East Asia (Kuruma Group, central Japan).

Description.—The whorls are moderately evolute (Fig. 8). The umbilici are relatively large and shallow with steep umbilical edges, as seen in TOYA-Fo-2974 (Fig. 7.1). The whorl sections seem to be subelliptical with flat flanks, recognized in the holotype (TOYA-Fo-2974; Fig. 7.1), but details are unknown because of compression. The venter bears a broad and round keel.

This species' surface ornaments show some intraspecific variations. First, the serrations of the crenulation are generally weak, fine, and strongly prorsiradiated (e.g., Fig. 7.1, 7.2, 7.6), but NU-MM0010 partly has coarse and strong serrations (Fig. 7.3, 7.4). Second, most ribs are radial, wide, strong, quite irregular, and projected toward the aperture on the dorsolateral edge, typically in the holotype (TOYA-Fo-2974; Fig. 7.1). However, the ribbing of NMNS PM23448 (Fig. 7.6) is partly rursiradiate near the umbilical edge and slightly projected backward at the dorsolateral part. Finally, the rib density also shows some variation. The holotype (Fig. 7.1) has a relatively high rib density with some intercalated ribs (19 ribs on half an outer whorl); however, NU-MM0010 (Fig. 7.3), TOYA-Fo-2986 (Fig. 7.5), and NMNS PM23448 (Fig. 7.6) are characterized by coarser and stronger ribbings without intercalations (16 ribs on half an outer whorl in TOYA-Fo-2986; Fig. 7.5).

The ribs start from the umbilical edge and become strong near the inner flank. They tend to disappear from the middle to the outer flank and are projected forward strongly in the ventrolateral part. Some of them pass through onto the

Northwest European Province (Dean et al., 1961; Dommergues et al., 1997; Page, 2003)			Northeast Russian Province (modified from Repin, 1968, 2009, 2016, 2017)	Kuruma Group (This study)	Toyora Group (Nakada and Matsuoka, 2011; This study)
Stage	Standard Zone	Standard Subzone	Zone	Assemblage Zone	Zone/ Assemblage Zone
Upper Pliensbachian	<i>Pleuroceras spinatum</i>	<i>P. hawskerense</i>	? <i>A. extremus</i>	(Canavaria)	<i>Canavaria japonica</i>
		<i>Pleuroceras apyrenum</i>	<i>Amaltheus viligaensis</i>		
	<i>Amaltheus margaritatus</i>	<i>Amaltheus gibbosus</i>	<i>Amaltheus talrosei</i>	<i>Amaltheus margaritatus</i>	
		<i>Amaltheus subnodosus</i>			
		<i>Amaltheus stokesi</i>	<i>Amaltheus stokesi</i>		

Figure 9. Biostratigraphic correlation for assemblage zones of the Teradani Formation recognized in this study with the upper Pliensbachian zonal schemes of the Northwest European province, the Northeast Russian region, and the Toyora Group area.

crenulated keel and constitute a part of the serrations. The present species has no tubercles, spines, or constrictions on the surface ornament.

Etymology.—The species name is derived from their distribution area, the oriental region (western Panthalassa area).

Materials.—The four specimens mentioned in the preceding are from the Teradani Formation, Kuruma Group.

Remarks.—The present species is quite similar to *Amaltheus talrosei*, described only from the Northeast Russian region by Repin (1968) and Dagis (1976). It displays evolute coiling, strongly prorsiradiate serration of the crenulated keel, the connection between the ribs and the serration of the keel, and the strong projection of ribs in the ventrolateral part. However, the present species has stronger and more irregular ribbing (see the holotype of the present species illustrated in Fig. 7.1) than *A. talrosei*, typical forms of which are illustrated by Dagis (1976, pl. 6, figs. 2–6). Consequently, the present new species from East Asia is closely related to *A. talrosei* from the Northeast Russian region.

The present species, especially TOYA-Fo-2974 (Fig. 7.1), is very similar to *Amaltheus sensibilis* (illustrated by Dagis, 1976, pl. 4, fig. 1), another of the endemic species of the Northeast Russian region, in the rursiradiate, strong, and wide ribbing and the evolute coiling. Nevertheless, the present new species is different from *A. sensibilis* by its irregular ribbing, most typical in the holotype (TOYA-Fo-2974) and the larger umbilicus.

The present species is similar to some Russian species, *Amaltheus (Nordamaltheus?) molodoensis* Repin, 2017 (pl. 1,

figs. 2, 12) and *Amaltheus striatus asiaticus* Repin, 1974 (see Repin, 2009), in terms of ribbing characteristics. However, the present new species is distinguishable from these species by the more evolute whorl.

Some specimens of the present species, TOYA-Fo-2974 (Fig. 7.1) and NU-MM0010 (Fig. 7.3), also have some affinities with *A. margaritatus* and *A. viligaensis* in terms of the characteristics of the ribbing; both of the latter species are characterized by weak and irregular sinuous ribs. In addition, *A. viligaensis* (e.g., Tuchkov, 1954, pl. 37, fig. 3; Repin, 1968) is similar to present species in the irregular ribbings. However, the present species is distinguishable from these two species by its more evolute whorl and the stronger projection of its ribs in the ventrolateral part.

The present specimens, especially NU-MM0010 (Fig. 7.3), are similar to *Amaltheus (Nordamaltheus?) borealis* Dagis, 1976 and *Amaltheus (Nordamaltheus?) bulunensis* Repin, 1968 (pl. 36, fig. 1) in terms of ribbing and crenulation characteristics. However, the present species differs from those Russian species in that it has more evolute whorl.

Biostratigraphic remarks

In previous studies, the Teradani Formation of the Kuruma Group has been thought to approximate to the upper Pliensbachian on the basis of the occurrence of *Amaltheus* sp. indet. and *Canavaria* sp. ex gr. *geyeriana* (Sato, 1955, 1992). However, detailed ammonoid biostratigraphy has not been discussed for the Kuruma Group because of difficulty in specific identification with the specimens' poor preservation and unrepresented fossil-bearing horizons. In the *Amaltheus* species identified in this study from the Kuruma Group, *A. stokesi* and *A. repressus*

co-occurred in the Northeast Russian *Amaltheus stokesi* Zone, which is correlated with the *stokesi* Standard Subzone (Fig. 9) (Dagis, 1976; Repin, 2009), and were not coeval with the longer range of *A. margaritatus*, which extends from the *subnodosus* through the *apyrenum* standard subzones (Fig. 9). On the basis of this biostratigraphic distribution, two successive *Amaltheus*-based assemblage zones are recognized in the Teradani Formation: in ascending order, the *Amaltheus stokesi*–*Amaltheus repressus* and the *margaritatus* assemblage zones (Fig. 9). As mentioned in the preceding, the range of *Amaltheus orientalis* n. sp. seems to be correlated with the *margaritatus* Assemblage Zone and the overlying *Canavaria* Assemblage Zone, which are middle–late late Pliensbachian (Figs. 2, 9). In addition, the occurrence of *A. stokesi* in the lowermost part of the Teradani Formation (Fig. 2) clearly demonstrates that the base of this formation biostratigraphically corresponds to the earliest late Pliensbachian.

In the Toyora Group, four successive ammonoid zones, the *japonica*, the *paltus*, the *helianthoides*, and the *inouyei* zones, in ascending order, were proposed for the Lower Nishinakayama Formation by Nakada and Matsuoka (2011). The lowermost part of the *japonica* Zone was characterized by a form of *A. margaritatus* (Fig. 6.4, 6.5) that is typical of the *apyrenum* Standard Subzone, as mentioned. The same morphological characteristics are also recognized in some specimens of *A. margaritatus*

obtained from the Kuruma Group (see the description of this species). Therefore, the late specimens of *A. margaritatus* from the Kuruma Group are probably coeval with the early fauna of the *japonica* Zone (Fig. 9) and are thus included in the overlying *Canavaria* Assemblage Zone. Moreover, in this study, the *Amaltheus stokesi* Assemblage Zone is newly established in the Higashinagano Formation (Fig. 9) on the basis of the occurrence of *A. stokesi* (GK.G.11293; Fig. 4.3). The faunal association of this assemblage zone is similar to that of the *stokesi*–*repressus* Assemblage Zone in the lowermost Teradani Formation proposed in this study (Fig. 9).

Paleobiogeographic remarks

The paleobiogeographic distribution of *Amaltheus* is shown in Figure 10. The species of *Amaltheus* were divided into three groups—the pan-Boreal, the Northwest European, and the Arctic groups—on the basis of their paleobiogeographic distributions. The pan-Boreal group, represented by *A. stokesi*, *A. bifurcus*, and *A. margaritatus*, has been recognized across the Boreal Realm, including in the Northwest European province, the North American Cordillera, the Canadian Arctic, Russia, and Asia (Japan and Iran). The Northwest European group, represented by *A. margaritatus* form *subnodosus* (Young and Bird, 1828) and *A. margaritatus* form *gibbosus* (Schlotheim,

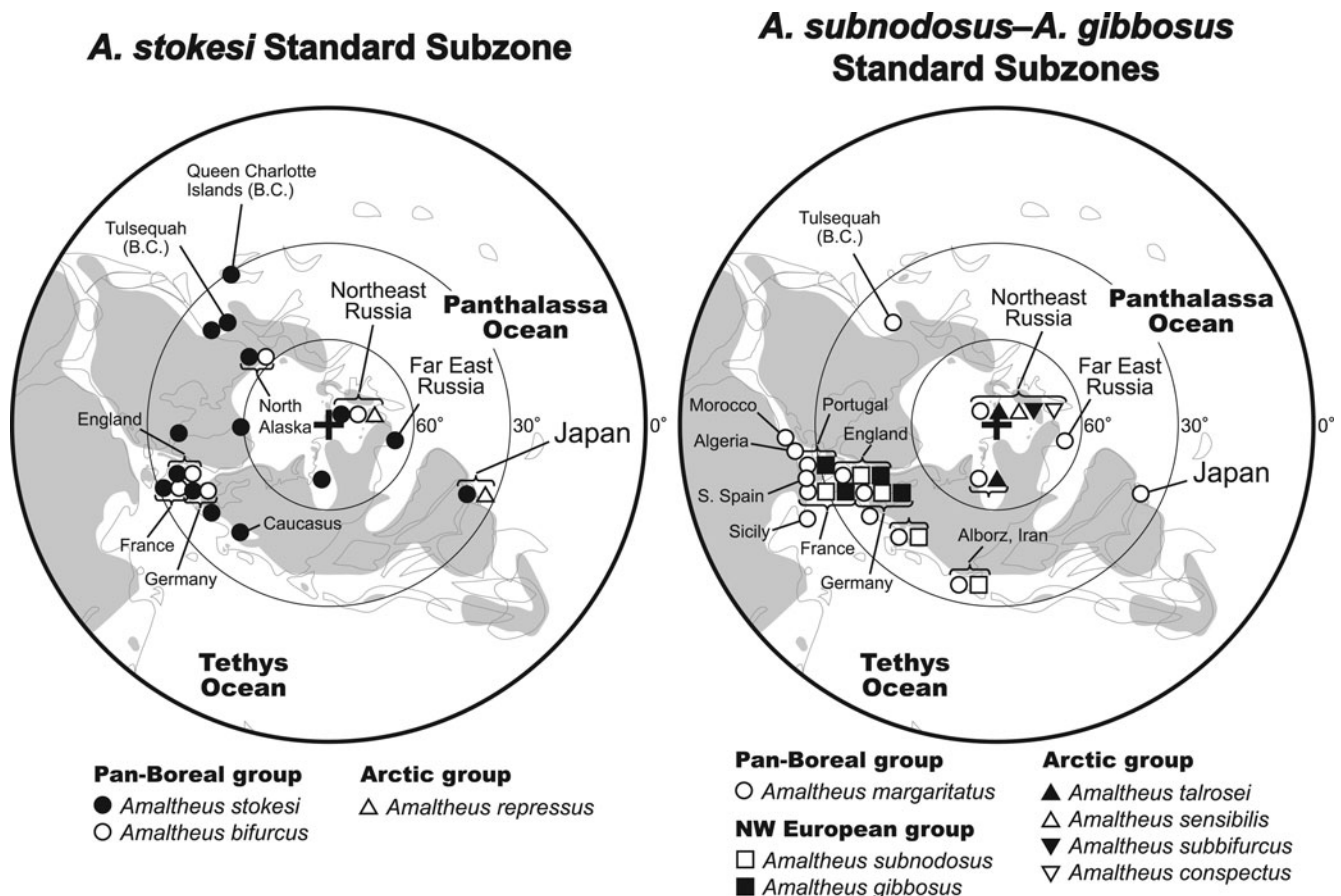


Figure 10. Specific distribution of *Amaltheus* spp. in the *stokesi* and the *Amaltheus gibbosus*–*Pleuroceras apyrenum* standard subzones, the Northwest European *margaritatus* Standard Zone. The paleogeographic map of late Early Jurassic is modified from the reconstructions of Smith and Briden (1977), Damborenea (2002), Golonka (2007), and Dera et al. (2009).

1820), evolved from *A. stokesi* or *A. bifurcus*, and their distribution was limited to the Northwest European province (Meister, 1988). The Arctic group, represented by *A. repressus*, *A. talrosei*, *A. sensibilis*, *A. viligaensis*, *A. conspectus*, and *A. subbifurcus*, also developed from the pan-Boreal group (Dagis, 1976). But they were distributed only in the Russian provinces, except for the occurrences of *A. viligaensis* in Alaska (Imlay, 1955) and a species formerly considered a Russian endemic reported from Japan in this study (Fig. 10).

In the *stokesi* Standard Subzone, the faunal composition from the Teradani Formation is characteristic of mixing of the pan-Boreal group, *A. stokesi*, and the Arctic group, *A. repressus*. This faunal association is recognized only in the Japanese assemblage (this study) and the Northeast Russian assemblage (e.g., Dagis, 1976) during this time interval, and other faunas, such as the Northwest European province and the North American Cordillera, are composed of only the pan-Boreal group (Fig. 10). This faunal similarity shows a high paleobiogeographic correlation between the East Asian and the Northeast Russian faunas throughout the *margaritatus* Standard Zone. Smith et al. (2001) suggested that the Arctic and northern North Atlantic (Viking Corridor) were the main dispersal routes of *Amaltheus* because of the poor occurrence of this genus from eastern Eurasia. The presence of the remarkable Amaltheinae assemblage from East Asia described in this study, which exhibit specific diversity equal to or higher than that of the coeval North American Cordillera fauna, probably indicates a strong Boreal influence from the Arctic to the middle-latitude areas of the western Panthalassa during the *margaritatus* Standard Zone. In addition, the morphological diversity of *A. margaritatus* was also recognized in middle- to low-latitude areas within the *margaritatus* Standard Zone. In North Africa, *A. gr. margaritatus* form *volubilis* and *A. gr. margaritatus* form *idris-sensis* have some homeomorphic ornamentations of *A. stokesi*, fine and delicate ornaments (no tubercles) with a slightly rounded and not-individual venter, but they clearly correspond to the *margaritatus* Standard Zone (Dommergues and Meister, 2017). These diversifications in Russia, Japan, and North Africa suggest that wide geological expansion seemed to increase endemism in *Amaltheus* during this period.

Conclusion

The taxonomy of Japanese *Amaltheus* is analyzed using already-reported collections and specimens newly obtained from the Kuruma and Toyora groups. Four species, including a new species, are described from the Kuruma Group in central Japan as follows: *A. stokesi* (Sowerby, 1818), *A. margaritatus* de Montfort, 1808, *A. repressus* Dagis, 1976, and *A. orientalis* n. sp. The first two species are also recognized in the Toyora Group in southwest Japan.

On the basis of the taxonomic analysis, two successive *Amaltheus* assemblage zones are recognized in the Lower Teradani Formation of the Kuruma Group: the *stokesi*–*repressus* and *margaritatus* assemblage zones. The former assemblage zone biostratigraphically corresponds to the *stokesi* Assemblage Zone, newly established in the Higashinagano Formation of the Toyora Group. The range of the late-type *A. margaritatus*

from the Kuruma Group is perhaps coeval with the early fauna from the *japonica* Zone of the Toyora Group.

The faunal composition of the Japanese ammonoid assemblage from the lower upper Pliensbachian is characterized by mixing of pan-Boreal and Arctic *Amaltheus* species and is quite similar to that of the Northeast Russian region. This affinity suggests a high paleobiogeographic similarity between the East Asian and the Northeast Russian faunas throughout this time interval.

Acknowledgments

We thank T. Sato (Tsukuba University) for providing us with information about the Kuruma Group fossil localities. We also thank K. Miyakita (Niigata City), M. Kawaguchi (Koriyama City), K. Nagata (Niigata City), K. Terabe (JX Nippon Oil & Gas Exploration), H. Ishida (Mine City), Y. Kubo (Nagano City), and T. Aoki (Kawasaki City) for offering abundant ammonoid specimens.

We are grateful to T. Sasaki (University Museum, University of Tokyo), Y. Ibaraki (Fossa Magna Museum), Y. Shigeta (National Museum of Nature and Science), and Y. Tanaka (Toyama Science Museum, retired) for providing access to samples considered in this study.

We thank J. Bardin and T. Poulton for their constructive comments on the manuscripts as the reviewers. We also thank K. Tanabe (University of Tokyo), P. Neige (University of Burgundy), G. Dera (University of Burgundy), and J. Guex (University of Lausanne) for their helpful comments.

References

- Bardin, J., Rouget, I., and Cecca, F., 2013, Late Pliensbachian (Early Jurassic) ammonites from Lac de Charmes (Haute-Marne, France): systematic, biostratigraphy and palaeobiogeography: *Geodiversitas*, v. 35, p. 309–334.
- Bardin, J., Rouget, I., and Cecca, F., 2017, Ontogenetic data analyzed as such in phylogenies: *Systematic Biology*, v. 66, p. 23–37.
- Buckman, J., 1845, *Outline of the Geology of the Neighbourhood of Cheltenham*: London, John Murray, 109 p.
- Callomon, J.H., and Gradinaru, E., 2005, From the thesaurus of the museum collections I, Liassic ammonites from Munteana (Svinita Zone, Southern Carpathians, Romania): *Acta Palaeontologica Romaniaae*, v. 5, p. 49–65.
- Cuvier, G., 1798, *Tableau élémentaire de l'histoire naturelle des animaux*: Paris, Baudouin, 710 p.
- Dagis, A.A., 1976, Late Pliensbachian Ammonites (Amaltheidae) of the North Siberia: Academy of Sciences of the USSR, Siberian Branch, *Transactions of the Institute of Geology and Geophysics*, issue 309, 77 p. [in Russian]
- Damborenea, S.E., 2002, Jurassic evolution of Southern Hemisphere marine palaeobiogeographic units based on benthonic bivalves: *Geobios*, v. 35, suppl. 1, p. 51–71.
- Dean, W.T., Donovan, D.T., and Howarth, M.K., 1961, The Liassic ammonite zones and subzones of the North-West European Province: *Bulletin of the British Museum (Natural History), Geology*, v. 4, p. 435–505.
- de Montfort, D., 1808, *Conchyliologie systématique et classification méthodique des coquilles*: Paris, F. Schoell, 410 p.
- Dera, G., Pellenard, P., Neige, P., Deconinck, J.-F., Pucéat, E., and Dommergues, J.-L., 2009, Distribution of clay minerals in Early Jurassic Peritethyan seas: palaeoclimatic significance inferred from multiproxy comparisons: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 271, p. 39–51.
- Dommergues, J.-L., 1987, L'évolution chez les Ammonitina du Lias moyen (Carixien, Domérien basal) en Europe occidentale: *Documents des Laboratoires de Géologie de Lyon*, v. 98, 297 p.
- Dommergues, J.-L., 2002, Les premiers Lytoceratatoidea du Nord-Ouest de l'Europe (Ammonoidea, Sinémurien inférieur, France). Exemple de convergence évolutive vers les morphologies “capricornes”: *Revue de Paléobiologie*, v. 21, p. 257–277.
- Dommergues, J.-L., and Meister, C., 1999, Cladistic formalisation of relationships within a superfamily of Lower Jurassic Ammonitina: Eoderocerataceae: *Revue de Paléobiologie*, v. 18, p. 273–286.

- Dommergues, J.-L., and Meister, C., 2017, Ammonites du Jurassique inférieur (Hettangien, Sinémurien, Pliensbachien) d'Afrique du Nord (Algérie, Maroc et Tunisie), Atlas d'identification des espèces: *Revue de Paléobiologie*, v. 36, p. 189–367.
- Dommergues, J.-L., Meister, C., and Mouterde, R., 1997, Pliensbachian, in Cariou, E., and Hantzpergue, P., eds., *Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles: Groupe français du Jurassique*, Bulletin des Centres de Recherches Elf Exploration–Production Elf-Aquitain, Mémoire 17, p. 15–23, 114–119.
- Dommergues, J.-L., Dugué, O., Gauthier, H., Meister, C., Neige, P., Raynaud, D., Savary, X., and Trevisan, M., 2008, Les ammonites du Pliensbachien et du Toarcién basal dans la carrière de la Roche Blain (Fresnay-le-Puceux, Calvados, Basse-Normandie, France). Taxonomie, implications stratigraphiques et paléogéographiques: *Revue de Paléobiologie*, v. 27, p. 265–329.
- Elmi, S., Atrops, F., and Mangold, C., 1974, Les zones d'ammonites du Domérien–Callovien de l'Algérie occidentales 1: Domérien–Toarcién: Lyon, Documents des Laboratoires de Géologie de la Faculté des Sciences, v. 61, 84 p.
- Fauré, P., 2002, Le Lias des Pyrénées: *Strata*, Série 2, v. 39, 761 p.
- Fauré, P., 2006, Le Domérien (Pliensbachien supérieur) des Corbières (Aude, France) Biostratigraphie, évolution sédimentaire, paléogéographie: *Bulletin de la Société d'Etudes scientifiques de l'Aude*, v. 103, p. 29–44.
- Fauré, P., and Teodori, D., 2019, Les ammonites du Pliensbachien des Pyrénées ariégeoises (Zone nord-pyrénéenne, France): étude taxonomique et stratigraphique, implications paléogéographiques: *Revue de Paléobiologie*, v. 38, p. 269–361.
- Frebald, H., 1964, Lower Jurassic and Bajocian Ammonoid faunas of Northwestern British Columbia and Southern Yukon: *Geological Survey of Canada Bulletin*, v. 116, 31 p.
- Frebald, H., 1975, The Jurassic faunas of the Canadian Arctic—Lower Jurassic ammonites, biostratigraphy and correlations: *Geological Survey of Canada Bulletin*, v. 243, 24 p.
- Frebald, H., Mountjoy, E.W., and Tempelman-Kluit, D.J., 1967, New occurrences of Jurassic rocks and fossils in Central and Northern Yukon Territory: *Geological Survey of Canada Paper*, no. 67-12, 35 p.
- Géczy, B., and Meister, C., 1998, Les ammonites du Domérien de la montagne du Bakony (Hongrie): *Revue de Paléobiologie*, v. 17, no. 1, p. 69–161.
- Giebel, C.G., 1852, *Fauna der Vorwelt*, Band 3, Die Cephalopoden: Leipzig, F.A. Brockhaus, 856 p.
- Golonka, J., 2007, Late Triassic and Early Jurassic palaeogeography of the world: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 244, p. 297–307.
- Goto, M., 1983, Some bivalves from the Lower Jurassic Kuruma Group of Central Japan: *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series, no. 130, p. 79–84.
- Goto, M., 1994, Discovery of *Seirocrinus* (an Early Jurassic crinoid) from the Kuruma Group, Toyama Prefecture, Central Japan: *Bulletin of the Toyama Science Museum*, no. 17, p. 91–94.
- Haas, O., 1913, Die Fauna des mittleren Lias von Ballino in Südtirol, pt. 2: Beiträge zur Paläontologie und Geologie Österreichs-Ungarn, v. 26, p. 1–161.
- Hayami, I., and Akahane, H., 1981, A new species of *Plagiostoma* from the Kuruma Group and Domerian transgression in the Inner Zone of southwest Japan: *Bulletin of the Toyama Science Museum*, no. 3, p. 1–6.
- Hirano, H., 1971, Biostratigraphic study of the Jurassic Toyora Group, part 1: *Memoirs of Faculty of Science, Kyushu University, Series D*, v. 21, p. 93–128.
- Hirano, H., 1973a, Biostratigraphic study of the Jurassic Toyora Group, part 2: *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series, no. 89, p. 1–14.
- Hirano, H., 1973b, Biostratigraphic study of the Jurassic Toyora Group, part 3: *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series, no. 90, p. 45–71.
- Hirano, H., Mikami, T., and Miyagawa, H., 1978, Lower Jurassic ammonites from the Higuchi Group, southwest Japan: *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series, no. 112, p. 410–416.
- Housa, V., 1965, Sexual dimorphism and the system of Jurassic and Cretaceous Ammonoidea: *Časopis Národního Muzea*, v. 134, no. 7, p. 33–35.
- Howarth, M.K., 1958, A Monograph of the Ammonites of the Liassic Family Amaltheidae in Britain: London, Palaeontographical Society, 53 p.
- Hyatt, A., 1867, The fossil cephalopods of the Museum of Comparative Zoology: *Bulletin of the Museum of Comparative Zoology*, v. 3, p. 71–102.
- Iba, Y., Sano, S., and Goto, M., 2015, Large belemnites were already common in the Early Jurassic—new evidence from Central Japan: *Paleontological Research*, v. 19, p. 21–25.
- Imlay, R.W., 1955, Characteristic Jurassic mollusks from northern Alaska: *United States Geological Survey Professional Paper*, 274-D, p. 69–96.
- Jakobs, G.K., and Pálffy, J., 1994, Upper Triassic to Middle Jurassic biostratigraphic and facies studies in the Iskut River map area, northwestern British Columbia: *Current Research, Geological Survey of Canada*, Ottawa, no. 1994-E, p. 17–28.
- Johansson, G.G., Smith, P.L., and Gordey, S.P., 1997, Early Jurassic evolution of the northern Stikinian arc: evidence from Laberge Group, northwestern British Columbia: *Canadian Journal of Earth Sciences*, v. 34, p. 1030–1057.
- Kimura, T., and Tsujii, M., 1980–1984, Early Jurassic plants in Japan, part 1–6: *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series, Part 1, no. 119, p. 339–358 (1980); Part 2, no. 120, p. 449–465 (1980); Part 3, no. 124, p. 187–207 (1981); Part 4, no. 125, p. 259–276 (1982); Part 5, no. 129, p. 35–57 (1983); Part 6, no. 133, p. 265–287 (1984).
- Kimura, T., Ohana, T., and Tsujii, M., 1988, Early Jurassic plants in Japan, part 8, supplementary description and concluding remarks: *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series, no. 151, p. 501–522.
- Kobayashi, T., Konishi, K., Sato, T., Hayami, I., and Tokuyama, A., 1957, On the Lower Jurassic Kuruma Group: *Journal of the Geological Society of Japan*, v. 63, p. 182–194. [in Japanese]
- Krymholts, G.Y., Mesezhnikov, M.S., and Westermann, G.E.G., 1988, The Jurassic ammonite zones of the Soviet Union: *Geological Society of America Special Papers*, v. 223, 116 p.
- Kumazaki, N., and Kojima, S., 1996, Depositional history and structural development of the Kuruma Group (Lower Jurassic) on the basis of clastic rock composition: *Journal of the Geological Society of Japan*, v. 102, p. 285–302. [in Japanese]
- Matsumoto, T., and Ono, A., 1947, A biostratigraphic study of the Jurassic Toyora Group, with special reference to ammonites: *Science Reports of the Faculty of Science, Kyushu University, Geology*, v. 2, p. 20–31. [in Japanese]
- Meister, C., 1988, Ontogenèse et évolution des Amaltheidae (Ammonoidea): *Eclogae Geologicae Helvetiae*, v. 81, p. 763–841.
- Meister, C., and Friebe, J.G., 2003, Austroalpine Liassic ammonites from Vorarlberg (Austria, Northern Calcareous Alps): *Beiträge zur Paläontologie*, v. 28, p. 9–99.
- Mouterde, R., Dommergues, J.-L., Meister, C., and Rocha, R.B., 2007, Atlas des fossiles caractéristiques du Lias portugais, IIIa) Domérien (Ammonites): *Ciências da Terra*, v. 16, p. 67–111.
- Nakada, K., 2008, The first Occurrence of *Petraoceras*, Harpoceratinae, Ammonoidea from the Lower Jurassic Toyora Group in Yamaguchi Prefecture, southwest Japan: *Bulletin of the Firefly Museum of Toyota Town*, v. 1, p. 85–91. [in Japanese with English abstract]
- Nakada, K., and Matsuoka, A., 2009, On the Pliensbachian/Toarcian boundary in the Lower Jurassic Toyora Group in southwest Japan: *Volumina Jurassica*, v. 7, p. 47–54.
- Nakada, K., and Matsuoka, A., 2011, International correlation of the Pliensbachian/Toarcian (Lower Jurassic) ammonoid biostratigraphy of the Nishinakayama Formation in the Toyora Group, southwest Japan: *Newsletters on Stratigraphy*, v. 42, p. 89–111.
- Neumayr, M., 1875, Die Ammoniten der Kreide und die Systematik der Ammonitiden: *Zeitschrift der Deutschen geologischen Gesellschaft*, v. 27, p. 854–892.
- Nützel, A., Schneider, S., Hülse, P., Kelly, S.R.A., Tilley, L., and Veit, R., 2016, A new Early Jurassic gastropod from Ellesmere Island, Canadian Arctic—an ancient example of holoplanktonic gastropods: *Bulletin of Geosciences*, v. 91, no. 2, p. 1–14.
- Page, K.N., 2003, The Lower Jurassic of Europe: its subdivision and correlation: *Geological Survey of Denmark and Greenland Bulletin*, v. 1, p. 23–59.
- Pálffy, J., and Hart, C.J.R., 1994, Biostratigraphy of the Lower to Middle Jurassic Laberge Group Whitehorse map area (105D), Southern Yukon: *Yukon Exploration and Geological Services Division, Yukon, Indian and Northern Affairs Canada, Part C*, p. 73–86.
- Poulton, T.P., 1991, Hettangian through Aalenian (Jurassic) guide fossils and biostratigraphy, Northern Yukon and adjacent northwest territories: *Geological Survey of Canada*, v. 410, 95 p.
- Pourmotamed, F., and Motamed, A., 1976, Sur l'existence du Domérien marin dans l'Elbourz central (Iran): *Comptes rendus sommaires de la Société Géologique de France*, v. 3, p. 105–108.
- Quenstedt, F.A., 1882–1885, Die Ammoniten des schwäbischen Jura I, Der Schwarze Jura (Lias): Stuttgart, Schweizerbart, 440 p.
- Quenstedt, F.A., 1858, Der Jura: Tübingen, H. Laup, 842 p.
- Rakus, M., and Guex, J., 2002, Les ammonites du Jurassique inférieur et moyen de la dorsale tunisienne: *Mémoires de Géologie*, v. 39, 217 p.
- Repin, Y.S., 1968, Lower and Middle Jurassic ammonites, in Efimova, A.F., Kinasov, V.P., Paraketsov, K.V., Polubotko, I.V., Repin, Y.S., and Dagus, A.S., eds., *Field Atlas of the Jurassic Flora and Fauna of North-East USSR*: Magadan, Ministry of Geology, RSFSR, Severo Vostochnoye Ordena Trydovogo Krasnogo Znamenii Geologicheskoe Vpravlénie, p. 5–18.
- Repin, Y.S., 1974, Amaltheidae representatives from the upper Pliensbachian deposits in the north-eastern parts of the USSR and their stratigraphical significance, in Sachs, V.N., ed., *Biostratigraphy of Boreal Mesozoic*: Academy of Sciences of the USSR Siberian Branch, *Transactions of the Institute of Geology and Geophysics*, v. 136, p. 50–174.
- Repin, Y.S., 2009, The ammonite scale of the upper Pliensbachian of North-East Asia, in Zakharov, V.A., ed., *Third All-Russian Meeting, "Jurassic*

- System of Russia: Problems of Stratigraphy and Paleogeography”: Saratov, Saratov State University, p. 183–186. [in Russian]
- Repin, Y.S., 2016, Lower Jurassic ammonite geologic time scale of Northeast Asia: *Neftegazovaya geologiya Teoriya i praktika*, v. 11, no. 4, p. 1–45. [in Russian]
- Repin, Y.S., 2017, Late Pliensbachian Amaltheidae (Ammonoidea) of the North–East of Asia: Problems of Paleocology and Historical Geocology. Proceedings of the All-Russian Scientific Conference Dedicated to the Memory of Professor V.G. Ocheva, Saratov, p. 73–80. [in Russian]
- Rulleau, L., Guiffroy, A., and Dommergues, J.-L., 2007, Biostratigraphie et paléontologie de la région lyonnaise, Tome II: du socle au Lias moyen: *Lozanne, Géologie-Paléontologie du Comité d’établissement des carrières Lafarge*, 229 p.
- Sato, T., 1955, Les ammonites recueillies dans le groupe de Kuruma, nord du Japon central: *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 20, p. 111–118.
- Sato, T., 1956, Corrélation du Jurassique inférieur japonais en basant sur les Ammonites Fossiles: *Journal of the Geological Society of Japan*, v. 62, p. 490–503. [in Japanese with French abstract]
- Sato, T., 1992, Southeast Asia and Japan, in Westermann, G.E.G., ed., *The Jurassic of the Circum-Pacific*: New York, Cambridge University Press, p. 194–213.
- Schubert, S., 2004, Das Pliensbachium im Grenzbereich Unteres/Oberes Pliensbachium (Carixium/Domerium) von Pödinghausen in der Herforder Liasmulde: *Berichte des Naturwissenschaftlichen Verein für Bielefeld und Umgegend*, v. 44, p. 7–39.
- Sey, I.I., and Kalacheva, E.D., 1980, Biostratigraphy of Lower and Middle Jurassic deposits of the Far East: *VSEGEI Transactions, New Series*, v. 285, 151 p. [in Russian]
- Seyed-Emami, K., Fürsich, F.T., Wilmsen, M., Majidifard, M.R., and Shekarifard, A., 2008, Lower and Middle Jurassic ammonoids of the Shemshak Group in Alborz, Iran and their palaeobiogeographical and biostratigraphical importance: *Acta Palaeontologica Polonica*, v. 53, p. 237–260.
- Smith, A.G., and Briden, J.C., 1977, *Mesozoic and Cenozoic Paleogeographic Maps*: New York, Cambridge University Press, 63 p.
- Smith, P.L., and Tipper, H.W., 1996, Pliensbachian (Lower Jurassic) Ammonites of the Queen Charlotte Islands, British Columbia: *Bulletins of American Paleontology*, v. 348, 122 p.
- Smith, P.L., Tipper, H.W., and Ham, D.M., 2001, Lower Jurassic Amaltheidae (Ammonitina) in North America: paleobiogeography and tectonic implications: *Canadian Journal of Earth Science*, v. 38, p. 1439–1449.
- Sonoda, T., Goto, M., and Terada, K., 2015, Discovery of the Early Jurassic turtle from the Kuruma Group, Central Japan: *Memoir of the Fukui Prefectural Dinosaur Museum*, v. 14, p. 19–24. [in Japanese with English abstract]
- Sowerby, J., 1812–1822, *The Mineral Conchology of Great Britain, Part 1–4*: London, Meredith, 383 p.
- Takeuchi, M., Tokiwa, T., Kumazaki, N., Yokota, H., and Yamamoto, K., 2017, Depositional age of the Lower Jurassic Kuruma Group based on zircon U–Pb age: *The Journal of the Geological Society of Japan*, v. 123, p. 335–350. [in Japanese with English abstract]
- Takizawa, F., 1984, Upper boundary and veneer rock of the Kuruma Group, Hida–Gaien Belt: Abstracts of the 91st Annual Meeting of the Geological Society of Japan, p. 202. [in Japanese]
- Tanabe, K., 1991, Early Jurassic macrofauna of the oxygen-depleted epicontinental marine basin in the Toyora Area, West Japan, in Kotaka, T., Dickins, J.M., McKenzie, K.G., Mori, K., Ogasawara, K., and Stanley, G.D., Jr., eds., *Shallow Tethys*, v. 3: Proceedings of the International Symposium on Shallow Tethys, Sendai, p. 147–157.
- Topchishvili, M., Lominadze, T., Tsereteli, I., Todria, V., and Nadareishvili, G., 2006, Stratigraphy of the Jurassic of Georgia: *Proceedings of the Georgian Academy of Sciences*, new ser. 122, 455 p.
- Tuchkov, I.I., 1954, Jurassic ammonites and belemnites north-east part of USSR: *Data on the Geology and Natural Resources of Northeastern USSR, Magadan*, v. 8, p. 98–125. [in Russian]
- van de Schootbrugge, B., et al., 2018, The Schandelah Scientific Drilling Project: A 25-million year record of Early Jurassic palaeo-environmental change from northern Germany: *Newsletters on Stratigraphy*, v. 52, p. 249–296.
- von Schlotheim, E.F., 1820, *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt*: Gotha, Becker, 499 p.
- von Zittel, K.A., 1884, *Cephalopoda*, in von Zittel, K.A., *Handbuch der Paläontologie, Abteilung 1, Band 2*: München und Leipzig, R. Oldenbourg, p. 329–522.
- Westermann, G.E.G., 1992, *The Jurassic of the Circum-Pacific*: New York, Cambridge University Press, 676 p.
- Young, G.M., and Bird, J., 1828, *A Geological Survey of the Yorkshire Coast: Describing the Strata and Fossils Occurring Between the Humber and the Tees, from the German Ocean to the Plain of York* (second edition): Whitby, G. Clark, 332 p., 17 pls.

Accepted: 18 April 2021