Late Cretaceous Dimorphic Scaphitid Ammonoid Genus Yezoites from the Circum-North Pacific Regions

Author: Tanabe, Kazushige

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Late Cretaceous dimorphic scaphitid ammonoid genus *Yezoites* from the circum-North Pacific regions

KAZUSHIGE TANABE

The University Museum, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan (e-mail: kazu-tanabe@ug.ecc.u-tokyo.ac.jp)

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Abstract. ***Yezoites*** **is a Late Cretaceous (Cenomanian–Campanian) small to very small dimorphic ammonoid genus belonging to the Scaphitidae, whose microconchs have a pair of long lateral lappets at the aperture. Based on examination of previously described material including type and figured specimens and newly recovered ones, five species of *Yezoites* are described herein from the circum-North Pacific regions (Japan, Sakhalin, Kamchatka, Alaska, Oregon, and California); i.e., *Y. perrini* (Anderson), *Y. seabeensis* (Cobban and Gryc), and *Y. puerculus* (Jimbo) from the Turonian, and *Y. pseudoaequalis* (Yabe) and *Y. matsumotoi* (Tanabe) from the Coniacian. Of these species, both microconchs and macroconchs are recognized in *Y. puerculus* and *Y. pseudoaequalis*, whereas only microconchs are known in the other three species. These *Yezoites* species characteristically occur in very fine-grained sandstone to silty mudstone facies suggesting an intermediate between nearshore and offshore environments, and can be used supplementarily for biozonation and correlation of the Turonian and Coniacian deposits in the North Pacific regions.**

Keywords: Ammonoidea, Late Cretaceous, North Pacific, Scaphitidae, taxonomy, *Yezoites*

Introduction

Heteromorph ammonoids of the family Scaphitidae Gill, 1871 are characterized by having a planispirally coiled phragmocone and a loosely coiled body chamber, consisting of a long or short shaft and a terminal hook with a constricted aperture. Species of this family are known worldwide from the upper Albian to the upper Maastrichtian marine strata. Recent data from the Cretaceous–Paleogene sequences in the Atlantic Coastal Plain (USA), the Netherlands, northeast Belgium, and Denmark suggest that some ammonoids including scaphitids (species of *Discoscaphites* and *Hoploscaphites*) have survived for a very short period during the early Danian after the end-Cretaceous bolide impact (see Landman *et al*., 2015 for a recent review).

In the circum-North Pacific regions, taxonomic studies of scaphitid ammonoids were initiated by Jimbo (1894), who described three species from the Turonian of Hokkaido, northern Japan. Shortly thereafter, Anderson (1902) described six new species of *Scaphites* Parkinson, 1811 from the Upper Cretaceous of Oregon and California on the Pacific coasts of the United States. Subsequently, Yabe (1910) described eight species including six new species from the Upper Cretaceous (Turonian–Santonian) strata of Hokkaido, and proposed a new genus, *Yezoites* for species with the internal part of the suture comprising a high internal saddle and small lobes in it. Afterwards, scaphitid ammonoids have been described from the Cenomanian to the Campanian deposits of Japan (Saito, 1962; Tanabe, 1975, 1977a, b; Inoma, 1980; Matsumoto and Yokoi, 1987; Misaki and Maeda, 2009; Inose, 2018), southern Sakhalin (Vereshchagin *et al*., 1965; Tanabe, 1975, 1977a, b; Alabushev and Wiedmann, 1997; Yazykova, 2004; Yazykova *et al*., 2004) and northern Kamchatka (Vereshchagin *et al*., 1965; Alabushev, 1989; Alabushev and Wiedmann, 1994, 1997) of Far East Russia, and Alaska (Cobban and Gryc, 1961) and Pacific coasts (Oregon and California) (Anderson, 1958; Wiedmann, 1965) of the United States.

These previous taxonomic works have shown that the scaphitid ammonoids from the circum-North Pacific regions include two morphotypes in their mature conchs; namely one with a simple constricted aperture and the other with pair of lateral lappets that extend from the constricted aperture. Based on this fact, Wright (1953) proposed the new subfamily Otoscaphitinae for the lappeted scaphitids, in which *Worthoceras* Adkins, 1928 and *Otoscaphites* Wright, 1953 were included.

Meanwhile, Tanabe (1977a) suggested that the two

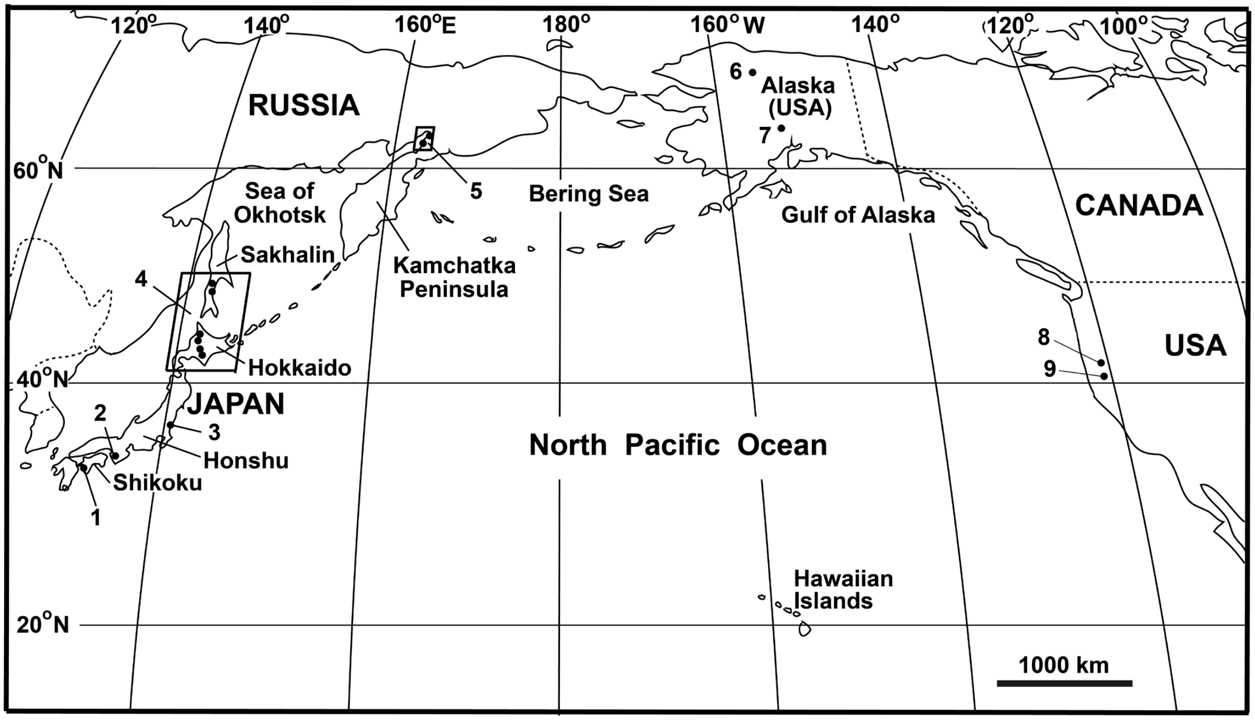

Figure 1. Geographic distribution of *Yezoites* in the circum-North Pacific regions. **1**, Coniacian Furushiroyama Formation, Uwajima area, southwest Japan (Tanabe, 1972, 1977b); **2**, Campanian Toyajo Formation, Aridagawa area, west Japan (Misaki and Maeda, 2009); **3**, Coniacian Ashizawa Formation, Futaba area, northeast Honshu (Saito, 1962; Inose, 2018); **4**, Turonian-Santonian strata of the Yezo Group, Hokkaido and south Sakhalin (Jimbo, 1894; Yabe, 1910; Matumoto, 1942; Vereshchagin *et al*., 1965; Tanabe, 1975, 1977a, b; Alabushev and Wiedmann, 1997; Yazykova, 2004; Yazykova *et al*., 2004); **5**, Turonian (upper part of Penzhina Formation) and Coniacian (upper Penzhinskaya Formation), northern Kamchatka, Far East Russia (Pergament, 1961; Vereshchagin *et al*., 1965; Alabushev, 1989; Alabushev and Wiedmann, 1994, 1997; Zakharov *et al*., 2004, 2005; this study); **6**, Turonian Seabee Formation, northern Alaska (Cobban and Gryc, 1961); **7**, Turonian and Coniacian unit of the Matanuska Formation, Talkeetna Mountains, southern Alaska (Jones, 1967; this study); **8**, Turonian and Coniacian strata, Phoenix, Oregon and Henley, California (Anderson, 1902, 1958); **9**, Turonian strata, Redding area, northern California (Matsumoto and Popenoe, 1960; Wiedmann, 1965).

Turonian scaphitids, which were classified under *Otoscaphites puerculus* (Jimbo, 1894) of the Otoscaphitinae and *Yezoites planus* Yabe, 1910 of the Scaphitinae Gill, 1871, represent sexual dimorphs of a single species, because of their contemporaneous and sympatric mode of occurrences, similarities in ontogenetic shell shape during early–middle stages and suture development, and parallel microevolutionary changes of certain shell characters. This view was accepted by subsequent workers, and distinctly dimorphic scaphitid species with a pair of lappets for microconchs and without lappets for macroconchs were included in *Yezoites* (e.g. Kaplan *et al*., 1987; Kennedy, 1988; Davis *et al*., 1996; Kirkland, 1996; Wright *et al*., 1996; Kennedy and Klinger, 2013). Sexual dimorphism has also been recognized in many species of the Scaphitinae; e.g. species of *Hoploscaphites* and *Discoscaphites* (Landman and Waage, 1993), since Cobban (1969) demonstrated it unequivocally in *Scaphites leei* Reeside, 1927 and *Scaphites hippocrepis* (DeKay, 1827) from the Upper Cretaceous (upper Santonian–lower Campanian) in the Western Interior of the United States.

As a result of these previous works, scaphitid ammonoids known from the circum-North Pacific regions must be re-investigated taxonomically by taking into account the possibility of sexual dimorphism. This paper aims to revise the systematics of five *Yezoites* species from the Upper Cretaceous deposits in the circum-North Pacific regions based on previously described material including type- and figured specimens and newly recovered ones from the Turonian and Coniacian strata of Japan, northern Kamchatka and southern Alaska.

Material and methods

Material.—A total of 1,458 specimens belonging to the following five species of *Yezoites* were examined in this study; *Yezoites perrini* (Anderson, 1902) (five microconchs), *Y. seabeensis* (Cobban and Gryc, 1961)

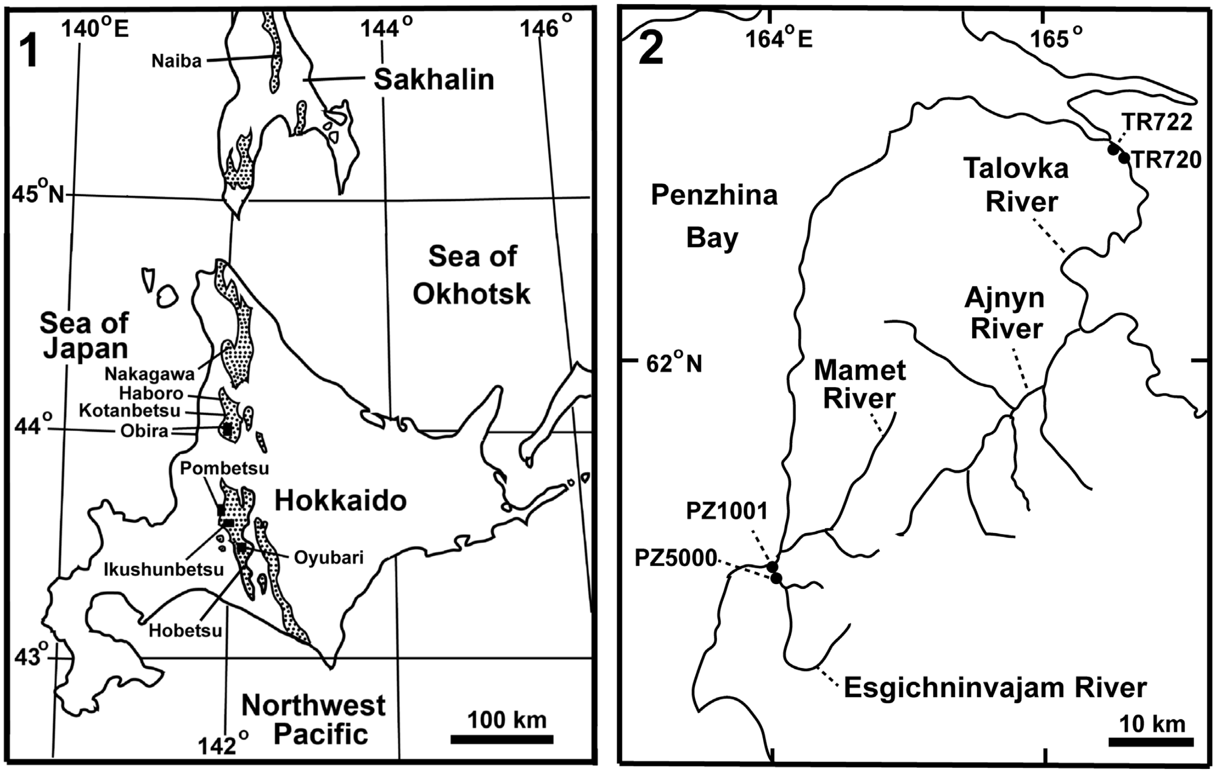

Figure 2. Occurrence of *Yezoites* in Hokkaido, southern Sakhalin and northern Kamchatka. **1**, map of Hokkaido and southern Sakhalin, showing the distribution of the post-Aptian Cretaceous Yezo Group (dotted) and the distribution areas of *Yezoites* treated in this paper (area 4 in Figure 1); **2**, map of northern Kamchatka, showing the localites of *Yezoites* specimens examined (area 5 in Figure 1).

(one microconch), *Y. puerculus* (Jimbo, 1894) (1075 specimens; 564 microconchs and 511 macroconchs), *Y. pseudoaequalis* (Yabe, 1910) (332 specimens; 165 microconchs and 167 macroconchs), and *Y. matsumotoi* (Tanabe, 1977b) (45 microconchs). Of these species, *Y. perrini*, *Y. seabeensis*, and *Y. puerculus* were collected from the Turonian of Hokkaido, southern Sakhalin, northern Kamchatka (mouth of the Esgichninvajam River facing the Penzhina Bay), whereas *Y. pseudoaequalis* and *Y. matsumotoi* came from the Coniacian of western Shikoku (Uwajima area), northeast Honshu (Futaba area), and Hokkaido, Japan, northern Kamchatka (Talovka River), and southern Alaska (Talkeetna Mountains). The specimens examined include those studied by Tanabe (1975, 1977a, b). Details of the localities, horizons, and age of the *Yezoites* specimens examined are summarized in Figures 1–4 and Supplement material (S-Appendixes I and II). In addition, I re-examined the type and figured scaphitid specimens described by previous authors (Jimbo, 1894; Anderson, 1902, 1958; Yabe, 1910).

Based on available fossil records, geographic distributions of the Late Cretaceous (Turonian–Campanian) *Yezoites* species in the circum-North Pacific regions are shown in Figure 1. Localities of the *Yezoites* specimens examined from northern Kamchatka, Far East Russia and central Hokkaido, Japan are respectively shown in Figures 2.2 and 3. Tanabe (1977b, fig. 2) figured the stratigraphic distributions of *Yezoites* species in the Turonian–Coniacian sequences of the Yezo Group in the Obira and Ikushunbetsu-Pombetsu areas, Hokkaido, and his figure is partly revised with additional new fossil records and reproduced in Figure 4.

Institutional abbreviations.—BGS GSM: British Geological Survey and Museum, Keywarth, UK; SMC: The Sedgwick Museum, Cambridge, UK; CAS: California Academy of Science, San Francisco, California, USA; USNM: U.S. National Museum of Natural History, Washington, D.C., U.S.A.; GK. H: Kyushu University Museum, Fukuoka, Japan; UMUT: University Museum, The University of Tokyo, Tokyo, Japan; NMNS: National Museum of Nature and Science, Tsukuba, Japan; YCM: Yokosuka City Museum, Yokosuka, Japan.

Methods.—The following shell portions (their abbreviations are given in parentheses) were measured by a slide caliper (accuracy ± 0.05 mm) for mature microconchs and macroconchs of *Yezoites* species examined:

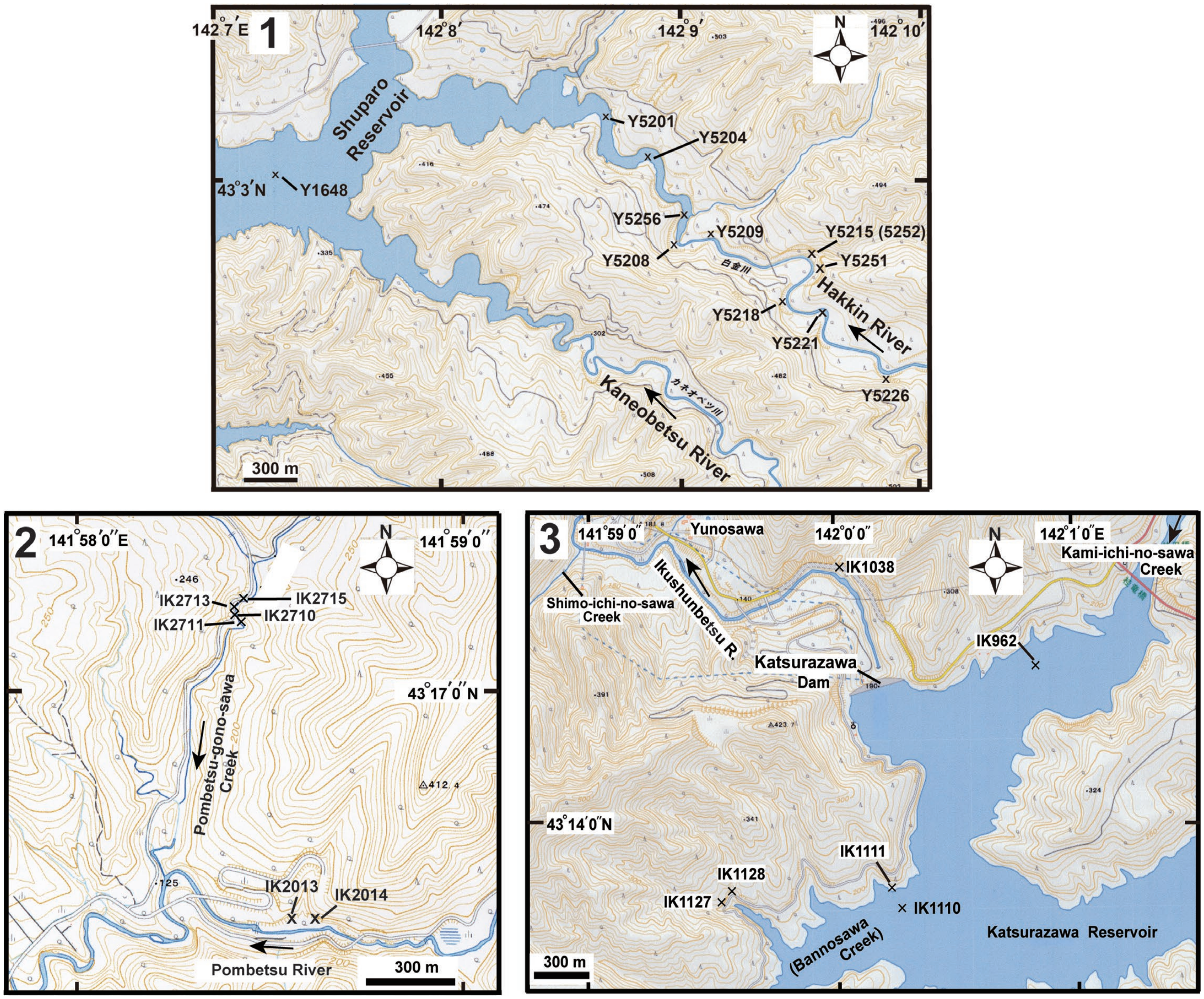

Figure 3. Maps of the Oyubari (**1**), Pombetsu (**2**) and Ikushunbetsu (**3**) areas, central Hokkaido, showing the localities of *Yezoites* specimens examined. Topographic maps are reproduced from the website of the Geospatial Information Authority of Japan (https://maps.gsi.go.jp).

Maximum shell length (*L*), maximum shell width (*W*), whorl height at aperture (*WH*), whorl breadth at aperture (*WB*), length of paired lateral lappets at aperture of microconch (*LLp*), phragmocone diameter (*PD*), whorl height of phragmocone (*PH*), whorl breadth of phragmocone (*PB*), umbilical diameter of phragmocone (*U*) (Figures 5.1, 5.2). A number of micro- and macroconch specimens of *Y. puerculus* and *Y. pseudoaequalis* were polished and/or thin-sectioned along the median dorso-ventral plane, and the maximum and minimum diameter of the initial chamber ("protoconch") and the maximum diameter of the ammonitella (= embryonic shell) were measured by means of a digital micrometer attached to the Nikon model V-20B Profile Projector at the Tsukuba Research Departments of the National Museum of Nature and Science (accuracy ± 1 μm). I follow the terminology and abbreviations of suture elements proposed by Kullmann and Wiedmann (1970) for description of sutures of the examined species.

The following abbreviations were used for the statistical description. *N*: number of specimens in a sample, $\bar{X}$: mean, $\bar{X} \pm t_{0.05}\sigma\bar{x}$: 95% confidence interval of the mean, *V*: coefficient of variation, *s*: standard deviation, *O.R.*: observed range.

Systematic descriptions

Subclass Ammonoidea von Zittel, 1884
Suborder Ancyloceratina Wiedmann, 1966
Superfamily Scaphitoidea Gill, 1871
Family Scaphitidae Gill, 1871
Subfamily Otoscaphitinae Wright, 1953

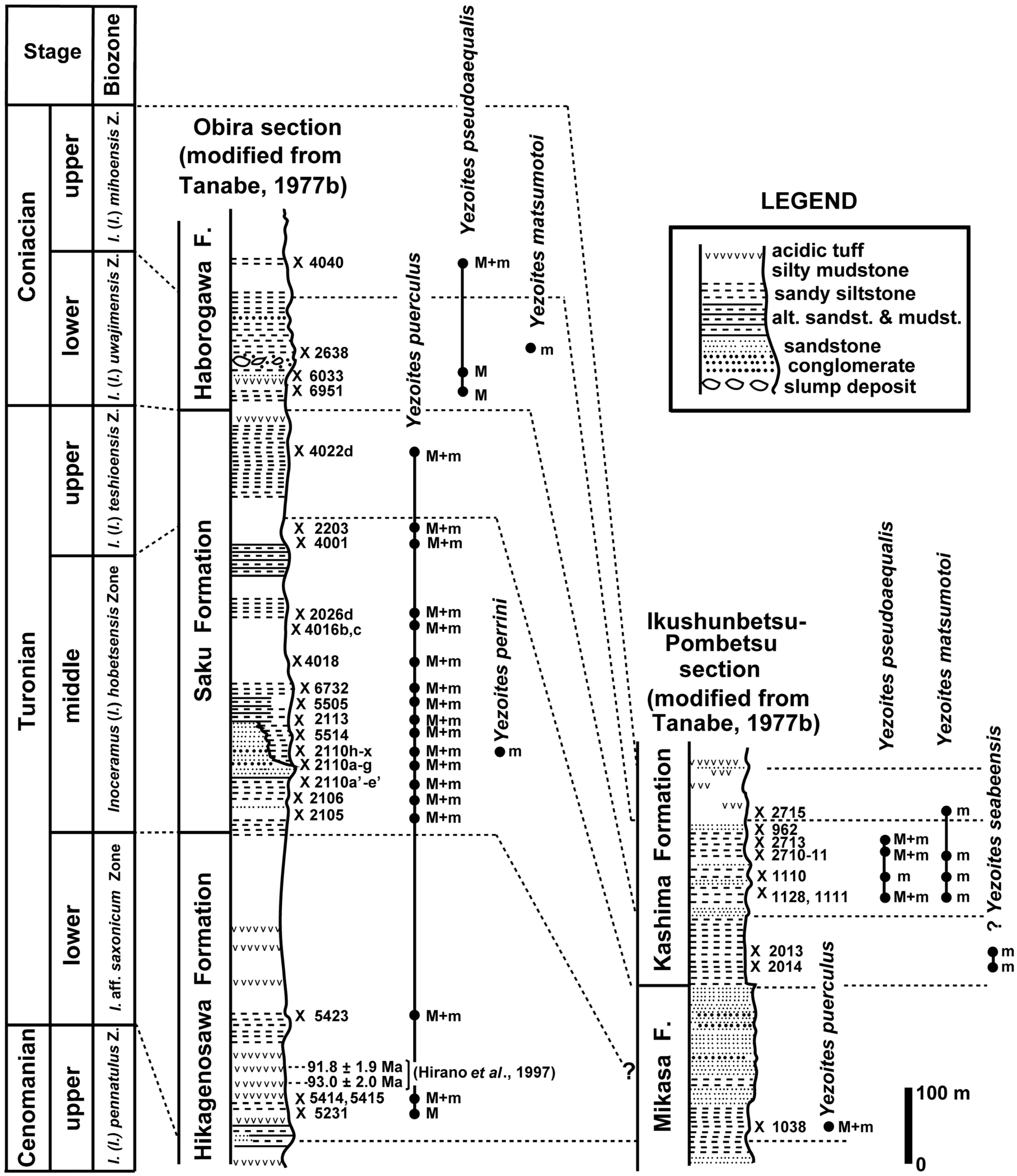

Figure 4. Stratigraphic distributions of *Yezoites* species in the Turonian–Coniacian sequences of the Yezo Group in the Obira and Ikushunbetsu-Pombetsu areas, Hokkaido (modified from Tanabe, 1977b, fig. 2). Prefixes R and IK for the fossil localities in the Obira and Ikushunbetsu-Pombetsu areas are omitted in this figure. Abbreviations; M, macroconch; m, microconch.

Revised diagnosis.—Small to very small dimorphic scaphitids; tightly coiled whorls generally evolute to subinvolute except in some late macroconchs; umbilicus of macroconchs not concealed by beginning of shaft in early forms but concealed in later forms; shaft very to moderately long; surface weakly or strongly ribbed, with ventrolateral tubercles in some forms; hook of macroconchs terminated by simple constricted aperture whose opening

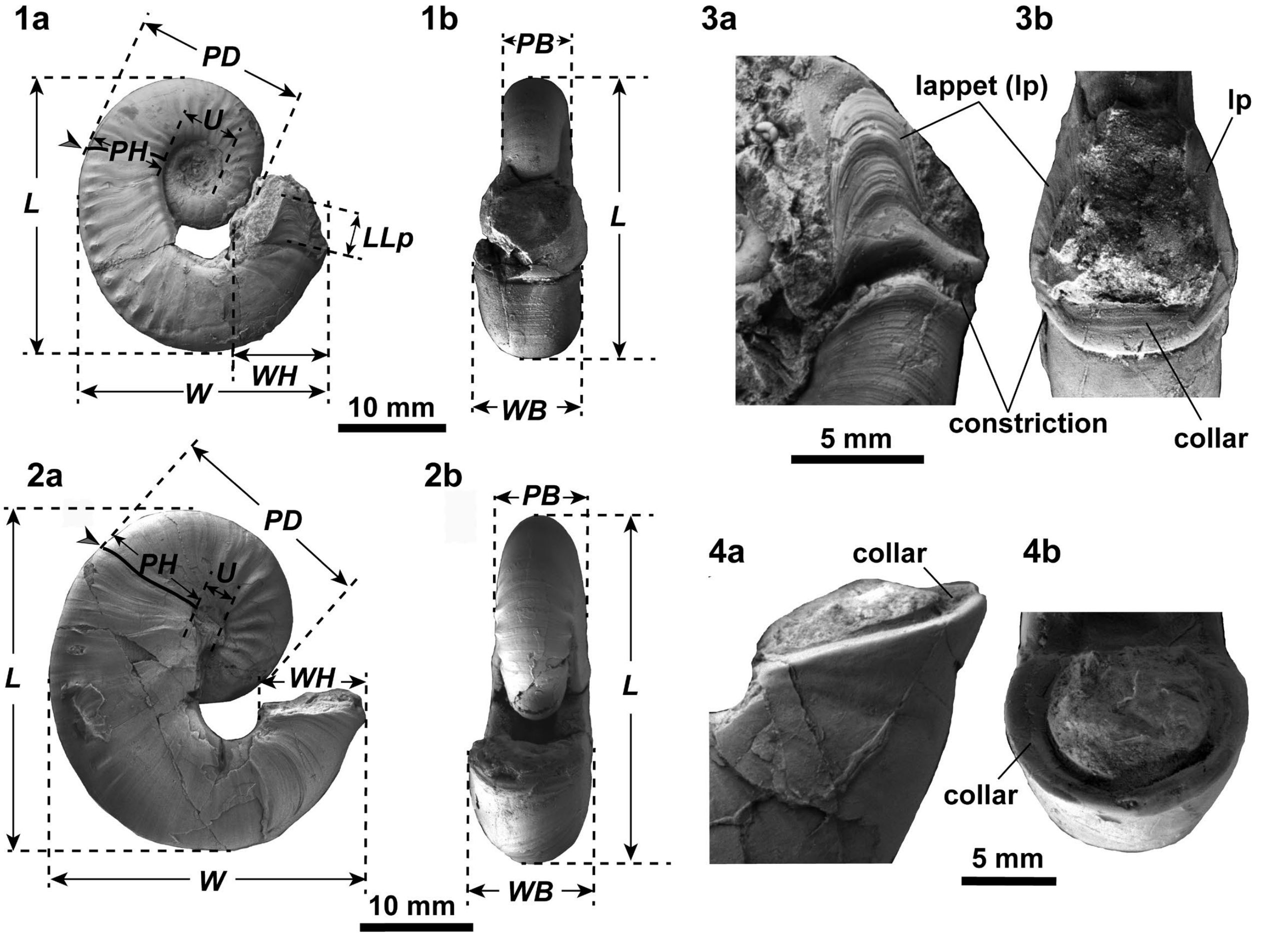

Figure 5. Microconchs and macroconchs of *Yezoites* (exampled by *Y. puerculus*) showing the conch morphology and measurements. **1**, mature microconch, GK. H. 20003 from loc. R4001, Obira area; **2**, mature macroconch, GK. H. 5780 from loc. R2112, Obira area; **3**, **4**, enlarged apertural portions of mature microconch, GK. H. 20006 from loc. R4001, Obira area (3) and mature macroconch, GK. H. 5781 from loc. R5505, Obira area (4). Right lateral (1a, 2a, 3a, 4a) and frontal (1b, 2b, 3b, 4b) views. An arrowhead in 1a and 2a points to the base of body chamber. See the text for explanation of abbreviations for measurements.

distinctly sealed by a collar; microconchs have longer shaft than macroconchs, less inflated, hook terminated by distinct constriction, from which a pair of long lateral lappets extended forward.

Remarks.—This subfamily was proposed by Wright, 1953 for species with a pair of lateral lappets. Although *Otoscaphites* Wright, 1953 is a junior synonym of *Yezoites* Yabe, 1910, the subfamily name is retained under ICZN Article 40 (Wright *et al*., 1996, p. 258).

Included genera.—*Yezoites*, Yabe, 1910 and *Worthoceras* Adkins, 1928.

Discussion.—Wright *et al*. (1996, p. 260) provisionally included *Eorhaeboceras* Alabushev, 1989 in this subfamily, but this monospecific genus with *E. derivatum* as the type-species (Alabushev, 1989, p. 39, figs. 14, 15, pl. 1, figs. 2, 3; see also Alabushev and Wiedmann, 1994, fig. 4G–K; Alabushev and Wiedmann, 1997, pl. 3, figs. 8–13) should be excluded from this subfamily, because the above-mentioned diagnostic characters of this subfamily were not recognized in any of the type and figured specimens of *E. derivatum*, all of which are represented by immature conchs.

Genus ***Yezoites*** Yabe, 1910

Synonymy.—*Otoscaphites* Wright, 1953, p. 475; *Scaphites* (*Hyposcaphites*) Wiedmann, 1965, p. 436.

Type-species.—*Scaphites perrini* Anderson, 1902, p. 114, by subsequent designation by Diener (1925, p. 213).

Revised diagnosis.—Whorl section compressed to inflated, even coronate, almost smooth to strongly ribbed, with or without mid-lateral or ventrolateral tubercles; ribs rectiradiate to prorsiradiate, straight or convex adorally. Microconchs small to very small; straight or ventrally curved shaft weakly to strongly ribbed, hook rather sharply recurved, not overlapping body chamber; aperture constricted and collared with paired spatula-like lateral lappets. Macroconchs with inner margin of shaft nearly straight to well curved, slightly to largely occluding the umbilicus; aperture with slight to strong constriction and collar. Suture with elements more incised than in *Worthoceras*; lateral lobe L irregularly bifid; saddle U/L wide and becoming subdivided by auxiliary lobe. Both microconchs and macroconchs were recognized in some species, whereas only microconchs are known for the rest species.

Discussion.—*Yezoites* was proposed by Yabe (1910, p. 167) for scaphitids with the internal part of the suture comprising a high internal saddle and small lobes in it. Its name came from "Yezo", the old name of Ainu, who are indigenous people in Hokkaido Island. Other diagnostic features of this genus described by Yabe (1910) are mature shells consisting of more or less widely umbilicate, coiled whorls and a loosened, first straight and then bending last whorl, as in *Scaphites*, and the apertural rim either thickened or with a constriction with lateral lappets. Yabe (1910) included three species, *Y. perrini*, *Y. puerculus*, and *Y. planus* in this genus, all of which are known from the Turonian *Scaphites* beds (= Saku Formation) of Hokkaido. He classified the three *Yezoites* species into two form groups; one is represented by *Y. planus* with a narrow umbilicus and a simple constricted aperture and the other comprising *Y. puerculus* and *Y. perrini*, with a completely open umbilicus and a constricted aperture with a pair of lateral lappets.

Wright (1953) stated that Yabe (1910) designated the non-lappeted *Y. planus* as the type-species form, which is a true *Scaphites*, and that the name *Yezoites* is therefore not available for the distinct lappeted group. Instead Wright (1953, p. 475) proposed the new genus *Otoscaphites* for the lappeted group, with *Ammonites bladenensis* Schlüter, 1871 (p. 30, pl. 10, figs. 5 and 6) as the type-species, and changed the generic position of Yabe's *Yezoites puerculus* (Jimbo) to *Otoscaphites*. As Kaplan *et al.* (1987, p. 18) pointed out, this treatment was doubly mistaken, because Yabe (1910) in fact did not designate a type-species for *Yezoites*. Since Diener (1925, p. 213) later designated *Scaphites perrini* Anderson, 1902, with lateral lappets for the type-species of *Yezoites*, *Otoscaphites* Wright, 1953 is regarded as a junior synonym of *Yezoites* Yabe, 1910, as well as *Scaphites* (*Hyposcaphites*) Wiedmann (1965, p. 436), who designated the lappeted *Scaphites stephanoceroides* Yabe, 1909, p. 442 (= *Olcostephanus* sp. by Jimbo, 1894, p. 33 [179], pl. 9 [25], fig. 8) as the type-species.

Tanabe (1977a) suggested that the smaller lappeted and larger non-lappeted forms, which have been respectively described under *Y. puerculus* and *Y. planus* by Yabe (1910) from the Turonian of Hokkaido, are sexual dimorphs of a single species because of their contemporaneous and sympatric occurrences and similarities in juvenile shell shape, ornamentation and suture ontogeny between them. This view was accepted by subsequent workers (e.g. Kaplan *et al*., 1987; Kennedy, 1988; Kirkland, 1996; Wright *et al*., 1996; Kennedy and Klinger, 2013). It is now conclusively regarded that *Yezoites* is a distinct dimorphic genus with lappeted microconchs and non-lappeted macroconchs.

Included species.—See Klein (2017, p. 10–11) for the complete list of described species.

Stratigraphic range and geographic distribution.—From the lower Cenomanian to the lower Campanian; western and central Europe, Zululand, South Africa, Madagascar, New Zealand, Japan, Far East Russia (Sakhalin and Kamchatka), Alaska, Oregon, California, Montana, Texas, and Mexico (Wright, 1957, 1979; Cobban and Gryc, 1961; Collignon, 1965; Jones, 1967; Tanabe, 1977b; Kaplan *et al*., 1987; Kennedy, 1988; Wright and Kennedy, 1996; Wright *et al*., 1996; Misaki and Maeda, 2009; Kennedy and Klinger, 2013).

Yezoites perrini (Anderson, 1902)

Figures 6, 7.1

Microconch synonymy.

Scaphites perrini Anderson, 1902, p. 114, pl. 2, figs. 71–73; Reeside, 1927, p. 33; Verechagin *et al*., 1965, p. 42, pl. 34, fig. 2a–c.
Yezoites Perrini (Anderson); Yabe, 1910, p. 172, pl. 15, fig. 28a–d.
non. Yezoites Perrini (Anderson); Yabe, 1910, pl. 15, fig. 29.
Otoscaphites perrini (Anderson); Wright, 1953, p. 476; Cobban and Gryc, 1961, p. 183, pl. 38, figs. 1–12.
Scaphites ("*Yezoites*") *perrini* Anderson; Anderson, 1958, p. 252, pl. 25, fig. 6, 6a, 6b.
Otoscaphites (*Hyposcaphites*) *perrini* (Anderson); Tanabe *et al*., 1977, p. 193, table 2b; Tanabe, 1977b, fig. 3-(10, 11); pl. 1, fig. 3a, b.
Yezoites perrini (Anderson); Kennedy, 1988, p. 113; Cooper, 1994, p. 173; Hayakawa, 2003, pl. 26, figs. p1–p3; Klein, 2017, p. 18.

Type.—The holotype, by monotypy, is a microconch, CAS Geol. 61625.01 (formerly SuTy 5625), from Fitch (formerly Smith) Ranch, 4.8 km west of Phoenix, Jackson County, Oregon, USA; basal Turonian (?). The plaster model of the holotype is shown in Figure 6.1a–d.

Material examined.—Five mature microconchs including the holotype were examined, among which four (UMUT MM 7598, GK. H. 5826, GK. H. 20009, and GK. H. 20010) came from the Obira area, northwestern Hokkaido, and one (GK. H. 5825) from the Oyubari area, central Hokkaido (Figure 2.1). UMUT MM 7598 was collected from the Obirashibe River (detailed locality unknown), together with microconchs of *Yezoites puerculus*, and was described and figured by Yabe (1910, p. 172, pl. 15, fig. 28a–d); GK. H. 5826 was recovered from

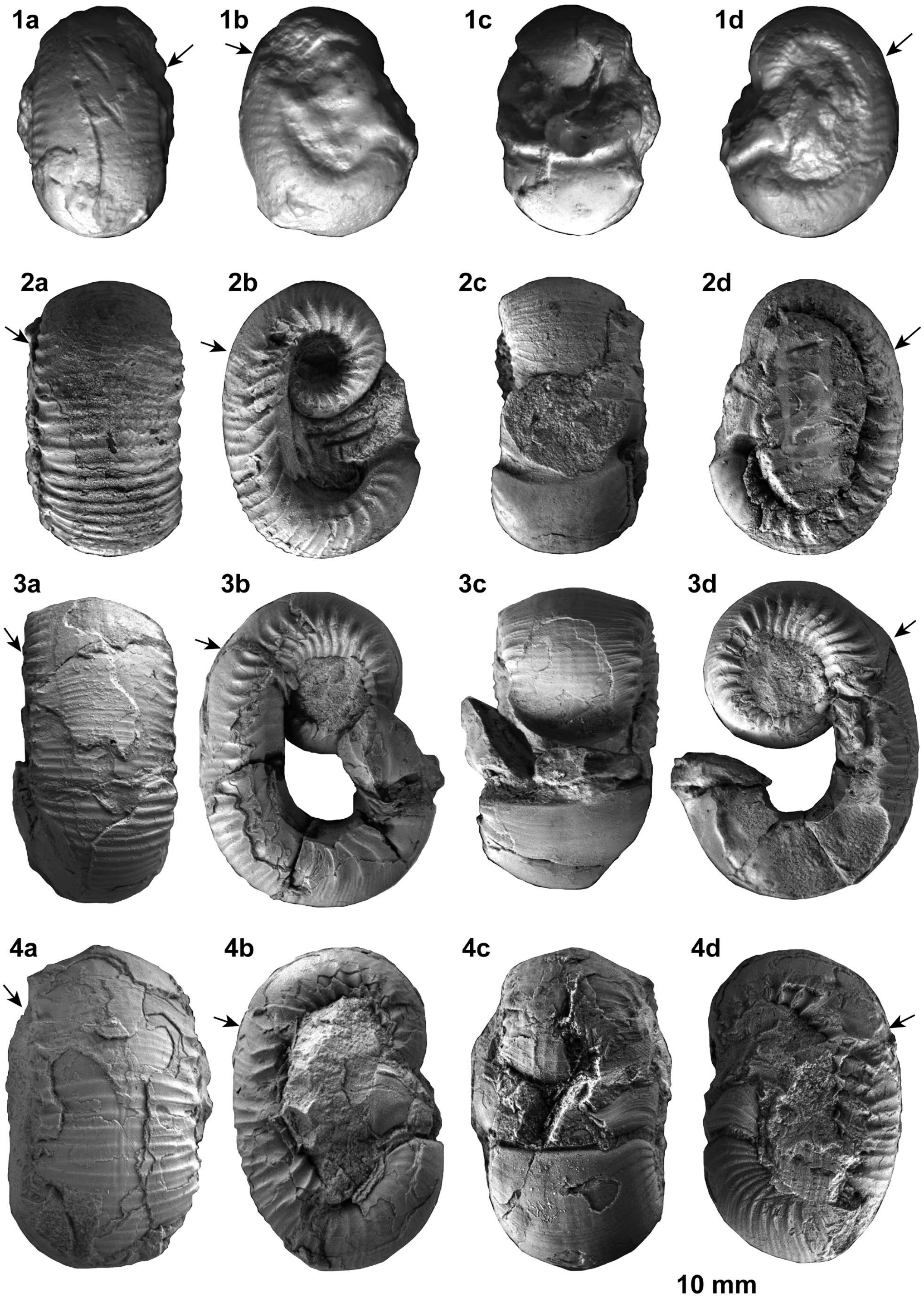

Figure 6. *Yezoites perrini* (Anderson, 1902). Mature microconchs. Ventral (a), right lateral (b), frontal (c), and left lateral (d) views for each specimen. Arrows point to the base of body chamber. **1**, plaster model of holotype, CAS Geol. 61625.01 from Phoenix, Oregon; **2**, UMUT MM 7598 from the Obirashibe River, Obira area; **3**, GK H 5826, from a float nodule at R6551p, Obira area; **4**, GK H. 20009, from a float nodule in the Sato-no-sawa Creek, Obira area. Arrows point to the base of body chamber. All photos other than 1a–d are whitened with ammonium chloride.

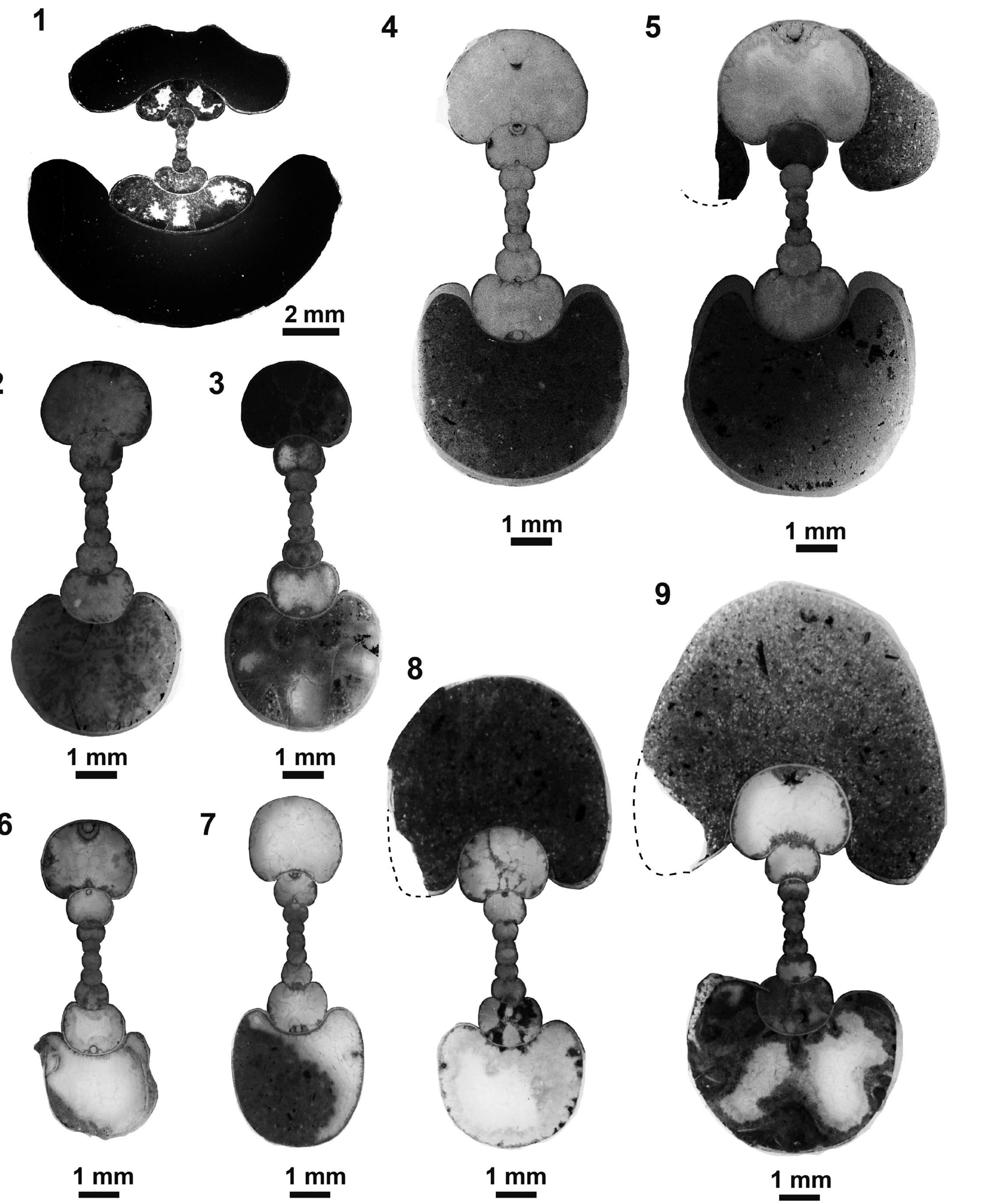

Figure 7. Cross sections of mature macroconchs and microconchs of three *Yezoites* species from Hokkaido. **1**, *Yezoites perrini* (Anderson, 1902), microconch. GK. H. 20010 from loc. R2110i, Obira area; **2**–**5**, *Yezoites puerculus* (Jimbo, 1894), microconchs (2, 3) and macroconchs (4, 5). GK. H. 5731 from loc. R2110e' (2) and GK. H. 5732 from loc. R2110b' (3), Obira area; **4, 5**, *Yezoites puerculus* (Jimbo, 1894), macroconchs. GK. H. 5788 (4) from loc. R 2110e'and GK. H. 5787 (5) from loc. R2110b', Obira area; **6**–**9**, *Yezoites pseudoaequalis* (Yabe, 1910), microconchs (6, 7) and macroconchs (**8**, 9). GK. H. 20011 (6), GK H. 20012 (7), GK. H. 20013 (8), GK. H. 20014 (9), all from a float nodule at loc. IK 2715, Pombetsu area.

Table 1. Measurements (in mm) of mature microconch shells of Y*ezoites perrini* (Anderson) and *Y. seabeensis* Cobban and Gryc.

Species	Specimen no.	*L*	*W*	*WB*	*WH*	*WB/WH*	*PD*	*PB*	*PH*	*PB/PH*	*U*	*U/PD*	*LLp*
Yezoites perrini	CAS Geol. 61625.01 (holotype)	12.5	10.0	7.5	2.8	2.7	?	?	?	?	2.4	?	>2.0
	UMUT MM 7598	14.9	10.0	7.5	3.0	2.5	9.2	7.8	3.3	2.36	3.0	0.33	6.9
	GK. H. 5826	16.5	11.6	8.0	4.3	1.9	10.1	8.3	4.2	1.98	3.9	0.39	5.0
	GK. H. 20009	16.4	10.3	8.4	3.2	2.6	9.3	8.4	3.4	2.47	4.4	0.47	3.9
Y. seabeensis	UMUT MM 7518	23.3	16.1	9.9	?	?	14.1	10.4	5.5	1.89	5.0	0.35	10.5

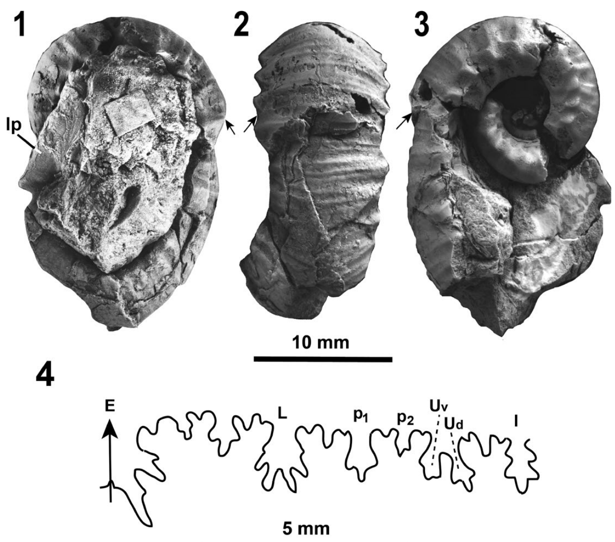

Figure 8. *Yezoites seabeensis* (Cobban and Gryc, 1961). Mature microconch. Left lateral (**1**), ventral (**2**), and right lateral (**3**) views, and drawing of mature suture (**4**). UMUT MM 7518, from a float nodule in the Pombetsu River, Pombetsu area (same specimen as that figured by Jimbo, 1894, pl. 9[25], fig. 3). Abbreviation; lp: lateral lappet. Arrows point to the base of body chamber. A–C are whitened with ammonium chloride.

a float nodule in the middle course of the Nakakinenbetsu River and figured by Tanabe (1977b, pl. 1, fig. 3a, b); GK. H. 20009 was found in a float nodule in the Satono-sawa Creek, a tributary of the Kamikinenbetsu River; GK. H. 20010 was collected *in situ* from silty mudstone outcrop at loc. 2110i in the Obirashibe River (see Tanabe *et al*., 1977, fig. 6 for the location); GK. H. 5825 was collected *in situ* from silty mudstone beds at loc. Y 5218 in the Hakkin River, a tributary of the Shiyubri River (Figure 3.1). GK. H. 5825 and GK. H. 20010 came from the middle Turonian *Inoceramus hobetsensis* Zone in the Saku Formation. The other three specimens were possibly derived from the lower to the middle Turonian unit of the Saku Formation.

Dimensions.—See Table 1.

Diagnosis.—See Cobban and Gryc (1961, p. 183) for a recent diagnosis of microconchs.

Description and discussion.—The holotype, CAS Geol. 61625.01 is a very small microconch, measuring 12.5 mm in shell length. I observed this specimen and confirmed the appropriateness of the descriptions by Anderson (1902, p. 114) and Cobban and Gryc (1961, p. 183). Namely, the conch is stout, consisting of extremely depressed whorls with coronate cross sections. The aperture is strongly constricted with a pair of large lateral lappets. Coiled whorls of the phragmocone have a wide umbilical area, followed by a loosely coiled body chamber consisting of relatively long and weakly arched shaft and sharply recurved hook portions. The shell is ornamented with dense and evenly spaced weak ribs, which become weaker near the aperture. The primary ribs terminate in bullae along the umbilical margin. Ribbing on the ventral side of the body chamber is scarcely discernible.

UMUT MM 7598, GK. H. 5826 and GK. H. 20009 are mature microconchs, all of which preserve a complete aperture (Figures 6.2–6.4). They are slightly larger than the holotype from Oregon (Figure 6.1), and range from 14.9 to 16.5 mm in shell length (Table 1). All closely fit Anderson's holotype and microconch specimens described by Cobban and Gryc (1961, pl. 38, figs. 1–12) from the basal Turonian of northern Alaska, in their degree of stoutness, depressed whorls with coronate section, and mode of ribbing. Ontogenetic change of the whorl shape and overlapping pattern can be observed in the cross-sectioned specimen, GK. H. 20010; the first three whorls are subcircular in cross section and have a relatively wide umbilicus. In going from the fourth to the fifth whorl, whorl shape changes to be strongly depressed with coronate cross section in association with the narrowing of umbilicus (Figure 7.1). The equally spaced primary ribs are straight and prorsiradiate across the umbilical wall. They terminate in low inconspicuous bullae at the mid-flank from which two or three secondary ribs and one or two intercalaries extend across the venter. These secondaries on the body chamber are well preserved in the three specimens, and they cross straightly or gently arched adorally on the venter. The ribbing on the venter tends to disappear near the constricted aperture. A pair of spatula-like lateral lappets, ornamented with fine and adorally arched growth lines, are present in these specimens; they are especially well developed in GK. H. 20009 (Figure 6.4b–d). Adult sutures are partly preserved in GK. H. 5825 and GK. H. 5826 (Tanabe, 1977b, fig. 3.10, 3.11), and are characterized by two pseudolobes on the saddle L U and three minor lobes on the saddle E L. They may be expressed by the suture formula, E L U p_1 p_2 U I, although U and I were not recognized in the two specimens.

Macroconchs of *Yezoites perrini* have not been described to date. Kennedy (1988, p. 113) suggested that *Scaphites* of *S. delicatulus* group is a probable candidate for the macroconch of this species. If this interpretation is correct, *Scaphites subdelicatulus* Cobban and Gryc, 1961 which co-occurred with lappeted microconchs of *Y. perrini* from the basal Turonian Seabee Formation in the Nanushuk River, northern Alaska may correspond to the macroconchs of this species, because of the similarities in the stout and inflated shape, depressed whorl sections, broadly rounded venter, and surface ornamentation, consisting of nearly straight prorsiradiate primary ribs in bullae and more numerous secondary ribs, which cross straightly or gently arched adorally on the venter.

Yezoites perrini is similar in having depressed whorls with coronate section to *Y. seabeensis* Cobban and Gryc, 1961 from the lower Turonian of northern Alaska, but the latter has the much stronger ribbing with sharp nodes on the flank (see Cobban and Gryc, text-fig. 2n), instead of inconspicuous bullae in the former.

Occurrence.—Basal to middle Turonian in Hokkaido (Obira and Oyubari areas) (Yabe, 1910; Tanabe, 1977b; this study), northern Kamchatka (mouth of Esgichninvajam River) (Vereshchagin *et al*., 1965), northern Alaska (Cobban and Gryc, 1961), and Oregon (Anderson, 1902).

Yezoites seabeensis (Cobban and Gryc, 1961)

Figure 8

Microconch synonymy

Olcostephanus sp., Jimbo, 1894, p. 33[179], pl. 9[25], fig. 3.3a, 3b.
nom. nud. Scaphites stephanoceroides Yabe, 1909, p. 442, 443.
Yezoites Perrini Anderson, Yabe, 1910, p. 172, pl. 15, fig. 29.
Otoscaphites seabeensis Cobban and Gryc, 1961, p. 184, pl. 38, figs. 13–17; text-fig. 2d, e, n.
Otoscaphites perrini (Anderson) (?); Matsumoto, 1963, p. 46, pl. 68, fig. 3.
Scaphites (*Hyposcaphites*) *stephanoceroides* Wiedmann, 1965, p. 436, pl. 59, fig. 3.
? *Otoscaphites* aff. *perrini* (Anderson); Futakami *et al*., 1980, table 1; Matsumoto *et al*., 1981, table 1.
non. Otoscaphites seabeensis Cobban and Gryc; Cobban, p. 11, pl. 5, figs. 6–11, 16, 17.
Yezoites seabeensis (Cobban and Gryc); Wright *et al*., 1996, p. 260, fig. 201.c, d.
Yezoites stephanoceroides (Yabe); Wright *et al*., 1996, p. 260, fig. 201.*i*.

Type.—The holotype, USNM 130805 designated by Cobban and Gryc (1961, p. 183, pl. 38, figs. 16–19) is a mature microconch from the Seabee Formation at U.S.G.S. Mesozoic locality 26560, Maybe Creek, northern Alaska.

Material examined.—A single microconch, UMUT MM 7518 found as a float in the Pombetsu River, a tributary of the Ikushunbetsu River, Pombetsu area, central Hokkaido.

Dimensions.—See Table 1.

Diagnosis.—See Cobban and Gryc (1961, p. 184) for diagnosis of microconchs.

Description and discussion.—The conch is small-sized and stout. Earlier coiled whorls are not preserved. The last coiled whorl of the phragmocone is extremely depressed with a coronate cross section and a wide and deep umbilical area (Figures 8.1–8.3). A loosely coiled body chamber, although the right lateral half of the hook portion is missing in this specimen, consists of a relatively long, ventrally weakly arched shaft and a sharply recurved hook with a constricted aperture, from which a very long lappet is extended forward on the left lateral side (lp in Figure 8.1; see also Yabe, 1910, pl. 15, fig. 29). The shell is ornamented with evenly spaced strong primary ribs that end in small and sharp nodes along the mid-flank, from which bifurcated secondary ribs extend across the venter, in association with one or two intercalaries between the secondaries (Figures 8.2, 8.3). Mature suture is expressed by the formula E L p_1 p_2 Uv Ud I (Figure 8.4). The saddle E L incised with two minor lobes.

This specimen was first described by Jimbo (1894, p. 33[179], pl. 9[25], fig. 3.3a, 3b) under *Olcostephanus* sp. of the family Olcostephanidae (Perisphinctoidea). Yabe (1909, p. 442–443) listed the new species name, *Scaphites stephanoceroides* Yabe for Jimbo's *Olcostephanus* sp. without description nor citation from Jimbo (1894). The taxon name, *S. stephanoceroides* is, therefore, regarded as *nomen nudum*. Later, Yabe (1910, p. 172, pl. 15, fig. 29) re-examined UMUT MM 7518 and described it under *Yezoites perrini* (Anderson, 1902), together with the other better- preserved specimen of true *Y. perrini* (UMUT MM 7598) from the Obira area. Matsumoto (1963) supported Yabe's (1910) view with reservation, and gave the revised name *Otoscaphites perrini* (Anderson, 1902) (?) for Jimbo's (1894) *Olcostephanus* sp. UMUT MM 7518 was subsequently described under *Scaphites* (*Hyposcaphites*) *stephanoceroides* (Yabe) by Wiedmann (1965, p. 436, pl. 59, fig. 3) and figured under *Yezoites stephanoceroides* (Yabe) by Wright *et al*. (1996, p. 260, fig. 201.l). However, the taxon name, *S. stephanoceroides* Yabe, 1909 is *nomen nudum*, so that it should be replaced by *Yezoites stephanoceroides* (Wiedmann, 1965), if it is a valid taxon, according to the ICZN, Article 13.1.

In the presence of sharply pointed nodes on the mid-flank and depressed whorls with coronate section, UMUT MM 7518 is regarded to be conspecific with mature microconchs of *Yezoites seabeensis* (Cobban and Gryc, 1961) from the lower Turonian Seabee Formation in northern Alaska. Wright *et al*. (1996, p. 260, fig. 201.a, b) figured one of the specimens described under *Scaphites delicatulus* Warren, 1930 (USNM 130801b) by Cobban and Gryc (1961, pl. 37, figs. 21, 22), which co-occurred with microconchs of the present species in the Maybe Creek, northern Alaska, as the macroconch of the present species, without description nor discussion. Microconchs described under *Yezoites delicatulus* (Warren, 1930) from the upper Cenomanian of Texas, however, differ from those of the present species by much smaller conch size (10–12 mm long) and the absence of sharp nodes along the mid-flank (Kennedy, 1988, p. 120, pl. 24, figs. 1, 3–5, 9–11). The co-occurring macroconchs of *Y. delicatulus* from the upper Cenomanian of Texas (Kennedy, 1988, pl. 24, figs. 12–23), as well as those of Warren's (1930, p. 66, pl. 3, fig. 3, pl. 4, figs. 7 and 8) syntypes of *S. delicatulus* from the upper Cenomanian Smoky River Shale in west central Alberta can be distinguished from the lower Turonian Alaskan *S. delicatulus* of Cobban and Gryc (1961, p. 182, pl. 37, figs. 16–24; text-fig. 2a–c) in the smaller conch size, less depressed whorls and weaker flank tubercles. The aforementioned judgement for the sexual dimorphism in *Y. seabeensis* by Wright *et al*. (1996, p. 260, fig. 201.a, b) should be confirmed by future morphological analysis of the Alaskan material described under *Otoscaphites seabeensis* and *S. delicatulus* by Cobban and Gryc (1961).

Occurrence.—This species was first described from the lower Turonian Seabee Formation in northern Alaska (Cobban and Gryc, 1961). UMUT MM 7518 was found in a dark gray sandy silty nodule and retains a white-colored shell wall. Based on this fact, Matsumoto (1963, p. 46) suggested that this specimen came from the upper Turonian sandy siltstone beds that are exposed in the lower stream of the Pombetsu River. Indeed, lappeted microconchs of *Yezoites*, which may be comparable to the present species, were reported under *Otoscaphites* aff. *perrini* from the upper Turonian sandy siltstone outcrops at locs. IK 2013 and 2014 in the lower course of the Pombestu River (Figure 3.2), together with *Prionocyclus* spp. and *Inoceramus* (*I.*) *teshioensis* (Futakami *et al*., 1980; Matsumoto *et al*., 1981, figs. 2, 3). These lines of evidence indicate that this species ranged from the lower to the upper Turonian.

Yezoites puerculus (Jimbo, 1894)

Figures 5, 7.2–7.5, 9–11, 12.1, 12.2, 13, 14

Microconch synonymy

Scaphites puerculus Jimbo, 1894, p. 37 [183], pl. 5[21], fig. 4, 4a, 4b; Reeside, 1927, p. 33, pl. 10, fig. 8; Yabe, 1909, p. 441.
Scaphites inermis Anderson, 1902, p. 113, pl. 3, figs. 74–77; Reeside, 1927, p. 30; Anderson, 1958, p. 251, pl. 27, fig. 1, 1a–c.
Yezoites puerculus (Jimbo); Yabe, 1910, p. 170, pl. 15, figs. 20–22 (missing for specimen shown in fig. 22); Wright *et al*., 1996, fig. 201e–h; Davis *et al*., 1996, fig. 9H; Shigeta, 2001, pl. 45, fig. 5; Tanabe and Landman, 2002, pl.1, fig. 4; Tanabe *et al*., 2003, tables 1, 2; Hayakawa, 2003, pl. 26, figs. g–l; Takahashi *et al*., 2007, pl. 7, fig. 4.
Yezoites puerculus var. *teshioensis* Yabe, 1910, p. 171, pl. 15, figs. 23–27.
Scaphites puerculus Jimbo var. *teshioensis* Yabe, Reeside, 1927, p. 33.
Scaphites (? *Yezoites*) sp.; Nagao, 1931b, p. 219, pl. 15, fig. 9, 9a.
Otoscaphites puerculus (Jimbo); Wright, 1953, p. 475; Matsumoto and Popenoe, 1960, p. 4–6, fig. 1; Matsumoto, 1963, p. 44, pl. 6, fig. 4; Tanabe, 1975, pl. 10, figs. 1–15, pl. 11, figs. 1–9; Tanabe, 1977a, p. 401, pl. 62, figs. 1–9, pl. 64, figs. 1–5; Tanabe, 1977b, pl. 1, figs. 1, 2; Tanabe *et al*., 1979, pl. 1, fig. 3, pl. 3, fig. 5; Takahashi *et al*., 2007, pl. 7, fig. 4.
Otoscaphites cf. *puerculus* (Jimbo); Matsumoto and Popenoe, 1960, p. 7, fig. 1.
Scaphites (*Otoscaphites*?) *puerculus* Jimbo; Wiedmann, 1965, p. 433, 434, text-fig. 9, pl. 59, fig. 2a–c.
Scaphites (*Otoscaphites*) *yabei* Wiedmann, 1965, p. 434.
Otoscaphites teshioensis Yabe; Jones, 1967, p. 27, pl. 4, figs. 15–18; text-fig. 8, table 1.
? *Otoscaphites* sp., Noda, 1969, p. 4.
non. Otoscaphites puerculus (Jimbo); Tanabe, 1972, table 7.
non. Otoscaphites teshioensis (Yabe); Tanabe, 1972, table 7.
Otoscaphites (*O.*) *puerculus* (Jimbo); Tanabe *et al*., 1977, tables 2b, 3a.
non. Yezoites cf. *puerculus* (Jimbo); Kaplan *et al*., 1987, p. 21, pl. 6, fig. 4a, b.
Scaphites (*Otoscaphites*) *teshioensis* Yabe; Alabushev, 1989, fig. 5; Alabushev and Wiedmann, 1997, pl. 2, fig. 9a, b.
non. Scaphites (*Otoscaphites*) *puerculus* Jimbo; Alabushev, 1989, fig. 4d–f; Alabushev and Wiedmann, 1994, fig. 4D–F; Alabushev and Wiedmann, 1997, p. 13, pl. 3, figs. 2, 4.
Scaphites (*Otoscaphites*) *puerculus* Jimbo; Alabushev and Wiedmann, 1997, p. 13, pl. 3, figs. 3, 5–7.
non. Yezoites teshioensis (Yabe), Shigeta, 2001, pl. 45, fig. 6.

Macroconch synonymy

Scaphites Yokoyamai Jimbo, 1894, p. 37[183], pl. 5[21], fig. 3, 3a, b; Reeside, 1927, p. 36.
Scaphites condoni Anderson, 1902, p. 111, pl. 2, figs. 58–63; Anderson, 1958, p. 249, pl. 24, figs. 6, 6a–e.
Scaphites condoni var. *appressus* Anderson, 1902, p. 112, pl. 2, figs. 64–66.
Scaphites roguensis Anderson, 1902, p. 112–113, pl. 2, figs. 67–69.
nom. nud. Scaphites planus Yabe, 1909. p. 441.
Yezoites planus Yabe, 1910, p. 167, pl. 15, figs. 11–18.
Yezoites planus var. *gigas* Yabe, 1910, p. 169, pl. 15, fig. 19.
Scaphites (?) *Yokoyamai* Jimbo; Yabe, 1910, p. 166, pl. 15, fig. 5a, b.
Scaphites (?) *gracilis* Yabe, 1910, p. 166, pl. 15, figs. 9, 10.
non. Scaphites planus Roman and Mazeran, 1920, p. 13, pl. 4, figs. 15–17.
Scaphites planus Yabe; Reeside, 1927, p. 23, 33, pl. 10, figs. 4–7;

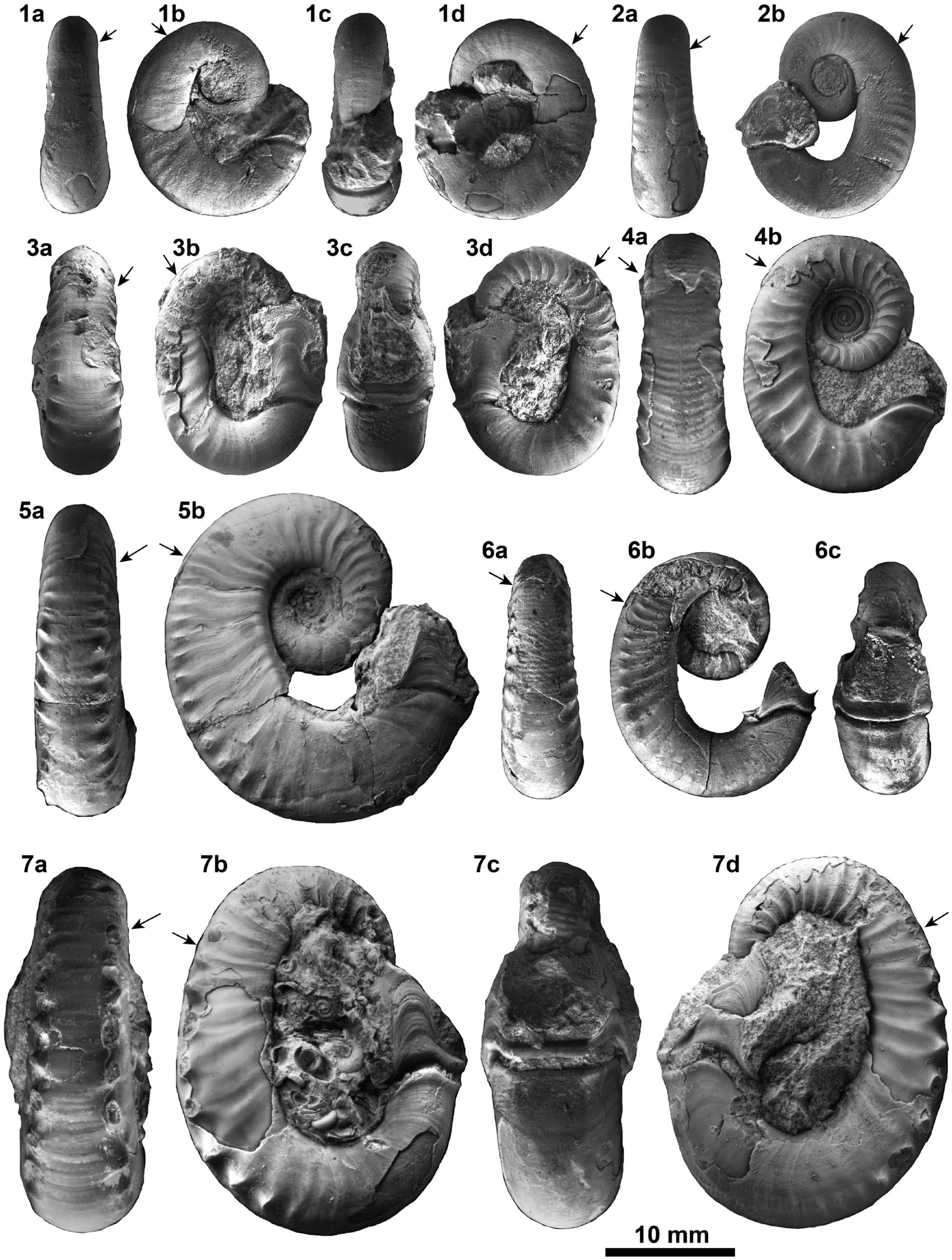

Figure 9. *Yezoites puerculus* (Jimbo, 1894). Mature microconchs from Hokkaido. Ventral (a), right lateral (b), frontal (c), and left lateral (d) views for each specimen, except for left lateral view for 2b. Arrows point to the base of body chamber. **1**, lectotype, UMUT MM 7520 from the Pankemoyuparo River, Oyubari area; **2**, GK. H. 5753 from loc. R2110e, Obira area; **3**, GK. H. 5734 from loc. R2110b', Obira area; **4**, GK. H. 20004 from loc. Y1648d, Oyubari area; **5**, GK. H. 20003, from loc. R4001, Obira area; **6**, GK. H. 20021 from a float nodule in the Sato-no-sawa Creek, Obira area; **7**, GK. H. 20006, from loc. R4001, Obira area. All photos whitened with ammonium chloride.

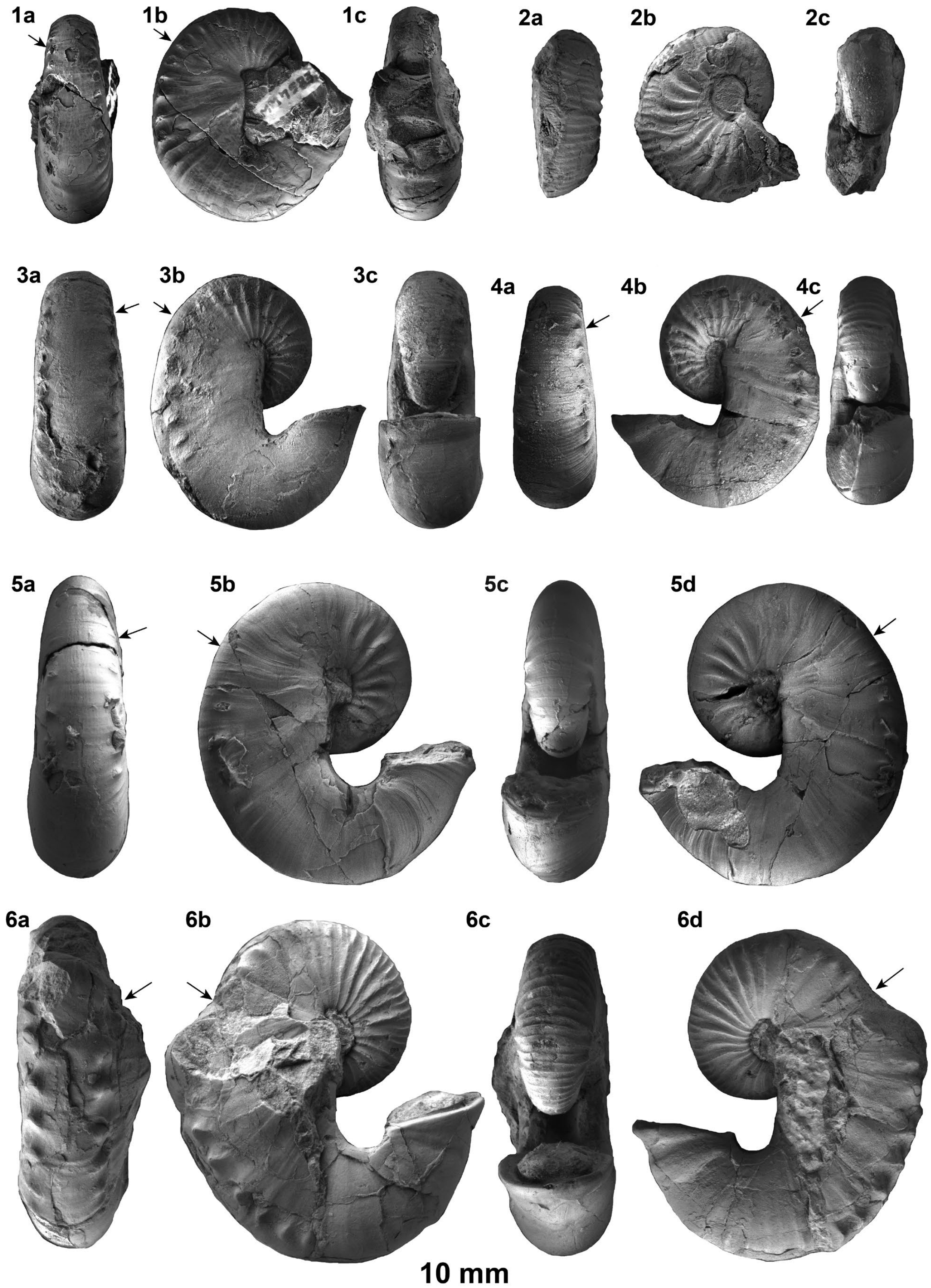

Figure 10. *Yezoites puerculus* (Jimbo, 1894). Mature (1, 3–6) and immature (2) macroconchs from Hokkaido. Ventral (a), right lateral (b), frontal (c), and left lateral (d) views for each specimen, except for left lateral view for 4b. Arrows point to the base of body chamber. **1**, UMUT MM 7583 from the Shiyubari River, Oyubari area; **2**, UMUT MM 7591 (holotype of *Scaphites yokoyamai* Jimbo, 1894) from the Pankemo-yubari River, Oyubari area; **3**, GK. H. 5779 from loc. Y5256a, Oyubari area; **4**, GK. H. 5777 from loc. R2110b', Obira area; **5**, GK. H. 5780 from a float nodule at loc. R2112, Obira area; **6,** GK. H. 5781 from loc. R5505, Obira area. All photos whitened with ammonium chloride.

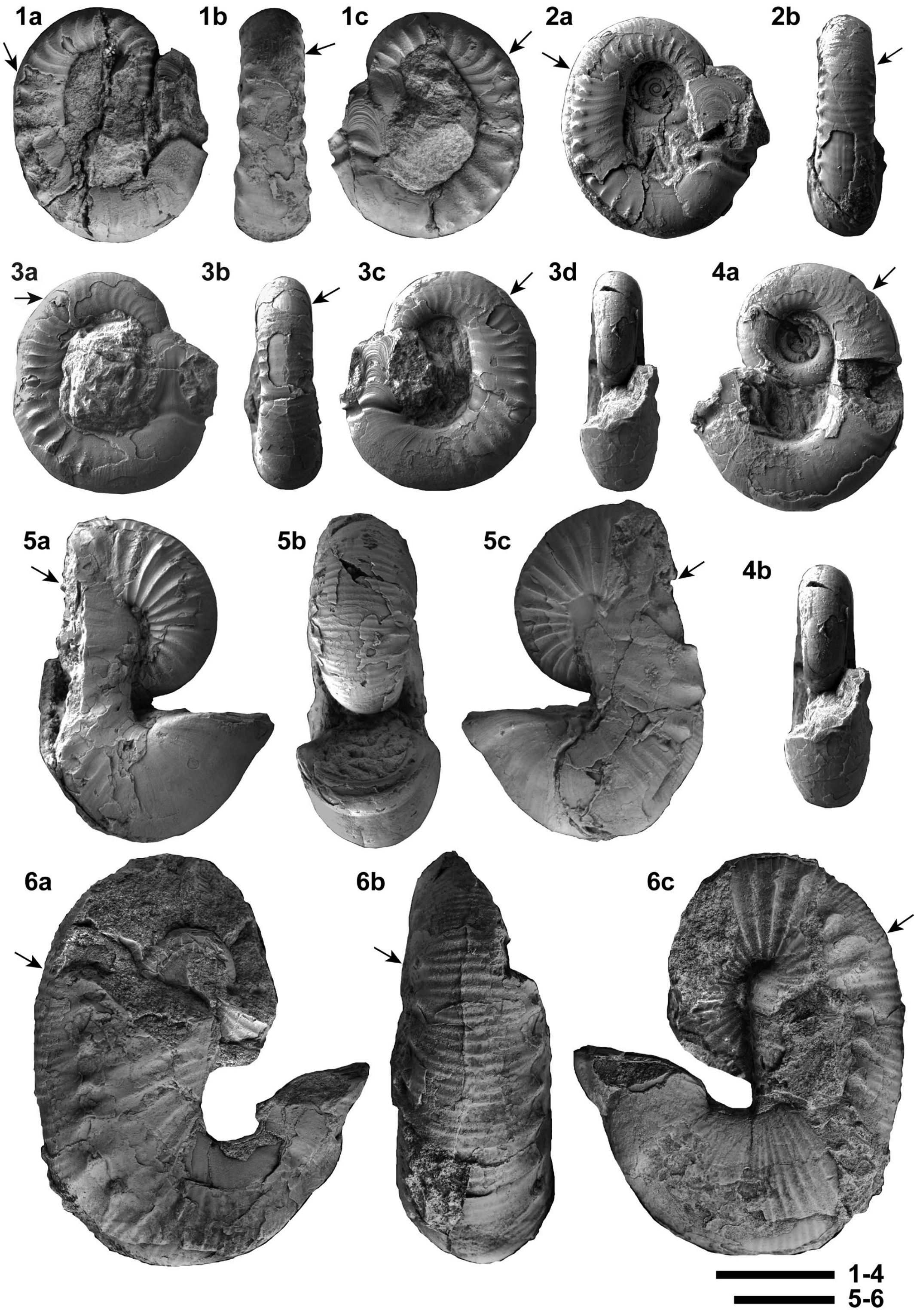

Figure 11. *Yezoites puerculus* (Jimbo, 1894). Mature microconchs (1–4) and macroconchs (5, 6) from loc. PZ 1001, northern Kamchatka. **1**, NMNS PM35465. Right lateral (a), ventral (b), left lateral (c) views; **2**, NMNS PM35480. Right lateral (a) and ventral (b) views; **3**, NMNS PM35482. Right lateral (a), ventral (b), left lateral (c), and frontal (d) views; **4**, NMNS PM35481. Left lateral (a) and frontal (b) views; **5**, NMNS PM35466. Right lateral (a), frontal (b) and left lateral (c) views; **6**, NMNS PM35467. Right lateral (a), ventral (b), and left lateral (**c**) views. Arrows point to the base of body chamber. All photos whitened with ammonium chloride. Scale bars represent 10 mm.

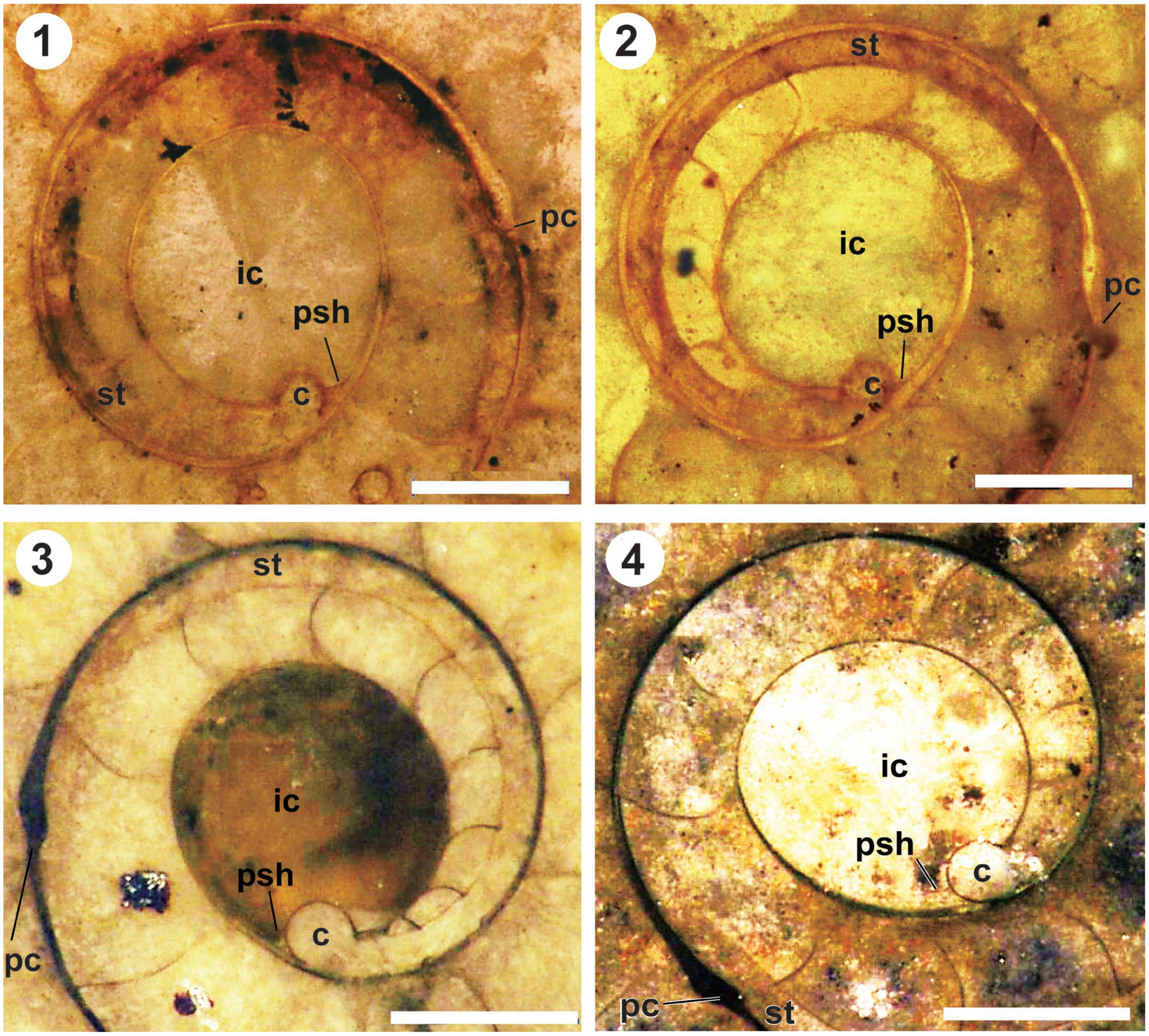

Figure 12. Optical micrographs of median sectioned early shell portions of *Yezoites puerculus* (Jimbo, 1894) (**1**, **2**) and *Yezoites pseudoaequalis* (Yabe, 1910) (**3**, **4**) from Hokkaido. **1**, GK. H. 20015, microconch from loc. R2105x, Obira area; **2**, GK. H. 5790, macroconch from loc. Y5201a, Oyubari area; **3**, GK. H. 20016, microconch from a float nodule at loc. IK2711, Pombetsu area; **4**, GK. H. 20017, macroconch from a float nodule at loc. IK2711. Abbreviations, c: caecum, ic: initial chamber ("protoconch"), pc: primary constriction, psh: prosiphon, st: siphuncular tube. Scale bars represent 250 μm.

Vereshchagin *et al*., 1965, p. 41, pl. 33, fig. 3a, b.
Scaphites planus Yabe var. *gigas* Yabe; Reeside, 1927, p. 33.
nom. nud. Yezoites subplanus Shimizu, 1935, p. 177.
nom. nud. Yezoites planus var. *paucicostata* Shimizu, 1935, p. 177.
nom. nud. Yezoites ainuanus Shimizu, 1935, p. 177.
Scaphites roguensis Anderson, 1958, p. 250, pl. 19, figs. 3, 3a.
Scaphites yokoyamai Jimbo; Matsumoto, 1963, pl. 64, figs. 3, 3a, 3b; Tanabe, 1977b, pl. 1, figs. 10, 11; Tanabe *et al*., 1977, tables 2a, 3a; Shigeta, 2001, pl. 45, fig. 3; Aiba *et al*., 2017, p. 5, pl. 7, fig. 3; Takahashi *et al*., 2007, pl. 7, fig. 2.
Scaphites pittensis Anderson, 1958, p. 252, pl. 19, fig. 4, 4a.
Scaphites (*Otoscaphites*?) *puerculus* Jimbo; Wiedmann, 1965, p. 433, 434, pl. 59, fig. 1a, b.
Scaphites aff. *planus* Yabe; Vereshchagin *et al*., 1965, p. 42, pl. 34, fig. 1a–c; Kanie, 1966, pl. 2, figs. 4a, b, 5a, b.
Scaphites aff. *planus* Yabe; Kanie, 1966, pl. 6, figs. 4, 5.
non. Scaphites cf. *planus* (Yabe); Tanabe, 1972, table 7.
non. Scaphites yokoyamai Jimbo; Tanabe, 1972, table 7.
Scaphites planus (Yabe); Tanabe *et al*., 1977, tables 2a, 3a; Tanabe, 1977a, p. 402, pl. 63, figs. 1–8, pl. 64, figs. 6–9; Tanabe *et al*., 1979, fig. 3.3, pl. 3, fig. 6; Shigeta, Y., 2001, pl. 45, fig. 2; Hayakawa, 2003, pl. 26, figs. a–e, q, r; Yazykova *et al*., 2004, fig. 9. 4–6; Arai and Wani, 2012, fig. 2.10; Yahada and Wani, 2013, p. 406, table 1, fig. 3.1; Aiba *et al*., 2017, p. 5, pl. 7, fig. 3.
Scaphites (*Scaphites*) *obscurus* Alabushev, 1989, p. 36, fig. 13, pl. 1, fig. 1.
Scaphites sp.; Hayakawa, 2003, pl. 26, figs. q, r.
Scaphites planus Yabe; Yazykova, 2004, pl. 2, fig. 1.

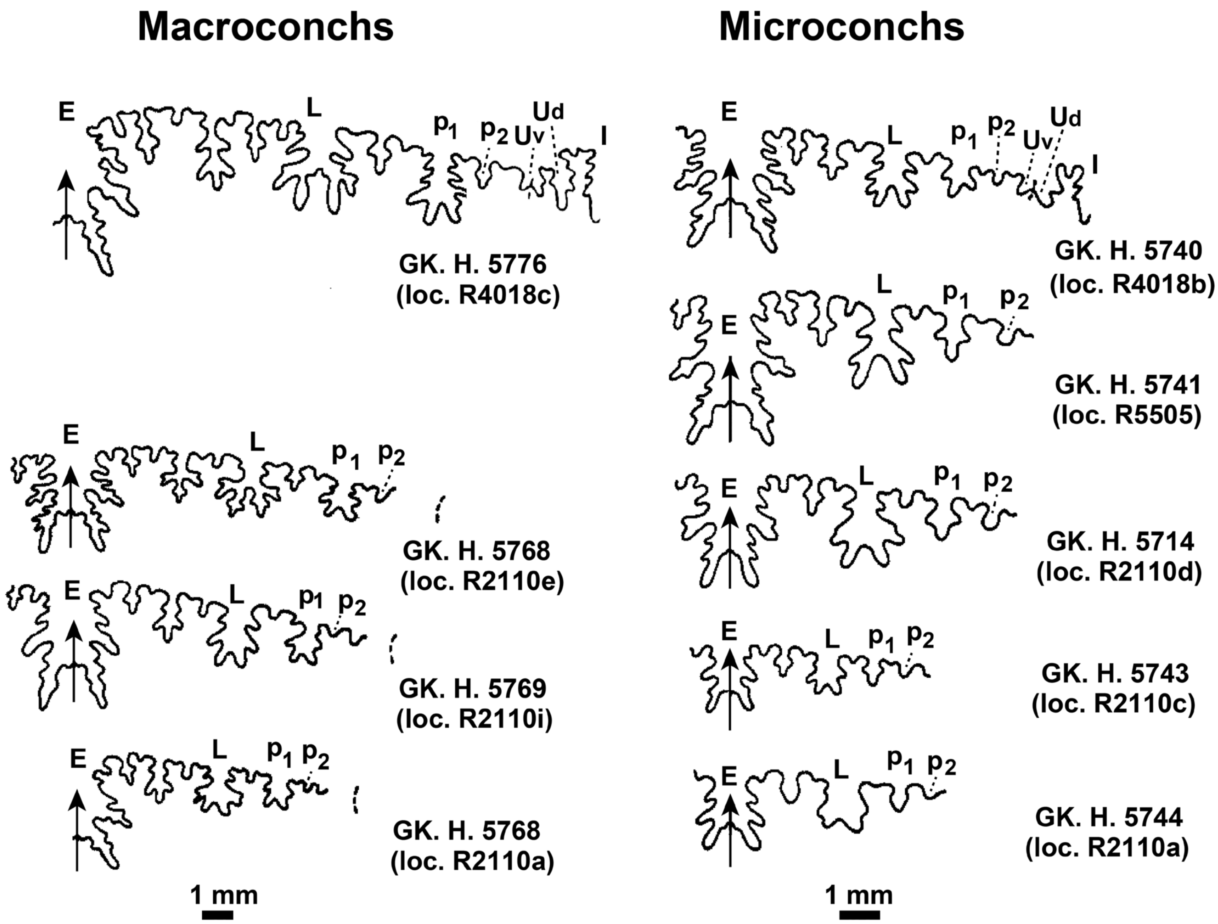

Figure 13. Trend of microevolution of adult sutures of *Yezoites puerculus* (Jimbo, 1894) in the middle Turonian sequence of the Obira area (modified from Tanabe, 1977a, fig. 12).

Yezoites puerculus (Jimbo); Davis *et al*., 1996, fig. 9G; Takahashi *et al*., 2007, pl. 7, fig. 3.

Type.—The lectotype, UMUT MM 7520 (Figure 9.1a–d), designated by Matsumoto (1963, p. 44) is a mature microconch that was originally figured as one of the syntypes by Jimbo (1894, pl. 5, fig. 4, 4a, b). It was collected from a calcareous nodule in the Turonian mudstone beds of the Saku Formation in the lower course of the Pankemoyubari (= Pankemoshuparo) River, a tributary of the Yubari River, Oyubari area, central Hokkaido (approximately 5 km south from the Kaneobetsu River), lat. 43°00′N, long. 142°09′E, according to Matsumoto, 1963).

Material examined.—In addition to the type-specimens described under S*caphites puerculus* Jimbo, 1894, *Scaphites Yokoyamai* Jimbo, 1894, *Scaphites* (?) *gracilis* Yabe, 1910, and *Yezoites planus* Yabe, 1910, all of which are housed in UMUT, a total of 1063 specimens (556 microconchs and 507 macroconchs) used by Tanabe (1975, 1977a) were examined. Furthermore, the following twelve specimens newly recovered from the middle Turonian *Inoceramus hobetsensis* Zone in Hokkaido (Obira and Oyubari areas) and northern Kamchatka (Penzhina Bay area) were studied; three microconchs (GK. H. 20003, GK. H. 20006, GK. H. 20019) from loc. R4001, Obira area, one microconch, GK. H. 20005 from a float nodule in the Sato-no-sawa Creek, Obira area, one macroconch, GK. H. 20008 from a float nodule at R4016p, Obira area, and two microconchs (GK. H. 20004, GK. H. 20020) and one macroconch (GK. H. 20007) from loc. Y1648d, Oyubari area, two microconchs (NMNS PM35464, NMNS PM35465) and two macroconchs (NMNS PM35466, NMNS PM35467) from loc. PZ1001, a large outcrop exposed at the mouth of the Esgichninvajam River facing the Penzhina Bay (see Figures 2.2, 3.1, 3.3, and Tanabe *et al*., 1977, fig. 9 for their locations).

Dimensions.—See Table 2.

Revised diagnosis.—Distinctly dimorphic species; microconchs and macroconchs share essentially identi-

Table 2. Measurements (in mm) of mature specimens of *Yezoites puerculus* (Jimbo). Locality of each specimen is given in parentheses.

Specimen no.	Conch type	*L*	*W*	*WB*	*WH*	*WB*/*WH*	*PD*	*PB*	*PH*	*PB*/*PH*	*U*	*U*/*PD*	*LLp*
UMUT MM 7520 (lectotype; Oyubari)	microconch	15.5	14.6	5.7	5.0	1.14	9.1	3.7	3.9	0.95	3.6	0.40	>3.2
GK. H. 5753 (R2110e)	ditto	16.3	13.6	6.1	4.7	1.30	9.4	4.2	3.9	1.08	3.7	0.39	>3.9
GK. H. 5754 (R2110b')	ditto	17.9	13.0	7.1	5.1	1.39	10.0	4.6	4.1	1.12	3.7	0.37	7.6
GK. H. 20004 (Y1648d)	ditto	19.8	14.7	6.8	5.9	1.15	11.6	5.5	5.1	1.08	4.6	0.40	>1.2
GK. H. 20020 (Y1648d-2)	ditto	17.3	14.3	6.3	4.5	1.40	10.2	4.7	4.3	1.09	4.5	0.44	?
GK. H. 20005 (Sato-no-sawa)	ditto	19.1	16.1	8.1	6.2	1.31	11.9	5.1	4.8	1.06	4.3	0.36	5.5
GK. H. 20006 (R4001)	ditto	30.0	23.3	10.3	8.3	1.24	16.5	7.2	7.5	0.96	5.6	0.34	8.0
GK. H. 20003 (R4001)	ditto	24.9	22.2	8.2	8.1	1.01	15.6	5.4	7.1	0.76	6.3	0.40	5.7
GK. H. 20019 (R4001)	ditto	26.5	22.4	9.0	8.7	1.03	16.0	6.2	6.6	0.94	6.0	0.38	8.8
NMNS PM35464 (PZ1001)	ditto	?	14.3	7.2	4.6	1.57	?	?	?	?	?	?	3.4
NMNS PM35465 (PZ1001)	ditto	18.3	15.0	6.9	5.4	1.28	10.6	4.6	3.7	1.24	3.7	0.35	6.5
NMNS PM35480 (PZ1001)	ditto	17.5	14.7	6.0	4.1	1.46	10.8	4.1	4.1	1.00	4.7	0.44	6.4
NMNS PM35481 (PZ1001)	ditto	21.5	18.5	7.5	6.1	1.23	12.5	5.1	5.3	0.96	5.1	0.41	>3.0
NMNS PM35482 (PZ1001)	ditto	17.6	15.7	6.8	4.8	1.42	11.5	4.6	5.0	0.92	3.8	0.33	6.3
NMNS PM35483 (PZ1001)	ditto	16.3	14.4	6.8	4.8	1.42	?	4.6	4.1	1.12	?	?	6.5
UMUT MM 7583 (syntype; Oyubari)	macroconch	27.0	24.0	10.1	9.8	1.03	17.1	7.7	10.1	0.76	1.8	0.11	–
GK. H. 5777 (R2110b')	ditto	26.1	23.9	>10.8	8.5	>1.27	15.6	6.9	8.4	0.82	2.6	0.17	–
GK. H. 5779 Y5256a)	ditto	31.0	25.8	11.8	10.2	1.16	17.1	9.2	9.7	0.95	1.6	0.09	–
GK. H. 5780 (R2112p)	ditto	33.7	30.3	10.3	11.0	0.94	19.1	7.2	9.8	0.73	3.2	0.17	–
GK. H. 20007 (Y1648d)	ditto	28.5	25.6	10.1	10.0	1.01	17.2	8.4	9.4	0.89	2.3	0.13	–
GK. H. 5781 (R5505)	ditto	42.8	36.1	14.5	13.4	1.08	22.7	10.2	12.0	0.85	3.9	0.17	–
GK. H. 20008 (R4016p4)	ditto	43.5	?	?	?	?	25.7	10.5	14.0	0.75	2.7	0.11	–
NMNS PM35466 (PZ1001)	ditto	33.1	?	13.8	12.0	1.15	19.4	9.9	11.2	0.88	2.4	0.12	–
NMNS PM35467 (PZ1001)	ditto	38.6	31.0	14.4	12.7	1.13	21.9	?	13.6	?	2.9	0.13	–

cal diagnoses in suture developmental patterns and early internal shell features, and surface ornament. Coiled whorls sculptured by weak to strong primary (umbilical) and fine secondary ribs; the latter generally bifurcating on the mid-flank; primary ribs tuberculate at the ventrolateral shoulder of body chamber; they become weaker toward aperture; hook part ornamented with numerous fine ribs only. Mature sutures of microconchs and macroconchs expressed by the formula E Lp$_1$ p$_2$ Uv Ud I, whose p$_1$ lobe essentially quadrifid. The E L saddle incised with one or two minor lobes; it becomes lengthen during ontogeny and phylogeny.

Description

Microconchs.—Mature conchs very small to small in maximum length, ranging from 15.5 mm to 30.0 mm in the specimens examined (Table 2; Figures 9, 11.1–4). Coiled whorls characterized by having somewhat compressed whorl section with rounded venter and moderately wide umbilicus (Figures 7.2, 7.3). Aperture of mature microconchs distinctly constricted with a pair of long, spatula-like lappets (Figures 5.1, 5.3, 9, 11.1–4). Whorl surface ornamented with weak to rather strong primary (umbilical) ribs and fine secondary ribs on the venter. Primary ribs on the mature body chamber tuberculated on the ventrolateral portion and tend to be weaken toward aper-

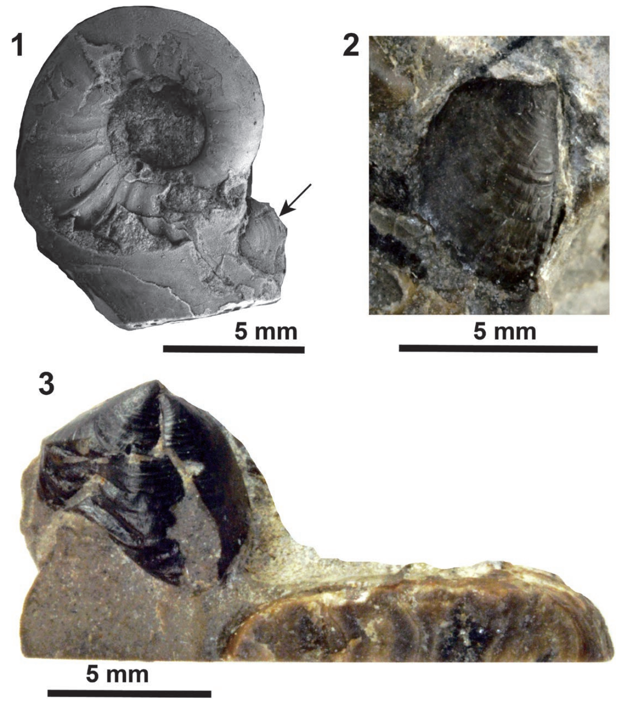

Figure 14. Lower jaws of *Yezoites puerculus* (Jimbo, 1894) from Hokkaido. **1**, GK. H. 8082, a microconch with preserved lower jaw *in situ* in the body chamber, from loc. 2110x, Obira area; **2**, GK. H. 8079, right lateral view of an isolated lower jaw attributed to *Y. puerculus*, co-occurred with many conchs of this species from a float nodule at loc. R4546, Obira area; **3**, GK. H. 8081, ventral view of an isolated lower jaw preserved near the aperture of a macroconch, from loc. Y5218b, Oyubari area.

ture (Figures 5.1, 9, 11.1–4). Apertural part ornamented with numerous very fine ribs only. Whorl width index (= whorl breadth/whorl height) and the degree of development of surface ornament exhibit wide individual variation in sympatric specimens.

Macroconchs.—Mature conchs small in maximum length ranging from 26.1 mm to 43.5 mm in the specimens examined (Table 2), quadrangular in outline with a narrow to moderately narrow umbilicus (Figures 5.2, 10, 11.5, 11.6). Coiled whorls circular to slightly wider than high in cross section, but the last coiled whorl always compressed laterally (Figures 7.4, 7.5). Umbilicus relatively wide in the first four whorls, but abruptly narrowing thereafter (Figure 7.5). Umbilical swelling well developed at the base of body chamber of mature conchs, but the grade of its development varies from specimen to specimen. Final hook of body chamber weakly to moderately compressed with ventrally expanded, constricted rip-like apertural margin. Apertural opening partly sealed by reflected shell (Figures 5.4, 11.5b). Surface on the first three whorls ornamented with fine ventral ribs only. Stronger ribs first appear in the early fourth whorl, and the last two coiled whorls sculptured by relatively strong ribs, generally bifurcating on the mid-flank. Primary ribs tuberculate at the ventrolateral shoulder of body chamber; they tend to be weaker toward aperture. Hook part ornamented with numerous fine ribs only.

Early shell features.—Both microconchs and macroconchs are similar in the early internal shell features in having a short and ventrally curved prosiphon, a circular caecum with a constricted base in median dorsoventral section, and a ventrally located siphuncle in the first whorl, the position of which is unchanged throughout ontogeny (Figures 12.1, 12.2). In the specimens examined, maximum initial chamber diameter ranges from 405 to 581 μm for microconchs and from 399 to 576 μm for macroconchs (Table 3), and ammonitella (= embryonic shell) diameter varies from 714 to 891 μm for microconchs and from 730 to 949 μm for macroconchs (Table 4). The variation of the two dimensions in the co-occurring microconchs and macroconchs is relatively small ($V < 7$).

Suture development.—The mature sutures of microconchs and macroconchs resemble those of *Scaphites equalis* stock (Wiedmann, 1965, text-fig. 3), and are expressed by the formula E Lp_1 p_2 Uv Ud I, whose p_1 lobe essentially quadrifid. Microconchs and macroconchs exhibit a similar temporal increase in the subdivision and depth of incision in the adult sutures in the Turonian sequence of the Obira area, northwestern Hokkaido, although the first pseudolobe, p_1 incised on the saddle LU is essentially quadrifid in macroconchs, whereas it is trifid in microconchs (Figure 13). According to Tanabe (1977a, fig. 13), microconchs and macroconchs of this species exhibit similar ontogenetic patterns of suture development, starting from ELUI in the first to the second whorls and ending to E Lp_1 p_2 Uv Ud I in the mature suture, via E L Uv Ud I and E Lp_1 Uv Ud I in the second to the third whorls. Furthermore, the suture developmental patterns of this species show a clear peramorphic trend in the Turonian sequence of the Obira area, since the first and second pseudolobes, p_1 and p_2 appear progressively earlier with time.

Jaws.—The lower jaw of this species is occasionally preserved *in situ* within and/or close near the body chambers of microconchs and macroconchs (Figure 14; see also Nagao, 1931a, fig. 2; Nagao, 1931b, pl. 15, fig. 9, 9a; Tanabe and Landman, 2002, pl. 1, fig. 4), but the upper jaw is still unknown. The lower jaw of this species is characterized by a widely open outer black chitinous lamella with a long and distinct commissure and a weakly pointed rostral tip. The outer chitinous lamella is ornamented with regular-spaced concentric growth rings and fine radiation striation (Figures 14.2, 14.3). Based on these features, the lower jaw of this species can be classified as the so-

Table 3. Statistical data of maximum diameter of initial chamber (in μm) in *Yezoites puerculus* (Jimbo).

Sample	Microconch				
	N	$\bar{X} \pm t_{0.05}\sigma_{\bar{x}}$	V	s	$O.R.$
N317d	10	488 ± 11	3.4	17	464–510
N315d	6	510 ± 39	7.2	37	472–581
N320	6	488 ± 25	4.9	24	454–516
R2105b	2	533 ± 292	6.2	33	510–556
R2110a	31	476 ± 7	4.2	20	446–528
R2110b	2	499 ± 217	4.9	24	482–516
R2110c	18	480 ± 8	3.5	17	454–522
R2110d	6	481 ± 11	2.1	10	468–494
R2110f	6	473 ± 23	4.6	22	436–494
R2110x	19	478 ± 9	4.1	20	438–507
R2113g	5	489 ± 20	3.3	16	480–518
R2113h	4	478 ± 54	7.1	34	440–518
R5505	13	521 ± 10	3.2	17	496–544
R4018b	8	523 ± 15	3.4	18	499–550
R4001d	7	492 ± 29	6.3	31	447–528
Y5226e	3	419 ± 67	5.5	23	405–446
Y5221g	8	456 ± 25	6.5	30	427–508
Y5251a	6	473 ± 23	4.7	22	452–514
Y5252b	3	470 ± 28	2.4	11	458–480
Y5218b	10	468 ± 19	5.9	27	419–494
Y5201r	8	470 ± 23	5.8	27	421–511

Sample	Macroconch				
	N	$\bar{X} \pm t_{0.05}\sigma_{\bar{x}}$	V	s	$O.R.$
R2110a	22	485 ± 7	3.3	16	440–512
R2110b	4	502 ± 36	4.5	23	476–530
R2110c	9	484 ± 12	3.4	16	463–506
R2110d	2	485 ± 89	2.1	10	477–488
R2110g	2	504 ± 203	4.5	23	488–520
R2110x	15	491 ± 8	2.8	14	461–527
R2113g	1	489	–	–	489
R2113h	3	513 ± 37	2.9	15	500–529
R5505	2	537 ± 330	6.9	37	511–563
R4018b	8	510 ± 29	6.7	34	485–576
R4018c	2	506 ± 114	2.5	13	497–515
R4001d	2	502 ± 4	1.7	1	469–508
R4022d	2	520 ± 178	3.8	20	506–534
Y5226e	5	490 ± 10	1.7	8	486–500
Y5221g	16	461 ± 17	6.8	31	399–496
Y5251a	4	470 ± 26	3.4	16	446–482
Y5218b	8	468 ± 23	6.0	28	425–498
Y5201r	11	474 ± 16	4.9	23	440–522
Y5201a	3	459 ± 68	6.0	27	434–488
Y5204	3	491 ± 37	3.1	15	476–506
Y5209a	8	492 ± 16	4.0	20	466–516
Y5208b	2	493 ± 13	0.3	1	462–464

called striaptychus of the aptychus-type jaws (Tanabe and Landman, 2002; Tanabe *et al*., 2015). In the lower jaws of other scaphitids described previously, the outer chitinous layer is covered by a pair of thin calcitic plates (aptychi *sensu stricto*) (e.g. Landman and Waage, 1993, fig. 42). The bivalved calcitic plates, however, could not be observed in the lower jaws of this species examined; they were presumably exfoliated before recovery.

Intraspecific variation of shell shape and ornament.— Yabe (1910) documented a wide intraspecific variation in the mature conch size, whorl shape and the strength of ribbing in both microconchs and macroconchs of this species. He examined more than two dozen microconch specimens, among which three large specimens (23–27 mm in maximum shell length) with strong ventral ribs figured in Yabe, 1910, pl. 15, figs. 23 (UMUT MM 7596), 25 (UMUT MM 7595), 26 (UMUT MM 7451) and one unfigured incomplete one (UMUT MM 7497) were described under *Yezoites puerculus* var. *teshioensis* Yabe. These specimens are comparable in size and ornament with the large microconchs shown in Figures 9.5a, b and 9.7a–d, and probably came from the upper part of the middle Turonian or from the upper Turonian. Similarly, Yabe (1910, p. 169, pl. 15, fig. 19) described a relatively large and strongly ribbed macroconch (UMUT MM 7591), measuring 32 mm in maximum shell length, from the Oyubari area under *Yezoites planus* var. *gigas* Yabe. However, this specimen is just a large macroconch

Table 4. Statistical data of ammonitella (= embryonic shell) diameter (in μm) in *Yezoites puerculus* (Jimbo).

Sample	Microconch					Sample	Macroconch				
	N	$\bar{X} \pm t_{0.05}\sigma\bar{x}$	V	s	$O.R.$		N	$\bar{X} \pm t_{0.05}\sigma\bar{x}$	V	s	$O.R.$
N317d	10	809 ± 16	3.0	7	770–867	R2110a	20	812 ± 14	3.7	30	748–877
N315d	6	826 ± 46	5.3	43	782–889	R2110b	4	828 ± 20	1.5	12	816–840
N320	5	810 ± 35	3.4	28	780–843	R2110c	9	823 ± 14	2.2	18	792–854
R2105b	2	853 ± 483	6.3	54	815–891	R2110d	2	823 ± 44	0.6	5	819–826
R2110a	27	812 ± 10	3.0	24	766–873	R2110g	2	849 ± 108	1.4	12	840–857
R2110b	2	819 ± 25	0.4	3	817–821	R2110x	15	835 ± 14	3.1	26	816–909
R2110c	18	803 ± 12	2.9	23	754–845	R2113g	1	799	–	–	799
R2110d	5	801 ± 38	3.8	31	752–829	R2113h	3	860 ± 82	3.9	33	823–887
R2110f	6	814 ± 17	1.9	16	800–843	R5505	3	873 ± 88	4.1	36	845–913
R2110x	20	813 ± 11	2.9	24	780–853	R4018b	8	844 ± 44	6.3	53	796–949
R2113g	5	811 ± 40	4.0	32	774–853	R4018c	2	850 ± 13	0.2	1	849–851
R2113h	4	777 ± 37	3.0	23	754–806	R4001d	1	839	–	–	839
R5505	13	850 ± 16	7.1	26	808–891	R4022d	1	859	–	–	859
R4018b	8	843 ± 18	2.6	22	815–889	Y5226e	4	816 ± 27	2.1	17	800–835
R4001d	7	814 ± 29	3.9	32	780–867	Y5221g	16	774 ± 15	3.8	29	730–817
Y5226e	3	733 ± 75	4.1	30	714–768	Y5251a	4	801 ± 38	3.0	24	768–825
Y5221g	8	762 ± 25	4.0	30	728–813	Y5252b	8	823 ± 23	3.4	28	793–867
Y5251a	5	797 ± 35	3.5	28	770–839	Y5218b	8	791 ± 24	4.0	32	744–837
Y5252b	3	788 ± 59	3.0	24	762–808	Y5201r	11	795 ± 15	2.8	22	766–851
Y5218b	10	791 ± 26	4.8	4	720–837	Y5201a	3	782 ± 53	2.7	21	770–807
Y5201r	8	800 ± 16	2.4	19	766–828	Y5204	3	801 ± 10	0.5	4	798–806

form of this species, as those shown in Figures 10.6a–d and 11.6a–c. The lectotype of *Scaphites puerculus* Jimbo, 1894 (UMUT MM 7520; Figure 9.1a–c) and one of the syntypes of *Yezoites planus* Yabe, 1910 (UMUT MM 7583; Figure 10.1a–d) are representatives of small-sized microconch and macroconch of this species respectively.

Quantitative morphological analysis of large population samples from Hokkaido and southern Sakhalin demonstrated that the strength of ribbing and whorl breadth/whorl height ratio, and the degree of development of paired lateral lappets exhibit a wide intraspecific variation for both macroconchs and microconchs (Figures 9–11; see also Tanabe, 1975, pl. 10; Tanabe, 1977a, pls. 62, 63). Yahada and Wani (2013) documented a significant difference in the shell thickness ratio (whorl breadth/maximum shell length) between two macroconch samples from the middle Turonian of the Oyubari and Kotanbetsu areas, Hokkaido, but further analysis of successively collected samples is needed to confirm whether the difference reflects the geographic variation or microevolutionary change of shell inflation in this species.

In the Turonian sequences of the Obira and Oyubari areas, Hokkaido, both microconchs and macroconchs of this species exhibit a similar microevolutionary trend to increase shell length and phragmocone diameter (see Tanabe, 1975, table 4; Tanabe, 1977a, table 2). Also, the spiral length of body chamber for mature microconchs tends to decrease toward the upward sequence (Tanabe, 1975, fig. 13; Tanabe, 1977a, table 3), but this trend is not observed in macroconchs (Tanabe, 1977a, table 3).

Discussion and comparison

Microconchs.—Wiedmann (1965, p. 434) pointed out that three microconchs of *Yezoites puerculus* (Jimbo) figured by Yabe (1910, pl. 15, figs. 20–22) differ from other microconchs of this species, by having distinct concave ribs, ventrolateral tubercles, and a high number of dense secondary ribs on the venter. Based on this fact, he newly proposed *Scaphites* (*Otoscaphites*) *yabei* Wiedmann, 1965 for them and designated the specimen UMUT MM 7592 figured by Yabe (1910, pl. 15, fig. 20a, b) as the holotype. However, my observation of two of the three specimens (UMUT MM 7592, UMUT 7594; note UMUT MM 7450 figured in Yabe's pl. 15, fig. 22 is now missing) indicates that they merely represent a coarsely ornamented form of the present species. As suggested by previous authors (Yabe, 1910, p. 170; Matsumoto, 1959, p. 172; Tanabe, 1977a, p. 401, 402), microconchs described under *S. inermis* Anderson (Anderson, 1902, p. 113, pl. 3, figs. 74–77; Anderson, 1958, p. 251, pl. 27, figs. 1, 1a–c) from the Turonian in the Forty-nine Mine, near Phoenix, Oregon and from a locality in the Little Cow Creek, Redding area, Shasta County, northern California, resemble the smooth-type microconchs of the present species in the overall conch shape and surface ornament. Wiedmann (1965, p. 433, 434, text-fig. 9; pl. 59, fig. 2a–c) figured two submature microconchs from the same locality as that of two paratypes of *S. inermis* by Anderson (1958) under *S.* (*O.*) *puerculus*. Tanabe (1977a, p. 402) attributed the two submature specimens described by Wiedmann (1965) to *O. bladenensis* (Schlüter, 1871) (= *Y. bladenensis*), but I now regard that they are microconchs of the present species in view of similarities in the surface ornament and sutural patterns at premature stage, expressed by the formula E L p_1 Uv Ud I (compare submature sutures shown in Wiedmann, 1965, text-fig. 9 and Tanabe, 1977b, fig. 4A, B).

Microconchs described under *Yezoites bladenensis* (Schlüter, 1871) from the Turonian in northwest and central Europe are similar in overall shape to those of the microconchs of the present species. *Yezoites bladenensis* is a very doubtful species, first described under *Ammonites* (?) *bladenensis* by Schlüter (1871, p. 30) based on several specimens (syntypes) from Bladen in Schlesien (see Wiedmann, 1965, p. 429; Kaplan *et al*., 1987, p. 19). Wright (1957, p. 807) designated an immature microconch figured by Schlüter (1871, pl. 10, figs. 5, 6) as the lectotype. Kaplan *et al*. (1987) studied many microconch specimens of *Y. bladenensis* from the middle to the upper Turonian at the type and other localities in northwest and central Europe. Those specimens differ from the microconchs of the present species by having much weaker primary and secondary ribs without ventrolateral tubercles. Unlike *Y. puerculus*, ribs on the microconchs of *Y. bladenensis* are maintained on the hook portion of the body chamber (see Wright, 1979, pl. 3, figs. 19, 20; Kaplan *et al*., 1987, pl. 6, figs. 1–3, 7–14, 16–29; Kennedy and Kaplan, 2019, pl. 50, figs. 8–12, pl. 52, figs. 5, 6). Kaplan *et al*. (1987, p. 21, pl. 6, fig. 4a, b) described a single microconch specimen without coiled phragmocone (BGS GSM 114753) from the upper Turonian at Dover, Kent, England under *Yezoites* cf. *puerculus* (Jimbo). Afterwards this specimen was redescribed under *Y*. aff. *puerculus* (Jimbo) by Kennedy (2020, p. 201, pl. 62, fig. 9, 10). BGS GSM 114753, however, differs from the microconchs of the present species by the presence of strong ribs on the hook portion.

Microconchs of the present species fairly resemble those of *Otoscaphites awanuiensis* Wright, 1957 (= *Yezoites awanuiensis* (Wright)) from the Upper Cretaceous in New Zealand by having a compressed whorl section with rounded venter and moderately wide umbilicus. As Wright (1957, p. 807) pointed out, the latter species is distinguished from the former by the total absence of ventrolateral tubercles. Wright (1957) suggested the age of *O. awanuiensis* as the upper Turonian, but Henderson (1973) correlated the *O. awanuiensis*-bearing horizon (upper Ngaterian in the local stage) with the Cenomanian in the international standard scale. Microconchs of the present species are similar to microconchs of *Yezoites concinna* Kennedy and Klinger (2013, p. 537, text-fig. 5J–Q) from the middle Coniacian of northern KwaZulu-Natal, South Africa in the mode ribbing on the phragmocone and shaft, but are distinguished from the latter by the absence of primary (umbilical) and fine secondary ribs on the hook portion. The depressed whorl section of *Y. concinna* fairly resembles that of the present species in the overall conch shape, but the latter is distinguishable from the former by a different branching pattern on mid-flank without developing ventrolateral tubercles.

Macroconchs.—*Scaphites yokoyamai* Jimbo (1894, p. 37[183], pl. 5[21], fig. 3, 3a, b), that was established based on a single submature macroconch (UMUT MM 7519) from the middle Turonian Saku Formation in the Pankemoyubari River, central Hokkaido (Matsumoto, 1963, p. 44), is regarded to be conspecific with the present species by the following reasons. In UMUT MM 7519 (Figure 10.2a–c), coiled whorls are slightly wider than high in cross section with a narrow umbilicus, and the last coiled whorl is ornamented with ventrally arched strong ribs that are bifurcated on the mid-flank, with an occasional intercalation of a weaker rib between them. These shell features indicate that the specimen can be identified as a strongly ribbed submature macroconch of the present species.

Scaphites (?) *gracilis* Yabe (1910, p. 166, pl. 15, figs. 9, 10) and *S.* (*Scaphites*) *obscurus* Alabushev (1989, p. 38, fig. 13, pl. 1, fig. 1) are monotypic species, that were proposed based on a single mature conch from the Turonian of the Obira area, Hokkaido and Penzhina Bay region, northern Kamchatka, respectively. They are regarded to be synonymous with the macroconchs of the present species, because of the similarities in the conch shape and mode of ribbings, whose primaries tuberculate at the ventrolateral shoulder of body chamber and tend to be weaker toward the constricted simple aperture. The relatively short shaft with a straight dorsal margin and the short hook in the holotype (UMUT MM 7581) of *S.*(?) *gracilis* are regarded as reflecting a wide intraspecific variability of macroconchs in the present species.

Anderson (1902, 1958) proposed *Scaphites condoni* Anderson, 1902, *S. condoni* var. *appressus* Anderson, 1902, *S. roguensis* Anderson, 1902, and *S. pittensis* Anderson, 1958, from the U.S. Pacific coast. Each of these species was established based on a single or a few macroconch specimens, and all specimens of the first three species came from the Turonian at the Forty-nine Mine near Phoenix, Oregon, whereas the holotype of the fourth species was recovered from a locality, about 15 km east of Redding, Shasta County, California. The holotypes of *S. condoni* and *S. condoni* var. *appressus* (see Anderson, 1902, pl. 2, figs. 58–59, 64–65) both possess an inflated body chamber on which strong ribs with paired ventrolateral tubercles on the shaft portion. These features are also observed in the strongly ribbed macroconchs of the present species; for examples, UMUT MM 7591 figured under *Yezoites planus* var. *gigas* (see Yabe, 1910, pl. 15, fig. 19) and YCM. GP. 2–1, 2 figured under *S.* aff. *planus* (see Kanie, 1966, pl. 6, figs. 4, 5) and *S. yokoyamai* (see; Tanabe, 1977b, pl. 1, fig. 10a, b). In view of the essential similarities in overall conch shape and surface ornamentation, the above listed four species described by Anderson (1902, 1958) are regarded as junior synonyms of the present species.

The mature macroconch of *Yezoites concinna* Kennedy and Klinger (2013, text-fig. 5R–T) from the middle Coniacian of northern KwaZulu-Natal resembles those of the present species in the mode ribbing on the phragmocone and shaft, but can be distinguishable from the latter by the absence of umbilical swelling at the base of body chamber and the persistence of primary ribs on the hook portion.

Occurrence.—This species is known from the Turonian in the circum-North Pacific regions (Hokkaido, southern Sakhalin, Kamchatka, southern Alaska, Oregon and California) (Appendix 1), i.e., from the middle Turonian (*Inoceramus hobetsensis* Zone) in northern Kamchatka (near the mouth of the Esgichninvajam River facing the Penzhina Bay) (Verechagin *et al*., 1965; Alabushev, 1989; Alabushev and Wiedmann, 1997) and southern Sakhalin (Naiba area) (Matsumoto, 1942; Tanabe, 1977a, b; Alabushev and Wiedmann, 1997; Yazykova, 2004), from the lowest Turonian (*Euomphaloceras septemseriatum* Zone) to the upper Turonian (*I. teshioensis* Zone) in Hokkaido (Saku, Kotanbetsu, Obira, Mikasa, Oyubari and Hobetsu areas) (Tanabe, 1977a, b), from the Turonian (unit C-1 of the lower part of Matanuska Formation) at USGS Mesozoic locality nos. M24853 and M2391, and 24239 (?), near the Glenn Highway, Nelchina area, southern Alaska (Granz in Jones, 1967), from the middle to the upper Turonian in Smith Ranch and Forty-nine Mine, near Phoenix, Oregon (Anderson, 1902), and from the upper Turonian (top of Member I to Member II of Redding Formation) in the Little Cow Creek, Salt Creek, and Sand Creek in Redding area, Shasta County, northern California (Matsumoto and Popenoe, 1960, fig. 1; Wiedmann, 1965). Noda (1969, p. 4) listed the occurrence of *Otoscaphites* sp. from the middle Turonian *I. hobetsensis* Zone of the Ryozen Formation, Onogawa Group in eastern Kyushu, southwestern Japan. It is highly probable that this species is attributed to the microconch of the present species. In Hokkaido, this species occurs throughout the Turonian and is found most abundantly in the *I. hobetsensis* Zone.

Yezoites pseudoaequalis (Yabe, 1910)

Figures 7.6–7.9, 12.3, 12.4, 15–17

Microconch synonymy

Scaphites klamathensis Anderson, 1902, p. 115, pl. 3, figs. 78–81; Reeside, 1927, p. 30; Anderson, 1958, p. 251, pl. 19, fig. 2a, b.
Otoscaphites teshioensis (Yabe); Saito, 1962, p. 80, text-fig. 11a, b, pl. 5, figs. 5, 7.
Otoscaphites klamathensis (Anderson); Tanabe, 1977b, p. 19, figs. 3.13, 3.14, 4D; pl. 1, figs. 4–6; Tanabe *et al*., 1977, table 3a.
Scaphites (*Otoscaphites*) *teshioensis* (Yabe); Alabushev, 1989, fig. 5.
Yezoites klamathensis (Anderson); Hayakawa, 2003, pl. 26, fig. m.
non. Yezoites klamathensis (Anderson); Walaszczyk *et al*., 2004, fig. 10Ba, b.
Yezoites pseudoaequalis (Yabe), microconch; Zakharov *et al*., 2005, p. 119.

Macroconch synonymy

nom. nud. Scaphites pseudoaequalis Yabe, 1909, p. 415.
Scaphites (?) *pseudoaequalis* Yabe, 1910, p. 163, pl. 15, figs. 1–3.
Scaphites pseudoequalis Yabe; Tanabe, 1977b, pl. 1, figs. 17–19; Tanabe *et al*., 1977, table 3a; Tanabe, 1989, figs. 1C–D, 3A; Shigeta, 2001, pl. 45, fig. 4; Hayakawa, 2003, pl. 26, fig. f.
non. Scaphites pseudoaequalis Yabe; Wright, 1979, p. 305, pl. 3, fig. 5; pl. 7, fig. 1.
Scaphites planus Yabe; Alabushev, 1989, fig. 6c; Alabushev and Wiedmann, 1997, pl. 2, fig. 7a, b.
Yezoites klamathensis (Anderson); Tanabe *et al*., 2010, p. 121, fig. 8A–C.
Yezoites pseudoaequalis (Yabe), macroconch; Zakharov *et al*., 2005, p. 119.
non. Scaphites pseudoaequalis Yabe; Kennedy, 2020, p. 181, text-fig. 85A, pl. 56, figs. 42–47.

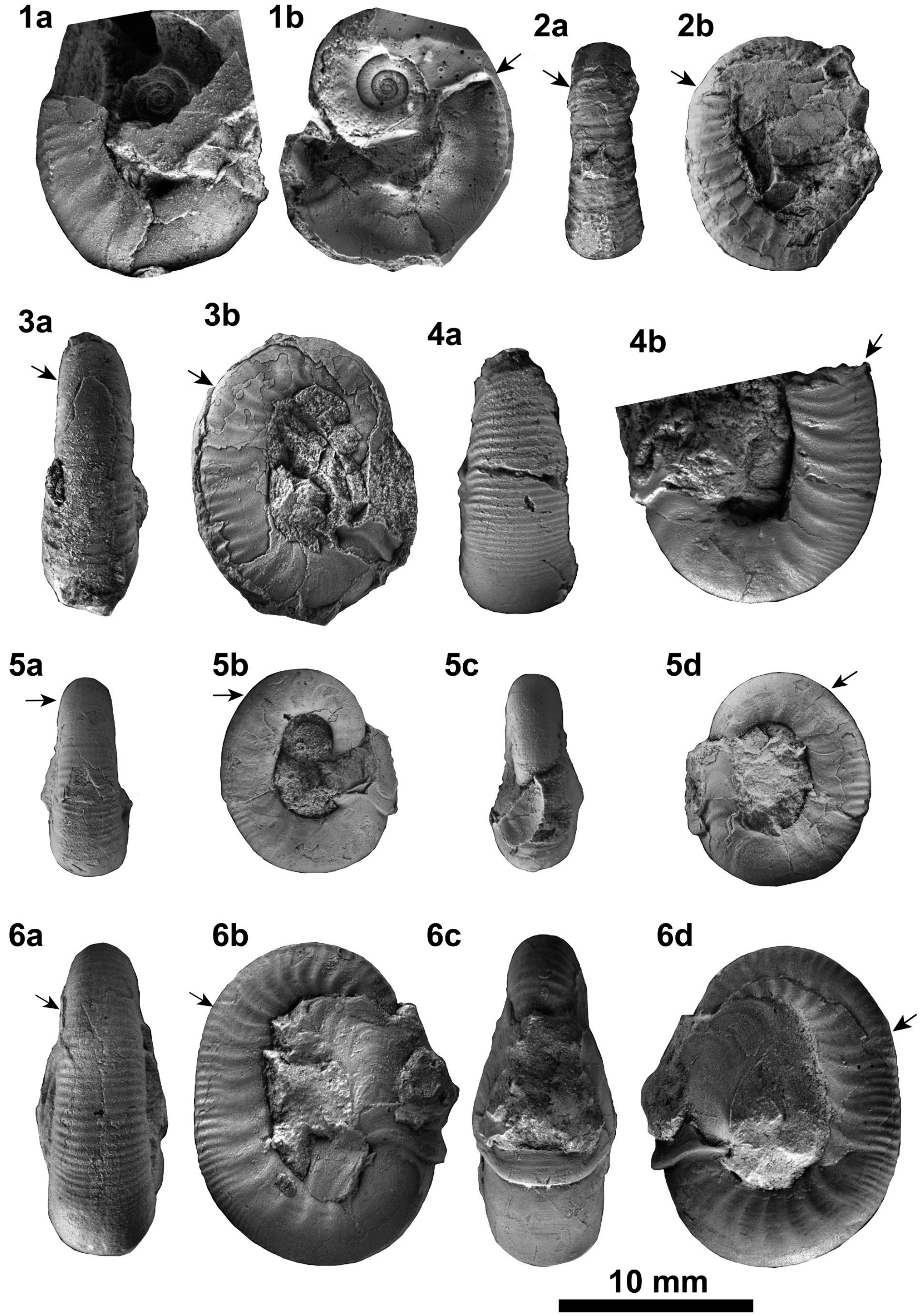

Figure 15. *Yezoites pseudoaequalis* (Yabe, 1910). Mature microconchs. Arrows point to the base of body chamber. Ventral (a), right lateral (b), frontal (c), and right lateral (d) views for each specimen, except for right lateral and left lateral views for 1a, and 1b and 4b respectively. **1**, NMNS PM35470 from loc. U8, Koike, Uwajima area. 1b is the silicon rubber cast of 1a; **2**, NMNS PM35475 from Anthracite Ridge, southern Alaska; **3**, GK. H. 20002 from a float nodule at loc. R4046, Obira area; **4**, NMNS PM15703 from Koike, Uwajima area; **5**, GK. H. 20024 from a float nodule at loc. IK2711, Pombetsu area; **6**, GK. H. 5835 from a float nodule at loc. IK 2711. All photos whitened with ammonium chloride.

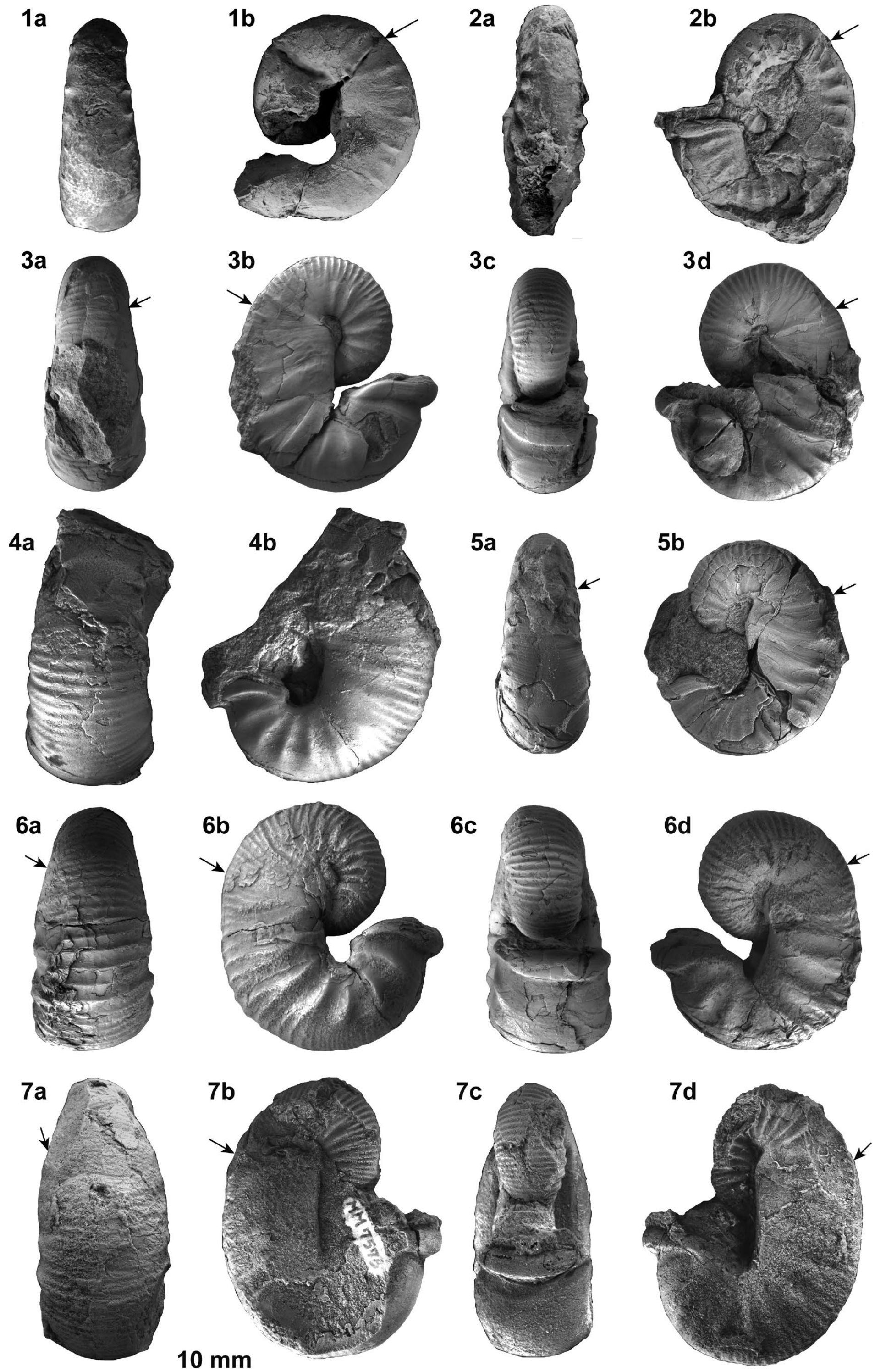

Figure 16. *Yezoites pseudoaequalis* (Yabe, 1910). Mature macroconchs. Ventral (a), right lateral (b), frontal (c), and left lateral (d) views for each specimen, except for left lateral views for 1a, 2b, 4b, and 5b. Arrows point to the base of body chamber. **1**, NMNS PM35476 from Anthracite Ridge, southern Alaska; **2**, NMNS PM35477 from the same locality as that of 1; **3**, GK. H. 5818 from a float nodule in the Pombetsu-gono-sawa Creek, Pombetsu area; **4**, NMNS PM35469 from Hode, Uwajima area; **5**, GK. H. 20001 from a float nodule at R4046p, Obira area; **6**, GK. H. 5817 from a float nodule in the Pombetsu-gono-sawa Creek, Pombetsu area; **7**, lectotype, UMUT MM 7576 from the Bannosawa Creek, Ikushunbetsu area. All photos whitened with ammonium chloride.

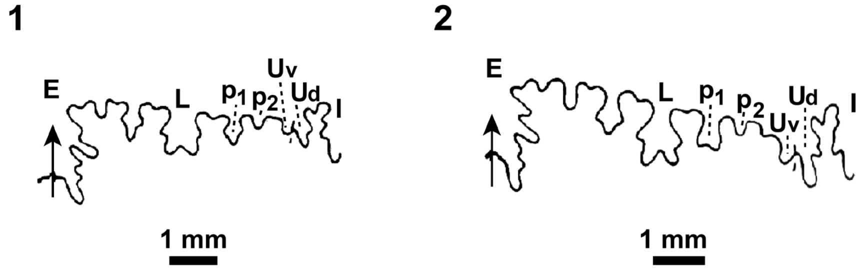

Figure 17. Drawings of mature sutures of *Yezoites pseudoaequalis* (Yabe, 1910). **1**, mature microconch, GK. H. 5836; **2**, submature macroconch, GK. H. 5821. Both specimens were collected from a fallen nodule at loc. IK2711, Pombetsu-gono-sawa Creek, Pombetsu area.

Type.—The lectotype, UMUT MM 7576 (Figure 16.7a–d), designated by Kennedy (2020, p. 181) is a mature macroconch that was originally described as one of the two syntypes described and figured by Yabe (1910, p. 165, pl. 15, fig. 1) from the Coniacian in the Bannosawa Creek (detailed locality undescribed), Ikushunbetsu area, central Hokkaido.

Remarks.—Anderson (1902, p. 115) established *Scaphites klamathensis* based on two microconchs from the northern border of Shasta Valley, California, to the south of the Klamath River, Oregon. However, the holotype (mature conch) and the paratype (immature conch) of this species were lost in the 1906 San Francisco fire (Anderson, 1958, p. 251). Anderson (1902) did not describe the detailed locality and horizon of these type specimens, although Reeside (1927, p. 30) later remarked the age of this species as the Cenomanian. Currently, additional specimens referable to this species are unavailable from the Upper Cretaceous of Oregon and California. For these reasons, I judge *S. klamathensis* as a doubtful species; hence *Yezoites pseudoaequalis* (Yabe) is adopted herein as a valid name for the corresponding *Yezoites* species from the Coniacian in the circum-North Pacific regions, whose microconchs are presumably conspecific with the holotype of Anderson's (1902) *S. klamathensis.*

Material examined.—In addition to the lectotype and a total of 325 specimens (162 microconchs and 163 macroconchs) studied by Tanabe (1977b), the following seven specimens newly recovered from the lower–middle Coniacian *Inoceramus uwajimensis* Zone in Japan and southern Alaska were examined. One microconch (NMNS PM35470) from loc. U8 (Koike) (Figure 15.1a, b) and one macroconch (NMNS PM35469) from loc. U49 (Hode) (Figure 16.4a, b), Uwajima area, Shikoku, southwest Japan; one microconch (GK. H. 20002) (Figure 15.3a, b) and one macroconch (GK. H. 20001) (Figure 16.5a, b) from loc. R4046p (found in a float nodule), Obira area, northwest Hokkaido, northern Japan; one microconch (NMNS PM35475) (Figure 15.2a, b) and two macroconchs (NMNS PM35476, 35477) (Figures 16.1a, b, 16.2a, b) from the Anthracite Ridge, southern Talkeetna Mountains, southern Alaska.

Dimensions.—See Table 5.

Revised diagnosis.—Distinctly dimorphic species; microconchs and macroconchs share essentially identical diagnoses in suture development and early internal shell features, shell shape in the early to premature stages, and surface ornament. Phragmocone and body chamber whorls ornamented with a combination of weak primary and fine secondary ribs; the latter bifurcated from the former on mid-flank, with intercalation of one or two fine secondary ribs; both primary and secondaries present on the whole body chamber; they disappear near the constricted aperture where numerous fine striations occur. Mature sutures expressed by the formula E Lp_1 p_2 Uv Ud I, whose p_1 and p_2 are weakly incised.

Description

Microconchs.—Mature conchs very small to small in maximum length ranging from 12.8 mm to 15.9 mm in the specimens examined (Table 5), ovate in lateral view (Figure 15). Coiled phragmocone whorls characterized by having moderately compressed whorl section with rounded venter and moderately wide umbilicus (Figures 7.6, 7.7). Aperture of mature microconchs bordered by a distinct lip-like elevation, being immediately preceded by a rather wide and shallow constriction. A pair of very long, spatula-like lappets ornamented with fine growth lines extend from the lateral side of the aperture; they partly cover the umbilical portion of coiled whorls (Figures 15.5d, 15.6b, d). Whorl surface ornamented with a combination of weak primary ribs and fine secondary ribs; the latter bifurcated from the former on mid-flank, with intercalation of one or two fine secondary ribs. The primaries prorsiradiate and weakly convex adorally. Both primary and secondary ribs weaken toward the hook portion of body chamber and disappear near the constricted aperture where numerous fine striations occur.

Macroconchs.—Mature conchs small in maximum length ranging from 21.1 mm to 32.2 mm in the specimens

Table 5. Measurements (in mm) of mature specimens of *Yezoites pseudoaequalis* (Yabe). Locality of each specimen is given in parentheses.

Specimen no.	Conch type	*L*	*W*	*WB*	*WH*	*WB*/*WH*	*PD*	*PB*	*PH*	*PB*/*PH*	*U*	*U*/*PD*	*LLp*
GK. H. 5835 (IK2711p-5)	microconch	15.9	10.8	5.6	4.5	1.24	10.0	4.0	3.8	1.05	?	?	8.2
GK. H. 5792 (IK2711p-1)	ditto	14.4	10.4	5.4	4.1	1.32	8.9	3.6	3.2	1.13	4.1	0.46	3.4
GK. H. 20024 (IK2711p-1)	ditto	12.8	10.6	5.1	3.7	1.38	7.9	3.5	3.2	1.09	3.6	0.46	3.5
GK. H. 20002 (R4046p)	ditto	15.0	11.6	?	4.2	?	8.7	3.4	3.4	1.00	3.8	0.44	?
NMNS PM35470 (U8)	ditto	13.5	11.9	4.7	3.6	1.31	10.6	?	3.7	?	4.2	0.40	>2.7
NMNS PM15703 (U8)	ditto	?	14.0	6.6	5.1	1.29	?	?	?	?	?	?	>2.0
NMNS PM35475 (southern Alaska)	ditto	13.8	11.0	5.1	?	?	9.1	3.9	3.1	1.25	4.0	0.44	>3.1
UMUT MM 7576 (lectotype; Ikushunbetsu)	macroconch	32.2	25.3	11.9	10.0	1.19	15.7	11.6	11.3	1.03	1.3	0.08	–
GK. H. 5817 (Pombetsu-gono-sawa Creek, float)	ditto	27.3	24.5	12.0	10.0	1.20	14.8	9.0	8.5	1.06	1.6	0.11	–
GK. H. 5818 (Pombetsu-gono-sawa Creek, float)	ditto	25.5	22.2	10.7	9.4	1.14	15.2	7.6	8.4	0.90	1.6	0.11	–
GK. H. 5820 (IK 1128)	ditto	25.1	19.9	10.3	8.7	1.18	15.2	8.0	8.7	0.92	1.0	0.07	–
GK. H. 20018 (Pombetsu-gono-sawa Creek, float)	ditto	28.1	22.9	11.5	9.4	1.22	15.4	8.9	9.3	0.96	1.2	0.08	–
GK. H. 20001 (R4046p)	ditto	23.3	19.6	9.5	7.7	1.23	14.2	7.1	7.8	0.91	1.7	0.12	–
NMNS PM35469 (U8)	ditto	?	23.5	11.9	8.7	1.37	?	?	?	?	?	?	–
NMNS PM35476 (southern Alaska)	ditto	21.3	17.5	8.0	6.9	1.16	14.4	5.9	6.5	0.91	?	?	–
NMNS PM35477 (southern Alaska)	ditto	21.1	18.7	7.7	7.3	1.05	12.6	4.9	5.5	0.89	4.3	0.34	–

examined (Table 5), quadrangular in lateral view (Figure 16). First four coiled whorls circular or slightly wider than high in cross section with rounded venter, but the last coiled whorl always weakly compressed with steeply sloping umbilical shoulder and broadly rounded venter (Figures 7.8, 7.9). Umbilicus relatively wide in the first four whorls, but suddenly becomes narrower thereafter. Body chamber moderately inflated with well-developed umbilical swelling at its base. It weakly compressed with flattened wide venter, and final hook portion relatively short with well-developed lip-like apertural edge on flank and ventral sides. Apertural edge surrounded by a bulge at about 2 mm wide and high on the outside, being narrower on the umbilical side, and lower and slightly curved backwards, and lacks conspicuous shell thickening. Coiled whorls and succeeding loosely coiled body chamber are sculptured by a combination of primary ribs and fine secondary ribs; the latter is bifurcated from the former on mid-flank, with intercalation of one or two fine secondary ribs. The primaries are weakly prorsiradiate and convex adorally. Both primary and secondary ribs become widely spaced and appear on the whole body chamber. The strength of primary ribs is especially conspicuous on the flank of hook portion (Figure 16).

Early shell features.—Microconchs and macroconchs share common early internal shell features by having a short and ventrally curved prosiphon, a subcircular caecum with a constricted base in median dorso-ventral section, and a ventrally located siphuncle in the first whorl, the position of which keeps throughout ontogeny (Figures 12.3, 12.4). Maximum initial chamber and ammonitella (embryonic shell) diameters in median section are similar between sympatric samples of microconchs and macroconchs, and respectively range from 366 to 439 μm and 657 to 777 μm for the specimens from the Pombetsu-gonosawa Creek, Pombetsu area, central Hokkaido (Table 6).

Suture development.—The sutures of microconchs and macroconchs resemble those of *Scaphites equalis* stock (Wiedmann, 1965, text-fig. 3) and exhibit similar ontogenetic patterns, starting from ELUI in the first to the second whorls and ending to E Lp_1 p_2 Uv Ud I in the mature suture, via E L Uv Ud I and E Lp_1 Uv Ud I in the second to the third whorls (Figures 17.1, 17.2; see also Tanabe, 1977b, fig. 4D, E).

Intraspecific variation of shell shape and ornament.—Both microconchs and macroconchs examined exhibit little intraspecific variation in shell shape and surface ornament. Yabe (1910) described that in UMUT MM 7576, designated herein as the lectotype, the flank and

Table 6. Measurements (in µm) of initial chamber and ammonitella diameters of *Yezoites pseudoaequalis* (Yabe). Abbreviations: *MaxID*, maximum initial chamber diameter, *MinID*, minimum initial chamber diameter, *AD*, ammonitella diameter.

Specimen no.	*MaxID*	*MinID*	*AD*
IK2711p5-1 (microconch)	393	376	730
IK2711p5-3 (ditto)	384	365	703
IK2711p5-4 (ditto)	406	384	767
IK2711p5-5 (ditto)	386	368	742
IK2711p5-6 (ditto)	383	369	713
IK2711p5-7 (ditto)	356	337	686
IK2711p5-8 (ditto)	399	382	742
IK2711p5-9 (ditto)	385	359	711
IK2711p5-10 (ditto)	385	366	696
IK2711p5-11(ditto)	389	353	723
IK2711p5-12 (ditto)	367	340	718
IK2711p5-13 (ditto)	366	351	657
IK2711p5-20 (ditto)	408	396	774
IK1127-1 (ditto)	439	418	782
IK2711p5-2 (macroconch)	411	378	711
IK2711p5-3 (ditto)	403	363	717
IK2711p5-4(ditto)	406	365	719
IK2711p5-6 (ditto)	425	404	777
IK2711p5-8 (ditto)	374	367	716

ventral ribs gradually disappear in the hook region of the body chamber, so that the ventral side appears smooth. My observation of the specimen, however, reveals that the outer surface of the body chamber portion has been largely eroded away before recovery, especially on the right lateral side (Figure 16.7b); hence it is highly probable that the lectotype originally had well-developed primary and secondary ribs on the hook, as in other macroconchs examined.

Discussion.—Microconchs of *Yezoites pseudoaequalis* are similar in shell shape to those described under *Otoscaphites reidi* Wright, 1979 and *Y. bladenensis* (Schlüter, 1871) from the upper middle Turonian to the upper Turonian in northwest and central Europe (Wright, 1979; Kaplan *et al*., 1987; Kennedy and Kaplan, 2019; Kennedy, 2020), in having strong flexuous blunt ribs branching at mid-flank or with intercalated secondaries. Especially, the specimens figured under *O. reidi* by Wright (1979, pl. 3, figs. 17, 18, pl. 7, fig. 8) and under *Y. bladenensis* by Kaplan *et al*. (1987, pl. 6, fig. 1), Kennedy and Kaplan (2019, pl. 50, fig. 8), and Kennedy (2020, pl. 62, figs. 20, 36) are comparable to the microconch of the present species shown in Figure 15.6a–d in the mode of ribbing pattern, whereas other microconchs of *Y. bladenensis* figured by Kaplan *et al*. (1987, pl. 6, figs. 16–29) and Kennedy (2020, pl. 62, figs. 1–8, 11–14, 23–24) are distinguishable from those of the present species by having much finer primary and secondary ribs on the body chamber. Macroconchs of *Y. bladenensis* (see Kaplan *et al*., 1987, pl. 2, fig. 14; pl. 6, fig. 15a, b; Kennedy, 2020, pl. 62, figs. 15–18), as well as those described under *Scaphites geinitzii* d'Orbigny, 1850 (Wright, 1979, p. 300, pl. 3, figs. 1–4; pl. 7, fig. 9; Kaplan *et al*., 1987, p. 10, pl. 1, figs. 1–4, 6–10, pl. 2, figs. 1–13, pl. 3, figs. 1–5, 9–11; pl. 4, figs. 1, 2, 7; Kennedy and Kaplan, 2019, pl. 50, figs. 14–32, pl. 51, figs. 5–17; Kennedy, 2020, pl. 55, figs. 4–35, pl. 56, figs. 1–19, pl. 57, figs. 1–31) from the upper Turonian in northwest Europe (England, France and Germany), differ from those of the present species by the development of ventrolateral tubercles on the body chamber. Three macroconchs (BGS GSM 115259, SMC B4205, SMC B76638) described under *Y. pseudoaequalis* Yabe from the upper Turonian in England by Wright (1979, p. 305, pl. 3, fig. 5; pl. 7, fig. 1a, b) and Kennedy (2020, p. 181, pl. 56, figs. 42–46) differ from those of the present species by having ventrolateral bullae on the body chamber and a much weaker umbilical swelling at the body chamber base. To sum up, further works with better-preserved microconchs and macroconchs comparable to those of *Y. pseudoaequalis* from the Coniacian of circum-North Pacific regions are needed to confirm the distribution of this species in northwestern and central Europe.

Microconchs and macroconchs of this species are easily distinguished from those of *Yezoites puerculus* (Jimbo, 1894) from the Turonian of circum-North Pacific regions by the absence of ventrolateral tubercles, and by having much simpler mature sutures (Figures 13, 17; see also Tanabe, 1977b, fig. 4) and smaller-sized initial chamber and ammonitella (Tables 3–4, 6; see also Tanabe, 1977b, fig. 5).

Occurrence.—From the Coniacian of Japan (Uwajima area, west Shikoku; Futaba area, northeast Honshu; Pombetsu, Ikushunbetsu, Obira, Kotanbetsu and Haboro areas, Hokkaido), Far East Russia (Naiba area, southern Sakhalin, and Talovka River, northern Kamchatka), and southern Alaska (Anthracite Ridge, southern Talkeetna Mountains).

Yezoites matsumotoi (Tanabe, 1977b)

Figure 18

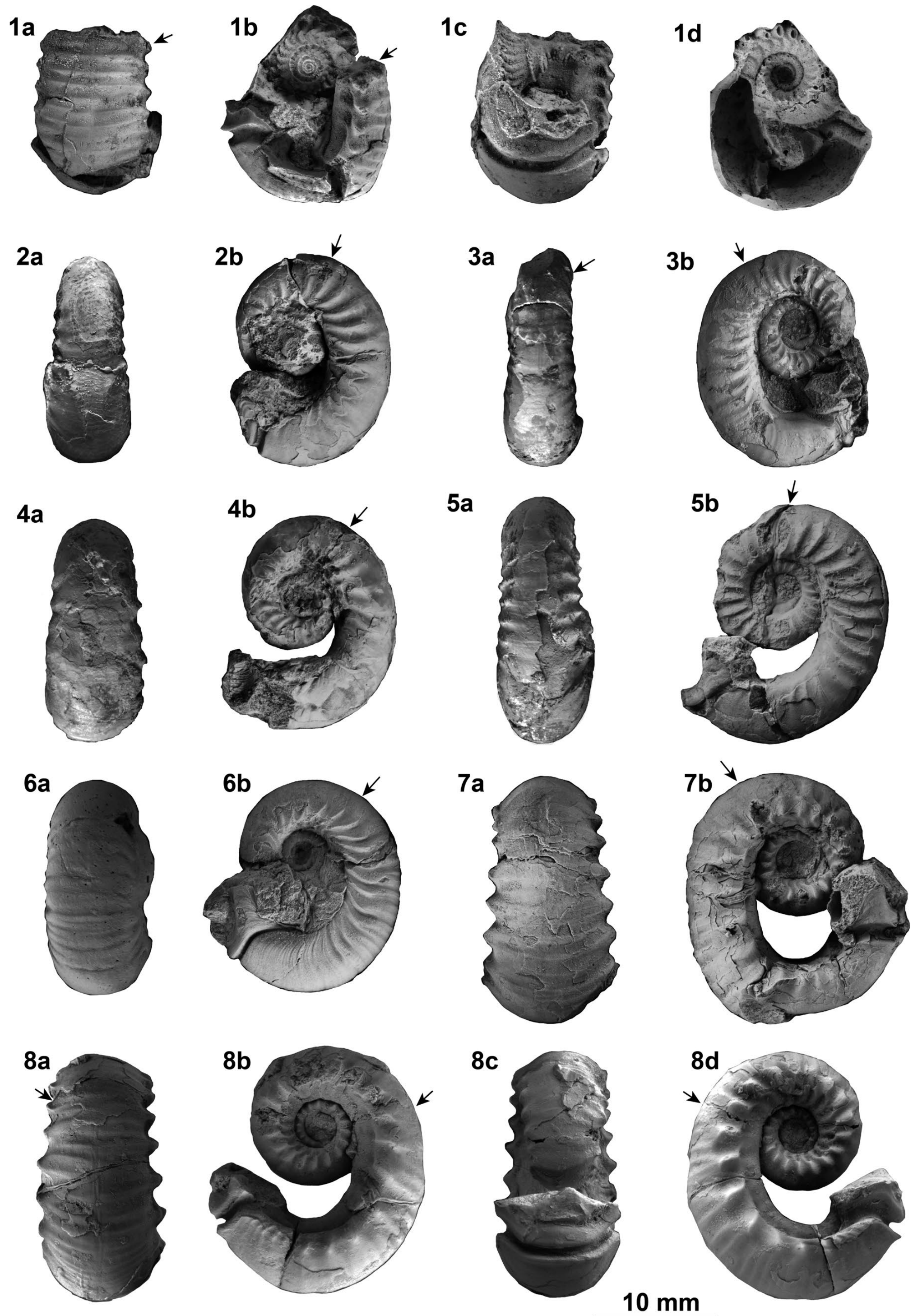

Figure 18. *Yezoites matsumotoi* (Tanabe, 1977b). Mature microconchs. Ventral (a), left lateral (b), frontal (c), and right lateral (d) views for each specimen, except for right lateral views for 3b and 7b. Arrows point to the base of body chamber. **1**, NMNS PM15702 (= GIYU. M. 106 of Tanabe, 1977b) from Hode, Uwajima area. 1d is the rubber cast of 1b; **2**, **3**, NMNS PM35471 (2) and NMNS PM35472 (3) from loc. TR722, Talovka River, northwestern Kamchatka; **4**, NMNS PM35473 from loc. TR720, Talovka River; **5**, NMNS PM35474 from a float nodule in the Takemi-zawa Creek, Haboro area; **6**, GK. H. 5831 from loc. R 2638j, Obira area; **7**, paratype, GK. H. 5832 from a float nodule derived from loc. IK 2710–11, Pombetsu area; **8**, holotype, GK. H. 5827 from a float nodule derived from loc. IK 2710–11. All photos whitened with ammonium chloride.

Table 7. Measurements (in mm) of adult specimens of *Yezoites matsumotoi* (Tanabe) *: After Tanabe (1977b). Locality of each specimen is given in parentheses.

Specimen number	Conch type	*L*	*W*	*WB*	*WH*	*WB*/*WH*	*PD*	*PB*	*PH*	*PB*/*PH*	*U*	*U*/*PD*	*LLp*
GK. H. 5827 (holotype) (IK2710-11)	microconch	21.0	17.4	10.3	6.2	1.66	13.6	7.8	5.7	1.37	4.7	0.35	>1.7
GK. H. 5832 (paratype)* (IK2710-11)	ditto	20.3	17.7	10.6	7.3	1.45	13.9	8.7	5.6	1.55	3.5	0.25	2.7
GK. H. 5830 (paratype)* (IK2710-11)	ditto	20.0	15.5	8.5	6.5	1.31	13.6	6.6	5.2	1.27	?	?	?
GK. H. 5831* (R2638j)	ditto	18.1	15.1	8.8	4.9	1.80	12.9	7.0	5.6	1.25	3.8	0.29	5.1
GK. H. 5829 (IK1127)	ditto	21.2	16.8	10.1	7.2	1.40	12.3	8.2	6.4	1.28	4.3	0.35	?
NMNS PM7351 (Futaba)*	ditto	22.1	?	9.4	?	?	12.9	6.5	6.2	1.05	4.5	0.35	?
NMNS PM15702 (paratype) (U8)	ditto	17.0	14.6	8.3	5.6	1.48	10.7	8.0	4.6	1.74	3.6	0.34	>2.5
NMNS PM35471 (TR722)	ditto	17.4	14.5	6.8	5.6	1.21	10.4	4.4	4.4	1.00	?	?	3.1
NMNS PM35472 (TR722)	ditto	18.0	14.5	6.2	5.6	1.11	11.6	4.4	4.4	1.00	5.2	0.45	2.5
NMNS PM35473 (TR720)	ditto	16.8	13.1	7.1	6.0	1.18	10.9	5.4	4.0	1.35	4.7	0.43	0.8
NMNS PM35474 (Haboro)	ditto	19.3	17.6	7.9	6.3	1.25	13.0	5.7	5.0	1.14	5.8	0.45	>3.6

Microconch synonymy

Scaphites puerculus Jimbo; Vereshchagin *et al*., 1965, p. 42, pl. 33, fig. 4.
Otoscaphites (*Hyposcaphites*) *matsumotoi* Tanabe, 1977b, p. 20, fig. 3–(12), pl. 1, figs. 7, 8a, b.
Scaphites (*Otoscaphites*) *puerculus* Jimbo; Alabushev, 1989, fig. 4a–f; Alabushev and Wiedmann, 1994, fig. 4D–F; Alabushev and Wiedmann, 1997, p. 13, pl. 3, figs. 2–5.
Yezoites teshioensis (Yabe); Shigeta, 2001, pl. 45, fig. 6.
Yezoites matsumotoi (Tanabe); Shigeta, 2001, pl. 45, fig. 7.
Yezoites perrini (Anderson); Inose, 2018, pl. 1, fig. 1a–d.

Types.—The holotype, GK. H. 5827 (Figure 18.8a–d) is the original of Tanabe (1977b, p. 20, pl. 1, fig. 8a, b) from a fallen nodule derived from the Coniacian *Inoceramus uwajimensis* Zone at loc. IK 2710-11, upper course of the Pombetsu-gonosawa Creek, Pombetsu area, central Hokkaido (location 43°17′07.5″N, 141°58′24.5″E; Figure 3.2). Paratypes, GK. H. 5830, 5832 (Figure 18.7a, b), and 5833, all from fallen nodules also collected at the type-locality.

Material examined.—In addition to the 41 specimens studied by Tanabe (1977b) from the Coniacian in the Pombetsu and Obira areas in Hokkaido, Futaba area in Northeast Honshu, and Uwajima area in Shikoku, one mature microconch (NSM PM35474) found in a float nodule in the Takemi-zawa Creek, Haboro area and three mature microconchs (NMNS PM35471, 35472, 35403), all recovered from mudstone beds of the Upper Penzhinskaya Formation exposed at locs. 714–722 of Zakharov *et al*. (2005, figs. 1, 5) on the west bank in the lower stream of Talovka River, northern Kamchatka were examined.

Dimensions.—See Table 7.

Revised diagnosis.—Mature microconchs small, characterized by stout, depressed coiled whorls with coronate cross sections, loosely coiled shaft and relatively short hook terminated by strongly constricted aperture with a pair of long and narrow lappets. Sculpture consists of strong, adorally concave primary ribs that are bifurcated on the ventrolateral side and extended to the venter, occasionally with developing a weak keep and distinct nodes on the inner flank, which slopes steeply inward. Adult suture resembles those of other *Yezoites* species. Macroconchs unknown.

Intraspecific variation.—As stated by Tanabe (1977b, p. 20), microconchs of the present species are characterized by stout, depressed whorls with coronate cross sections, moderately involute, deep umbilicus and strong, adorally concave primary and secondary ribs, occasionally with a weak keel and distinct nodes on the inner flank. However, strength of ribs and development of nodes exhibit marked intraspecific variation, and the holotype, GK. H. 5827 (Figure 18.8a–d), one of the paratypes, GK. H. 5832 (Figure 18.7a, b), and NMNS PM15702 from the Uwajima area (Figure 18.1a–d) represent the strongly ribbed type with sharp nodes, whereas NMNS PM35471 (Figure 18.2a, b) and NMNS PM35472 (Figure 18.3a, b) from northern Kamchatka, NMNS PM35474 (Figure 18.5a, b) from the Haboro area, and GK. H. 5831 (Figure 18.6a, b) from the Obira area, northwest Hokkaido are of weakly ribbed type without sharp nodes on the inner flank. NMNS PM35473 (Figure 18.4a, b) with weak nodes on the inner flank of the body chamber from northern Kamchatka represents an intermediate form.

Discussion.—The microconch specimens described under *Scaphites* (*Otoscaphites*) *puerculus* Jimbo by Alabushev (1989, fig. 4a–f), Alabushev and Wiedmann (1994, fig. 4D–F), and Alabushev and Wiedmann (1997, p. 13, pl. 3, figs. 2–5) from the Coniacian at locs. TR 720 and 722 in the lower course of the Talovka River, northern Kamchatka (Figure 2.2) are undoubtedly identified as microconchs of the present species because of the presence of diagnostic features including the depressed whorls with coronate cross sections and strong primary ribs with ventrolateral tubercles. Alabushev and Wiedmann (1994) described the strata that yielded microconchs of the present species as the Santonian/Campanian boundary beds, but they are, indeed, correlated to the Coniacian because of the co-occurred ammonites *Mesopuzosia yubarensis*, *Kossmaticeras japonicum*, *Anagaudryceras limatum*, and inoceramids *Sphenoceramus naumanni* and *Inoceramus uwajimensis* are commonly known in the contemporaneous strata in Hokkaido and Sakhalin (Zakharov *et al*., 2005).

Strongly noded micoroconchs of the present species including the holotype are similar to those of *Yezoites seabeensis* (Cobban and Gryc, 1961, p. 184, pl. 38, figs. 13–27) from the lower Turonian of northern Alaska and from the upper Turonian of Hokkaido, the latter of which was previously described under *Olcostephanus* sp. by Jimbo (1894, p. 33[179], pl. 9[25], fig. 3, 3a–b; see Figures 8.1–8.4), in the surface ornament and suture. However, in the latter species, coiled whorls are more compressed, and the nodes occur on the mid- to ventrolateral side of flank as against the inner flank in the present species. *Yezoites perrini* from the Turonian of Oregon (Anderson, 1902, p. 114, pl. 2, figs. 71–73; see also Figure 6.1), northern Alaska (Cobban and Gryc, 1961, p. 183, pl. 38, figs. 1–12), and Hokkaido (Yabe, 1910, p. 172, pl. 15, fig. 28a–d; Tanabe, 1977b, pl. 1, fig. 3a, b; see also Figures 6.2–6.4) resembles the present species in having depressed coiled whorls with a deep umbilicus, but is distinguished by finer ribbing pattern and smaller-sized adult shells.

Occurrence.—From the Coniacian (Zones of *Inoceramus uwajimensis* and *I. mihoensis*) in Japan (Uwajima, Futaba, Hokkaido), northern Kamchatka (Talovka River), and southern Alaska (Anthracite Ridge, Talkeetna Mountains).

Discussion

Other scaphitid ammonites from the circum-northwest Pacific regions

In addition to the five *Yezoites* species described herein, Misaki and Maeda (2009) reported two scaphitid species from the middle Campanian *Sphenoceramus schmidti* Zone of the Nakaibara Siltstone Member of Toyajo Formation in Wakayama Prefecture, west Japan (loc. 2 in Figure 1). The specimen figured under *Yezoites* sp. by Misaki and Maeda (2009, fig. 9H, I) is a small mature conch consisting of coiled whorls with a moderately wide umbilicus and a body chamber with a straight shaft and a sharply recurved hook. The overall shell shape fits well those of microconchs of other *Yezoites* species; however, a pair of lateral lappets, the diagnostic feature for the microconchs of this genus, could not be ascertained in the specimen as well as those of this morphotype from the Toyajo Formation, due to insufficient preservation (personal information from A. Misaki). The other two specimens figured under *Scaphites* sp. by Misaki and Maeda (2009, fig. 9E–G) are larger mature conchs with tightly coiled whorls, followed by a straight shaft and a recurved hook with a strong constricted aperture and collar, indicating that they represent macroconchs. It is highly probable that the specimens figured under *Yezoites* sp. and *Scaphites* sp. by Misaki and Maeda (2009) represent a dimorphic pair of the same species of *Yezoites*; however, better preserved microconch specimens with paired lateral lappets are needed to confirm this interpretation. I provisionally treat the scaphitid specimens described by Misaki and Maeda (2009) under *Yezoites* (?) sp. in this paper. Meanwhile, Matsumoto and Yokoi (1987, p. 43, figs. 1–4) described *Worthoceras pacificum* sp. nov. of the Otoscaphitinae, based on several tiny specimens with a long and straight shaft and paired lateral lappets from the Cenomanian of the Shumarinai area, northwestern Hokkaido.

Other scaphitid species described from the Upper Cretaceous deposits in the circum-North Pacific regions include *Scaphites japonicus* Inoma, 1980, p. 176, figs. 8–11 of the Scaphitinae, from the Cenomanian of the Shumarinai-Soeushinai area, northwestern Hokkaido, *S.* aff. *obliquus* J. Sowerby, 1813 from the basal Turonian of the Ikushunbetsu area, central Hokkaido (Tanabe, 1977b, pl. 1, fig. 9), *S.* (s.l.) *yonekurai* Yabe, 1910 from the lower to the middle Turonian of Hokkaido and southern Sakhalin (Naiba area) (Yabe, 1910, p. 165, pl. 15, figs. 4–7; Tanabe, 1977b, pl. 1, figs. 12, 13), *S. subdelicatulus* Cobban and Gryc (1961, p. 179, pl. 37, figs. 1–5; text-fig. 2c), and *S. delicatulus* Warren, 1930 (Cobban and Gryc, 1961, p. 182, pl. 37, figs. 16–24; text-fig. 2a, b, o) from the lower Turonian of northern Alaska, *S.* aff. *subdelicatulus* Cobban and Gryc, 1961 from the middle to the upper Turonian of Hokkaido (Tanabe, 1977b, p. 16, pl. 1, fig. 16) and northern Kamchatka (mouth of Esgichinvajam River, Benzhina Bay area) (Vereshchagin *et al.*, 1965, pl. 34, fig. 7a, b, figured under *S.* aff. *gracilis* Yabe), *S. talovkensis* Alabushev and Wiedmann, 1997, p. 12, pl. 1, fig. 1a–d (see also Alabushev and Wiedmann, 1994,

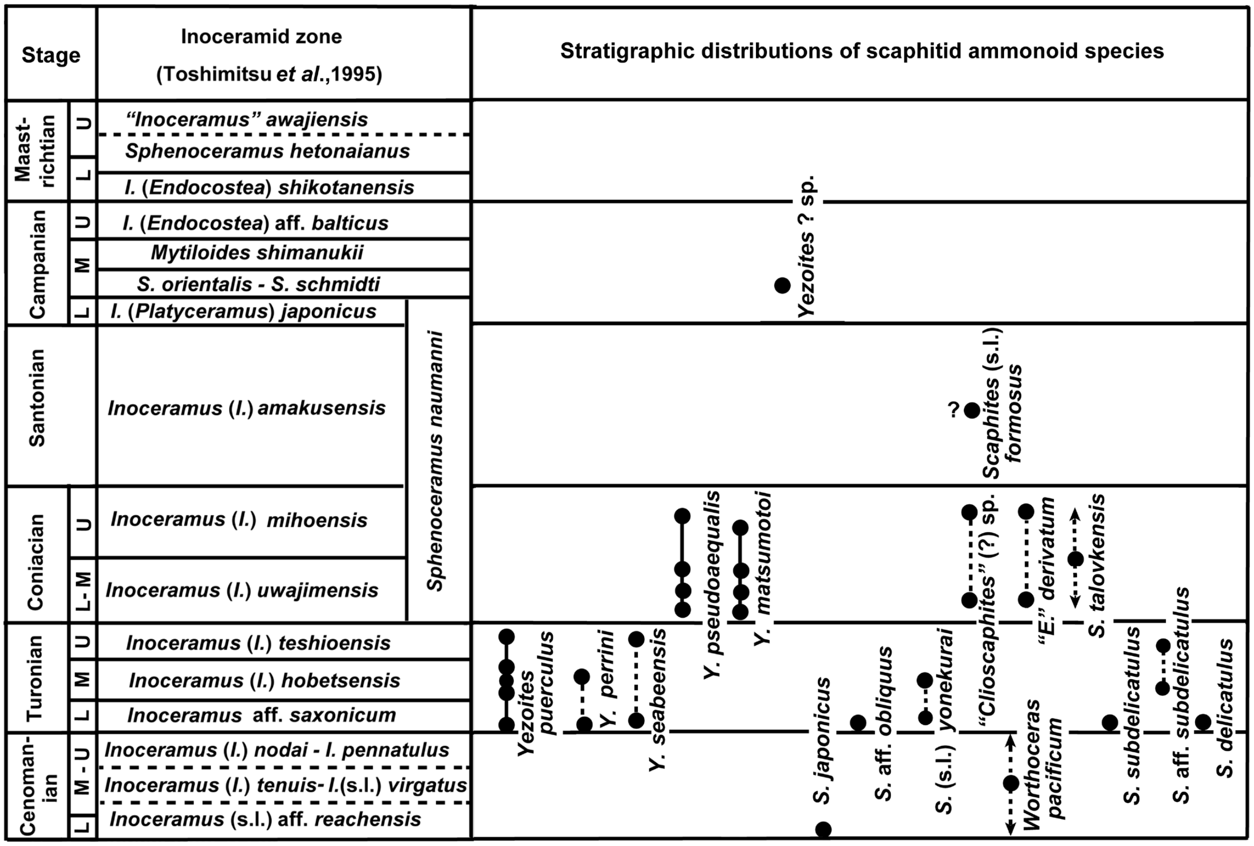

Figure 19. Stratigraphic distributions of scaphitid ammonoids in the Upper Cretaceous deposits in the North Pacific regions. See the text for the sources of fossil records. Vertical solid and dashed lines respectively indicate continuous and sporadic distributions. Age determination after Toshimitsu *et al*. (1995) and Shigeta *et al*. (2016).

fig. 4C) and *Eorhaeboceras derivatum* (Alabushev, 1989, p. 39, pl. 1, figs. 2, 3, text-fig. 3; see also Alabushev and Wiedmann, 1997, pl. 3, figs. 8–13, text-fig. 3) from the Coniacian in the lower course of Talovka River, northern Kamchatka, *Clioscaphites* (?) sp. from the Coniacian of Japan (central Hokkaido and Futaba area, northeastern Honshu) (Tanabe, 1977b, p. 18, pl. 1, fig. 21), and *Scaphites* (s.l.) *formosus* (Yabe, 1910, p. 166, pl. 15, fig. 8) from the Santonian of Ikushunbetsu area, central Hokkaido. These scaphitids are represented by either immature conchs for *Clioscaphites* (?) sp. and *E. derivatum* or mature conchs for the rest species, which are characterized by a straight shaft and a curved hook terminated by a constricted simple aperture without lateral lappets. Of these species, *C.* (?) sp. and *E. derivatum* are doubtful taxa, because they were proposed based on immature specimens. I provisionally refer them as to "*Clioscaphites*" (?) sp. and "*E.*" *derivatum* in this paper.

As suggested by Kennedy (1988, p. 113), *Scaphites* of *S. delicatulus* group, for examples, *S. subdelicatus* Cobban and Gryc, 1961 and *S. delicatulus* Warren, 1930 respectively are highly probable to constitute a dimorphic pair with the co-occurred microconchs of *Yezoites perrini* (Anderson, 1902) and *Y. seabeensis* (Cobban and Gryc, 1961) from the lower Turonian of northern Alaska. This view was followed for the relationship between *S. delicatulus* and *Y. seabeensis* by Wright *et al*. (1996, p. 260, fig. 201a–d). Kennedy's (1988) hypothesis should, however, be verified by detailed comparative morphological examination of sympatric mature specimens of these nominal species. Owing to the rare occurrence, it is still unsolved whether the rest of the above-listed scaphitid species from the circum-North Pacific regions represent macroconchs of *Yezoites* species or independent species of the Scaphitinae without a lappeted microconch.

Biostratigraphic and paleogeographic implications

Scaphitid ammonoids are known from the Cenomanian to the middle Campanian deposits in the circum-North Pacific regions (Figure 19). Of the five *Yezoites* species described, *Yezoites puerculus* occurs very abundantly in the Turonian sequences of Hokkaido, southern

Sakhalin, northern Kamchatka, southern Alaska, Oregon, and northern California. *Yezoites pseudoaequalis* and *Y. mastumotoi* are widespread in the Coniacian of Japan, northern Kamchatka, and southern Alaska, and can be used as the keys to biostratigraphic correlation of the Coniacian in these regions. In the Turonian-Coniacian sequences of the Cretaceous Yezo Group in Hokkaido, mature and immature shells of *Y. puerculus*, *Y. pseudoaequalis*, and *Y. matsumotoi* occur very abundantly together with other ammonoids such as the nostoceratids, diplomoceratids, and collignoniceratids in the silty to fine sandy lithofacies (Tanabe, 1977a, b, 1979). The whole litho- and biofacies of the scaphitid-bearing strata have been termed either the *Yezoites* beds (Yabe, 1927) or the *Scaphites* facies (Matsumoto and Okada, 1973; Tanabe, 1979), which represents a facies intermediate to the nearshore to offshore facies of the Yezo forearc sedimentary basin. In the Santonian and higher Cretaceous deposits in the circum-North Pacific regions, occurrences of scaphitid ammonites are sporadic, so that their exact stratigraphic ranges could not be determined (Figure 19). Late Cretaceous scaphitid ammonites from the circum-North Pacific regions are mostly represented by endemic taxa and characterize the faunal elements in the North Pacific biotic province (Jeletzky, 1971). None of genera known from the Santonian–Maastrichtian deposits of other bioprovinces, such as *Desmoscaphites*, *Acanthoscaphites*, *Rhaeboceras*, *Hoploscaphites* and *Discoscaphites* (e.g. Birkelund, 1965; Landman and Waage, 1993; Wright *et al.*, 1996; Machalski, 2005) have been found from the Upper Cretaceous in the circum-North Pacific regions.

Conclusions

Yezoites is a Late Cretaceous (Cenomanian–Campanian) dimorphic ammonoid genus of the family Scaphitidae, whose microconchs have a pair of long lateral lappets at the aperture. Based on the previously described material including type- and figured specimens and newly recovered ones, five species of *Yezoites* are described from the circum-North Pacific regions; i.e., *Y. perrini* (Anderson), *Y. seabeensis* (Cobban and Gryc), and *Y. puerculus* (Jimbo) from the Turonian, and *Y. pseudoaequalis* (Yabe) and *Y. matsumotoi* (Tanabe) from the Coniacian. Of these species, both microconchs and macroconchs are recognized in *Y. puerculus* and *Y. pseudoaequalis*, whereas only microconchs are known in the other three species. The five described *Yezoites* species characteristically occur in very fine-grained sandstone to silty mudstone lithofacies suggesting an intermediate between nearshore and offshore environments and can be used supplementarily for biozonation and correlation of the Turonian and Coniacian deposits in the North Pacific regions. The Late Cretaceous scaphitid ammonoids from the circum-North Pacific regions are mostly represented by endemic taxa and characterize the faunal elements in the North Pacific biotic province (Jeletzky, 1971).

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S-Appendix I. Locality guide of Turonian *Yezoites* specimens from the circum-North Pacific regions. *: locality is now under the reservoir.

Sample	Locality	Longitude and latitude	Horizon	Age	Source
PZ5000	Lower stream of Esgichninvajam R., northern Kamchatka, FER	61°39'03"N, 164°01'43"E	Penzhina Formation	middle Turonian (*Inoc.hobetsensis* Zone)	This study
PZ1000	Mouth of Esgichninvajam River, northern Kamchatka, FER	61°39'53"N, 164°00'53"E	Penzhina Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Same locality as loc. 700 in Zakharov *et al* ., 2004, fig. 1
N317d	Naiba River, southern Sakhalin, Far East Russia	47°18'46"N, 142°33'32"E	Bykov Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matumoto, 1942, pl. 8; Tanabe, 1977a; Kodama *et al* ., 2002, fig.2
N315d	Naiba River, southern Sakhalin, Far East Russia	47°18'36"N, 142°33'35"E	Bykov Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matumoto, 1942, pl. 8; Tanabe, 1977a; Kodama *et al* ., 2002, fig.2
N320	Naiba River, southern Sakhalin, Far East Russia	47°20'01"N, 142°33'24"E	Bykov Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matumoto, 1942, pl. 8; Tanabe, 1977a; Kodama *et al* ., 2002, fig.2
T43	Saku-gakko-no-sawa Creek, Nakagawa area, northern Hokkadio	44°44'18"N, 142°00'46"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matumoto, 1942, pl. 12; Tanabe, 1977a
T1083p	Saku-gakko-no-sawa Creek, Nakagawa area, northern Hokkadio	44°44'19"N, 142°00'48"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matsumoto and Okada, 1973, fig. 3; Tanabe,1977a
T1079p	Saku-gakko-no-sawa Creek, Nakagawa area, northern Hokkadio	44°44'20"N, 142°00'50"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matsumoto and Okada, 1973, fig. 3; Tanabe,1977a
R134p	Futamata Creek, Kotanbetsu area, northwestern Hokkadio	44°12'20"N, 142°01'43"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matsumoto and Okada, 1973, fig. 7; Tanabe,1977b
R5231	Obirashibe River, Obira area, northwestern Hokkaido	44°06'21"N, 142°00'12.5"E	Hikagenosawa Fm.	lower Turonian (*Inoc.* aff. *saxonicum* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R5232	Obirashibe River, Obira area, northwestern Hokkaido	44°06'22"N, 142°00'08"E	Hikagenosawa Fm.	lower Turonian (*Inoc.* aff. *saxonicum* Zone)	Tanabe et al., 1977, fig. 6
R5222	Obirashibe River, Obira area, northwestern Hokkaido	44°06'19"N, 142°00'10"E	Hikagenosawa Fm.	lower Turonian (*Inoc.* aff. *saxonicum* Zone)	Tanabe et al., 1977, fig. 6
R5414	Obirashibe River, Obira area, northwestern Hokkaido	44°06'14"N, 142°00'13"E	Hikagenosawa Fm.	lower Turonian (*Inoc.* aff. *saxonicum* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R5415	Obirashibe River, Obira area, northwestern Hokkaido	44°06'14"N, 142°00'12.5"E	Hikagenosawa Fm.	lower Turonian (*Inoc.* aff. *saxonicum* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R5423	Obirashibe River, Obira area, northwestern Hokkaido	44°06'22"N, 141°59'51"E	Hikagenosawa Fm.	lower Turonian (*Inoc.* aff. *saxonicum* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R2105	Obirashibe River, Obira area, northwestern Hokkaido	44°06'12"N, 141°59'47"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R2106	Obirashibe River, Obira area, northwestern Hokkaido	44°06'14"N, 141°59'45"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R2110	Obirashibe River, Obira area, northwestern Hokkaido	44°06'19"N, 141°59'43"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R2112	Obirashibe River, Obira area, northwestern Hokkaido	44°06'18"N, 141°59'39"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R2113	Obirashibe River, Obira area, northwestern Hokkaido	44°06'18"N, 141°59'36"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 6; Tanabe, 1977a
R4018	Obirashibe River, Obira area, northwestern Hokkaido*	44°04'05"N, 141°55'23"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R4016	Obirashibe River, Obira area, northwestern Hokkaido*	44°04'11"N, 141°55'31"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R4001	Obirashibe River, Obira area, northwestern Hokkaido*	44°04'00"N, 141°54'39"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R4022	Small creek near Nakakinenbetsu Br., Obira area, NW Hokkaido	44°04'18"N, 141°55'27"E	Saku Formation	upper Turonian (*Inoc. teshioensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R2203	Kamikinebetsu River, Obira area, northwestern Hokkaido	44°04'07"N, 141°57'13"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R2025	Nakakinenbetsu River, Obira area, northwestern Hokkaido	44°01'32"N, 141°56'58"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R2026	Nakakinenbetsu River, Obira area, northwestern Hokkaido	44°01'33"N, 141°57'05"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R5505	Nanbunosawa Creek, Obira area, northwestern Hokkaido	44°04'06"N, 141°56'08"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R5514	Nanbunosawa Creek, Obira area, northwestern Hokkaido	44°04'03"N, 141°56'15"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977a
R6732	Sannosawa Creek, Obira area, northwestern Hokkadio	44°01'10"N, 141°54'54"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe *et al* ., 1977, fig. 8; Tanabe, 1977a
IK1038	Ikushunbetsu River, Mikasa City, central Hokkadio	43°14'43"N, 142°00'02"E	Mikasa Formation	lowest Turonian (*E. septemseriatum* Z.)	Matsumoto, 1965, fig. 2; Tanabe, 1977b
Y5226	Hakkin River, Oyubari area, central Hokkadio	43°02'23"N, 142°09'51"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y5221	Hakkin River, Oyubari area, central Hokkadio	43°02'35"N, 142°09'36"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y5251	Hakkin River, Oyubari area, central Hokkadio	43°02'43"N, 142°09'34"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y5252	Hakkin River, Oyubari area, central Hokkadio	43°02'46"N, 142°09'31"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y5218	Hakkin River, Oyubari area, central Hokkadio	43°02'38"N, 142°09'26"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y5209	Hakkin River, Oyubari area, central Hokkadio	43°02'49"N, 142°09'08"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y5208	Hakkin River, Oyubari area, central Hokkadio	43°02'48"N, 142°08'58"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y5256	Hakkin River, Oyubari area, central Hokkadio*	43°02'53"N, 142°09'01"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe, 1977a
Y5204	Hakkin River, Oyubari area, central Hokkadio*	43°03'03"N, 142°08'53"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y5201	Hakkin River, Oyubari area, central Hokkadio*	43°03'12"N, 142°08'41"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Hirano *et al* ., 1977, fig. 2; Tanabe, 1977a
Y1648	Hakkin River, Oyubari area, central Hokkadio*	43°03'01"N, 142°07'17"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Tanabe, 1977a
H2073	Nutapomanai Creek, Hobetsu area, southern central Hokkaido	42°55'03"N, 142°10'37"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matsumoto and Okada, 1973, fig. 16; Tanabe, 1977b
H2115	Nutapomanai Creek, Hobetsu area, southern central Hokkaido	42°55'21"N, 142°10'16"E	Saku Formation	middle Turonian (*Inoc.hobetsensis* Zone)	Matsumoto and Okada, 1973, fig. 16; Tanabe, 1977b

S-Appendix II. Locality guide of Coniacian *Yezoites* specimens from the circum-North Pacific regions. *: locality is now under the reservoir.

Sample	Locality	Longitude and latitude	Horizon	Age	Source
AR1	Anthracite Ridge, southern Talkeetna Mts., southern Alaska	61°51'30"N, 148°07'18"W	Matanuska Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	This study
TR722	Lower course of Talovka River, northern Kamchatka, FER	62°21'09"N, 165°17'28"E	Upper Penzhinskaya Form.	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Zakharov *et al* ., 1995, figs.1, 5; this study
TR720	Lower course of Talovka River, northern Kamchatka, FER	62°20'38"N, 165°17'40"E	Upper Penzhinskaya Form.	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Zakharov *et al* ., 1995, figs.1, 5; this study
N26	Krasnoyarka River, Naiba area, southern Sakhalin, Far East Russia	47°20'20"N, 142°32'28"E	Bykov Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Matumoto, 1942, pl. 8; Tanabe, 1977b
H15	Takemizawa Creek, Haboro area, northwestern Hokkaido	44°16'05"N, 142°00'16"E	Haborogawa Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	This study
R140p	Futamata Creek, Kotanbetsu area, northwestern Hokkadio	44°12'22"N, 142°01'29"E	Haborogawa Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Matsumoto and Okada, 1973, fig. 7; Tanabe, 1977b
R6951	Obirashibe River, Obira area, northwestern Hokkaido	44°03'16"N, 141°53'36"E	Haborogawa Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe *et al* ., 1977, fig. 8; Tanabe, 1977b
R6033	Obirashibe River, Obira area, northwestern Hokkaido	44°03'20"N, 141°53'23"E	Haborogawa Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe *et al* ., 1977, fig. 8; Tanabe, 1977b
R2638	Obirashibe River, Obira area, northwestern Hokkaido	44°04'38"N, 141°56'19"E	Haborogawa Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977b
R4040	Obirashibe River, Obira area, northwestern Hokkaido	44°04'35"N, 141°56'39"E	Haborogawa Formation	upper Coniacian (*Inoc. mihoensis* Zone)	Tanabe *et al* ., 1977, fig. 9; Tanabe, 1977b
IK1127	Bannosawa forestry road, Mikasa City, central Hokkadio	43°13'47"N, 141°59'32"E	Kashima Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Matsumoto, 1965, fig. 2; Tanabe, 1977b
IK1128	Bannosawa forestry road, Mikasa City, central Hokkadio	43°13'48"N, 141°59'34"E	Kashima Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Matsumoto, 1965, fig. 2; Tanabe, 1977b
IK1111	Bannosawa Creek, Mikasa City, central Hokkadio*	43°13'49"N, 141°00'12"E	Kashima Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Matsumoto, 1965, fig. 2; Tanabe, 1977b
IK1110	Bannosawa Creek, Mikasa City, central Hokkadio*	43°13'45"N, 142°00'15"E	Kashima Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Matsumoto, 1965, fig. 2; Tanabe, 1977b
IK2710	Pombetsu-gonosawa Creek, Mikasa City, central Hokkaido	43°17'08"N, 141°58'24"E	Kashima Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe, 1977b
IK2711	Pombetsu-gonosawa Creek, Mikasa City, central Hokkaido	43°17'07"N, 141°58'25"E	Kashima Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe, 1977b
IK2713	Pombetsu-gonosawa Creek, Mikasa City, central Hokkaido	43°17'10"N, 141°58'24"E	Kashima Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe, 1977b
IK2715	Pombetsu-gonosawa Creek, Mikasa City, central Hokkaido	43°17'11"N, 141°58'25"E	Kashima Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe, 1977b
	Gokuraku-zawa, Ohku Town, Iwaki City, Fukushima Pref., NE Honshu	37°09'30"N, 140°56'22"E	Ashizawa Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Fukushima Prefectural Museum's collection
	600m NW of Oriki Spa, Hirono Town, Fukushima Pref., NE Honshu	37°12'22"N, 140°57'01"E	Ashizawa Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Fukushima Prefectural Museum's collection
U8	Koike coast, Uwajima City, Ehime Prefecture, western Shikoku	33°11'48"N, 132°30'20"E	Furushiroyama Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe, 1972, fig. 4; Tanabe, 1977b
U49	Hode, Uwajima City, Ehime Prefecturre, western Shikoku	33°12'43"N, 132°33'05"E	Furushiroyama Formation	lower-middle Coniacian (*Inoc. uwajimensis* Zone)	Tanabe, 1972, fig. 4; Tanabe, 1977b