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Dimorphism in the early Cenomanian (Late Cretaceous) ammonoid *Parajaubertella*

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Abstract. Ontogenetic development of ornamentation and whorl geometry of the Cretaceous ammonoids *Parajaubertella kawakitana* and *P. zizoh* are studied based on well-preserved specimens collected from the lower Cenomanian in the Horokanai area, Hokkaido, Japan. Our results indicate that their comparably sized immature stages share identical ornamentation and shell morphology, while the size of their adult shells is distinctly bimodal. They also share the same stratigraphic ranges in the lower Cenomanian and have overlapping geographic distributions in Northwest Pacific region, and lastly, they co-occur in the same concretions. This evidence strongly suggests that the two taxa should be considered as dimorphs, microconch and macroconch of a single species, which is herein described as *P. kawakitana*.

Keywords: ammonoid, Cenomanian, Cretaceous, dimorphism, Hokkaido, *Parajaubertella*

Introduction

Parajaubertella Matsumoto, 1943, a genus belonging to the family Tetragonitidae Hyatt, 1900 (Hoffmann, 2015), is one of the most common early Cenomanian ammonoid genera in the Northwest Pacific region (e.g. Matsumoto, 1995). Two species, the typically large shell sized *P. kawakitana* Matsumoto, 1943 and the small sized *P. zizoh* Matsumoto *et al*., 1997, have been described from the lower Cenomanian of the Yezo Group in Hokkaido, northern Japan and Sakhalin, Russian Far East (Figure 1). Matsumoto *et al*. (1997) concluded that the young shells of these two species could be separated, and excluded the possibility that they could represent a dimorphic pair (*ibid*, 1997, p. 198, l. 9–17). However, their observation of differences in the young shells of the two species was biased by the relatively low number of specimens at hand, therefore it was not possible to verify the range of intraspecific variation of each group. Moreover, the ontogenetic shell development of these two groups had not been examined. To determine if the young shells of *P. kawakitana* and *P. zizoh* are divergent, it is necessary to study the ontogenetic shell development of each species by utilizing several well-preserved adult specimens.

The National Museum of Nature and Science (NMNS), Tsukuba in Japan maintains a huge collection of Cretaceous ammonoids from Hokkaido collected by the late Yoshitaro Kawashita (1934–2000), which contains many specimens referable to *Parajaubertella* from the lower Cenomanian in Hokkaido (Shigeta, 2001). Furthermore, coauthor T. Sakai has spent more than 30 years investigating the lower Cenomanian of Hokkaido and collected many well-preserved specimens referable to *Parajaubertella*, which are housed in the NMNS.

In order to clarify the taxonomic relationship between the two species of *Parajaubertella*, we have examined the ontogenetic shell development (shell surface ornamentation and whorl geometry) and suture lines of the numerous specimens comprising the Kawashita and Sakai collections in the NMNS as well as the type specimens in the Kyushu University Museum (GK) and the University Museum, the University of Tokyo (UMUT).

Previous studies on *Parajaubertella*

The genus *Parajaubertella* was established by Matsumoto (1943) based on *P. kawakitana* as the type species. The comprehensive generic diagnosis is summarized as follows: 1) fairly involute, depressed shell with broadly rounded venter, inflated flanks, subangular

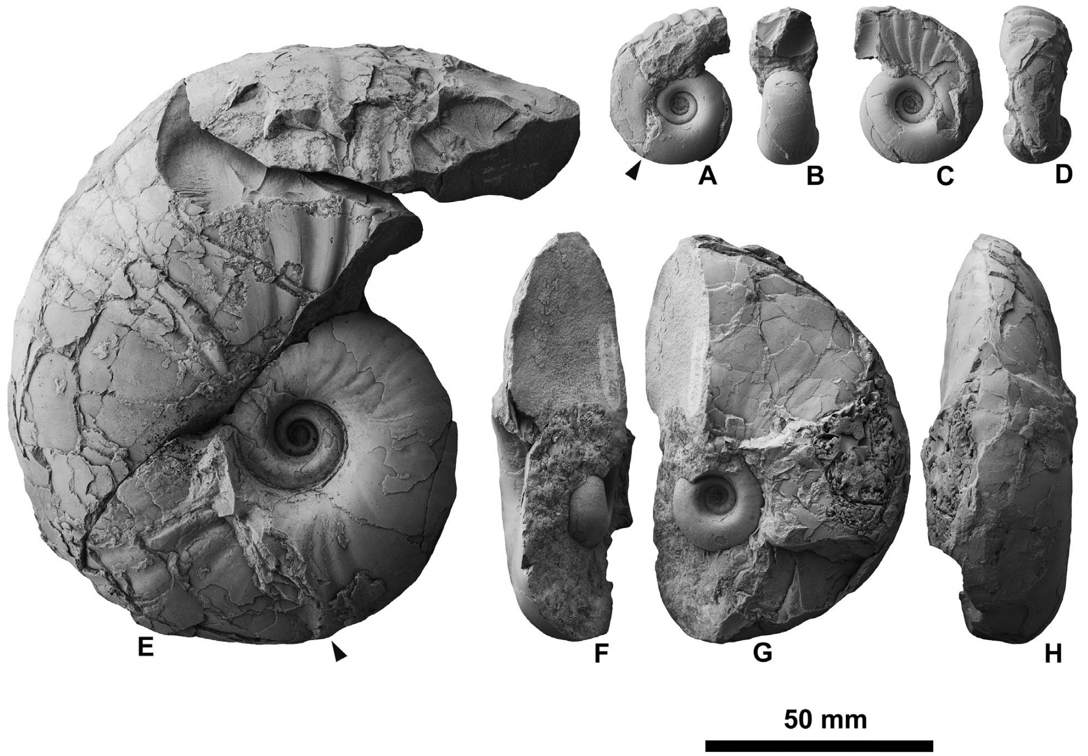

Figure 1. *Parajaubertella* from the lower Cenomanian of the Yezo Group. **A–D,** holotype of *P. zizoh* Matsumoto *et al*., 1997, GK.H8482, from the My3 Unit along the Suribachi-zawa River in the Horokanai area, which is here designated as a microconch of *P. kawakitana*. **E–H,** holotype of *P. kawakitana* Matsumoto, 1943, UMUT MM19698, from the Naiba area, Sakhalin, which is here designated as a macroconch of *P. kawakitana*. A, E, left lateral views; B, F, apertural views; C, G, right lateral views; D, H, ventral views. Black arrows indicate position of last septum.

umbilical edge, 2) fairly narrow and deep umbilicus with vertical umbilical wall, 3) ornamentation with slightly flexuous lirae on early whorls, and flexuous, narrow ribs or fold-like ribs at later stages and on the body chamber, which project forward on venter, and 4) gaudryceratid type suture line with large, incised, bifid major saddle, third lateral saddle situated on the umbilical shoulder, and bifid lateral lobe (Matsumoto *et al*., 1997; Hoffmann, 2015).

The holotype of *Parajaubertella kawakitana* (Figure 1E–H) was collected from a calcareous concretion in the lower Cenomanian Ky Unit of the Kawakita Group (= IV Unit of the Naiba Formation by Vereshchagin and Salnikov, 1968 and Poyarkova, 1987, and N2 Unit of the Naiba Formation by Kodama *et al*., 2002) at locality N94b of Matsumoto (1942, pl. 8) on the Yunosawa River. This river, also known as the Vesioly River, is a short eastern tributary of the Naibuchi River (= Naiba River), in the Bykov area, southern Sakhalin. The specific diagnosis is summarized as follows: 1) early growth stage with narrow and deep umbilicus, depressed whorl section, and slightly flexuous lirae, 2) long continuous middle growth stage in which several narrow ribs separated by narrow grooves appear periodically, and 3) large adult shell, about 200 mm in diameter on average, with rounded fold-like ribs separated by narrow interspaces on the body chamber (Matsumoto *et al*., 1997).

A second species of *Parajaubertella*, *P. imlayi* Matsumoto, 1959, whose holotype was collected from USGS Mesozoic locality 25445 (lower Cenomanian) in the upper Chitina Valley, southeastern Alaska, USA, is very similar to *P. kawakitana*, and the difference in the angularity at the umbilical shoulder of the inner whorls was given as one of the criteria to differentiate both species. Matsumoto (1995) suggested that *P. imlayi* should be suppressed as a junior synonym of *P. kawakitana*, because the umbilical shoulder is often modified by preservational conditions and the holotype of *P. imlayi* is somewhat weathered. This suggestion may have merit, but a thorough taxonomic study of *P. imlayi* is required, i.e., determine its intraspecific variation and examine its ontogenetic shell morphology.

Wiedmann and Dieni (1968) described *Gabbioceras kawakitanum occidentalis* based on a small specimen (diameter ~19 mm) collected from the uppermost Albian at Orosei, Sardinia, Italy. The small specimen described by Wiedmann and Dieni (1968) is very similar in shell form to juvenile specimens of *Parajaubertella kawakitana*, but the umbilical shoulder is located in the middle of the second lobe, thus suggesting that the holotype of *G. kawakitanum occidentalis* should be assigned to either *Gabbioceras*, Hyatt, 1900, or *Tanabeceras* Shigeta *et al*., 2012 (Hoffmann, 2010; Shigeta *et al*., 2012). The umbilical shoulder of *P. kawakitana* is located in the middle of the third saddle for a specimen with a diameter of 27.5 mm (Matsumoto, 1995, fig. 3d).

A third species of *Parajaubertella*, *P. zizho*, was described by Matsumoto *et al*. (1997) based on the holotype (Figure 1A–D) collected from a float calcareous concretion in the My3 Unit (lower Cenomanian) at locality R575 (Nishida *et al*., 1996) on the Suribachi-zawa River, a tributary of the Sounnai River, Horokanai area, northwestern Hokkaido. This species is characterized by a small adult shell, normally about 40 to 45 mm in diameter, but ranging up to 70 mm in extreme cases, with rounded fold-like ribs separated by narrow interspaces on the body chamber (Matsumoto *et al*., 1997).

Obata and Futakami (1977, fig. 1) designated a specimen as *Parajaubertella* aff. *kawakitana* from the upper Albian in the Manji area, central Hokkaido, but Shigeta *et al*. (2012) later established *Obataceras manjiense* based on this specimen. Shigeta *et al*. (2012) also erected *Tanabeceras pombetsense* based on a specimen reported as *P.* aff. *kawakitana* from the upper Albian in the Mikasa area, central Hokkaido by Futakami (1996, pl. 23, fig. 1).

Notes on stratigraphy

The Cretaceous Yezo Group in the Horokanai area, northwestern Hokkaido is complexly faulted (Hashimoto *et al*., 1965), but lower Cenomanian strata (= My3 to lower part of My5 units) are relatively well exposed along the Suribachi-zawa, Sanjussen-zawa, Kyoei-Sakin-zawa, Shumarinai, and Nakamata-zawa rivers (Nishida *et al*., 1996, 1997, 1998). The 500 m thick My3 Unit, consisting mainly of massive mudstone and mudstone with sandy laminae, contains many calcareous concretions in which not only *Parajaubertella kawakitana* and *P. zizoh* occur but other ammonoids as well. Two lower Cenomanian ammonoid zones, i.e., the basal Cenomanian *Graysonites wooldridge* Zone and the *Stoliczkaia japonica* Assemblage Zone, have been recognized in the My3 Unit (Matsumoto *et al*., 2003, 2004); the latter zone occurs below the lower Cenomanian *Mantelliceras saxbii* Zone in Hokkaido (Matsumoto *et al*., 2004). While the 250 m thick My4 Unit is composed mainly of unfossiliferous sandstone and conglomerates with well-rounded to subrounded pebbles and cobbles, the overlying 950 m thick My5 Unit, which is dominated by mudstone, contains *P. kawakitana* and *Neostlingoceras carcitanense* (Matheron, 1842) in the lower part. *Neostlingoceras carcitanense* also occurs in the lower Cenomanian *Mantelliceras japonicum* Zone in the Mikasa area, central Hokkaido (Matsumoto and Takahashi, 2000).

Material and methods

Material

The National Museum of Nature and Science, Tsukuba, maintains 252 specimens referable to *Parajaubertella* (NMNS PM16856, 16857, 17003–17007, 17009–17019, 17076, 35939–35956, 45000–45214). These specimens were collected from float or *in situ* calcareous concretions in the lower Cenomanian My3 Unit (*Graysonites wooldridge* Zone and *Stoliczkaia japonica* Assemblage Zone) along the Suribachi-zawa, Sanjussen-zawa, Kyoei-Sakin-zawa, Shumarinai and Nakamata-zawa rivers in the Horokanai area (Figure 2). The size distribution of those shells with rounded fold-like ribs separated by narrow interspaces, features that are characteristic of adult shells of *Parajaubertella kawakitana* and *P. zizoh*, is bimodal (Figure 3). According to Matsumoto (1995) and Matsumoto *et al*. (1997), the larger specimens (115–274 mm in diameter) are assigned to *P. kawakitana* and the smaller ones (34–55 mm in diameter) are identified as *P. zizoh*. From these, 18 well-preserved specimens were chosen for analysis of their ontogenetic shell development (whorl geometry and shell surface ornamentation). In addition to these specimens, the holotype (GK.H8482) and paratype (GK.H8446) of *P. zizoh* from the My3 Unit in the Horokanai area were also examined.

Methods

A total of 20 specimens were examined for ontogenetic shell development. The outer whorls of 18 specimens (NMNS PM16857, 17012, 35939–35954) were removed in two segments of about one-half whorl each, and then the four classic geometric parameters of the shell, i.e., diameter (D), umbilical diameter (U), whorl width (W) and whorl height (H), were measured with a slide caliper (accuracy, ± 0.05 mm) for each remaining shell down to a shell diameter of about 30 mm; in addition, three ratios, relative umbilical size (U/D), relative whorl thickness (W/H) and whorl expansion rate ($WER = [D/D']^2$; D', diameter before half whorl; see Klug *et al*., 2015a), were also calculated. Then, the inner whorls (diameter ~30 mm) of 7 well-preserved specimens (NMNS PM17014, 35940, 35943, 35945, 35947, 35950 and 35952) were further cut into cross sections, and each cross-sectioned surface was etched with 5% acetic acid for three minutes. Acetate

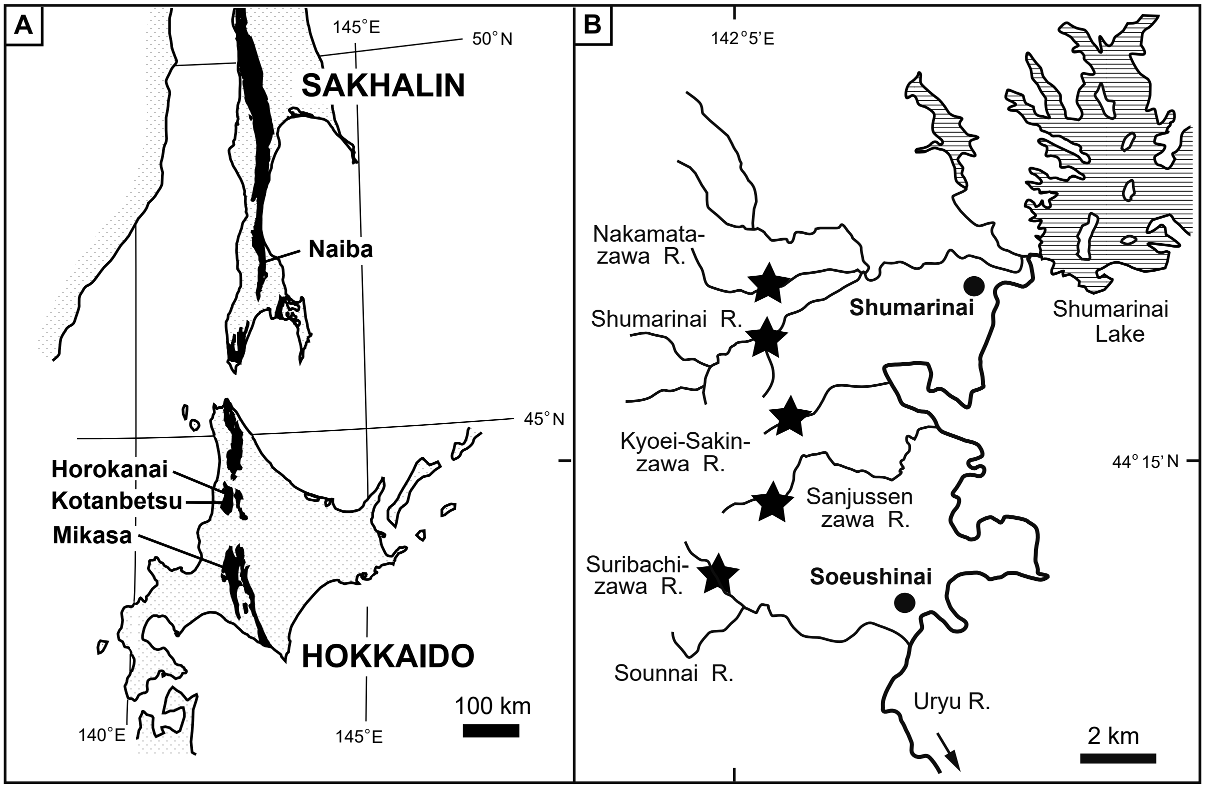

Figure 2. Index map (**A**) showing distribution of the Yezo Group (black areas) in Hokkaido, Japan and Sakhalin, Russia, and localities (**B**) from which specimens of *Parajaubertella* were collected in the Horokanai area (black stars).

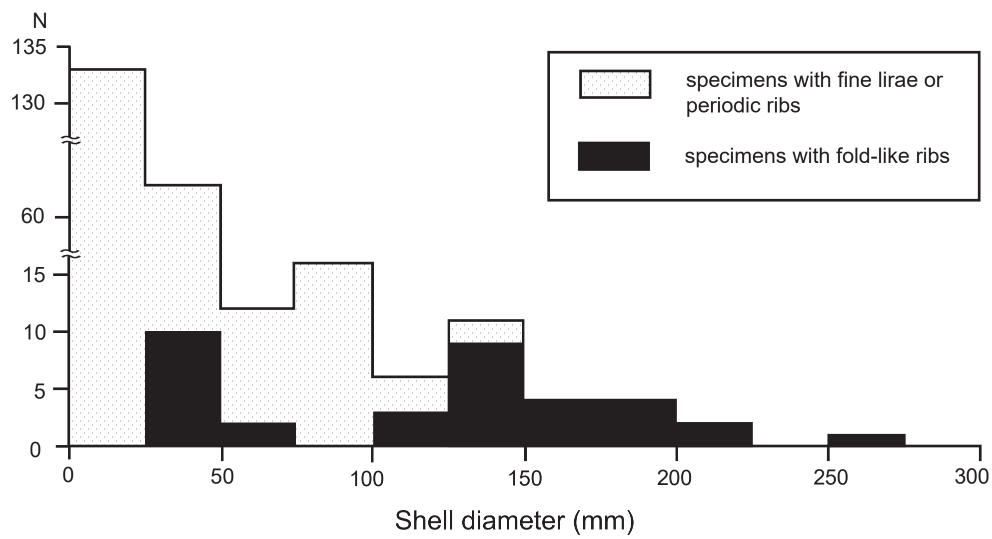

Figure 3. Histogram representing 252 *Parajaubertella* specimens separated by shell size (Kawashita and Sakai collections) collected from the My3 Unit of the Yezo Group in the Horokanai area, Hokkaido, which are stored at the NMNS. Two groups with rounded fold-like ribs are recognized. According to the species diagnosis (Matsumoto, 1995; Matsumoto *et al*., 1997), the larger group represents adult or subadult shells of *P. kawakitana* Matsumoto, 1943 and the smaller group is identified as *P. zizoh* Matsumoto *et al*., 1997. Specimens with fine lirae or periodic ribs are juveniles of *P. kawakitana* or *P. zizoh*.

peels were then prepared by pressing a sheet of triacetylcellulose film (0.025 mm in thickness) onto the etched surfaces while flooded with acetone. The four parameters (*D*, *U*, *W*, *H*) were then measured every half whorl using a digital micrometer (accuracy, ± 0.001 mm) attached to a profile projector (Nikon Model V-20B) on the peeled cross section and the three ratios (*U*/*D*, *W*/*H*, *WER*) were calculated.

The inner whorls of the holotype (GK.H8482) and paratype (GK.H8446) of *Parajaubertella zizoh* and specimens NMNS PM35948, 35949 and 35952 were scanned utilizing X-ray computed tomography (inspeXio SMX-225CT FPD HR, Shimadzu), and the four parameters (*D*, *U*, *W*, *H*) were measured every half whorl using an X-ray CT image of the cross section and the three ratios (*U*/*D*, *W*/*H*, *WER*) were calculated.

The phragmocones of many specimens are three-dimensionally preserved without deformation, but the body chambers are often deformed or lacking in part. The original shell diameter with a complete aperture was estimated by allometry of the shell in relation to whorl volution of the phragmocone, based on the observation that the length of the living chamber is 225 degrees, which was determined from specimens with perfectly preserved body chambers (e.g. PM35940, 35952).

Results

Shell surface ornamentation

Parajaubertella kawakitana.—Shell ornamentation consists mainly of fine growth lines, lirae, narrow ribs and fold-like ribs. The mode of ribbing changes with growth, and the following three successive stages are observable (Figures 4–6). First stage; nearly smooth with only fine growth lines and slightly flexuous lirae, which are recognized in the early growth stage with a shell diameter less than about 50 mm. Second stage; at shell diameters between about 37 mm and 155 mm, segments appear periodically that consist of a set of 3 to 5 narrow grooves followed by flexuous narrow ribs. Each segment extends for 30–40 degrees in spiral length, while the interval without ribs and grooves extends between 50–70 degrees. Third stage; characterized by rounded, fold-like ribs separated by narrow interspaces, a feature that appears in shells larger than the size range of 80–150 mm in diameter.

Parajaubertella zizoh.—Shell ornamentation consists mainly of fine growth lines, lirae and fold-like ribs. The early growth stage is nearly smooth with only fine growth lines and slightly flexuous lirae, but rounded fold-like ribs separated by narrow interspaces appear from 28–36 mm in shell diameter (Figures 6, 7).

Adult features

It is quite common for the adult body chamber of ammonoids to exhibit a change in ornamentation (e.g. Davis *et al*., 1996; Klug *et al*., 2015b). Among the tetragonitids, it is well known that fold-like or flat-topped ribs appear only on the later part of the phragmocone and/or adult body chamber in *Anagaudryceras* (e.g. Kennedy and Klinger, 1979; Matsumoto, 1995). Although the usual adult indicators such as apertural modification, abrupt change of body chamber shape, septal thickening and/or septal crowding have not been observed in *Parajaubertella*, the presence of fold-like ribs similar to *Anagaudryceras* on the body chamber suggests that the shell is an adult or a sub-adult.

Parajaubertella kawakitana.—The shell diameters at the last septum of the 10 adult or sub-adult specimens with rounded fold-like ribs on the body chamber used in this study range from 98 to 162 mm, and the diameters of shells with complete apertures are measured or estimated to be 187 to 284 mm (see Material and methods section; Figures 6, 8, Appendix 1).

Parajaubertella zizoh.—The 10 adult or sub-adult specimens in this study have a diameter of 21 to 31 mm at the last septum, and the measured or estimated shell diameters of specimens with complete apertures range from 34 to 51 mm (Figures 6, 8; Appendix 1).

Whorl geometry

The whorl geometry of *Parajaubertella kawakitana* and *P*. *zizoh* changes with growth, and these changes are almost identical, particularly in their immature stages (Figures 9–11; Appendix 2).

Parajaubertella kawakitana.—At about 2 mm in diameter, each specimen exhibits a fairly depressed whorl (*W*/*H* = 1.10–1.20), a moderately wide umbilicus (*U*/*D* = 0.39–0.41) and a whorl expansion rate (*WER*) of 2.04–2.27. As the shell grows, the *U*/*D* becomes progressively smaller, the whorl section becomes more depressed (*W*/*H* = 1.60–1.70), and the whorl expansion rate is slightly reduced, up to about 20 mm in diameter. Shells with diameters greater than 20 mm gradually become more compressed with an increasing whorl expansion rate, while shells with diameters larger than 100 mm exhibit a whorl section that is as high as broad (*W*/*H* = 0.95–1.05), a fairly narrow umbilicus (*U*/*D* = 0.25–0.26) and a whorl expansion rate close to 2.70.

Parajaubertella zizoh.—At a diameter of about 2 mm, each specimen exhibits a fairly depressed whorl (*W*/*H* = 1.20–1.25), a moderately wide umbilicus (*U*/*D* = 0.40) and a whorl expansion rate (*WER*) of 2.07–2.23. As the shell grows, the *U*/*D* decreases to 0.32–0.33 up to a diameter of 30 mm, and correspondingly, the *W*/*H* first increases to 1.55–1.64 up to a diameter of 20 mm

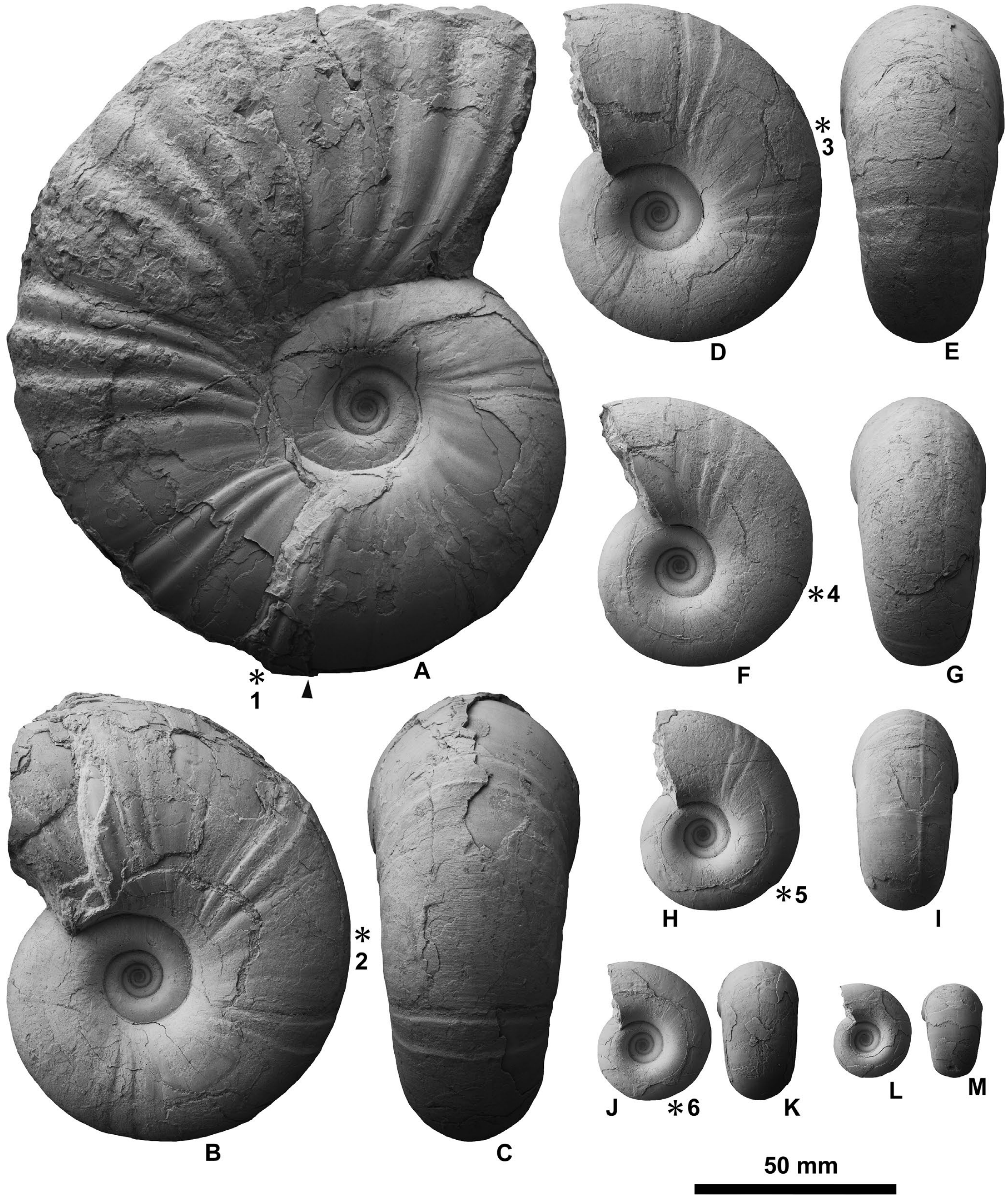

Figure 4. *Parajaubertella kawakitana* Matsumoto, 1943, NMNS PM35940, from the My3 Unit of the Yezo Group along the Suribachizawa River in the Horokanai area, which is here designated as a macroconch of *P. kawakitana*. **A,** original specimen; **B–M,** the same specimen following the removal of successive ~1/4 to 1/2 whorl segments. Numbered asterisks 1–6 indicate positions where whorl segments were removed, resulting in B–C, D–E, F–G, H–I, J–K and L–M, respectively (see Material and methods section). A, left lateral view; B, D, F, H, J, L, right lateral views; C, E, G, I, K, M, ventral views. Black arrow indicates position of last septum.

and then gradually decreases to 1.35–1.40 up to 30 mm in diameter. Similarly, the whorl expansion rate also first decreases to 1.92–1.97 up to a diameter of 20 mm and then gradually increases to 2.04–2.26 up to 30 mm in diameter.

Suture line

The suture lines of comparably sized specimens of

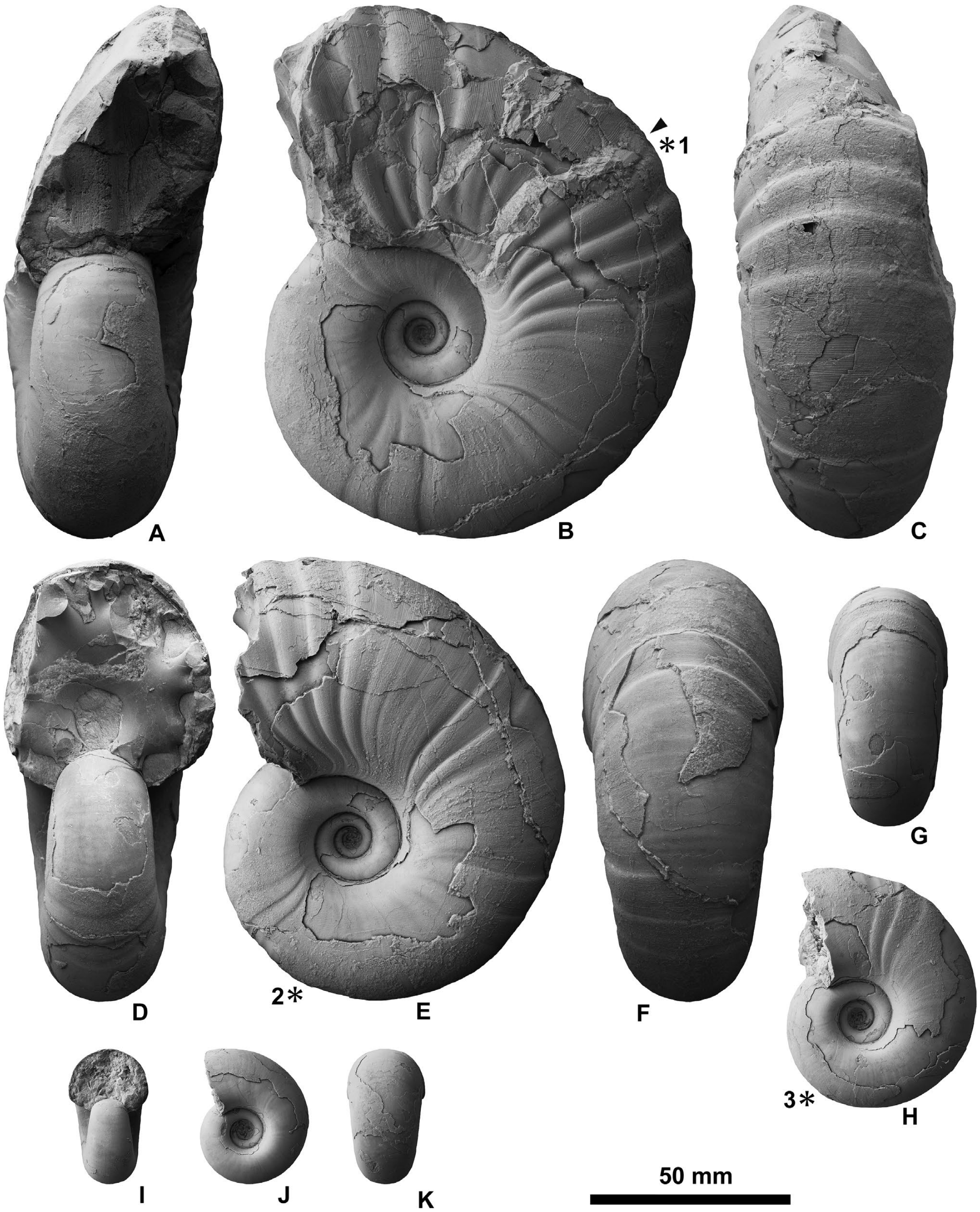

Figure 5. *Parajaubertella kawakitana* Matsumoto, 1943, NMNS PM35946, from the My3 Unit of the Yezo Group along the Suribachi-zawa River in the Horokanai area, which is here designated as a macroconch of *P. kawakitana*. **A–C,** original specimen; **D–K,** the same specimen following the removal of successive ~1/4 to 1/2 whorl segments. Numbered asterisks 1–3 indicate positions where whorl segments were removed, resulting in D–F, G–H and I–K, respectively (see Material and methods section). A, D, I, apertural views; B, E, H, J, right lateral views; C, F, G, K, ventral views. Black arrow indicates position of last septum.

Parajaubertella kawakitana and *P. zizoh* are almost identical (Figure 12). They have a large, deeply incised, asymmetric bifid first lateral saddle, a slightly smaller bifid second saddle, and a large, irregularly subdivided first lateral lobe. The third lateral saddle is situated on the umbilical shoulder.

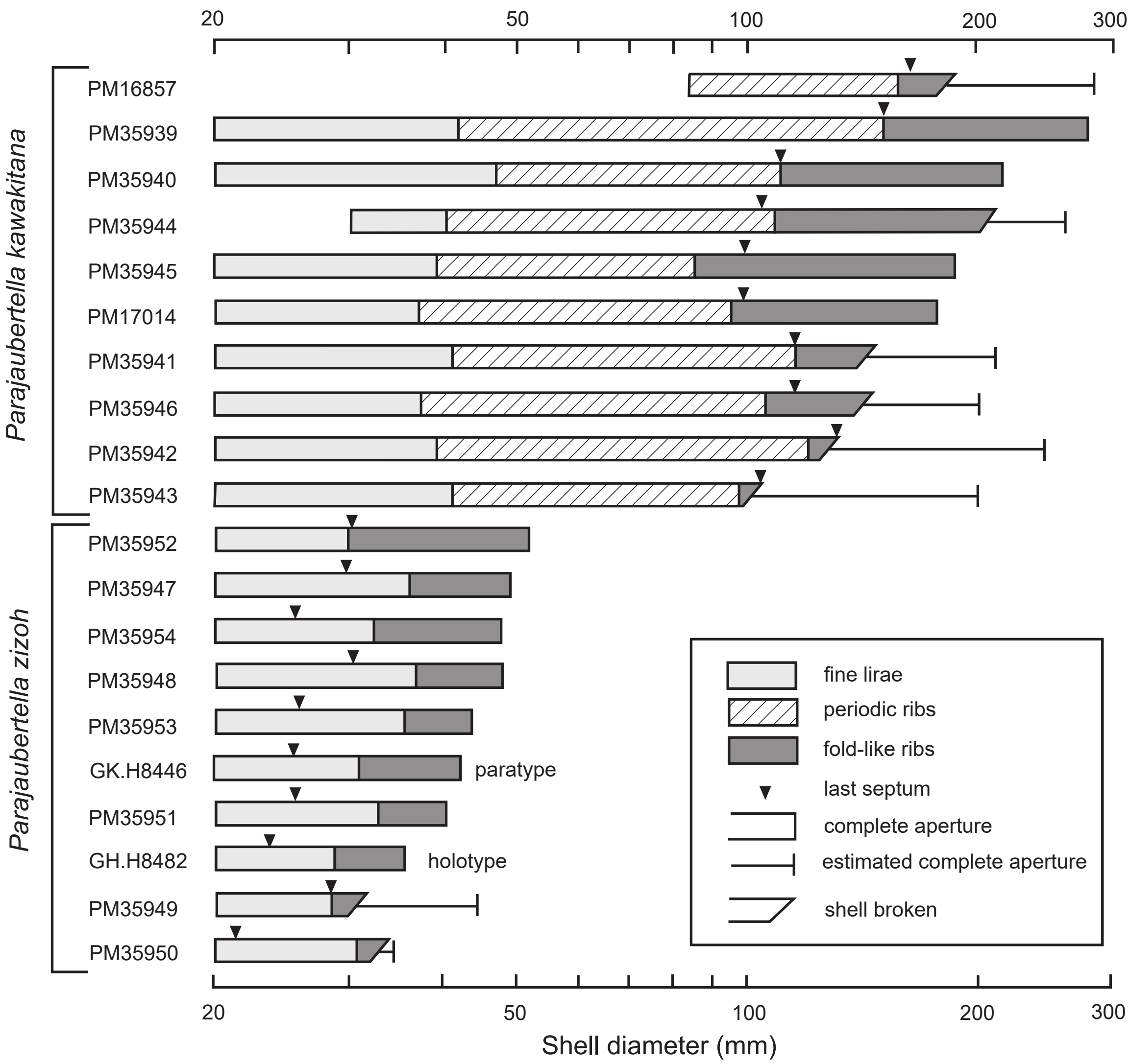

Figure 6. Schematic diagram showing ontogenetic changes in shell surface ornamentation in *Parajaubertella kawakitana* Matsumoto, 1943 and *P. zizoh* Matsumoto *et al*., 1997 from the My3 Unit of the Yezo Group in the Horokanai area, which are here designated as a macroconchs and microconchs of *P. kawakitana*. See Material and methods section for technique used to estimate the original shell diameter (with complete aperture) of specimens with deformed or partly chambers.

Discussion

Numerous examples of dimorphism have been reported in Paleozoic and Mesozoic ammonoids (see Davis *et al*., 1996; Klug *et al*., 2015b), and the following criteria have been proposed for the identification of dimorphism in ammonoids (Makowski, 1962; Callomon, 1963, 1981; Westermann, 1964; Davis, 1972; Kennedy and Cobban, 1976; Maeda, 1993; Davis *et al*., 1996; Klug *et al*., 2015b): The antidimorphs;

1. Should differ in adult morphology.
2. Should have identical early ontogenies.
3. Should have the same stratigraphic ranges.
4. Should have overlapping geographic distributions.
5. Should have identical phylogenies.
6. The ratio of numbers of one antidimorph to the other should be consistent through time.

Matsumoto *et al*. (1997) stated that the young shell of *Parajaubertella zizoh* has a wider umbilicus than *P. kawakitana*, and excluded the possibility that the two species could comprise a dimorphic pair of one species (*ibid*, 1997, p. 198, l. 9–17). However, their conclusion that the young shells of the two species could be separated was biased by the low number of specimens available for study at that time, and it was not possible to verify the range of intraspecific variation of each group. Our

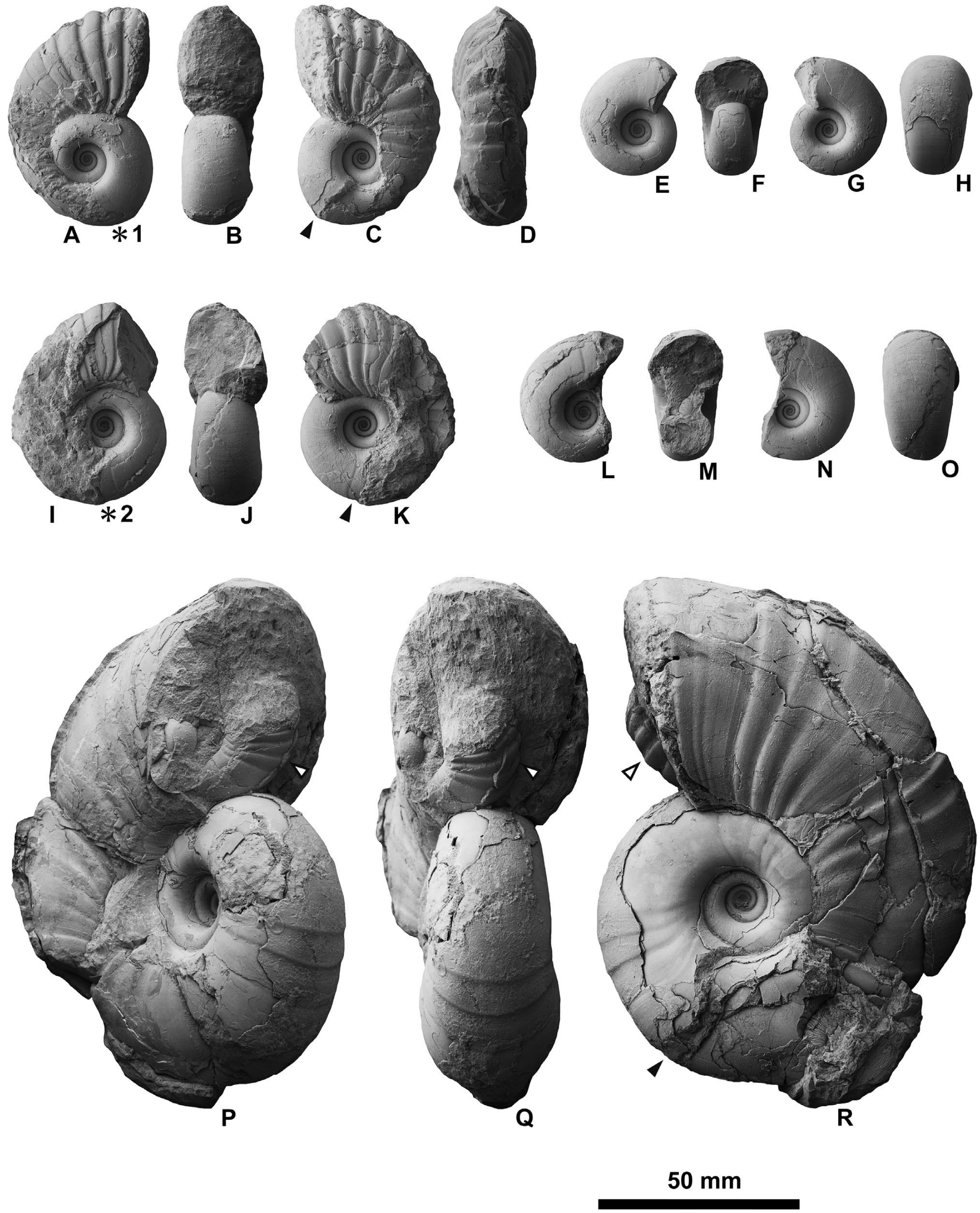

Figure 7. *Parajaubertella zizoh* Matsumoto *et al*., 1997 and *P. kawakitana* Matsumoto, 1943 from the My3 Unit of the Yezo Group in the Horokanai area, which are here designated as microconchs and a macroconch of *P. kawakitana*. **A–H,** *P. zizoh*, NMNS PM35947, from the Suribachi-zawa River; A–D, original specimen; E–H, its inner whorls; **I–O,** *P. zizoh*, NMNS PM35952, from the Kyoei-Sakin-zawa River; I–K, original specimen; L–O, its inner whorls; **P–R,** *P. kawakitana* (NMNS PM35955) with *P. zizoh* (white arrows, NMNS PM35956), from the Suribachi-zawa River. Numbered asterisks 1 and 2 indicate positions where whorl segments were removed, resulting in E–H and L–O, respectively (see Material and methods section). A, E, I, L, left lateral views; B, F, J, M, Q, apertural views; C, G, K, N, R, right lateral views; D, H, O, ventral views; P, oblique view rotated 45° from Q. Black arrows indicate position of last septum.

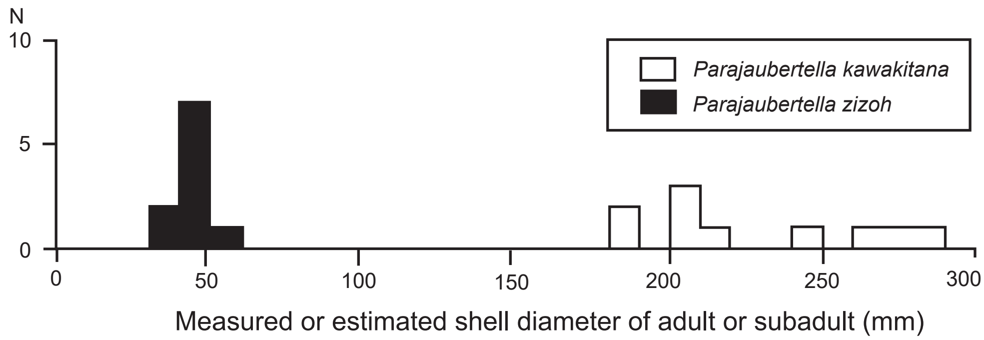

Figure 8. Histogram showing range of shell diameters of adult or sub-adult specimens illustrated in Figure 6 as *Parajaubertella kawakitana* Matsumoto, 1943 and *P. zizoh* Matsumoto *et al*., 1997, which are here designated as macroconchs and microconchs of *P. kawakitana*.

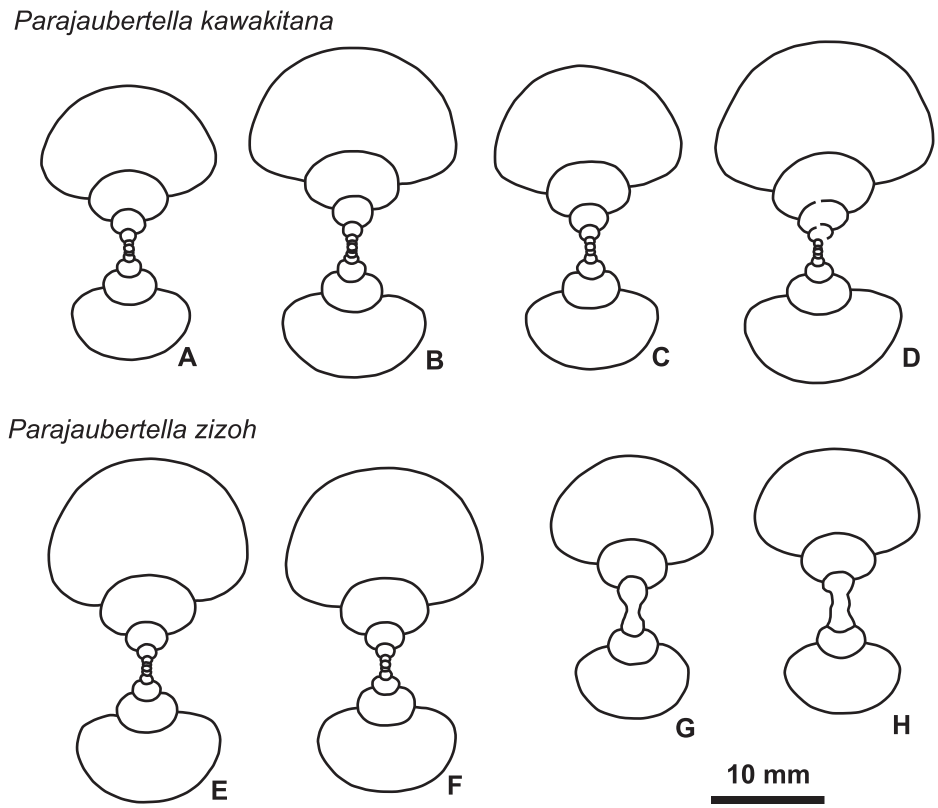

Figure 9. Whorl cross sections of *Parajaubertella kawakitana* Matsumoto, 1943 (A–D) and *P. zizoh* Matsumoto *et al*., 1997 (E–H) from the My3 Unit of the Yezo Group in the Horokanai area, which are here designated as macroconchs and microconchs of *P. kawakitana*. **A,** NMNS PM35940; **B,** NMNS PM35945; **C,** NMNS PM17014; **D,** NMNS PM35943; **E,** NMNS PM35952; **F,** NMNS PM35947; **G,** GK.H8446, paratype; **H,** GK.H8482, holotype.

new data clearly demonstrate that their whorl geometry overlaps with each other (Figures 10, 11). For example, relative umbilical size (*U*/*D*) and relative whorl thickness (*W*/*H*), both of which were considered diagnostic for two species, share almost identical patterns throughout the ontogeny (Figure 10). The sharing of identical and undistinguishable juvenile morphology is a strong argument for recognizing dimorphism (Palframan, 1966, 1967; Maeda, 1993).

Our study of the ontogenetic shell development (ornamentation and whorl geometry) and suture line revealed that *Parajaubertella kawakitana* and *P. zizoh* from the

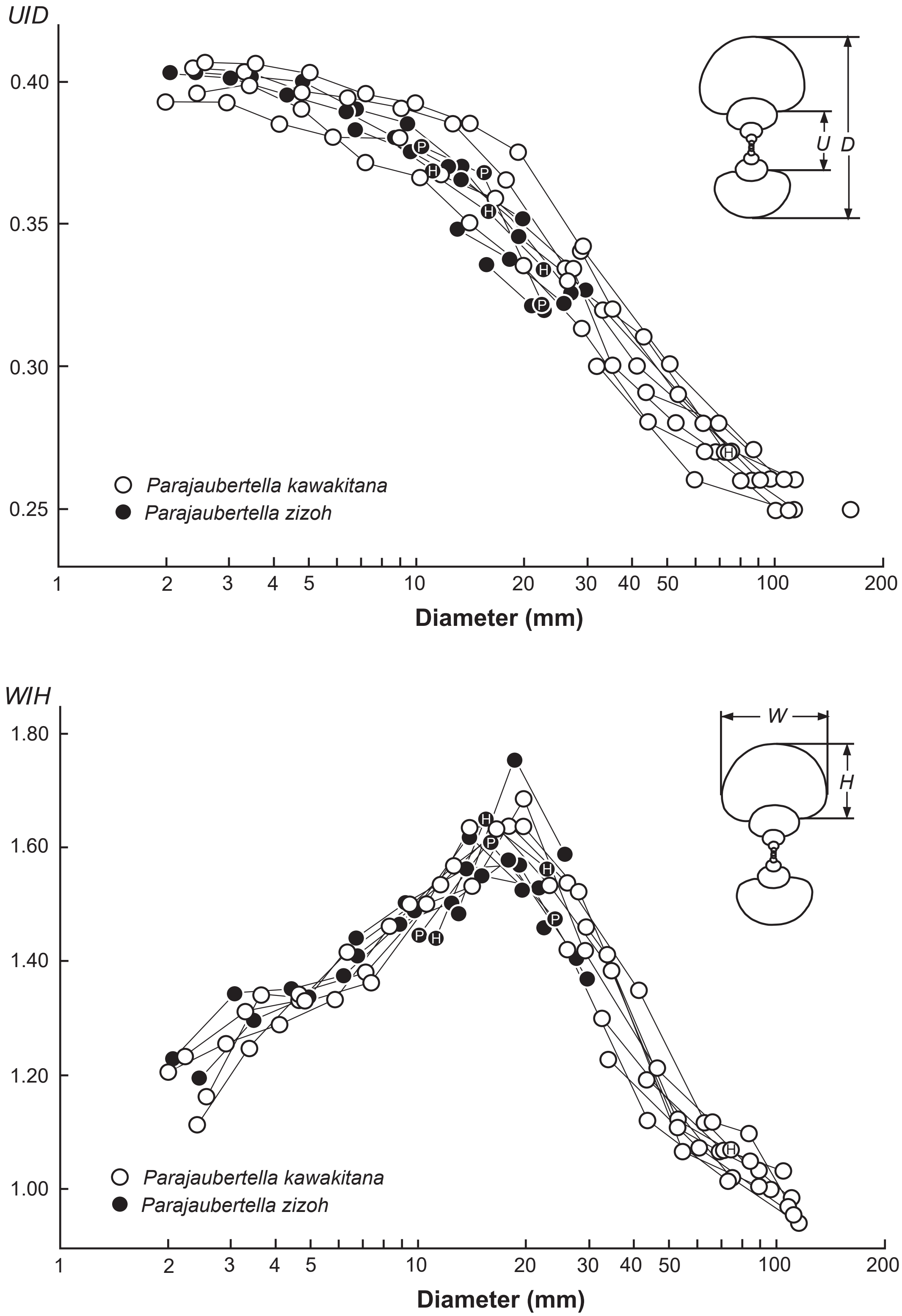

Figure 10. Scatter diagrams showing ontogenetic variation in umbilical diameter/shell diameter (*U*/*D*) versus shell diameter (*D*) and whorl width/whorl height (*W*/*H*) versus shell diameter for *Parajaubertella kawakitana* Matsumoto, 1943 and *P*. *zizoh* Matsumoto *et al*., 1997 from the My3 Unit of the Yezo Group in the Horokanai area, which are here designated as macroconchs and microconchs of *P*. *kawakitana*. Type specimens of *P*. *kawakitana* and *P*. *zizoh* are included; H, holotype; P, paratype.

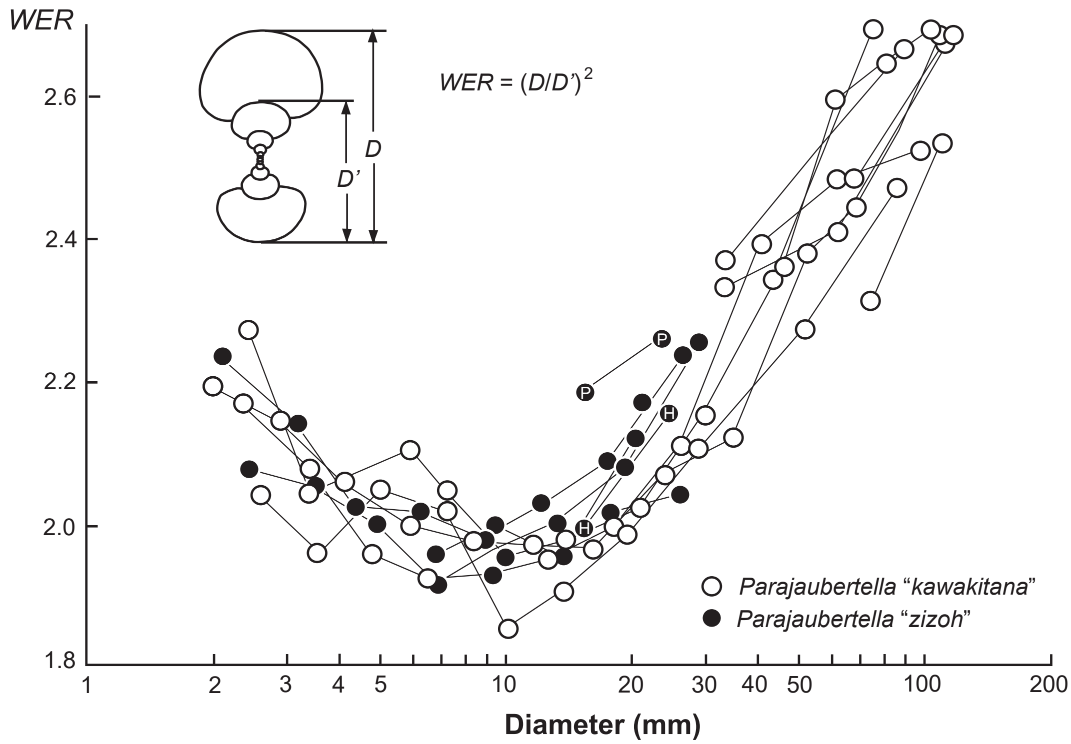

Figure 11. Scatter diagrams showing ontogenetic variation in whorl expansion rate (*WER*) versus shell diameter (*D*) for *Parajaubertella kawakitana* Matsumoto, 1943 and *P. zizoh* Matsumoto *et al.*, 1997 from the My3 Unit of the Yezo Group in the Horokanai area, which are here designated as macroconchs and microconchs of *P. kawakitana*. Type specimens of *P. zizoh* are included; H, holotype; P, paratype.

lower Cenomanian My3 Unit in the Horokanai area, Hokkaido satisfy criteria 1 and 2 above. That is, the size of their adult shells is distinctly bimodal (187 to 284 mm for *P. kawakitana*, 34 to 51 mm for *P. zizoh*; Figure 8), and their immature stages share similar ornamentation and shell morphology at comparable sizes (Figures 6, 9–11). Their stratigraphic ranges are restricted to the lower Cenomanian, and their geographic distribution is limited to the Northwest Pacific region (Matsumoto, 1995; Matsumoto *et al*., 1997); thus, criteria 3 and 4 are satisfied. Additionally, they sometimes co-occur in the same concretion (Figure 7P–R). Their morphological similarity indicates that they are phylogenetically very close, and thus, criterion 5 is satisfied. It is unclear whether criterion 6 (= numerical consistency through time) can be applied here, because their extremely short stratigraphic ranges are too short to test this criterion. On the other hand, numerical disparity is not necessarily a basis for rejecting dimorphism because the macroconch/microconch ratio could be biased by ecological and taphonomic factors (Kennedy and Cobban, 1976). These lines of evidence suggest that the two species should be considered as two dimorphs, microconch and macroconch (as proposed by Callomon [1955, 1963]) of a single species, which is described below as *Parajaubertella kawakitana*.

Systematic description

Morphological terms are those used in Arkell (1957). Quantifiers used to describe the shape of ammonoid shell replicate those proposed by Matsumoto (1954, p. 246) and modified by Haggart (1989, table 8.1).

Institution abbreviations.—GK, the Kyushu University Museum, Fukuoka; NMNS, National Museum of Nature and Science, Tsukuba; UMUT, the University Museum, the University of Tokyo, Tokyo.

Superfamily Lytoceratoidea Neumayr, 1875
Family Tetragonitidae Hyatt, 1900
Subfamily Gaudryceratinae Spath, 1927
Genus ***Parajaubertella*** Matsumoto, 1943

Type species.—*Parajaubertella kawakitana* Matsumoto, 1943.

Revised diagnosis.—A dimorphic genus of a fairly involute, depressed shell with broadly rounded venter, inflated flanks, subangular umbilical shoulder. Umbilicus fairly narrow and deep with vertical umbilical wall.

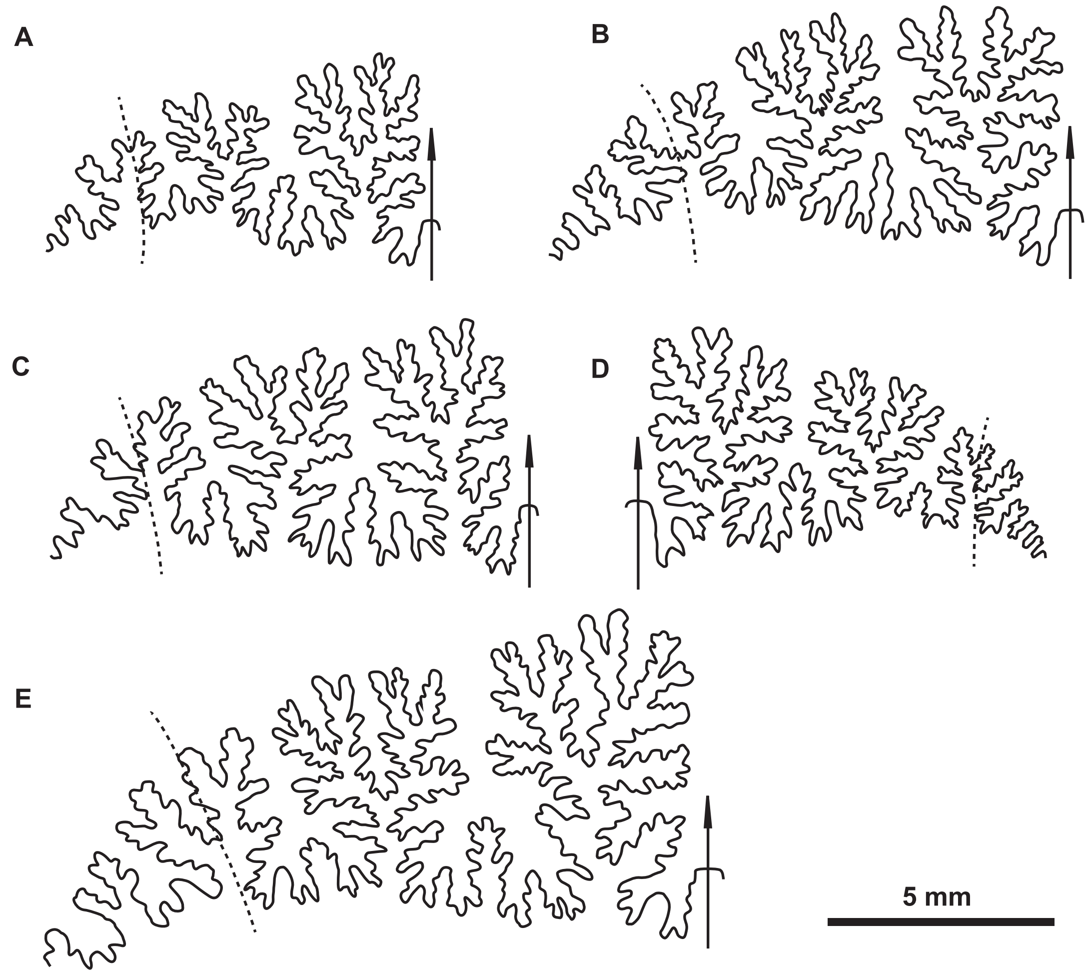

Figure 12. Suture lines of of *Parajaubertella zizoh* Matsumoto *et al*., 1997 (A, B) and *P. kawakitana* Matsumoto, 1943 (C–E) from the My3 Unit of the Yezo Group in the Horokanai area, which are here designated as microconchs and macroconchs of *P. kawakitana*. **A,** NMNS PM35953; **B,** NMNS PM35947; **C,** NMNS PM35940; **D,** NMNS PM35946; **E,** NMNS PM35941. Solid line represents the siphuncle, and dotted line indicates the position of the umbilical shoulder.

Ornamentation consists of slightly flexuous lirae on early whorls, and flexuous, narrow ribs or fold-like ribs that project forward on the venter at later stages and on the body chamber. Macroconch three to eight times larger than microconch.

Discussion.—*Gabbioceras kawakitanum occidentalis* described by Wiedmann and Dieni (1968) from the uppermost Albian at Orosei, Sardinia, Italy is very similar to *Parajaubertella kawakitana*, but the umbilical shoulder is located in the middle of the second lobe, suggesting that it should be assigned to either *Gabbioceras*, Hyatt, 1900, or *Tanabeceras* Shigeta *et al*., 2012 (Hoffmann, 2010; Shigeta *et al*., 2012). Specimens reported as *Parajaubertella* aff. *kawakitana* by Obata and Futakami (1977, fig. 1) and Futakami (1996, pl. 23, fig. 1) from the upper Albian in the Manji and Mikasa areas, central Hokkaido were later reassigned to *Obataceras* and *Tanabeceras*, respectively (Shigeta *et al*., 2012).

Occurrence.—Lower Cenomanian of Hokkaido, Sakhalin, southern Alaska and Queen Charlotte Islands (British Columbia).

Parajaubertella kawakitana Matsumoto, 1943

Figures 1, 4–13

Macroconch synonymy

Parajaubertella kawakitana Matsumoto, 1943, p. 667, fig. 2; Matsumoto, 1959, p. 70, pl. 23, fig. 1, text-fig. 11; Matsumoto, 1995, p. 11, figs. 3–13; Kawabe *et al*., 1996, pl. 2, figs. 1, 2; Nishida *et al*., 1996, pl. 30, fig. 1, pl. 31, figs. 1, 2, pl. 32, fig. 1; Matsumoto *et al*., 1997, p. 189, figs. 3–6; Nishida *et al*., 1997, pl. 8, fig. 3; Hayakawa and Nishino, 1999, p. 5, pl. 3; Shigeta, 2001, pl. 48, figs. 2, 3.

?*Parajaubertella imlayi* Matsumoto, 1959, p. 71, pl. 21, figs. 1, 2, text-

figs. 12, 13; Murphy, 1967, p. 26; Jones, 1967, p. 23, pl. 1, figs. 10–12, text-figs. 6D, 7B; McLearn, 1972, p. 40, pl. 21, fig. 1.
?*Gabbioceras imlayi* (Matsumoto). Wiedmann, 1962, p. 20.
Parajaubertella cf. *kawakitana* Matsumoto. Poyarkova, 1987, pl. 24, fig. 3.
non. Parajaubertella kawakitana Matsumoto. Vereshchagin *et al*., 1965, p. 39, pl. 27, figs. 2, 3 (= *Tanabeceras mikasaense*); Poyarkova, 1987, pl. 23, fig. 1 (= *T. yezoense*); Zonova *et al*., 1993, p. 149, pl. 63, fig. 7 (= *T. yezoense*), fig. 8, pl. 64, figs. 2, 3, pl. 65, figs. 1, 2 (= *T. mikasaense*); Alabushev and Wiedmann, 1997, p. 10, pl. 2, fig. 5 (= *Gabbioceras*); Abu-Zied, 2008, fig. 5C, D (= *Tanabeceras* or *Gabbioceras*).

Microconch synonymy

Parajaubertella n. sp. Nishida *et al*., 1996, pl. 33, figs. 1–4.
Parajaubertella zizoh Matsumoto *et al*., 1997, p. 197, figs. 7–9.
Parajaubertella cf. *zizoh* Matsumoto *et al*. Kawabe, 2000, pl. 4, fig. 4.

Holotype.—UMUT MM19698, figured by Matsumoto (1943, p. 667, fig. 2), from the Ky Unit of the Kawakita Group (= IV Unit of the Naiba Formation by Vereshchagin and Salinikova, 1968 and Poyarkova, 1987, and N2 Unit of the Naiba Formation by Kodama *et al*., 2002; lower Cenomanian) at locality N94b (Matsumoto, 1942, pl. 8) on the Yunosawa River (= Vesioly River), a short eastern tributary of the Naibuchi River (= Naiba River), Bykov area, southern Sakhalin, Russian Far East.

Diagnosis.—As for the genus.

Material examined.—In addition to the type specimens of *Parajaubertella kawakitana* (UMUT MM19698) and *P. zizoh* (GK.H8482, 8446), 18 specimens obtained from float calcareous concretions, which came from the lower Cenomanian My3 Unit (*Graysonites wooldridge* Zone and *Stoliczkaia japonica* Assemblage Zone) in the Horokanai area: 14 specimens (NMNS 16857, 17014, 35939–35943, 35945, 35946–35951) from the Suribachi-zawa River and 4 specimens (NMNS PM35944, 35952–35954) from the Kyoei-Sakin-zawa River, were examined for ontogenetic descriptions.

Description.—Fairly involute, fairly depressed shell with rounded whorl section (W/H = 1.10–1.25), arched venter, indistinct ventral shoulders, and slightly convex flanks with maximum whorl width at mid-flank in early growth stage at about 2 mm in diameter. Umbilicus moderately wide (U/D = 0.39–0.41) with moderately high, rounded wall and rounded shoulder. As shell grows, relative umbilical size (U/D) decreases, and whorl section with inflated flanks and subangular umbilical shoulder, becomes more depressed up to about 20 mm in diameter (W/H = 1.55–1.70), and then gradually becomes more compressed. Ornamentation, up to 30–45 mm in diameter, consists only of fine growth lines and slightly flexuous lirae. Suture line with large, deeply incised, asymmetric bifid first lateral saddle, slightly smaller bifid second saddle, and large, irregularly subdivided first lateral lobe. Third lateral saddle situated on the umbilical shoulder.

Macroconch: Estimated mature shells fairly large, ranging in size from 162 to 284 mm for the specimens examined (Appendix 1). Shells larger than 100 mm have whorls as high as broad (W/H = 0.95–1.05) and a fairly narrow and deep umbilicus (U/D = 0.25–0.26) with vertical wall and subangular umbilical shoulder. Ornamentation at a diameter of 37 to 155 mm consists of periodic segments with a set of 3 to 5 narrow grooves followed by flexuous narrow ribs. Each segment extends for 30–40 degrees in spiral length, while the interval without ribs and grooves extends between 50–70 degrees. Shells larger than 80–150 mm in diameter have rounded fold-like ribs separated by narrow interspaces.

Microconch: Estimated mature shells fairly small, ranging in size from 34 to 51 mm for the specimens examined (Appendix 1), and not exceeding 70 mm even in extreme cases (e.g. GK.H8445, paratype). Shells larger than 28–36 mm in diameter have rounded fold-like ribs separated by narrow interspaces.

Measurements.—See Appendixes 1, 2.

Discussion.—*Parajaubertella imlayi* is very similar to the macroconch of *P. kawakitana*, and the difference in angularity at the umbilical shoulder of the inner whorls was taken as one of the criteria for differentiating both species (Matsumoto, 1959). Because the umbilical shoulder is often modified by taphonomic processes and since the holotype of *P. imlayi* is somewhat weathered, Matsumoto (1995) pointed out that *P. imlayi* may be a junior synonym of *P. kawakitana*. However, in order to support this suggestion, a thorough taxonomic study is required, i.e., determine the taxon's intraspecific variation and examine its ontogenetic shell morphology.

Specimens assigned to *Parajaubertella kawakitana* by Vereshchagin *et al*. (1965), Poyarkova (1987), Zonova *et al*. (1993), Alabushev and Wiedmann (1997) and Abu-Zied (2008) from Sakhalin and Kamchatka in the Russian Far East and Egypt are identical to juvenile shells of *Tanabeceras* Shigeta *et al*., 2012 or *Gabbioceras* Hyatt, 1900.

The original diameter of GK.H8445 (Figure 13A, B), one of the paratypes of *Parajaubertella zizoh*, is about 65 mm and the mature shell diameter is estimated to be 77 mm, which is much larger than the other microconchs from the My3 Unit in the Horokanai area. This specimen was collected from a float concretion that probably came from the lower part of the My5 Unit, which is somewhat stratigraphically higher than the My3 Unit but still assignable to the lower Cenomanian (Nishida *et al*., 1996; Matsumoto *et al*., 1997). Specimen NMNS PM17079 (Figure 13C), collected from a float concretion that also probably came from the lower part of the My5 Unit, is a macroconch, and its mature shell diameter is estimated to

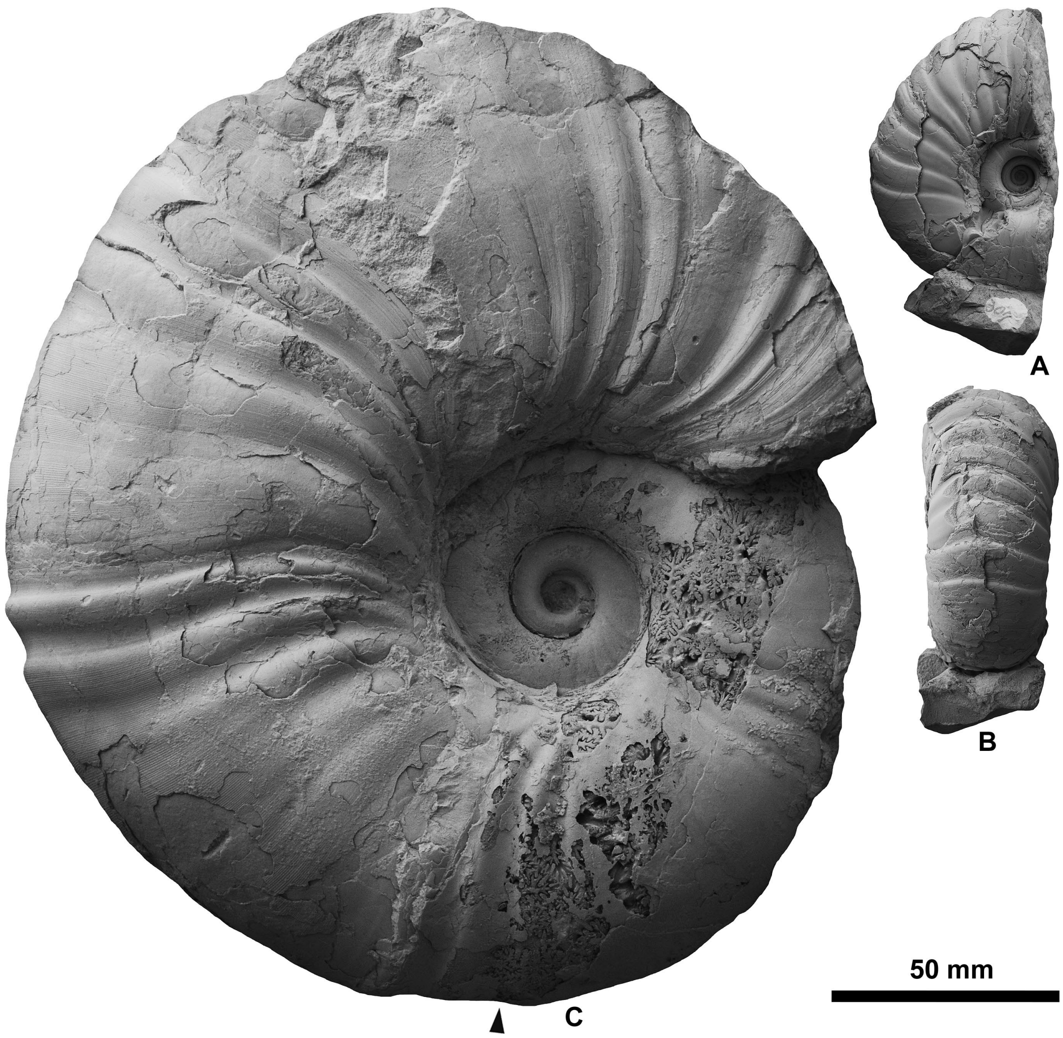

Figure 13. *Parajaubertella* from the lower Cenomanian My5 Unit of the Yezo Group in the Kotanbetsu area, Hokkaido. **A, B,** paratype of *P. zizoh* Matsumoto *et al*., 1997, GK.H8445, which is here designated as a microconch of *P. kawakitana* Matsumoto, 1943; **C,** *P. kawakitana*, NMNS PM17079, which is here designated as a macroconch of *P. kawakitana*. Black arrow indicates position of last septum.

be 276 mm, which is much larger than the other macroconchs. These specimens suggest that the taxon's mature size increases in stratigraphically higher horizons of the lower Cenomanian.

Occurrence.—Lower Cenomanian of Hokkaido and Sakhalin.

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Author contributions

T. S. collected fossils and contributed to the geological aspect of the study. Y. S. and H. M. conducted taxonomic study. All authors contributed to the writing of the paper.

Appendix 1. Shell diameter (in mm) at various growth stages of herein studied specimens of *Parajaubertella kawakitana* Matsumoto, 1943 from the My3 Unit of the Yezo Group in the Horokanai area. M, macroconch; m, microconch; *D1*, shell diameter at the start of observation; *D2*, shell diameter where periodic ribs appear; *D3*, shell diameter where fold-like ribs appear; *D4*, shell diameter at last septum; *D5*, maximum diameter of preserved shell; *D6*, measured or estimated diameter of complete aperture shell.

register number	M or m	*D1* (mm)	*D2* (mm)	*D3* (mm)	*D4* (mm)	*D5* (mm)	*D6* (mm)
NMNS PM16857	M	82.94	—	154.59	162.40	184.00	284.39
NMNS PM17014	M	20.00	37.00	95.00	98.40	175.09	188.29
NMNS PM35939	M	20.00	42.00	150.04	150.04	274.14	274.14
NMNS PM35940	M	20.00	47.00	110.30	110.30	215.32	215.32
NMNS PM35941	M	20.00	41.00	115.80	115.80	147.80	213.13
NMNS PM35942	M	20.00	39.00	120.00	130.00	130.00	248.04
NMNS PM35943	M	20.00	41.00	100.00	103.80	103.80	201.60
NMNS PM35944	M	30.00	39.60	109.38	103.00	211.95	261.70
NMNS PM35945	M	20.00	39.00	86.00	99.23	186.83	186.83
NMNS PM35946	M	20.00	38.00	106.90	116.60	145.30	202.43
NMNS PM35947	m	20.00	—	36.06	29.48	48.74	48.74
NMNS PM35948	m	20.00	—	36.43	30.02	48.71	48.71
NMNS PM35949	m	20.00	—	28.85	28.26	31.56	44.13
NMNS PM35950	m	20.00	—	30.85	21.18	33.90	33.90
NMNS PM35951	m	20.00	—	35.19	*ca.* 25.63	*ca.*43.47	*ca.*43.47
NMNS PM35952	m	20.00	—	29.65	30.63	50.93	50.93
NMNS PM35953	m	20.00	—	32.59	24.25	40.52	40.52
NMNS PM35954	m	20.00	—	32.70	25.40	47.73	47.73
GK.H8446	m	20.00	—	30.80	25.12	41.83	41.83
GK.H8482	m	20.00	—	28.48	23.50	34.52	38.00

Appendix 2. Measurements (in mm) of herein studied specimens of *Parajaubertella kawakitana* Matsumoto, 1943 from the My3 Unit of the Yezo Group in the Horokanai area . M, macroconch; m, microconch; *D*, shell diameter; *D′*, diameter before half whorl; *U*, umbilical diameter; *H*, whorl height; *W*, whorl width; *WER*, whorl expansion rate = $(D/D')^2$; M, macroconch; m, microconch.

register number	M or m	*D* (mm)	*D′* (mm)	*U* (mm)	*H* (mm)	*W* (mm)	*U*/*D*	*W*/*H*	*WER*
NMNS PM16857	M	162.40	—	40.30	—	—	0.25	—	—
NMNS PM17014	M	2.344	1.592	0.949	0.827	1.018	0.405	1.231	2.168
		3.378	2.344	1.361	1.197	1.569	0.403	1.311	2.077
		4.727	3.378	1.876	1.687	2.244	0.396	1.330	1.958
		6.559	4.727	2.582	2.294	3.243	0.394	1.414	1.925
		9.116	6.559	3.558	3.260	4.872	0.390	1.494	1.932
		12.736	9.116	4.903	4.569	7.162	0.385	1.568	1.952
		17.998	12.736	6.569	6.827	11.184	0.365	1.638	1.997
		26.156	17.998	8.859	10.354	15.881	0.339	1.534	2.112
		41.00	26.50	12.40	17.00	23.00	0.30	1.35	2.39
		63.00	40.00	17.40	29.10	32.70	0.28	1.12	2.48
		98.40	62.00	25.40	43.90	43.70	0.26	1.00	2.52
NMNS PM35939	M	33.00	—	10.40	13.80	18.00	0.32	1.30	—
		76.60	50.40	20.80	34.00	34.60	0.27	1.02	2.31
		112.10	70.50	29.50	52.60	49.40	0.26	0.94	2.53
NMNS PM35940	M	2.000	1.350	0.785	0.743	0.894	0.393	1.203	2.194
		2.927	2.000	1.149	1.040	1.305	0.393	1.255	2.142
		4.199	2.927	1.618	1.529	1.964	0.385	1.284	2.058
		5.935	4.199	2.253	2.161	2.880	0.380	1.333	1.998
		8.346	5.935	3.162	4.446	3.043	0.379	1.461	1.977
		11.717	8.346	4.298	4.377	6.703	0.367	1.531	1.971
		16.446	11.717	5.908	6.185	10.086	0.359	1.631	1.970
		23.687	16.446	7.926	9.510	14.579	0.334	1.533	2.074
		35.10	24.10	10.40	15.20	20.90	0.30	1.38	2.12
		52.40	34.10	14.90	24.60	27.20	0.28	1.11	2.38
		69.50	44.50	18.80	33.20	35.50	0.27	1.07	2.44
		87.90	55.00	22.60	40.00	42.20	0.26	1.06	2.55
		110.30	67.40	27.11	54.20	53.00	0.25	0.98	2.68
NMNS PM35941	M	26.50	—	8.70	11.30	16.10	0.33	1.42	—
		44.40	29.00	13.80	22.30	20.00	0.31	1.12	2.34
		76.80	46.80	20.50	35.60	36.40	0.27	1.02	2.69
NMNS PM35942	M	29.40	—	10.10	12.00	17.50	0.34	1.46	—

		34.30	22.30	10.90	14.10	19.90	0.32	1.41	2.37
		56.30	35.50	16.60	25.60	27.30	0.29	1.07	2.52
		90.10	55.20	23.40	42.10	42.40	0.26	1.01	2.66
NMNS PM35943	M	2.413	1.601	0.956	0.903	1.002	0.396	1.110	2.272
		3.449	2.413	1.371	1.214	1.517	0.398	1.249	2.043
		5.005	3.449	1.909	1.713	2.382	0.380	1.391	2.106
		7.165	5.005	2.659	2.801	3.858	0.371	1.377	2.049
		10.029	7.165	3.668	3.656	5.485	0.366	1.500	1.959
		14.113	10.029	4.939	5.760	8.800	0.350	1.528	1.980
		20.097	14.113	6.732	7.438	12.518	0.335	1.683	2.028
		29.496	20.097	9.236	12.798	18.087	0.313	1.413	2.154
		45.30	29.50	12.70	21.40	26.00	0.28	1.21	2.36
		64.40	40.00	17.40	29.10	32.50	0.27	1.12	2.59
		82.00	50.50	21.40	37.10	40.70	0.26	1.10	2.64
		103.80	63.30	25.90	51.00	49.60	0.25	0.97	2.69
NMNS PM35944	M	44.50	—	12.80	20.80	24.70	0.29	1.19	—
		69.00	43.80	19.40	32.10	34.40	0.28	1.07	2.48
		103.00	63.00	26.80	49.00	50.70	0.26	1.03	2.67
NMNS PM35945	M	2.600	1.820	1.058	0.919	1.066	0.407	1.160	2.041
		3.638	2.600	1.477	1.185	1.591	0.406	1.343	1.958
		5.087	3.638	2.066	1.768	2.354	0.403	1.330	2.043
		7.388	5.087	2.921	2.505	3.428	0.395	1.368	2.019
		10.066	7.388	3.944	3.468	5.152	0.392	1.486	1.856
		13.906	10.066	5.348	4.917	8.048	0.385	1.637	1.908
		19.618	13.906	7.364	7.332	11.996	0.375	1.636	1.990
		28.464	19.618	9.706	11.477	17.739	0.341	1.546	2.105
		50.50	33.50	14.90	23.40	26.10	0.30	1.12	2.27
		86.50	55.00	23.10	40.00	41.70	0.27	1.04	2.47
NMNS PM35946	M	34.20	22.40	10.30	16.20	20.00	0.30	1.23	2.33
		60.60	39.00	13.80	29.00	31.10	0.26	1.07	2.41
		114.60	70.00	28.70	53.70	51.50	0.25	0.96	2.68
NMNS PM35947	m	2.155	1.442	0.868	0.791	1.019	0.403	1.288	2.233
		3.153	2.155	1.266	1.132	1.522	0.402	1.345	2.141
		4.480	3.153	1.771	1.586	2.141	0.395	1.350	2.019
		6.368	4.480	2.480	2.324	3.200	0.389	1.377	2.020
		8.950	6.368	3.401	3.338	4.900	0.380	1.468	1.975

		12.747	8.950	4.715	4.804	7.211	0.370	1.501	2.028
		18.417	12.747	6.462	7.073	11.167	0.351	1.579	2.087
		27.536	18.417	8.977	11.443	16.074	0.326	1.405	2.235
NMNS PM35948	m	15.068	—	5.068	5.753	8.904	0.336	1.548	—
		22.192	15.068	7.123	9.315	14.246	0.321	1.529	2.169
NMNS PM35949	m	13.019	—	4.528	5.094	7.547	0.348	1.482	—
		18.491	13.019	6.226	6.981	12.264	0.337	1.756	2.017
		26.415	18.491	8.491	10.943	17.358	0.321	1.586	2.040
NMNS PM35950	m	6.940	4.956	2.659	2.454	3.460	0.383	1.410	1.960
		9.808	6.940	3.677	3.702	5.481	0.375	1.481	1.997
		13.790	9.808	5.033	4.964	8.055	0.365	1.623	1.977
		20.091	13.790	7.053	8.064	12.357	0.351	1.532	2.123
NMNS PM35952	m	2.459	1.706	0.991	0.820	0.981	0.403	1.196	2.078
		3.525	2.459	1.417	1.194	1.550	0.402	1.298	2.055
		4.981	3.525	1.990	1.735	2.320	0.400	1.337	1.997
		6.903	4.981	2.692	2.438	3.504	0.390	1.437	1.921
		9.684	6.903	3.730	3.513	5.240	0.385	1.492	1.968
		13.699	9.684	5.072	5.108	7.975	0.370	1.561	2.001
		19.743	13.699	6.817	7.851	12.329	0.345	1.570	2.077
		29.651	19.743	9.653	12.081	16.524	0.326	1.368	2.256
NMNS PM35953	m	23.00	—	7.40	9.60	14.00	0.32	1.46	—
GK.H8482	m	11.333	—	4.167	4.167	6.000	0.368	1.440	—
		16.000	11.333	5.667	6.167	10.167	0.354	1.649	1.993
		23.500	16.000	7.833	9.333	14.583	0.333	1.563	2.157
GK.H8446	m	10.538	—	3.871	4.301	6.237	0.367	1.450	—
		15.591	10.538	5.376	6.129	9.892	0.345	1.614	2.189
		23.441	15.591	7.527	9.677	14.194	0.321	1.467	2.260