A New Pliocene Species of Swiftopecten (Bivalvia: Pectinidae) from the Zukawa Formation in Toyama Prefecture, Central Japan

Author: Yoshimura, Taro

Source: Paleontological Research, 21(3) : 293-303

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/2016PR030

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Paleontological-Research on 06 Apr 2025
Terms of Use: https://bioone.org/terms-of-use

Paleontological Research, vol. 21, no. 3, pp. 293–303, July 1, 2017
© by the Palaeontological Society of Japan
doi:10.2517/2016PR030

A new Pliocene species of *Swiftopecten* (Bivalvia: Pectinidae) from the Zukawa Formation in Toyama Prefecture, Central Japan

TARO YOSHIMURA

Keio Senior High School, 4-1-2 Hiyoshi, Kohoku-ku, Yokohama, Kanagawa 223-8524, Japan (e-mail: t.yoshimura@keio.jp)

Received February 14, 2016; Revised manuscript accepted November 14, 2016

Abstract. A new pectinid species, *Swiftopecten djoserus* sp. nov. is described from the Pliocene Zukawa Formation in Takaoka City, Toyama Prefecture in Central Honshu. This species can be distinguished from *S. swiftii*, the type species of the genus, by its smaller size, the fewer fine radial riblets on both valves, the wider umbonal angle and the more uneven ledges. *Swiftopecten djoserus* sp. nov. is an extinct species of the Omma-Manganji fauna that occurred locally in the central part of the Sea of Japan borderland during the latest Pliocene.

Key words: Bivalvia, Japan, latest Pliocene, *Swiftopecten*, Zukawa Formation

Introduction

The pectinid genus *Swiftopecten* was proposed by Hertlein (1935), with *Pecten swiftii* Bernardi, 1858 as the type species. *Swiftopecten swiftii* is the only extant species in this genus (Masuda, 1959, 1960, 1972). *Swiftopecten swiftii* is a cold-water dweller distributed from Choshi, Chiba Prefecture in Japan to Alaska on the Pacific coast and from Gangwon-do in Korea and northward areas in the northern Sea of Japan. It lives on rocky and gravel bottoms in depths shallower than 50 m (Sinelnikova, 1975; Volova and Scarlato, 1980; Okutani, 2000; Min *et al.*, 2004).

Although the fossils of *Swiftopecten* in the North Pacific were studied taxonomically by Masuda (1959, 1960, 1962, 1972), variation of both fossil and recent specimens has not been studied in detail. In association with *S. swiftii*, a new species of *Swiftopecten*, *S. djoserus* sp. nov. has been found in the upper Pliocene Zukawa Formation (Mochiduki, 1930; Amano *et al.*, 2012) in Takaoka City, Toyama Prefecture. For a comparison between the new species and *S. swiftii*, the variation of these species has been examined in detail. In this paper, I describe the new species from the Zukawa Formation, reveal the variation of both fossil and Recent specimens of *S. swiftii*, and also discuss the taxonomy of the genus *Swiftopecten*. The paleogeographic significance of the new species is also discussed.

Material and methods

The Zukawa Formation consists mainly of medium- to coarse-grained sandstone, and yields many molluscan fossils including *Swiftopecten* (Kiyu and Mizuki, 1983; Matsuura, 1985, 1992, 2009; Fujii and Shimizu, 1992; Goto *et al.*, 1993; Amano *et al.*, 2012). The molluscan fossils are mainly composed of cold-water species, with fewer warm-water species (Amano *et al.*, 2012). Based on calcareous nannofossils from localities near the type locality of the Zukawa Formation, the age of the main part of this formation is late Pliocene while the lowermost part is early Pliocene (Amano *et al.*, 2012).

In this study, 49 specimens assignable to *Swiftopecten* were collected from the Zukawa Formation at four localities: Ikarabe (Loc. 1 = Loc. Z-4 in Amano *et al.*, 2012), Zukawa (Loc. 2), Nishiebizaka (Loc. 3) and Ishidutsumi (Loc. 4) in the western part of Takaoka City (Figure 1). Among them, 15 specimens belong to a new species: 13 specimens from Ikarabe, one from Zukawa and one from Nishiebizaka. The specimens from Ikarabe and Zukawa were recovered from the uppermost part of the formation. Judging from calcareous nannofossils, the uppermost part of the formation corresponds to the horizon just above Datum A (= 2.75 Ma after Sato and Kameo, 1996) (Amano *et al.*, 2012).

In this study, 390 specimens of *Swiftopecten swiftii* were also examined in total for comparison with the new

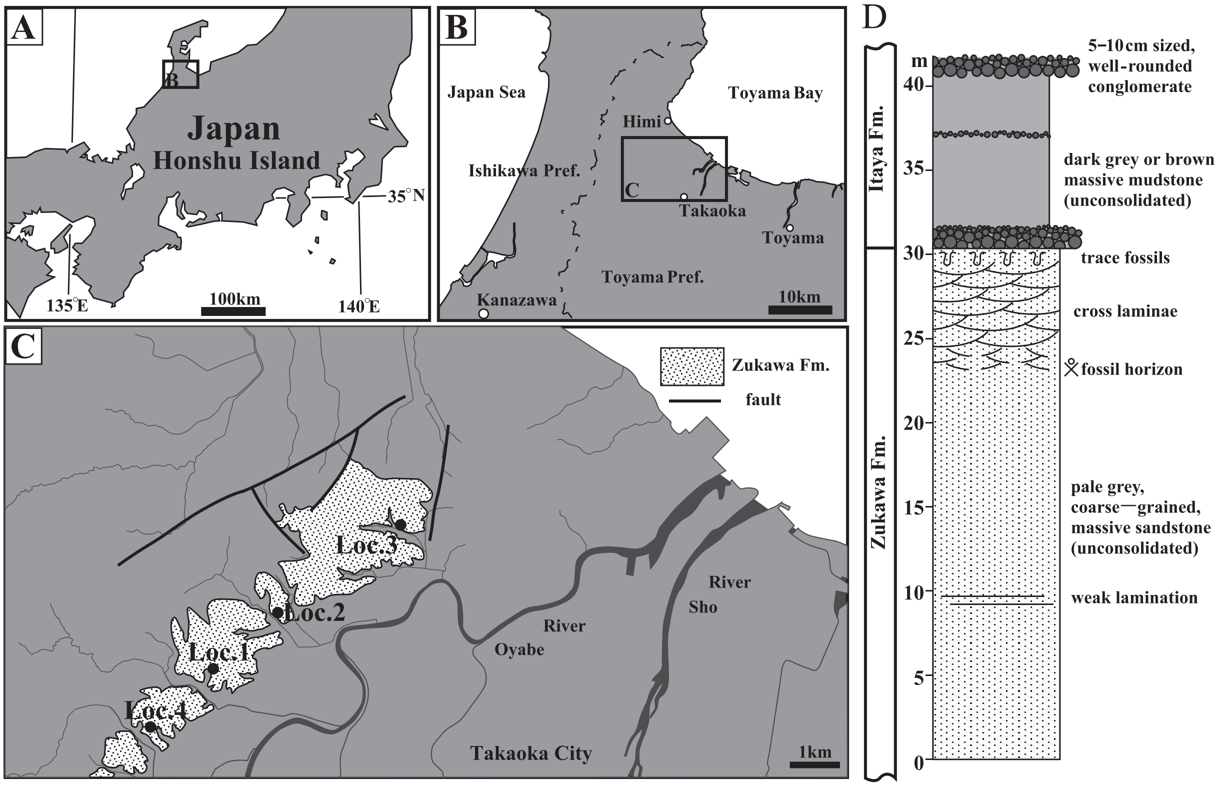

Figure 1. Index maps (A, B) showing the localities (C) and horizon (D) at Loc. 1 of the *Swiftopecten djoserus* sp. nov. specimens described from the Zukawa Formation. The geological map is modified from Sumi *et al.* (1989).

species. Among them, 179 were Recent specimens from 26 localities mainly in Hokkaido, Sakhalin and Primorye, and 192 were fossils from 11 formations represented at 18 localities in the Sea of Japan and the Pacific side of Honshu and Hokkaido (Figure 2, Appendix). Of these specimens, 102 of the recent ones were purchased at Yubetsu fishing port in Hokkaido and 49 of the fossil ones were collected from the Zukawa Formation by the author. Other Recent and fossil specimens stored at the following institutions were examined: JUE, Joetsu University of Education; NMNS, National Museum of Nature and Science, Tsukuba; TSM, Toyama Science Museum; NHMIC, Natural History Museum and Institute, Chiba; YFM, Yatsuo Fossil Museum, Kai-inkan; KSHS, Keio Senior High School.

In addition to measuring shell length and height, measurements and counting have been done of the following three characters: (1) number of radial ribs and fine riblets, (2) umbonal angle, and (3) unevenness of the ledges. Radial ribs were counted on both valves while fine riblets were counted on the third ledge of all the specimens and only on the left valve because few well preserved right valves of the new species are available. Umbonal angle is the angle between the anterior and posterior margins on each specimen, measured by a goniometer (Figure 3). The ledge is a morphological term referring to developed growth ribs, in accordance with Waller (1991). In growing order, the first formed ledge is called the first ledge, and ledges are formed sequentially such as the second ledge and the third ledge for the vertical margin. Growth increments towards the ventral margin (3a, 4a, 5a in Figure 3) and towards the interior (3b, 4b, 5b in Figure 3) were measured with vernier calipers. However, immature specimens having fewer than three ledges were excluded as invalid data because the ledges are not fully developed and have not grown towards the interior.

Systematic descriptions

Family Pectinidae Rafinesque, 1815
Subfamily Chlamydinae von Teppner, 1922
Genus ***Swiftopecten*** Hertlein, 1935

Type species.—*Swiftopecten swiftii* Bernardi, 1858 by original designation.

Remarks.—The original description of the genus *Swiftopecten* has been referred to Hertlein (1935) (e.g. Hertlein and Grant, 1972; Masuda, 1972) or Hertlein (1936) (e.g.

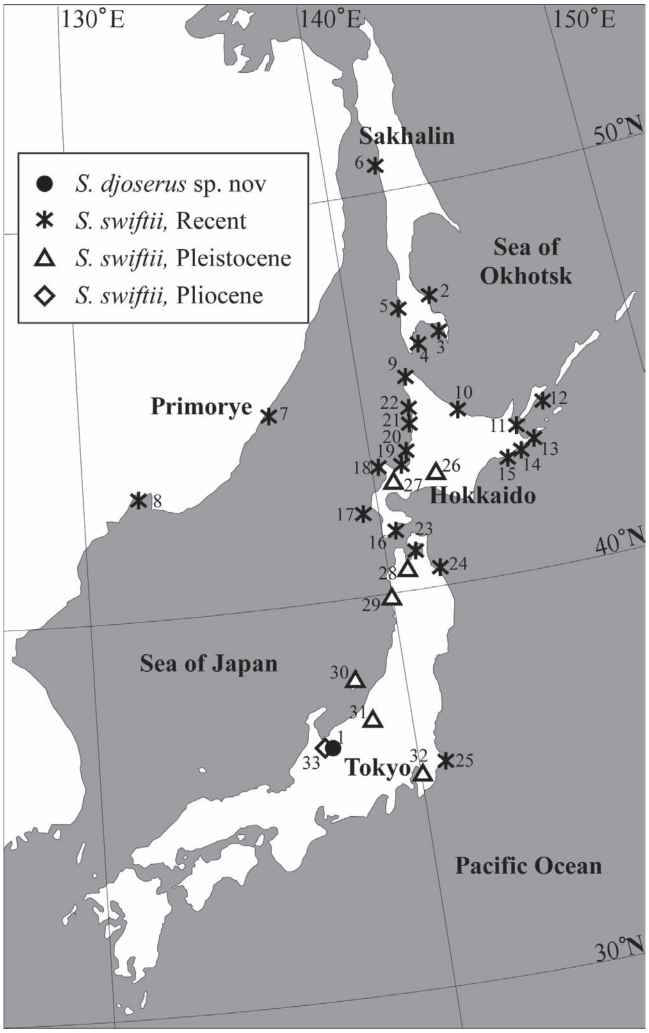

Figure 2. Map showing localities of the *Swiftopecten djoserus* sp. nov. (Pliocene) and *S. swiftii* (Plio-Pleistocene and Recent) specimens measured. 1, Takaoka; 2, Byellinszaueyena; 3, Okhotskoye; 4, Tret'ya Pad'; 5, Pochinka; 6, Due; 7, Cape Koinjo; 8, Syavyanka; 9, Veselyy Yar; 10, Mysovoy; 11, Vladivostok; 12, Wakkanai (JUE); 13, Yubetsu; 14, Notsukesaki; 15, Kunashiri; 16, Nemuro; 17, Akkeshi; 18, Kushiro; 19, Hakodate; 20, Okushiri; 21, Oshima; 22, Sapporo (?); 23, Hamamasu; 24, Mashike; 25, Rumoi; 26, Wakkanai (NMNS); 27, Mutsu; 28, Hachinohe; 29, Choshi; 30, Kamiiso; 31, Suttsu; 32, Minamitsugaru; 33, Oga; 34, Sado; 35, Kariwa; 36, Kisarazu; 37, Takaoka.

Del Rio, 1995; Matsubara, 2013). I accepted here the former opinion tentatively.

The genus *Swiftopecten* has been compared with three genera, *Nanaochlamys*, *Manupecten*, and *Semipallium*, in part. *Swiftopecten* can be separated from *Nanaochlamys* Hatai and Masuda, 1953 by having an inequivalve shell (nearly equivalve in *Nanaochlamys*; Yokoyama, 1929). These two genera are also distinguished by the differences in the allometric change of the umbonal angle versus shell height (Hayashida and Tanabe, 2006). Masuda (1960) noted that the character of the surface sculpture in the adult stage of *S. swiftii* is closely similar to the younger stage of *N. notoensis* and *N. otutumiensis*, but *Swiftopecten* can be distinguished by its nodular ribs in the adult stage, whereas *Nanaochlamys* has smooth ribs. Hertlein and Grant (1972) claimed that *Manupecten* Monterosato, 1872 lacks the ledges and hinge teeth present in *Swiftopecten*. Waller (1991) showed that *Semipallium* Jousseaume in Lamy, 1928 differs from *Swiftopecten* in having only incipient ledging, much less well developed than in *Swiftopecten*.

In conclusion, *Swiftopecten* is distinguished from other similar genera in an inequivalve shell, allometric change of the umbonal angle versus shell height, nodular ribs in the adult stage, developed ledges, hinge teeth and larger size.

Included species.—Although Kuroda (1931) ranked *Pecten turpiculus* Yokoyama, 1925 from the Pliocene Shigarami Formation as a subspecies of *Swiftopecten swiftii*, Masuda (1959) and Masuda and Noda (1976) considered it to be either a subspecies of *Chlamys cosibensis* (Yokoyama, 1911) or a separate species. Not including this one, five fossil species and one subspecies have been described in *Swiftopecten*: *S. swiftii*, *S. swiftii kindlei* (Dall, 1920), *S. parmeleei* (Dall, 1898), *S. donmilleri* (MacNeil, 1970) and *S. merklini* (Sinelnikova, 1975), all from the Asian and the North American side of the North Pacific, and *S. iheringii* Del Rio, 1995 from Argentina.

Hertlein and Grant (1972) and Moore (1984) indicated that the genus *Swiftopecten* from California is characterized by a small shell. Masuda (1972) claimed that *S. parmeleei* differs from the closely related *S. swiftii* in having a somewhat larger apical angle and a smaller shell that tends to become rounded with growth. MacNeil (1967) considered that *Chlamys kimurai* Kotaka, 1955 from the upper Oligocene Isomatsu Formation is the oldest species of the genus. After that, Del Rio (1995) described *S. iheringii* from upper Eocene deposits in Argentina as the oldest species of this genus. However, Matsubara (2013) mentioned that *C. kimurai* belongs to the genus *Nanaochlamys* and doubted whether *S. iheringii* is a species of *Swiftopecten*. If this is correct, the oldest record of this genus is *S. swiftii* from the middle Miocene deposits in northern Japan (Masuda, 1973, 1986).

Hertlein and Grant (1972) and Waller (1991) included *Pecten cosibensis* Yokoyama, 1911 in the genus *Swiftopecten*. However, Masuda (1972) argued that *Chlamys cosibensis* should not be allocated to *Swiftopecten* on the grounds that *Swiftopecten* can be distinguished from *C. cosibensis* by its large, higher, posteriorly contorted shell, smaller apical angle, triangular large anterior auricle and nearly flat left valve in the younger stage. In my opinion,

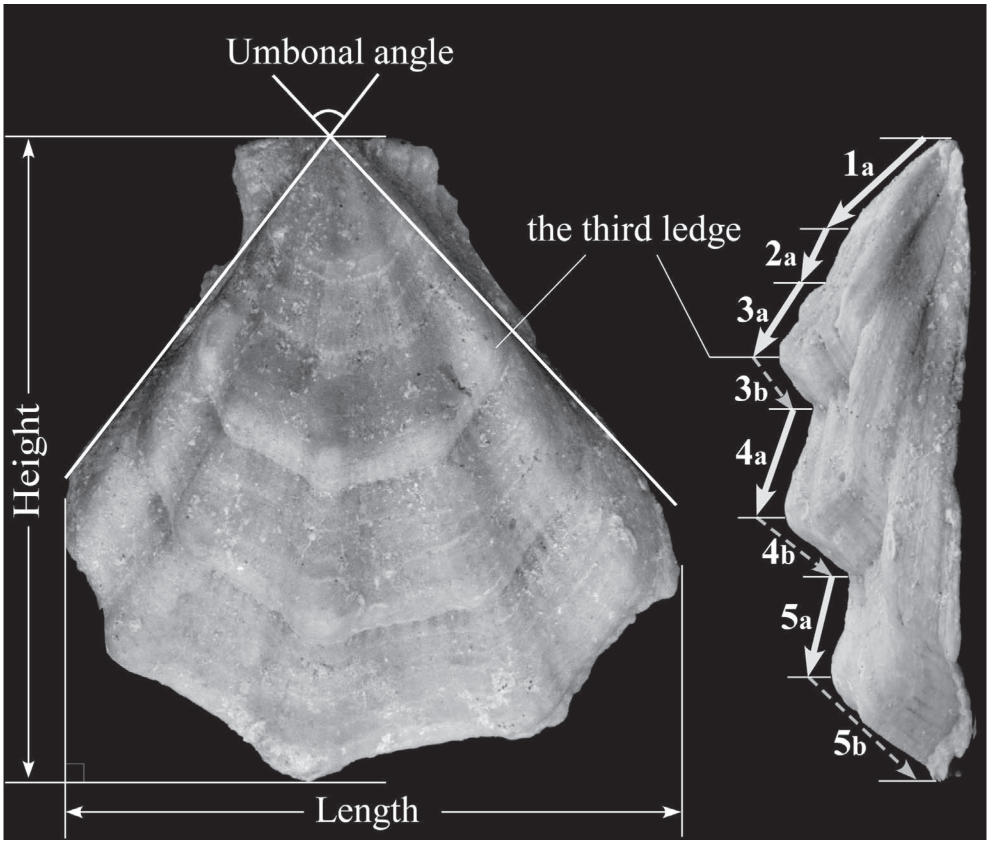

Figure 3. Morphology and measurements of *Swiftopecten*. 1a, 2a, 3a, 4a, 5a, growth increment toward ventral margin; 3b, 4b, 5b, growth increment toward inside.

C. cosibensis should not be assigned to the genus *Swiftopecten* due to differences in the deep byssal notch, the small maximum shell height, the small number of fine riblets and the lesser unevenness of the ledges. I believe that prominent ledges have evolved independently in *Swiftopecten* and *Nanaochlamys* species and in *Chlamys cosibensis*, therefore *C. cosibensis* should be excluded from *Swiftopecten*.

Swiftopecten djoserus Yoshimura, sp. nov.
[Japanese name: Zukawa-kinchakugai]

Figure 4

Swiftopecten swiftii (Bernardi, 1858). Kiyu and Mizuki., 1983, fig. 1.8; Amano *et al*., 2012, fig. 3.10.

Chlamys cosibensis (Yokoyama, 1911). Amano *et al*., 2012, fig. 3.2.

Etymology.—Named for the Pyramid of Djoser in Saqqara, Egypt because the commarginal constrictions of this species resemble the unique stepwise form of this pyramid. A noun in apposition.

Type material.—Holotype, NMNS PM27195 (Figure 4.1); Paratype, JUE No.15938 (Figure 4.2).

Type locality.—About 1.5 km northwest of the Kunisaki Bridge (crossing the Oyabe River), 7 m below the boundary of the Zukawa Formation and the Itaya Formation, Ikarabe area, Takaoka City, Toyama Prefecture, Central Japan (Loc. 1 in Figure 1 = Loc. Z-4 in Amano *et al*., 2012).

Dimensions.—See Table 1.

Diagnosis.—Medium-sized *Swiftopecten*, shell strongly convex; umbonal angle 85–90 degrees. Four radial ribs on right valve and five on left valve, covered with 42–44 fine riblets on the third ledge. Ledges very distinct. Adductor muscle scar slightly posterior and slightly dorsal from center of disc.

Description.—Shell medium-sized for genus, up to 75.4 mm in height, somewhat higher than long, fan-shaped, rather thick, very inflated; left valve slightly more inflated than right; umbonal angle 85–90 degrees, apical angle on first ledge 83–87 degrees. Right valve sculptured with four prominent radial ribs with interspaces each narrower than one rib, covered with 42–44 fine divaricated riblets on third ledge; 3–5 growth steps producing definite

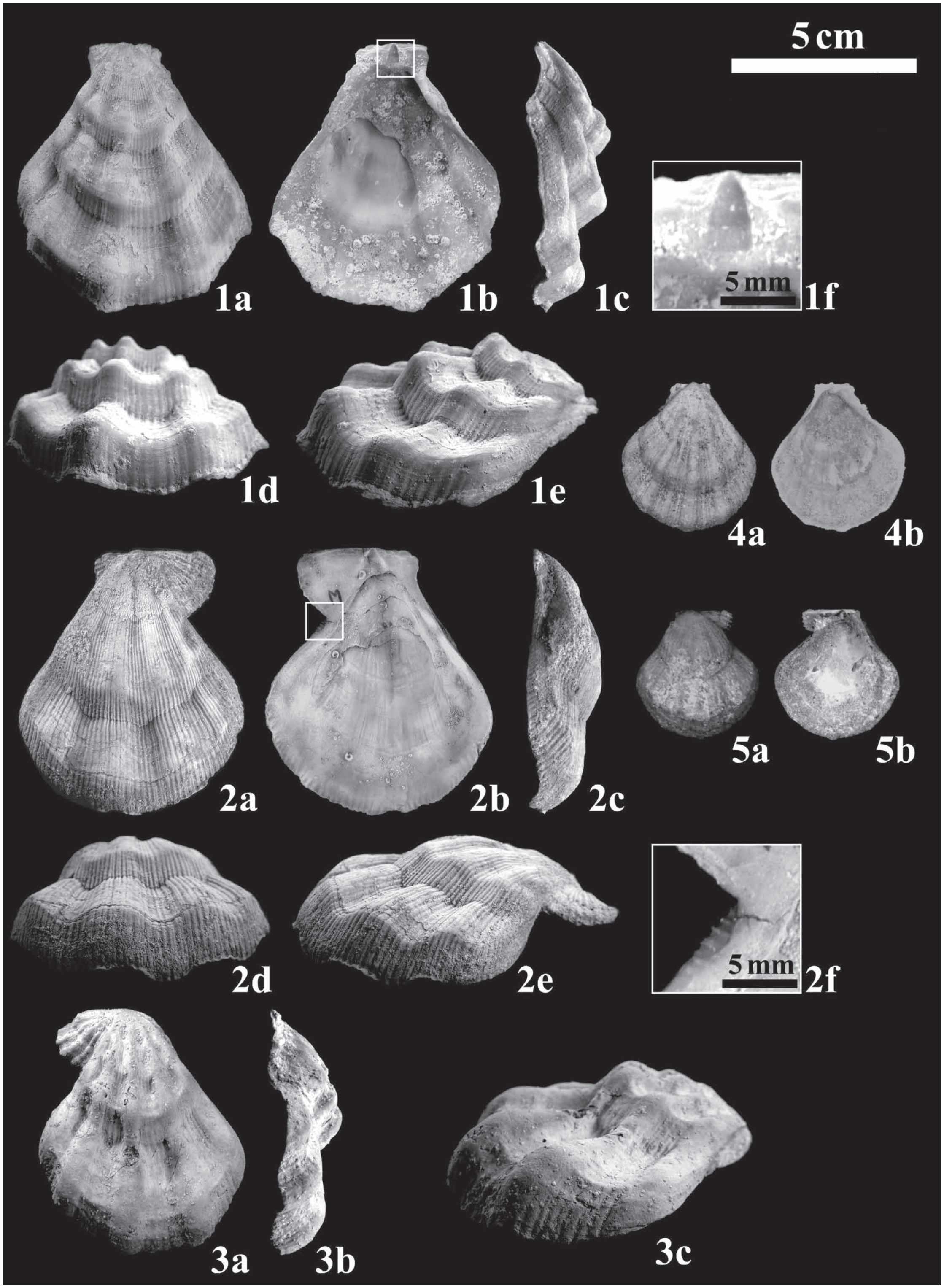

Figure 4. *Swiftopecten djoserus* sp. nov. from the Pliocene Zukawa Formation. **1,** holotype, NMNS PM27195, from Loc. 1; 1a, exterior view; 1b, interior view; 1c, lateral view; 1d, ventral view; 1e, oblique view from upper-right side; 1f, close-up of resilium; **2,** paratype, JUE no.15938, from Loc. 1; 2a, exterior view; 2b, interior view; 2c, lateral view; 2d, ventral view; 2e, oblique view from upper-right side; 2f, close-up of ctenolium; **3,** UMUT RM32338 from Loc. 2; 3a exterior view; 3b, lateral view; 3c, oblique view from upper-right side; **4,** UMUT RM32343 from Loc. 3; 4a, exterior view; 4b, interior view; **5,** UMUT RM32348 from Loc. 1; 5a, exterior view; 5b, interior view.

ledges. Left valve with five rather prominent ribs with broader interspaces than on right valve; divaricate riblets and ledges as on right valve. Anterior auricle large, triangular, with rounded margin, sculptured with 6–9 radial ribs. Posterior auricle much smaller than anterior, sculptured with 4–5 ribs. Byssal notch in right valve rather narrow; functional ctenolium consisting of six teeth. Resilial pit large, nearly triangular in shape; resilial teeth strong; cardinal crura distinct. Adductor muscle scar positioned slightly posterior and dorsal to center of valve, although aragonite area dissolved in all specimens. Interior surface of both valves distinctly or gently folded corresponding to external sculpture, with fine crenulations at ventral margin.

Table 1. Measurements of *Swiftopecten djoserus* sp. nov. * broken.

Specimens	Type	Height (mm)	Length (mm)	Valve	Loc.
NMNS PM27195	Holotype	73.8	64.7	Left	1
JUE No.15938	Paratype	75.4	64.0	Right	1
UMUT RM32338		71.0	62.6	Left	2
UMUT RM32339		56.9	50.1	Left	1
UMUT RM32340		53.8	47.2	Left	1
UMUT RM32341		51.5	43.6	Left	1
UMUT RM32342		42.0	36.4	Left	1
UMUT RM32343		42.0	38.8	Left	3
UMUT RM32344		41.3*	46.7	Right	1
UMUT RM32345		40.6	36.1	Right	1
UMUT RM32346		40.0	35.8	Left	1
JUE No.15938		39.3	34.9	Left	1
UMUT RM32347		39.2	34.8	Right	1
UMUT RM32348		36.8	32.3	Left	1
UMUT RM32349		21.8	20.2	Left	1

Comparison.—*Swiftopecten djoserus* sp. nov. is most similar to the modern species, *S. swiftii*. The anterior and posterior auricles are sculptured with 6–9 radial ribs, as in *S. swiftii*. Both auricles also are similar to those of *S. swiftii* in shape. The number of radial ribs also is the same in both species: four on the right valve and five on the left valve. However, the number of fine riblets differs, as *S. djoserus* sp. nov. has 42–44 radial riblets on the third ledge while *S. swiftii* has 55–57 (Table 2). As the result of a Mann-Whitney U test, a significant difference was found in median of the number of the fine riblets between the two species ($U = 0$, $p = 2.2\times10^{-16}$). *Swiftopecten djoserus* sp. nov. has an umbonal angle of 85–90 degrees versus a low of *ca.* 73 to a high of *ca.* 87 in *S. swiftii* (Figure 6). As the result of a Kolmogorov-Smirnov test, the null hypothesis of normal distribution was not rejected in either species ($D = 0.13977$, $p = 0.9473$). As a result of a t-test, a significant difference in mean was found between the two species ($t = 19.253$, $df = 14.486$, $p = 1.005\times10^{-11}$). On the unevenness of ledges, *S. djoserus* sp. nov. is stronger than *S. swiftii.* Although both species have rather strongly uneven ledges, the mean of the slope of the regression line of the width of growth increment towards inside against that towards ventral margin is 0.660 (9 specimens) for *S. djoserus* sp. nov. compared with 0.329 (213 specimens) for *S. swiftii* (Figure 7). As results of Kolmogorov-Smirnov test, the null hypothesis of the normal distribution was not rejected for the unevenness of the ledges in the samples of *S. djoserus* sp.

Table 2. Morphological comparison of *Swiftopecten djoserus* sp. nov. with the other species and subspecies of *Swiftopecten*.

Species Characters	Maximum shell height (mm)	Number of radial ribs on left valve	Number of fine riblets on left disc	Number of ledges	Umbonal angle (degree)
Swiftopecten djoserus sp. nov.	75.4	5	42–44	3–5	85–90
S. swiftii	114.5	5	55–57	3–6	72–77
S. parmeleei	100	5	48	3–5	70
S. donmilleri	59	9	65	3–4	80
S. merklini	48	5	60	3–5	80
S. iheringii	44.4	7	60	4–5	75–82
S. swiftii kindlei	70	5	56	3–5	70

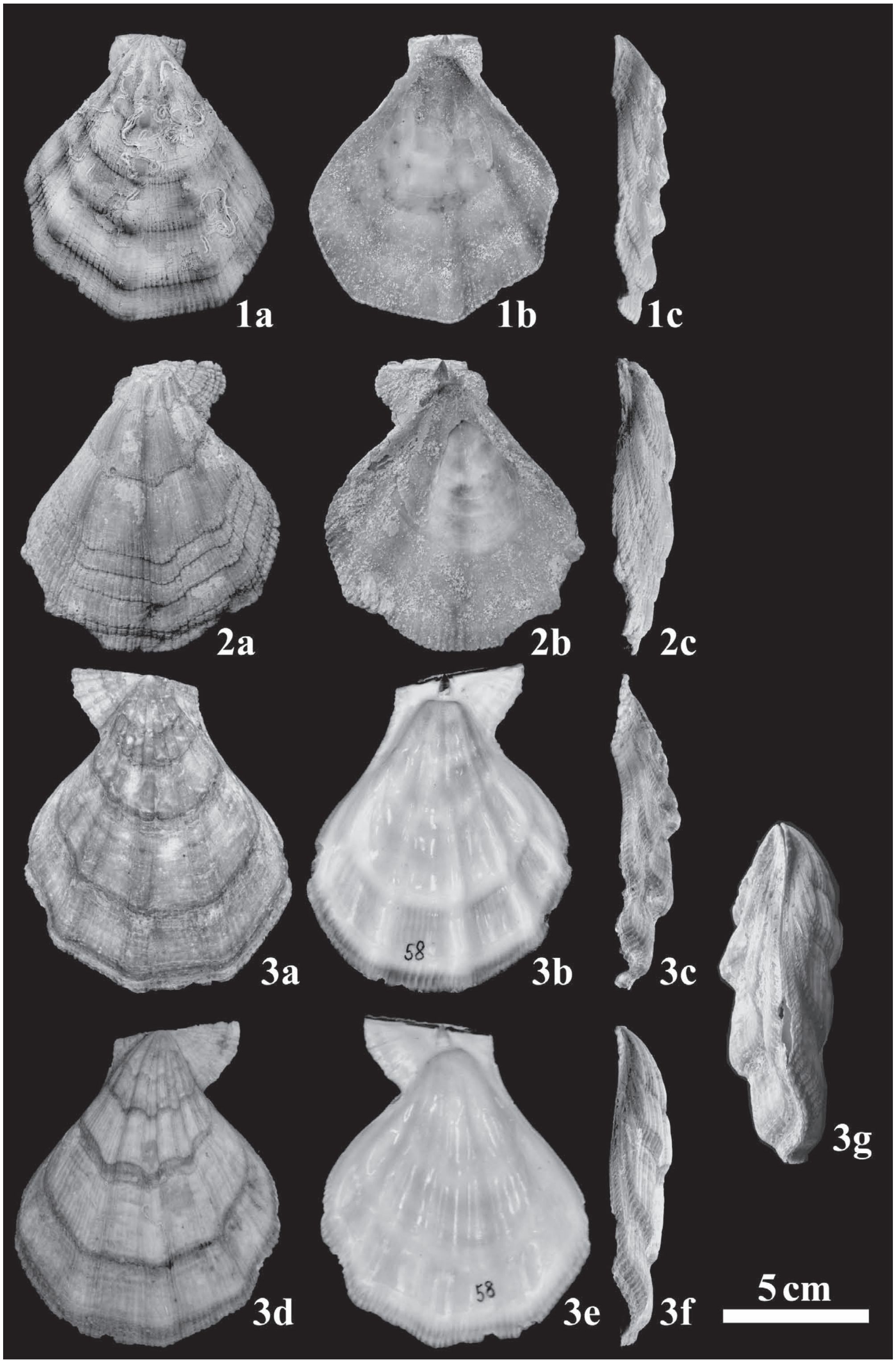

Figure 5. Recent and fossil specimens of *Swiftopecten swiftii* (Bernardi, 1858). **1,** KSHS-F1-001, fossil specimen from Loc. 1 in the Zukawa Formation; 1a, exterior view; 1b, inner view; 1c, lateral view; **2,** KSHS-F2-001, fossil specimen from Loc. 1 in the Zukawa Formation; 2a, exterior view; 2b, inner view; 2c, lateral view; **3,** KSHS-R1-058, Recent specimen from Yubetsu Town in Hokkaido, depth 50 m; 3a, d, exterior view of right and left valves; 3b, e, inner view of the right and left valves; 3c, f, lateral view of right and left valves; 3g, lateral view of articulated valve.

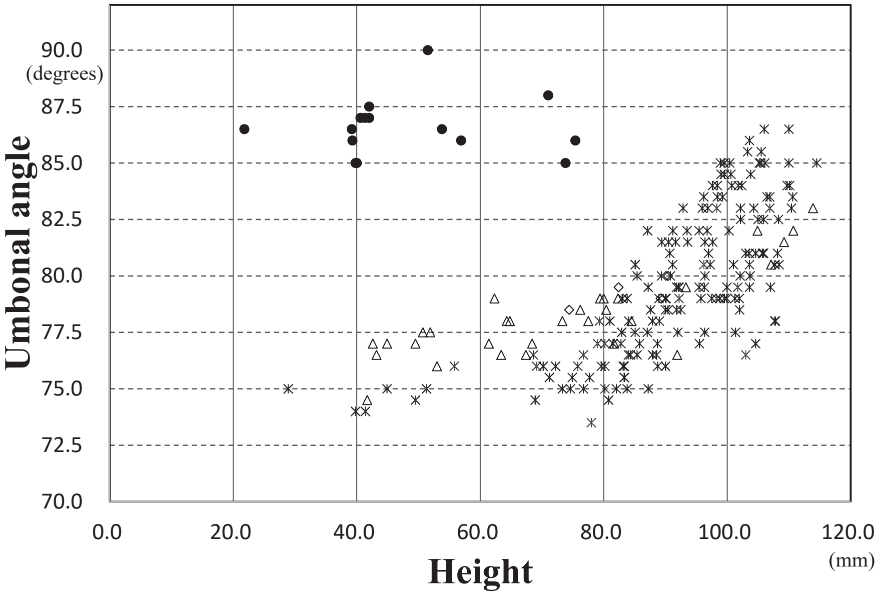

Figure 6. Relationship between shell height (mm) and umbonal angle (degrees) of *Swiftopecten djoserus* sp. nov. and *S. swiftii* (all symbols as in Figure 2).

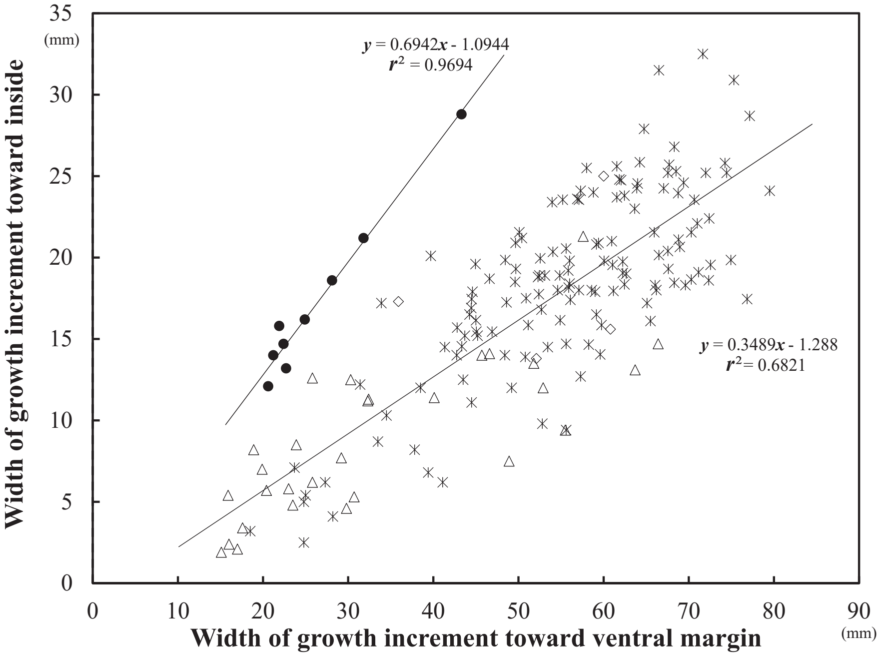

Figure 7. Scatter diagram showing the relationship between widths of growth increment towards the ventral margin (3a, 4a, 5a in Figure 3) and growth increment towards the inside (3b, 4b, 5b in Figure 3) for *Swiftopecten djoserus* sp. nov. and *S. swiftii*. Regression lines are shown for each species (all symbols as in Figure 2).

nov. ($D = 0.2201$, $p = 0.6609$), as well as in the samples of *S. swiftii* ($D = 0.060508$, $p = 0.6298$). As the result of the *t*-test, a significant difference was found between the two species ($t = 22.855$, $df = 14.341$, $p = 1.099 \times 10^{-12}$).

Stratigraphic and geographic range.—Recorded only from the upper part of the Pliocene Zukawa Formation.

Discussion

Appearance and extinction of the new species and its causes

From its Pliocene occurrences in only the Sea of Japan borderland, *Swiftopecten djoserus* sp. nov. can be judged to be an endemic species of the Omma-Manganji fauna (Otuka, 1939) as well as the only extinct species of *Swiftopecten* in Japan. In this research, I examined 179 Recent and 192 fossil specimens of *S. swiftii* in the late Pliocene, Pleistocene and Recent. Significant difference was not observed among various ages or localities. Therefore, *S. swiftii* is characterized by a constant range of morphological variations.

The new species also was found only from the upper part of the Zukawa Formation. This new species was collected in association with *S. swiftii* and apparently lived sympatrically with it. As mentioned above, *S. swiftii* appeared during the middle Miocene. From these occurrences, *S. djoserus* sp. nov. is judged to have originated from *S. swiftii* in the central part of the Sea of Japan borderland during or before the latest Pliocene, because almost all specimens (a total of 15 specimens; 14 specimens and one specimen which is impossible to discriminate) of the new species were recovered from just above Datum A at Ikarabe and Zukawa, corresponding with the Pliocene cooling event in the Northern Hemisphere (Sato and Kameo, 1996). As a result of this cooling, the percentage of cold-water mollusks became higher than in the horizons below Datum A. Moreover, species now living in Hokkaido and northwards appeared above Datum A in the Zukawa and Sasaoka formations in Akita Prefecture (Amano *et al.*, 2011, 2012). What can be assumed here is the possibility that the cooling event accelerated the speciation of the new species. However, we cannot judge whether the new species was alive before Datum A because *S. swiftii* was not present below the Datum A. In regard to the question of extinction, the new species has not been recorded from other formations in this research. Hence, the new species is likely to have become extinct in the latest Pliocene or later. It is considered that the new species became extinct as a result of the environmental deterioration caused by a fall in sea level during a glacial epoch in the Middle Pleistocene or later, as previously reported (Amano, 2001), but as yet I have no satisfactory evidence that would explain why only the new species became extinct.

Causes of the formation of ledges in the genus *Swiftopecten*

In this study, detailed measurements were carried out on the ledges on both valves. Generally, the formation of ledges along growth lines was caused by pauses in shell growth (Habe, 1977). In pectinids, Takenaka and Hayami (1998) considered that ledges reflect a reproductive cycle. As mentioned above, the average value of the ratio of growth increment towards inside to growth increment towards ventral margin of *S. djoserus* sp. nov. (0.660) is significantly different from that of *S. swiftii* (0.329). This means that in *S. swiftii*, the growth ratio of increments towards the ventral margin to increments towards the inside is 3 to 1. On the other hand, this ratio in *S. djoserus* sp. nov. is 3 to 2 (Figure 7). This result suggests that *S. djoserus* sp. nov. and *S. swiftii* had different breeding seasons, explaining how the two species were able to live sympatrically. In order to support this conclusion, further research is necessary to observe the growth lines microscopically and to measure the stable oxygen and carbon isotope ratios.

Acknowledgements

This research was greatly supported by Kazutaka Amano (Joetsu University of Education) who provided insight and expertise. I am grateful to Alan G. Beu (GNS Science, New Zealand) for reviewing the manuscript. I am also grateful to Takenori Sasaki (The University Museum, The University of Tokyo) and Taiji Kurozumi (Natural History Museum and Institute, Chiba) for providing a lot of information and discussing the subject minutely. I also thank Takehiro Sato (Kanagawa Prefectural Museum of Natural History) for cooperating with the measurement data verification. My thanks are also due to Hiroshi Saito (National Museum of Nature and Science, Tsukuba), Tasuku Yoshioka (Toyama Science Museum) and Yatsuo Fossil Museum, Kai-inkan for their help in examining specimens. Furthermore, Yoko Kumanoya (Keio University) cooperated by translating Russian literature. Additionally, Koya Yamada (The Sea of Japan Mining Corporation Limited) kindly provided access to the sampling locality. I would also like sincerely to thank Masahiro Kishima (Keio Senior High School). Without his persistent support, this research would not have been completed.

References

Amano, K., 2001: Pliocene molluscan fauna of Japan Sea borderland and the paleoceanographic conditions. *Biological Science*, vol. 3, p. 178–184. (*in Japanese with English title*)

Amano, K., Hamuro, M., Hamuro, T., Sato, T. and Ogihara, R., 2012: Influence of latest Pliocene cooling to the benthic fauna from the central part of the Japan Sea borderland: Molluscan fauna from the Zukawa Formation in Toyama Prefecture. *Journal of the Geological Society of Japan*, vol. 118, p. 810–822. (*in Japanese with English abstract*)

Amano, K., Yoshida, A. and Sato, T., 2011: Influence of cooling event at 2.75 Ma on the molluscan fauna from central and northern parts of Akita Prefecture. *Journal of the Geological Society of Japan*, vol. 117, p. 508–522. (*in Japanese with English abstract*)

Bernardi, M., 1858: Description d'espèces nouvelles. *Journal de Conchyliologie*, vol. 7, p. 90–94.

Dall, W. H., 1898: Contribution to the Tertiary fauna of Florida, with special reference to the silex-beds of Florida and the Pliocene beds of Caloosahatchie River. *Wagner Free Institute of Science of Philadelphia*, vol. 4, p. 571–947.

Dall, W. H., 1920: Pliocene and Pleistocene fossils from the Arctic coast of Alaska and the auriferous beaches of Nome, Norton Sound, Alaska. *United States Geological Survey Professional Paper 125-C*, p. 23–37.

Del Rio, C. J., 1995: The genus *Swiftopecten* Hertlein, 1936, (Bivalvia; Pectinidae) in the Tertiary of southern South America. *Journal of Paleontology*, vol. 69, p. 1054–1059.

Fujii, S. and Shimizu, M., 1992: On the molluscan fossils from Ikarabe, Takaoka-shi, Toyama Prefecture, Central Japan: Study of Omma molluscan fossils (Part 4). *Journal of the College of Liberal Arts*, *Toyama University*, *Natural Science*, no. 25, p. 13–23. (*in Japanese with English abstract*)

Goto, M., Kaneko, K. and Kanayama, S., 1993: Plio-Pleistocene fossils from the Zukawa and Omma formations, Toyama and Ishikawa. *Special Publication of Toyama Science Museum*, no. 6, p. 1–63. (*in Japanese with English title*)

Habe, T., 1977: *Systematics of Mollusca in Japan*, *Bivalvia and Scaphopoda*, 374 p. Hokuryukan, Tokyo. (*in Japanese with English title*)

Hatai, K. and Masuda, K., 1953: On the *Pecten notoensis* Yokoyama (On the Miocene Pectinidae from the environs of Sendai, part 2). *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 11, p. 75–82.

Hayashida, N. and Tanabe, K., 2006: The mode of life and taxonomy relationship of a Japanese Miocene pectinid bivalve *Nanaochlamys notoensis*. *Paleontological Research*, vol. 10, p. 1–10.

Hertlein, L. G., 1935: The Templeton Crocker Expedition of the California Academy of Sciences, 1932. *Proceedings of the California Academy of Sciences*, vol. 21, p. 301–328.

Hertlein, L. G., 1936: Three new sections and rectifications of some specific names in the Pectinidae. *Nautilus*, vol. 50, p. 24–27 and p. 54–58.

Hertlein, L. G. and Grant, U. S., IV, 1972: The geology and paleontology of the marine Pliocene of San Diego, California (Paleontology: Pelecypoda). *San Diego Society of Natural History*, *Memoir 2 (Part 2B)*, p. 134–409.

Kiyu, H. and Mizuki, M., 1983: Toyama sea was colder than current? —Story of approximately 5 million years ago. *Toyama and Nature*, *Toyama Science Museum*, vol. 6, p. 2–5. (*in Japanese; original title translated*)

Kotaka, T., 1955: Molluscan fauna from the Oligocene Isomatsu Formation, Aomori Prefecture, Northeast Japan. *Saito Ho-on Kai Museum Research Bulletin*, no. 24, p. 23–30.

Kuroda, T., 1931: Fossil Mollusca. *In*, Homma, F. *ed.*, *Geology of the Central Part of Shinano*, *Part 4*, p. 1–90. Kokon Shoin, Tokyo. (*in Japanese with English title*)

Lamy, E. 1928: Les Peignes de la Mer Rouge (d'après les Matériauc recueillis par le Dr. Jousseaume). *Muséum National d'Histoire Naturelle Bulletin*, vol. 34, p. 166–172.

MacNeil, F. S., 1967: Cenozoic pectinids of Alaska, Iceland, and other northern regions. *United States Geological Survey Professional Paper 553*, p. 25.

MacNeil, F. S., 1970: New Pliocene *Chlamys* (*Swiftopecten*) and *Beringius* from the Alaska Peninsula. *Nautilus*, vol. 84, p. 69–74.

Masuda, K., 1959: On the Miocene Pectinidae from the environs of Sendai: Part 14, On *Pecten swiftii* Bernardi. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 34, p. 101–111.

Masuda, K., 1960: On the morphogenesis of *Nanaochlamys*. *Science Reports of the Tohoku University*, *Second Series*, *Geology*, *Special Volume*, no. 4, p. 371–383.

Masuda, K., 1962: Notes on the Tertiary Pectinidae of Japan. *Science Reports of the Tohoku University*, *Second Series*, *Geology*, *Special Volume*, no. 5, p. 159–193.

Masuda, K., 1972: *Swiftopecten* of the northern Pacific. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 87, p. 395–408.

Masuda, K., 1973: Molluscan biostratigraphy of the Japanese Neogene. *Memoirs of the Geological Society of Japan*, vol. 8, p. 107–120.

Masuda, K., 1986: Notes on Origin and Migration of Cenozoic Pectinids in the Northern Pacific. *Palaeontological Society of Japan Special Publications*, no. 29, p. 95–110.

Masuda, K. and Noda, H., 1976: *Check List and Bibliography of the Tertiary and Quaternary Mollusca of Japan*, *1950–1974*, 494 p. Saito Ho-on Kai, Sendai.

Matsubara, T., 2013: Is *Nanaochlamys* (Bivalvia: Pectinidae) ancestral to *Swiftopecten*? *Abstracts of the 120th Annual Meeting of the Geological Society of Japan*, p. 135.

Matsuura, N., 1985: Successive change of the marine molluscan faunas from Pliocene to Holocene in Hokuriku Region, central Japan. *Bulletin of the Mizunami Fossil Museum*, no. 12, p. 71–158. (*in Japanese with English abstract*)

Matsuura, N., 1992: *Fossils from Ishikawa*, 156 p. Hokkoku Newspaper Company, Kanazawa. (*in Japanese; original title translated*)

Matsuura, N., 2009: *Fossils from Ishikawa*, *New Edition*, 273 p. Hokkoku Newspaper Company, Kanazawa. (*in Japanese; original title translated*)

Min, D.-K., Lee, J.-S., Koh, D.-B. and Je, J.-G., 2004: *Mollusks in Korea (Revised Supplementary Edition)*, 566 p. Min Molluscan Research Institute, Seoul. (*in Korean with English title*)

Mochiduki, K., 1930: Neogene and later history of Kanazawa area. *Journal of the Geological Society of Japan*, vol. 37, p. 278–280.

Monterosato, T. A., 1872: *Notizie Intorno alle Conchiglie Mediterranee*, 61 p. Ufficio tipografico di Michele Amenta, Palermo.

Moore, E. J., 1984: Tertiary marine pelecypods of California and Baja California: Propeamussiidae and Pectinidae. *United States Geological Survey Professional Paper 1228-B*, B1–B112, pls. 1–42.

Okutani, T. *ed.*, 2000: *Marine Mollusks in Japan*, 1173 p. Tokai University Press, Tokyo.

Otuka, Y., 1939: Mollusca from Cainozoic System of eastern Aomori Prefecture. *Journal of the Geological Society of Japan*, vol. 44, p. 23–31.

Rafinesque, C. S., 1815: *Analyse de la Nature, ou Tableau de l'Univers et des Corps Organisés*, 224 p. Privately printed, Palermo.

Sato, T. and Kameo, K., 1996: Pliocene to Quaternary calcareous nannofossil biostratigraphy of the Arctic Ocean, with reference to late Pliocene glaciation. *In*, Thiede, J., Myhre, A. M., Firth, J. V. *et al. eds.*, *Proceedings of ODP*, *Scientific Results*, vol. 151, p. 39–59. College Station, Texas (Ocean Drilling Program).

Sinelnikova, V. N., 1975: Mio-Pliocene Pectinidae of Kamchatka. *Transactions of the Geological Institute of the Academy of Sciences of the USSR*, vol. 229, p. 1–137. (*in Russian with English title*)

Sumi, Y., Nozawa, T. and Inoue, M., 1989: *Geology of the Isurugi District*, *Quadrangle Series*, *Scale 1:50,000*, 62 p. Geological Survey of Japan, Tsukuba. (*in Japanese with English title*)

Takenaka, N. and Hayami, I., 1998: The relation of reproductive cycle and growth rings on *Chlamys vesiculosus* (Dunker, 1877). *Abstract* *with Programs, the 1998 Annual Meeting of the Palaeontological Society of Japan*, p. 83. (*in Japanese; original title translated*)

Teppner, W. von., 1922: Lamellibranchiata tertiaria "Anisomyaria". *In*, Diener, C. *ed.*, *Fossilium Catalogus*, *I*, *Animalia*, *Pars 15*, p. 67–296. W. Junk, Berlin.

Volova, G. H. and Scarlato, O. A., 1980: *Bivalve Molluscs from Peter the Great Bay*, 93 p. Far East Science Center of the Academy of Sciences of the USSR, Vladivostok. (*in Russian with English title*)

Waller, T. R., 1991: Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). *In*, Shumway, S. A. *ed.*, *Scallops: Biology, Ecology and Aquaculture*, p. 1–73. Developments in Aquaculture and Fisheries Science 21, Elsevier, New York.

Yokoyama, M., 1911: Pectens from the Koshiba Neogene. *Journal of the Geological Society of Japan*, vol. 18, p. 1–5.

Yokoyama, M., 1925: Tertiary Mollusca from Shinano and Echigo. *Journal of the Faculty of Science*, *Imperial University of Tokyo*, *Section 2*, *Geology*, *Mineralogy*, *Geography*, *Seismology*, vol. 1, p. 1–23.

Yokoyama, M., 1929: Pliocene shells from near Nanao, Noto. *Report of the Imperial Geological Survey of Japan*, no. 104, p. 1–7.

Appendix

List of material of 371 specimens of *Swiftopecten swiftii* (Bernardi, 1858) for morphologic comparison with *S. djoserus* sp. nov.

Fossil specimens

1. Zukawa Formation, upper Pliocene: Ishidutumi (N = 19) and Iwatsubo (N = 7), Takaoka City, Yoyama Prefecture, TSM. Ikarabe (N = 44) and Zukawa (N = 1), Takaoka City, Toyama Prefecture, JUE. Ikarabe (N = 3), Ishidutsumi (N = 2) and Zukawa (N = 4), Takaoka City, Toyama Prefecture, YFM. Nishiebizaka (N = 4), Ikarabe (N = 33), Iwatsubo (N = 6) and Zukawa (N = 6) Takaoka City, Toyama Prefecture, KSHS.
2. Mita Formation, lower Pliocene: Fuchu, Toyama City, Toyama Prefecture (N = 1), TSM. Fuchu, Toyama City, Toyama Prefecture (N = 1), JUE.
3. Daishaka Formation, upper Pliocene: Daishakazawa, Minamitsugaru District, Aomori Prefecture (N = 1), JUE.
4. Shitoka Formation, upper Pliocene: Kamakurazawa River (N = 1) and Shitoka River (N = 1), Minamiuonuma City, Niigata Prefecture, JUE.
5. Haizume Formation, lower Pleistocene: Izumozakimachi (N = 1), Santo District, and Nishiyamacho (N = 9), Kariwa District, Niigata Prefecture, JUE.
6. Kamiizumi Formation, lower Pleistocene: Nagayoshi, Sodegaura City, Chiba Prefecture (N = 1), NHMIC.
7. Omma Formation, lower Pleistocene: Oyabe City, Toyama Prefecture (N = 3); Kanazawa City, Ishikawa Prefecture (N = 1), TSM.
8. Sawane Formation, lower Pleistocene: Sado City, Niigata Prefecture (N = 14), JUE.
9. Setana Formation, lower Pleistocene: Soibetsu River, Suttsu District, Hokkaido (N = 14), JUE.
10. Shibikawa Formation, middle Pleistocene: Yasuda, Oga City, Akita Prefecture (N = 11), JUE.
11. Tomikawa Formation, lower Pleistocene: Kamiisomachi, Kamiiso District, Hokkaido (N = 2), JUE.

Recent specimens

12. Sea of Japan: Hamamasu (N = 8), Mashike (N = 2), Okushiri (N = 1), Oshima (N = 2), Rumoi (N = 9), Sapporo (?) (N = 2) and Wakkanai (N = 1), Hokkaido, NMNS. Wakkanai (N = 1), Hokkaido; Vladivostok (N = 1) and Syavyanka (N = 1), Primorye, NHMIC. Cape Koinjo (N = 2) and Due (N = 1), Sakhalin, JUE.
13. Pacific Ocean: Nemuro (N = 1), Kunashiri, Kuril (N = 2) and Shirikishinai (N = 2), Hokkaido; Shiroganemachi, Hachinohe City, Aomori Prefecture (N = 2), NMNS. Kushiro, Hokkaido (N = 1); Choshi, Chiba Prefecture (N = 2), NHMIC. Akkeshi (N = 3), Notsukesaki (N = 1) and Nemuro (N = 4), Hokkaido, JUE.
14. Sea of Okhotsk: Yubetsu, Hokkaido (N = 102), KSHS. Okhotskoye (N = 6), Pochinka (N = 2) and Tret'ya Pad' (N = 7), Sakhalin, JUE.
15. Tsugaru Strait: Hakodate, Hokkaido (N = 2), NMNS.
16. Mutsu Bay: Mutsu City, Aomori Prefecture (N = 1), NMNS.