

Four new species of the Jurassic to Cretaceous seep-restricted bivalve *Caspiconcha* and implications for the history of chemosynthetic communities

Robert G. Jenkins,¹ Andrzej Kaim,² Yoshinori Hikida,³ and Steffen Kiel⁴

¹School of Natural System, College of Science and Engineering, Kanazawa University, Kanazawa City, Ishikawa Prefecture 920-1192, Japan (robertgj@staff.kanazawa-u.ac.jp)

²Institute of Paleobiology, Polish Academy of Sciences, ul. Twarda 51/55, PL-00-818 Warszawa, Poland (kaim@twarda.pan.pl)

³Nakagawa Museum of Natural History, 28-9 Yasukawa, Nakagawa Town, Hokkaido 098-2626, Japan (nmhikida@coral.ocn.ne.jp)

⁴Swedish Museum of Natural History, Department of Palaeobiology, Box 500 07 104 05 Stockholm, Sweden (steffen.kiel@nrm.se)

Abstract.—Four new species of the methane seep-inhabiting kalenterid bivalve genus *Caspiconcha* Kelly in Kelly et al., 2000 are described: *Caspiconcha basquensis* from the late Albian of northern Spain, *C. yubariensis* from the late Albian of northern Japan, *C. raukumaraensis* from the late Albian to mid-Cenomanian of New Zealand, and *C. lastsamurai* from the Campanian of northern Japan. The earliest confirmed record of the genus is known from the latest Jurassic. It reached its maximum diversity in the Albian and declined in diversity and abundance through the Late Cretaceous. The youngest species, *C. lastsamurai*, is currently known from a single specimen only.

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Introduction

Chemosynthesis-based ecosystems are most commonly found around hydrothermal vents and methane seeps in the deep sea. Most of the megafauna at these sites consist of highly specialized animals living in symbiosis with sulfur- and/or methane-oxidizing bacteria, which provide them with nutrients. At modern vents and seeps, these are mainly vestimentiferan tube worms, bathymodiolin mussels, and vesicomid bivalves—all restricted to these environments. Mesozoic vents and seeps were also inhabited by animals endemic to such environments, although their taxonomic affinities were different. Common were rhynchonellid brachiopods of the Dimerelloidea, a group that disappeared from vents and seeps by the end of the Early Cretaceous (Campbell and Bottjer, 1995a, b; Sandy, 2010; Peckmann et al., 2011; Kiel et al., 2014). Among mollusks, gastropods of the Abyssochrysoidea were common, including large-sized taxa (Goedert and Kaler, 1996; Kaim et al., 2008, 2009, 2014; Kiel et al., 2010), and bivalves restricted to the seep environment included several genera of Lucinidae (Kiel, 2013) and the large kalenterid genus *Caspiconcha* Kelly in Kelly et al., 2000.

Initially described from Greenland, *Caspiconcha* is now known from seep deposits from the Atlantic, Pacific, and Tethys Oceans and from both hemispheres (Kelly et al., 2000; Kiel and Peckmann, 2008; Kiel et al., 2010, 2013; Agirrezabala et al., 2013; Jenkins et al., 2013). Its shell morphology indicates the presence of a byssus, and when found in situ, it is usually oriented with the anterior part about 30° downward relative to the bedding plane, suggesting a semi-infaunal/epifaunal mode of life (Kelly et al., 2000; Kiel and Peckmann, 2008). Its large size (exceeding 300 mm in length) and its abundance at

many Early Cretaceous seep deposits suggest that *Caspiconcha* harbored chemotrophic bacteria in its gills, like the dominant bivalves at vents and seeps today (Kelly et al., 2000; Jenkins et al., 2013). So far, there are three nominal species of *Caspiconcha*: the type species *C. whitami* Kelly in Kelly et al., 2000 from the Barremian of Greenland; *Caspiconcha major* (Gabb, 1869) from Tithonian to Albian seep deposits in California (Jenkins et al., 2013); and *Caspiconcha rubani* Kiel, Campbell, and Gaillard, 2010 from the Berriasian of the Crimea. Several other species have been left in open nomenclature pending more exhaustive taxonomic work and/or collecting effort. Here we formally describe four of these species and discuss the evolutionary history of *Caspiconcha* and other seep-related kalenterids/modiomorphids.

Geologic setting

The material is from localities in Spain, New Zealand, and Japan that have been described elsewhere (Fig. 1). They are briefly outlined here, with references to more detailed reports.

Ispaster, Spain.—More than 50 limestone bodies crop out on an intertidal platform composed mostly of turbidites along the coast of the Bay of Biscay in the Basque country, Spain, between the villages Ea and Ispaster. They were identified as ancient methane-seep deposits using stable carbon isotope, petrographic, and biomarker evidence, are of late Albian age, and belong to the Ogella unit of the Black Flysch Group (Agirrezabala et al., 2013). All investigated specimens described here as *Caspiconcha basquensis* n. sp. are from float boulders of seep limestone found along the beach at this section.

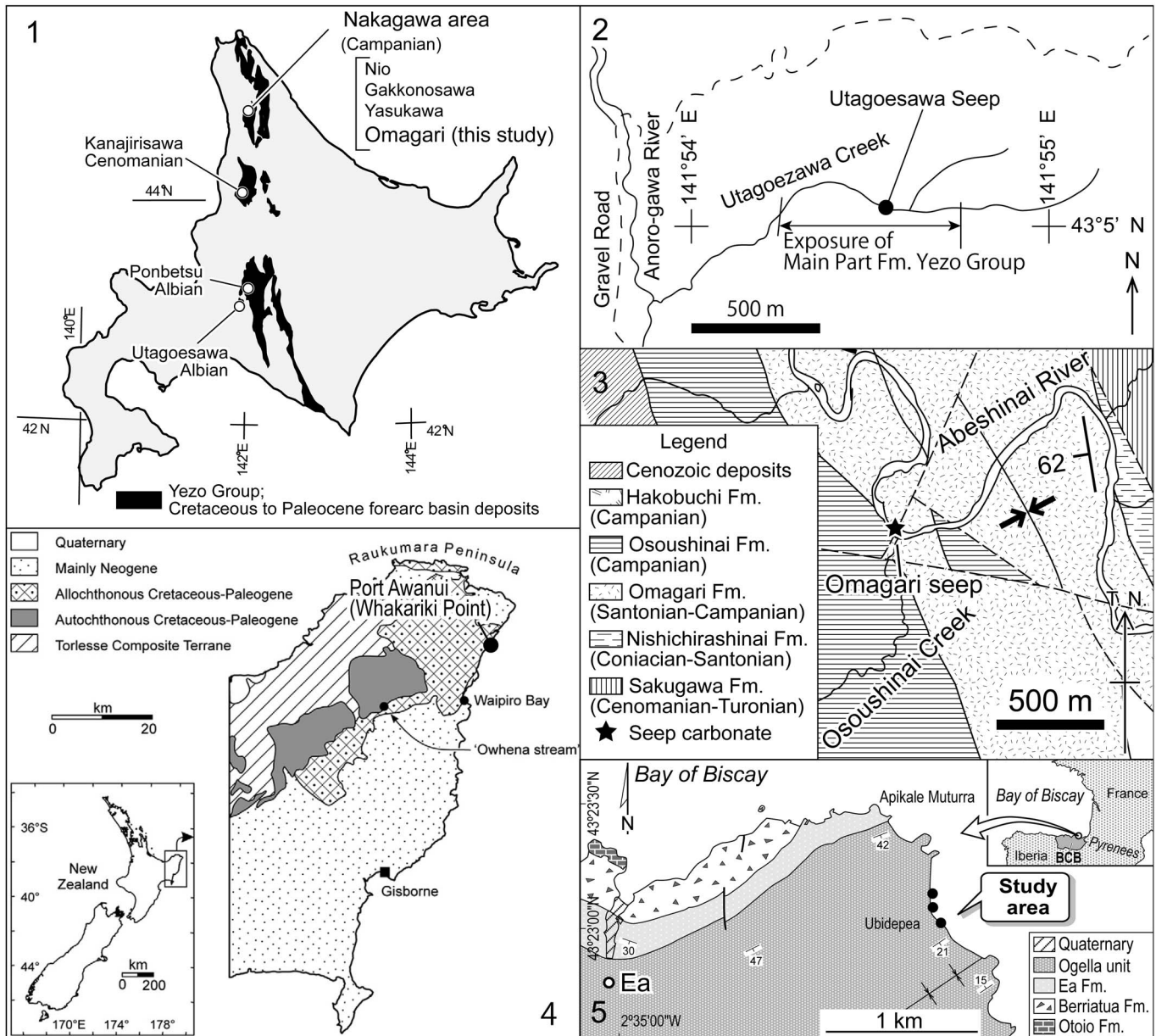


Figure 1. Maps showing the fossil localities of *Caspiconcha* described in the text. (1) Locality map of the Utagoesawa seep and the Omagari lens in Hokkaido, Japan. (2) Detailed map of the Utagoesawa Seep in Yubari City, Hokkaido, Japan. (3) Detailed map of the Omagari lens in Nakagawa area, Hokkaido, Japan. After Takahashi et al. (2003). (4) Locality map of the Raukumara Peninsula, northern New Zealand. After Kiel et al. (2013). (5) Locality map of Ispaster, Spain. After Agirrezabala et al. (2013).

Utagoesawa, Japan.—Large carbonate bodies crop out along the Utagoesawa Creek (also called Utagoshisawa Creek by local people) in Yubari City, central Hokkaido, Japan. The carbonate bodies are surrounded by late Albian (Early Cretaceous) muddy sediment of the Yezo Group. A detailed description of this locality is pending, but basic information was provided by Ogi-hara (2005) and Jenkins et al. (2013). The petrography of the carbonate bodies includes typical seep textures (e.g., isopachous radial carbonate cements and clotted fabrics), and those cements show a carbon isotope signature as low as -47‰ VPDB (Vienna Peedee belemnite), which clearly indicates seep origin.

Port Awanui, New Zealand.—Limestone boulders eroded from the well-exposed, calcareous mudstone unit that forms the shore

and is from within the undifferentiated Whangai–Wanstead formations float on the shore platform close to the headland of Whakariki Point at Port Awanui. Using stable carbon isotope, petrographic, and biomarker evidence, these limestone boulders were identified as ancient methane-seep deposits (Kiel et al., 2013). Most specimens described here as *Caspiconcha raukumaraensis* n. sp. are from locality Awanui GS688 (New Zealand Fossil Record File number FRF Z15/f7485) and are dated as mid-Cenomanian. A single specimen is from the locality Awanui II (FRF Z15/f82) dated as late Albian to mid-Cenomanian (Kiel et al., 2013).

Omagari seep site, Japan.—A ~10 m wide carbonate body is exposed as a small islet in the Abeshinai River near the mouth of its tributary, Osoushinai River, within strata of the Omagari

Formation, Yezeo Group, and dated as Campanian (Takahashi et al., 2003, 2007; Jenkins et al., 2007). It was identified as an ancient methane-seep deposit using stable carbon isotope, petrographic, and biomarker evidence (Hikida et al., 2003; Ogihara, 2005; Jenkins and Hikida, 2011). A single large bivalve from this deposit was previously identified as *Calyptogena* sp. (Hikida et al., 2003) and is here described as *Caspiconcha lastsamurai* n. sp.

Materials and methods

Most of the specimens described here were collected by the authors, and selected specimens were mechanically prepared. The comparative figured material of *C. whithami* Kelly in Kelly et al., 2000 and *C. major* (Gabb, 1869) is housed at the Sedgwick Museum, University of Cambridge, UK (SMUC) and the California Academy of Science (CAS), respectively.

Repositories and institutional abbreviations.—NMM, Nakagawa Museum of Natural History, Nakagawa Town, Hokkaido, Japan; NMNS, National Museum of Nature and Science, Tsukuba, Japan; NRM, Swedish Museum of Natural History, Department of Palaeobiology, Stockholm, Sweden; GNS, Geological and Nuclear Science, Lower Hutt, New Zealand; UMUT, University Museum, the University of Tokyo.

Systematic paleontology

Class Bivalvia Linnaeus, 1758
 Subclass Autobranchia Grobben, 1894
 Superorder Heteroconchia Gray, 1854
 Order Carditida Dall, 1889
 Superfamily Kalenteroidea Marwick, 1953
 Family Kalenteridae Marwick, 1953

Remarks.—Kalenterids were previously classified within the Pholadomyoidea (e.g., Waller, 1990; Fang and Morris, 1997; Kelly et al., 2000; Griffin and Pastorino, 2006), Palaeoheterodontia (Cox et al., 1969; Hautmann, 2001, 2008), or Carditida (e.g., Chavan, 1954, 1969; Newell, 1957, 1969; Neveeskaja, 2009). Here we follow the interpretation of Kaim and Schneider (2012) who placed the kalenterids among the Carditida based on the presence of complex cross-lamellar shell microstructure and the lack of a nacreous layer in two genera of kalenterids: *Caspiconcha* (Jenkins et al., 2013) and *Myoconcha* J. Sowerby, 1824 (Kaim and Schneider, 2012).

Genus *Caspiconcha* Kelly in Kelly et al., 2000

Type species.—*Caspiconcha whithami* Kelly in Kelly et al., 2000; Early Cretaceous (late Barremian), NE Greenland.

Occurrence.—Tithonian (Late Jurassic) to Campanian (Late Cretaceous). Barremian of Greenland, Tithonian to Albian of California, Hauterivian of Crimea and possibly Czech Republic, Albian of Basque Country, Spain, Albian–Cenomanian of New Zealand, and Albian and Campanian of Hokkaido, Japan.

Remarks.—Due to its similarity to *Myoconcha* regarding the modioliform shape, deeply set anterior adductor muscle scars

with myophoric buttress, and extreme reduction of the anterior side of the shell, Kelly et al. (2000) placed *Caspiconcha* among the Modiomorphidae, subfamily Myoconchidae. Later, Myoconchidae/Myoconchinae have been synonymized with Kalenteridae (Damborenea, 2004; Bouchet et al., 2010; Jenkins et al., 2013), and subsequently *Caspiconcha* is here classified in Kalenteridae. *Caspiconcha* differs from *Myoconcha* by lacking external radial ornament and by possessing an edentulous hinge and a caspiconchiid process.

The nominal species are *Caspiconcha whithami* Kelly in Kelly et al., 2000 from the Barremian of Greenland (Kelly et al., 2000), *C. rubani* Kiel, Campbell, and Gaillard, 2010 from the late Berriasian of the Crimean Peninsula (Kiel and Peckmann, 2008; Kiel et al., 2010), *C. major* (Gabb, 1869) from Tithonian to Albian localities in the Great Valley Group in California (Stanton, 1895; Kiel et al., 2008; Jenkins et al., 2013), and the new species *C. basquensis* n. sp. from the late Albian of northern Spain, *C. yubariensis* n. sp. from the late Albian of Utagesawa seep, central Hokkaido, Japan, *C. raukumaraensis* n. sp. from the late Albian to mid-Cenomanian of New Zealand, and *C. lastsamurai* n. sp. from the Campanian of the Omagari seep, northern Hokkaido. Illustrations with indication of selected key characters of all nominal species, including the four new species described herein, are in Figure 2. In addition, '*Myoconcha* aff. *transatlantica*' from the Early Cretaceous (Hauterivian) of the Czech Carpathians (Ascher, 1906) is most likely a species of *Caspiconcha* (Kiel and Peckmann, 2008; Kaim, et al., 2013). A specimen possibly belonging to *Caspiconcha* was found in a Santonian (Late Cretaceous) debris flow deposit in Amakusa, southwestern Japan (N. Kikuchi and Y. Kondo, Kochi University, personal communication, 2012); it reaches nearly 300 mm in length and has a broad, modioliform outline, but no internal shell features were observed.

Caspiconcha basquensis new species

Figure 3

2013 *Caspiconcha* sp. Agirrezabala et al., p. 102, fig. 16C, D.

Holotype.—NRM Mo 182801.

Paratypes.—NRM Mo 182802, 182803, and six unnumbered, fragmentary specimens.

Diagnosis.—Modioliform shell with strong anteroposterior elongation; nearly straight dorsal and ventral margin, broad ridge from the umbo to the posteroventral margin; no triangular depression runs below the ridge; moderately deep-set anterior adductor muscle scar.

Occurrence.—Seep carbonates in Ubidepea mudstone (informal subunit; late Albian), Ogalla unit, Black Flysch Group exposed along the shore between the villages Ea and Ispaster, west of Lekaitio, Basque country, northern Spain.

Description.—Shells elongate modioliform, up to 210 mm long, dorsal and ventral sides nearly straight; umbo subterminal, prosogyrate, very low, pointed; inflation moderate, greatest along a broad ridge from the umbo to the posteroventral margin,

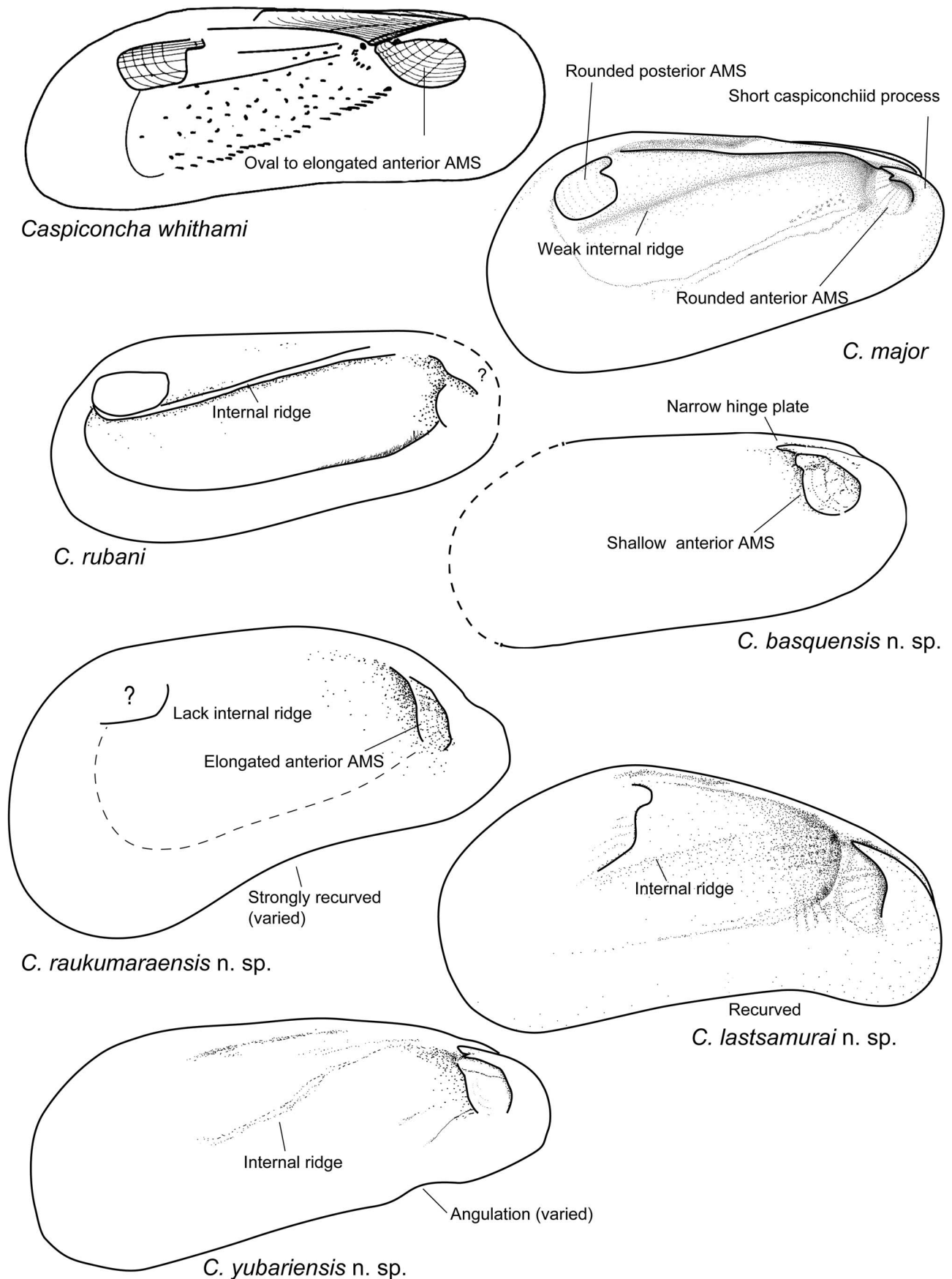


Figure 2. Schematic illustrations of all nominal *Caspiconcha* species with indications of selected key characters. AMS = adductor muscle scar. After Kelly et al. (2000) and Kiel et al. (2010) for illustrations of *C. whithami* and *C. rubani*, respectively.



Figure 3. *Caspiconcha basquensis* new species from Albian seep carbonates exposed along the shoreline between the villages Ea and Ispaster, west of Lekaitio, Basque country, in northern Spain. (1–4) Holotype (NRM Mo 182801), specimen with partially preserved shell; anterior part of right valve broken away, showing mold of anterior adductor muscle scar; (1) right valve; (2) dorsal view; (3) anterior view; (4) close-up of anterior end. (5) Paratype (NRM Mo 182802), small specimen with well-preserved shell. (6) Paratype (NRM Mo 182803), rubber cast of anterior side of specimen, showing adductor and pedal retractor scars (from Agirrezabala et al., 2013).

no triangular depression below ridge; surface with fine, irregular growth increments. Interior of shell with broad ridge and several fine striations from umbo to posterior end. Anterior adductor muscle scar oval, anteroposteriorly elongated, moderately impressed, deepest at anterodorsal side; curved, commarginal growth increments pointing toward the posterior on entire scar, crossed by fine, perpendicular striations; pedal retractor scar elongate trapezoid, directly adjacent posterodorsally to anterior adductor scar, separated by indistinct ridge; pedal elevator muscle scar elongate oval with longitudinal striations,

positioned posterior of pedal retractor scar, separated from it by strong ridge. Myophoric buttress indistinct; caspiconchiid process present; hinge plate narrow, edentulous.

Etymology.—For the Basque country, Spain, where the type locality is located.

Remarks.—*Caspiconcha basquensis* n. sp. is similar to the type species *C. whitthami* in being straight and elongate and having an anteroposteriorly elongated oval anterior adductor muscle

scar, but differs by having a narrow hinge plate and a more pointed anterior shell; *C. whithami* has a broad hinge plate and a broad anterior shell. The more pointed anterior side also distinguishes *Caspiconcha basquensis* from the similarly straight and elongate species *C. rubani*. *Caspiconcha basquensis* differs from all other known species of *Caspiconcha* by having a shallower anterior adductor muscle scar.

Caspiconcha yubariensis new species
Figure 4

2013 *Caspiconcha* sp. Jenkins et al., p. 371, fig. 11.

Holotype.—Best preserved specimen (NMNS PM27843).

Paratypes.—NMNS PM25523-25525, 27837-27842.

Diagnosis.—Shell modioliform to subtrapezoidal; strong ridge from the umbo to posteroventral margin, relatively narrow but clear depression runs below the ridge; varied angulation in anteroventral area especially in adult specimen; deep-set anterior muscle scar; strong internal ridge.

Occurrence.—Utagesawa seep site in late Albian (Early Cretaceous) deposit of 'main part formation,' Yezo Group exposed along the Utagesawa Creek, Yubari City, Hokkaido, Japan.

Description.—The shell large, up to 247 mm (NMNS PM25523); modioliform to subtrapezoidal, equivalve, strongly inequilateral, strong inflation in the dorsal part of the central flank running obliquely toward posterior part of the ventral margin, relatively well-developed triangular depression runs from the umbonal area widening toward the mid flank; dorsal margin slightly curved along its whole extent, posterior margin rounded, angulation of shell shape in anteroventral part, strength of angulation varies among species; umbones close to the anterior end, situated at, or slightly below, the hinge line; shell thick, especially in the anterior part; exterior ornament consists of commarginal growth lines, more pronounced on the shell anterior; shell interior generally smooth, large elongated anterior adductor muscle scar bordered posteriorly by a stout myophoric buttress, strong oblique ridge running from umbonal area toward posterodorsal area, probable posterior adductor muscle scar situated just above the oblique ridge in posterodorsal area; hinge stout with very long ligament groove.

Etymology.—For Yubari City, from the type area of the species.

Remarks.—Angulation of the shell shape in anteroventral part varies among observed specimens; for example, adult specimens of NMNS PM25523 (Fig. 4), 27837 and 27839 have strong angulation, although juvenile (paratype NMNS PM27841, Fig. 4) and young (holotype NMNS PM27843, Fig. 4) specimens have very weak angulation. *Caspiconcha yubariensis* n. sp. is similar to the type species *C. whithami* in general shell shape, but differs by having a much stronger ridge and a relatively narrow and strong depression from the umbonal area toward the posteroventral area. *Caspiconcha yubariensis* is also similar to *C. raukumaraensis* n. sp. in general shell shape, but

C. raukumaraensis differs by its shallow myophoric buttress and the lack of internal ridge. *Caspiconcha yubariensis* differs from other known *Caspiconcha* species by having angular anteroventral margins.

Caspiconcha raukumaraensis new species
Figures 5, 6

2013 *Caspiconcha* sp. Kiel et al., p. 26, fig. 13D, E.

Holotype.—TM8832.

Paratypes.—TM8831 (anterior portion of right valve; L = 56.4 mm), TM9255 (anterior portion of left valve; L = 36 mm), TM92556-9 (total: 14 specimens from GS668, one from Awanui II)

Diagnosis.—Shells strongly recurved as adults, with broad triangular depression in mid flank; anterior adductor muscle scar subrectangular, anterodorsal side deeply impressed, and posteroventral side projected.

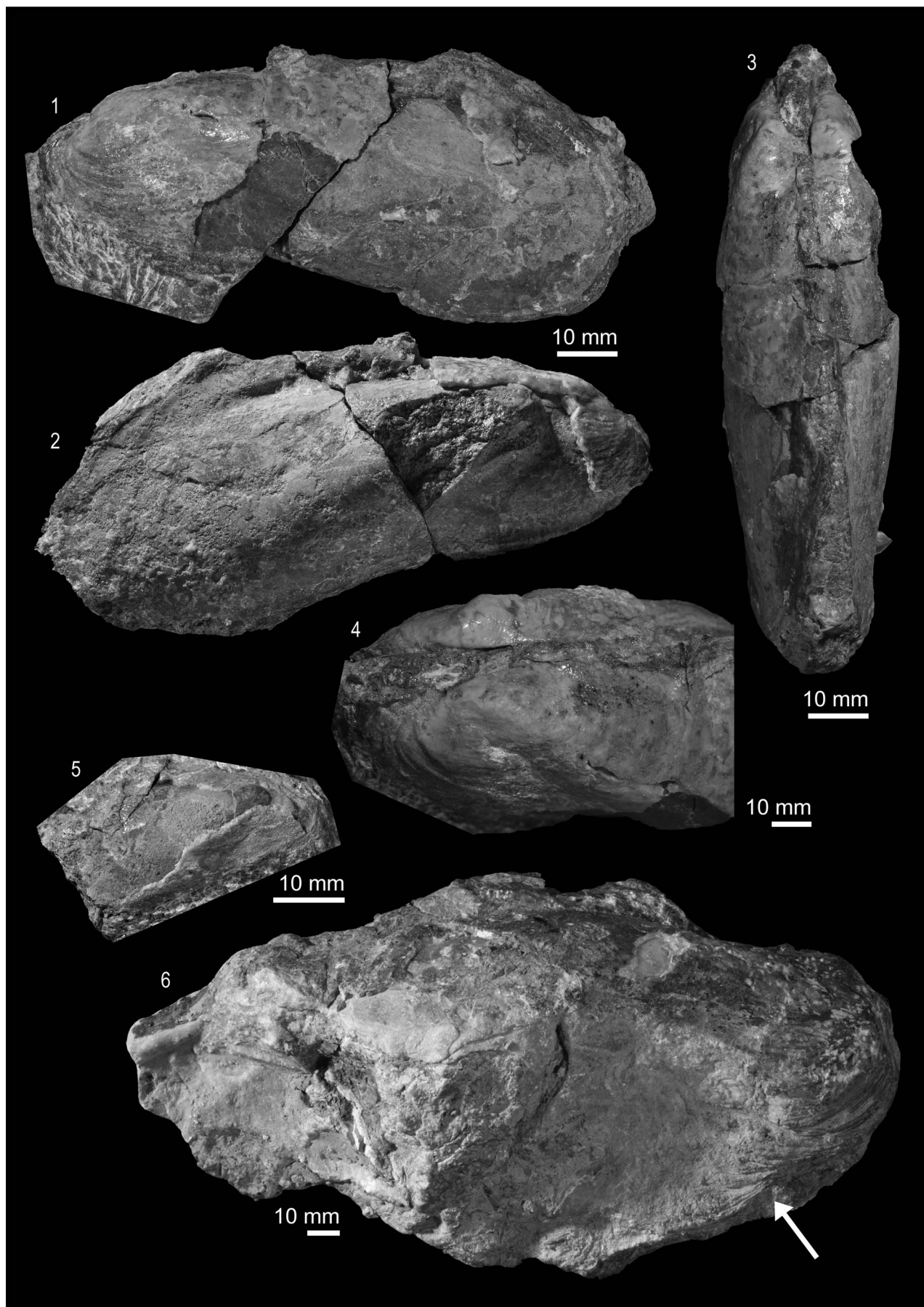
Occurrence.—Seep carbonates in undifferentiated Whangai-Wanstead formations, mid-Cenomanian at Port Awanui, North Island, New Zealand (FRF locality number Z15/f7485).

Description.—Shell recurved modioliform, up to 155 mm long; umbo subterminal, prosogyrate, very low; dorsal margin slightly to moderately curved with thick, external ligament; posterior margin broad, convex; ventral margin slightly concave; anterior margin short and blunt; shell inflated near umbo with curved, blunt ridge running toward the posteroventral margin, broad triangular depression below ridge; surface with rough, irregular growth increments.

Shell interior with numerous small pits above pallial line in posterior third of shell (mantle muscle scar area); faint, broad band running from umbo toward posterior end of shell; anterior adductor muscle scar subrectangular, slightly longer than high, ventral margin moderately convex, covered by commarginal growth increments, anterodorsal side deeply impressed; pedal retractor scar triangular, situated posterodorsal of adductor muscle scar and separated from it only by weak ridge. Myophoric buttress steep; caspiconchiid process present; hinge edentulous. Pallial line entire, indistinct, starting at posterior side of anterior adductor muscle scar, curved relative to ventral margin, posteriorly distant from shell margin, ending at posteroventral corner of posterior adductor muscle scar. Posterior adductor muscle scar weak, only known from a single small (42 mm long) specimen, elongate oval, parallel to posterodorsal shell margin, indistinct dorsally, ventrally with fine growth increments.

Etymology.—For the Raukumara Peninsula in northeastern New Zealand.

Remarks.—*Caspiconcha raukumaraensis* n. sp. is variable in shell shape, with nearly straight-sided specimens to recurved specimens. This variation may to some extent represent an ontogenetic change because all available small specimens are nearly straight-sided, while most, but not all, large specimens show curvature. At least in one specimen, the extreme concavity of the ventral margin appears to be due to an injury in this part of



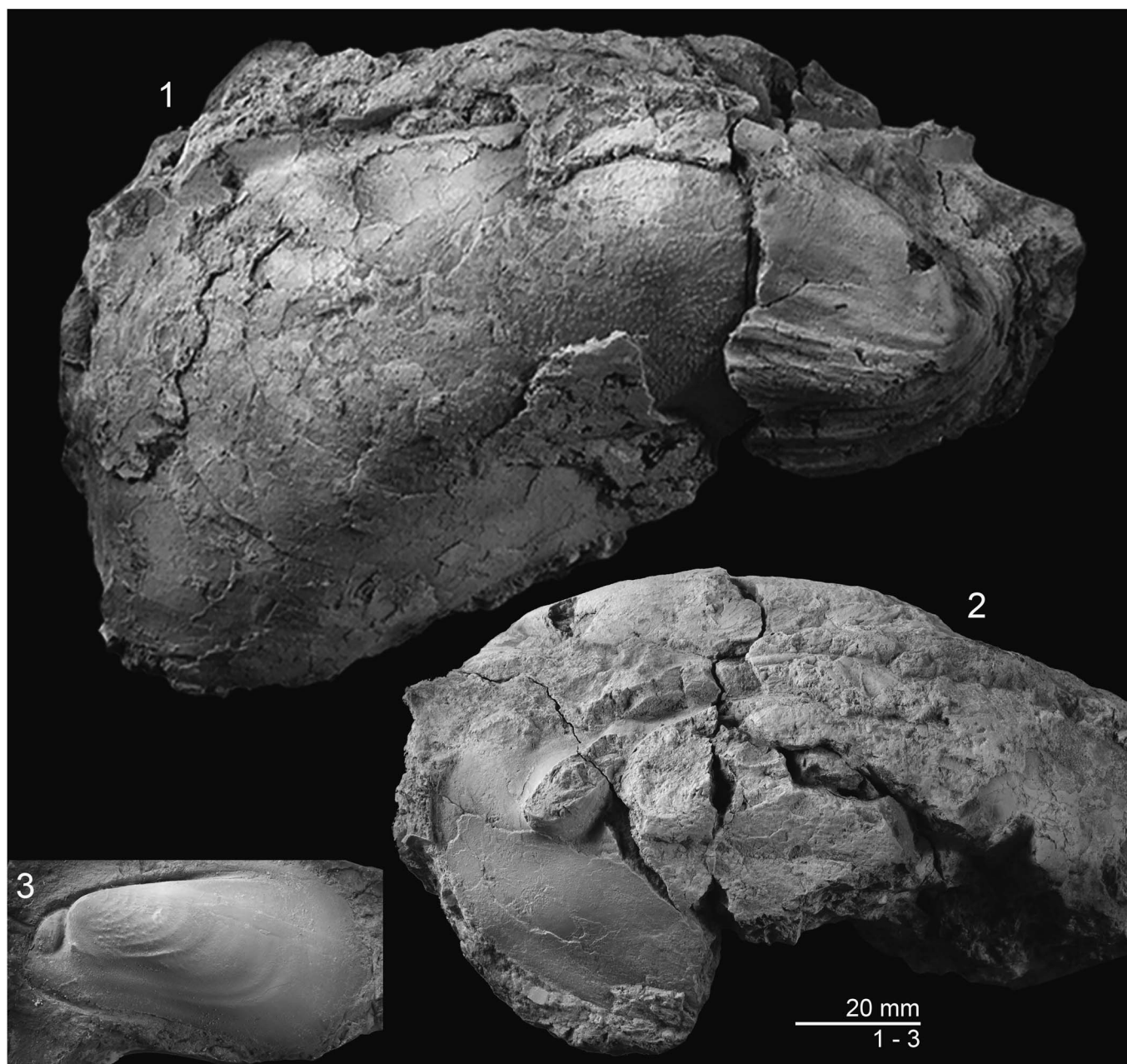


Figure 5. *Caspiconcha raukumaraensis* new species from Albian to Cenomanian seep carbonates at Port Awanui in New Zealand. (1, 2) Holotype (TM8832), semiarticulated specimen, right valve with partially preserved shell, internal mold of left valve showing anterior adductor muscle scar (fig. 1 from Kiel et al., 2013). (3) Paratype (TM9255), internal mold of left valve.

the shell. Two specimens of *Caspiconcha raukumaraensis* from the type locality are preserved in a way that the two shells are interlocking. This type of preservation has also been reported from *Caspiconcha basquensis* n. sp. (Agirrezabala et al., 2013).

Caspiconcha raukumaraensis differs from *C. major* mainly by its more rectangular anterior adductor muscle scar that is more elongate in an anterior–posterior direction. Unfortunately, the posterior adductor muscle scar of *Caspiconcha*

rauikumaraensis is known only from a single small specimen; therefore, these features cannot be compared with those other species. In addition, the Japanese *Caspiconcha lastsamurai* n. sp. reported herein differs from *Caspiconcha raukumaraensis* by having a larger, more rounded anterior adductor muscle scar. *Caspiconcha basquensis* n. sp. reaches larger sizes than *Caspiconcha raukumaraensis*, and all available specimens of *Caspiconcha basquensis* are very elongate and straight-sided.

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Figure 4. *Caspiconcha yubariensis* new species from late Albian seep carbonates in Utagoesawa Creek, northern Japan. (1–4) Holotype (NMNS PM27843), articulated specimen, most of shell of right valve peeled off, showing internal mold with myophoric buttress and partial anterior adductor muscle scar; (1) left valve; (2) right valve; (3) dorsal view; (4) oblique view, close-up of anterior part showing strong ridge and depression. (5) Paratype (NMNS PM27841), right valve of juvenile specimen. (6) Paratype (NMNS PM25523), right valve of articulated adult specimen, angulation in anteroventral area (arrow).

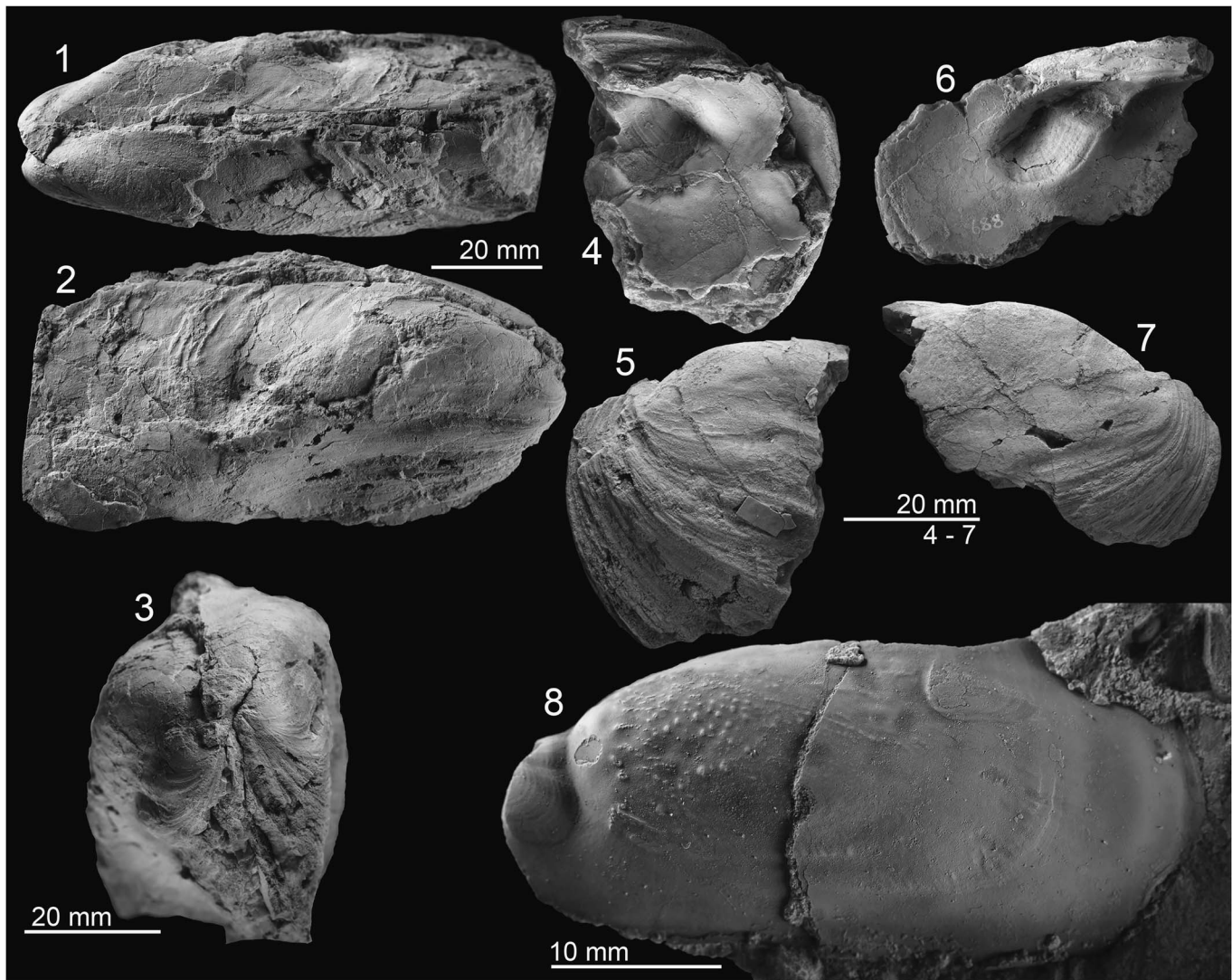


Figure 6. *Caspiconcha raukumaraensis* new species from Albian to Cenomanian seep carbonates in New Zealand. (1–3) Paratype (TM9256), articulated specimen; (1) view on dorsal side; (2) view on right valve; (3) view on anterior side. (4, 5) Anterior part of left valve (TM9257). (6, 7) Anterior part of right valve (TM9258) (fig. 6 from Kiel et al., 2013). (8) internal mold of small specimen (TM9259).

Caspiconcha lastsamurai new species
Figures 7–9

- 2003 *Calyptogena* sp. Hikida et al., p. 337, fig. 9–3.
2007 *Calyptogena* sp. Amano and Kiel, p. 228.
2008 *Calyptogena* sp. Kiel and Peckmann, p. 757.
2010 ‘*Calyptogena*’ sp. Kiel et al., p. 38.
2013 *Caspiconcha* sp.; Jenkins et al., p. 361, fig. 14.
2013 *Caspiconcha* sp.; Kiel et al., p. 26, table 1.

Holotype.—Internal mold of an articulated specimen (NMM-223); a cast of the type specimen is in the UMUT collection (UMUT MM 31127).

Diagnosis.—Shell strongly recurved with nearly straight dorsal margins and moderately curved ventral margin; weak internal ridge running from anterior pedal elevator muscle scar toward ventral margin of the posterior adductor muscle scar; elongated anterior adductor muscle scar deeply set.

Occurrence.—Omagari seep site, Omagari Formation, Yezo Group; Campanian, Upper Cretaceous exposed in Nakagawa Town, Hokkaido, Japan.

Description.—The description as follows is based on the single type specimen (NMM-223). The specimen is an internal mold with valves in occlusion, having very little shell substance adhering. Thus, we could observe only the internal features of this species. Shell large, strongly recurved with moderately concave ventral and nearly straight dorsal margins; equivalved, strongly inequilateral, moderately inflated in the anterior close to the umbones; dorsal margin straight in lateral profile for the full extent of the nymph and ligament area and then curved ventrally at the posterodorsal area; posterior margin well rounded; ventral margin moderately concave especially at one-third length from the anterior; anterior margin short and rounded; shell moderately inflated in dorsal aspect with wedge shape in both anterior and posterior margin, triangular depression running from the umbonal area widening toward the mid flank. Shell interior smooth apart from muscle scars, pallial line

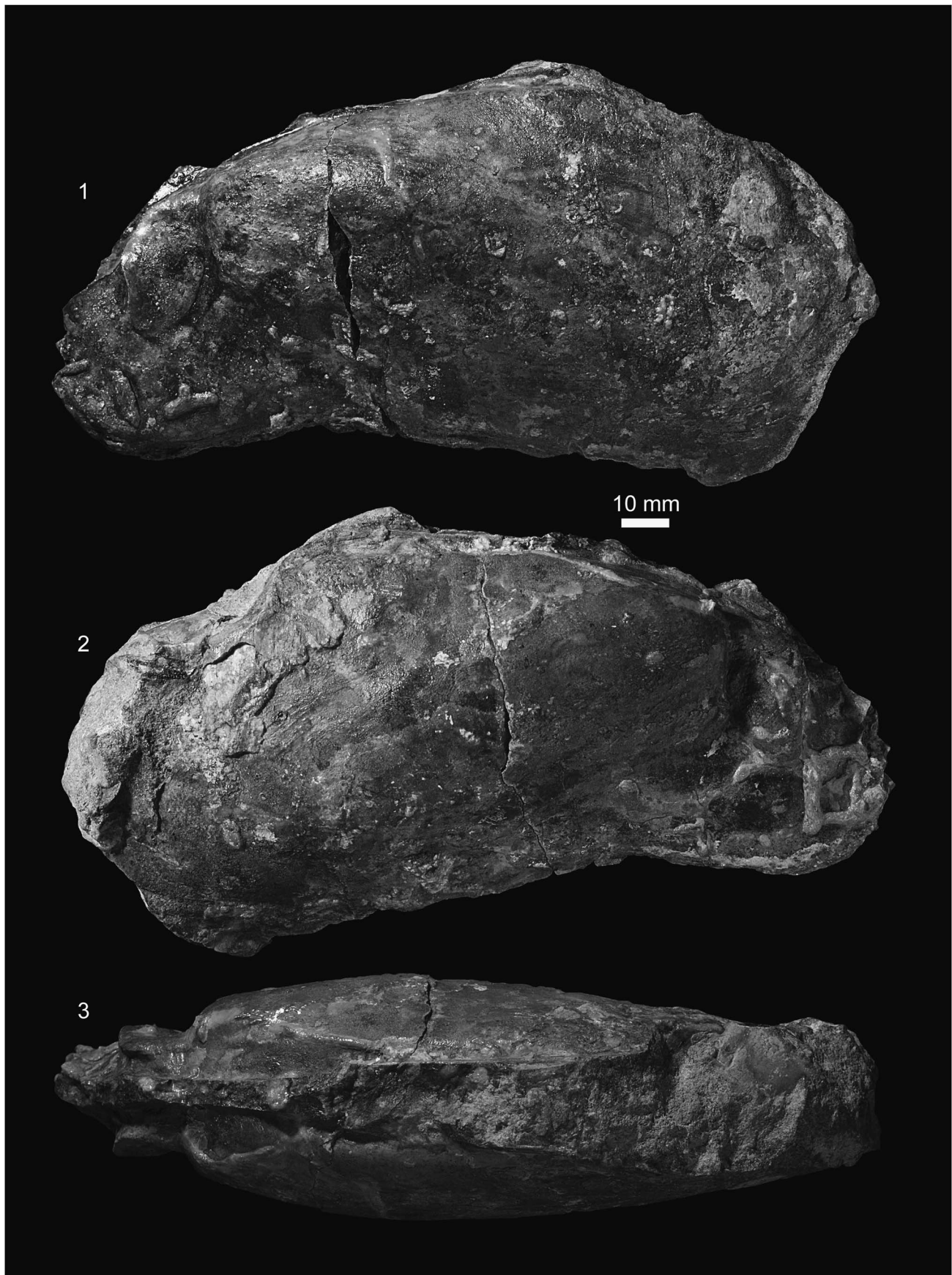


Figure 7. *Caspiconcha lastsamurai* new species from Campanian Omagari seep carbonate in northern Japan. (1–3) Holotype (NM-223), articulated specimen, almost no shell material remained; (1) left valve; (2) right valve; (3) dorsal view.

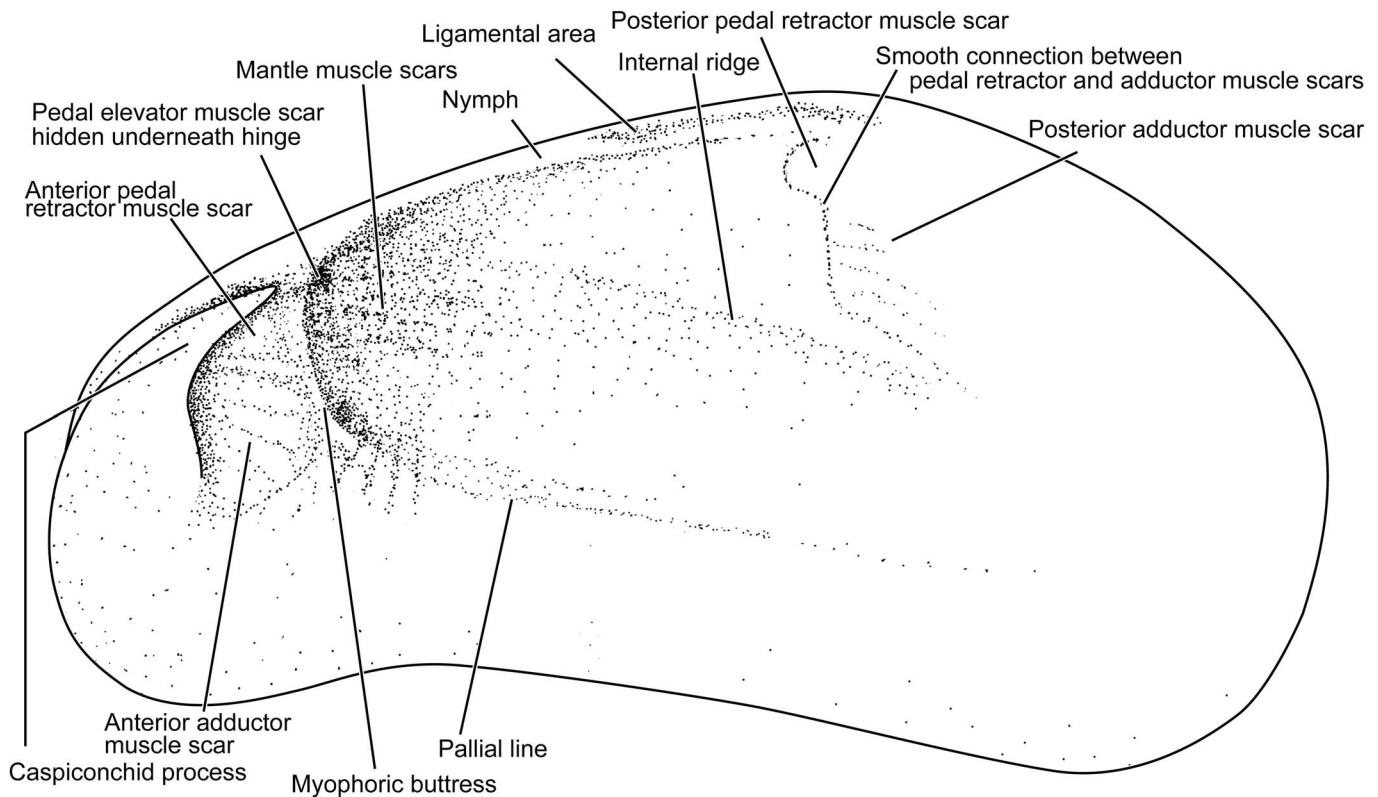


Figure 8. Schematic illustration of the right valve internal features of *Caspiconcha lastsamurai* new species from Omagari seep, northern Japan.

invisible; anterior adductor muscle scar elliptically rounded with pedal elevator muscle scars located dorsally; posterior adductor muscle scar is trapezoidal with dorsally located narrow posterior pedal retractor muscle scar projected anteriorly; connection between posterior pedal retractor muscle scar and posterior adductor muscle scar forms smoothly curved line (Figs. 7, 8); weak internal ridge running from anterior pedal elevator muscle scar toward ventral margin of the posterior adductor muscle scar; myophoric buttress moderately steep. Hinge area not perfectly preserved, apparently edentulous; caspiconchiid process present; nymph and ligament groove very long and straight.

Etymology.—The species is the last known occurrence of the genus and it was found in Japan. We coined the species name after Hollywood motion picture ‘The Last Samurai,’ 2003 © Warner Brothers.

Remarks.—*Caspiconcha lastsamurai* n. sp. was first reported as *Calypptogena* sp. based on its general shell shape (Hikida et al., 2003). This identification was subsequently questioned and instead affinities to *Caspiconcha* were suggested (Amano and Kiel, 2007; Kiel and Peckmann, 2008; Kiel et al., 2010; Jenkins et al., 2013). *Caspiconcha lastsamurai* differs from other *Caspiconcha* species (i.e., *C. whithami*, *C. rubani*, *C. basquensis*, and *C. major*) in having a strongly recurved shell, trapezoidal posterior adductor muscle scar, and smoothly curved connection line between posterior pedal retractor muscle scar and the posterior adductor muscle scar (Fig. 9). *Caspiconcha lastsamurai* n. sp. differs from *Caspiconcha raukumaraensis* n. sp. from New Zealand (Kiel et al., 2013) by

having a less recurved shell shape and an almost straight dorsal margin. *Caspiconcha lastsamurai* differs from *C. basquensis* n. sp. from Spain (Agirrezabala et al., 2013) by its strongly curved shell and its deeper anterior adductor muscle scar.

Discussion

History of Caspiconcha.—We demonstrate the currently known stratigraphic range of *Caspiconcha* from Tithonian to Campanian in Figure 10. The fossil record of *Caspiconcha* consists of seven nominal species and one uncertain species from Santonian (Upper Cretaceous) deposit of Amakusa area in Kyushu, Japan. *Caspiconcha* first appeared with *C. major* in the latest Jurassic (Tithonian) in the eastern Pacific, and shortly afterward the first Tethyan species, *C. rubani*, appeared in the earliest Cretaceous (Berriasian). Two further species appeared in the Barremian and Hauterivian. The diversity reached a peak in the Albian with four species distributed worldwide. Afterward, the genus seems to have declined in diversity and local abundance. The mid-Cenomanian seep site at Port Awanui, New Zealand, was the last seep deposit dominated by a species of *Caspiconcha* (*C. raukumaraensis*); the remaining Late Cretaceous records are single occurrences, including the youngest species, the Campanian *C. lastsamurai*. This fading abundance of *Caspiconcha* seems to be a real phenomenon rather than sampling bias because several well-investigated Late Cretaceous seep deposits exist and no additional specimens of *Caspiconcha* have been recovered up to now. Although Maastrichtian (Late Cretaceous) seeps are extremely rare at this moment, there is a newly found Campanian-Maastrichtian seep in Alaska (unpublished data, RGJ and AK, 2007) and there are

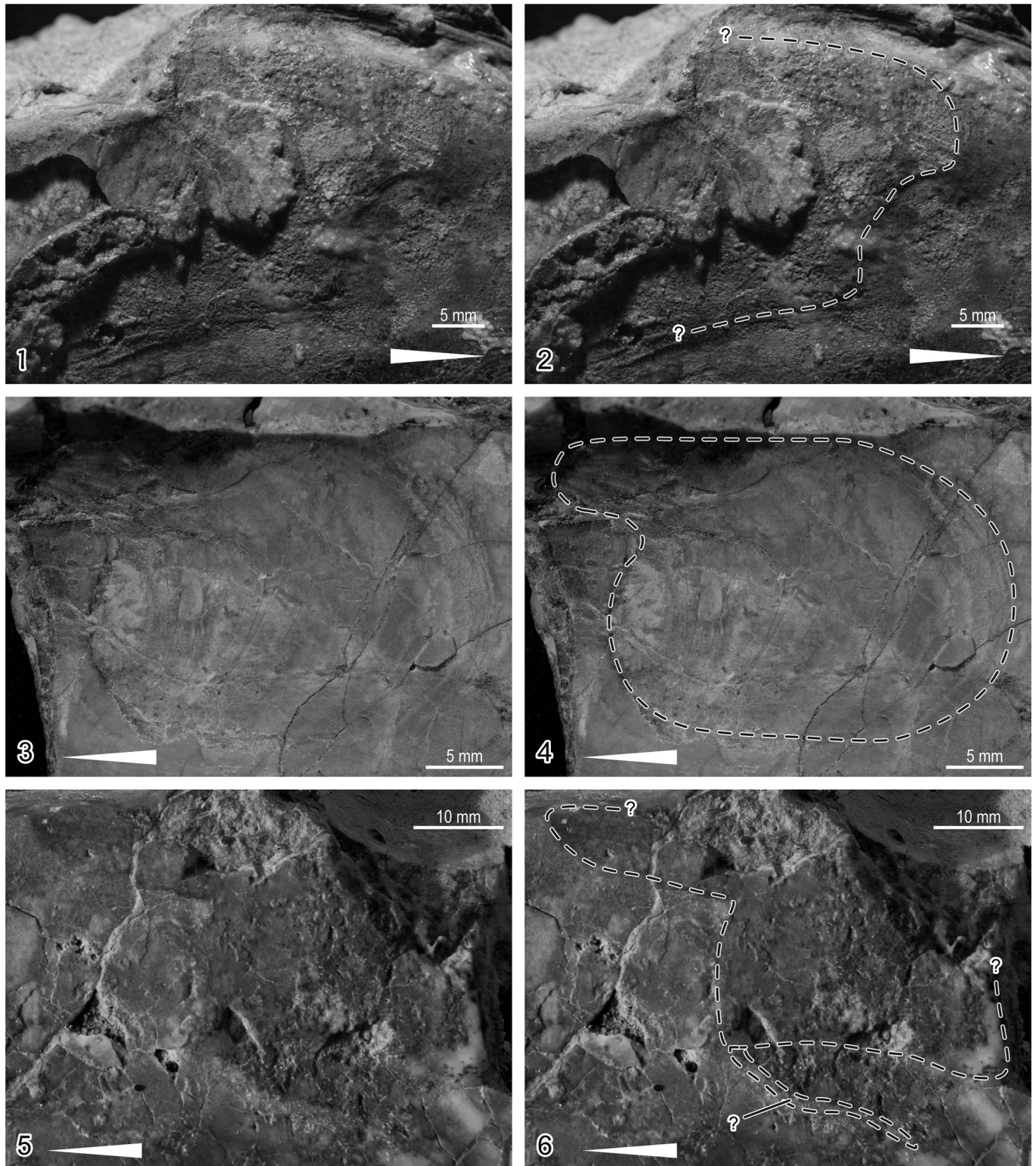


Figure 9. Photographs of posterior adductor muscle scars of some *Caspiconcha* species. (1, 2) *C. lastsamurai* new species from Omagari seep, northern Japan, mold of right valve. (3, 4) *C. major* (Gabb, 1869) CAS 72527–9, right valve. (5, 6) *C. whitami* Kelly in Kelley et al., 2000 CASP K9276 (SMUC number X30009), left valve. (1, 3, 5) Photographs only; (2, 4, 6) Photographs with explanatory drawing. Arrowheads indicate the shell anterior.

Maastrichtian seeps in Antarctica (Little et al., 2015). Why did this once successful bivalve genus slowly disappear from seep habitats during the Late Cretaceous? No obvious competitor for its ecological niche appeared in that time. The epifaunal and semi-

infaunal bivalves (i.e., bathymodiolin and vesicomid bivalves) that dominate modern seep environments did not appear in the geologic record before the mid-Eocene (Amano and Kiel, 2007; Kiel and Amano, 2013). One possible reason could be the

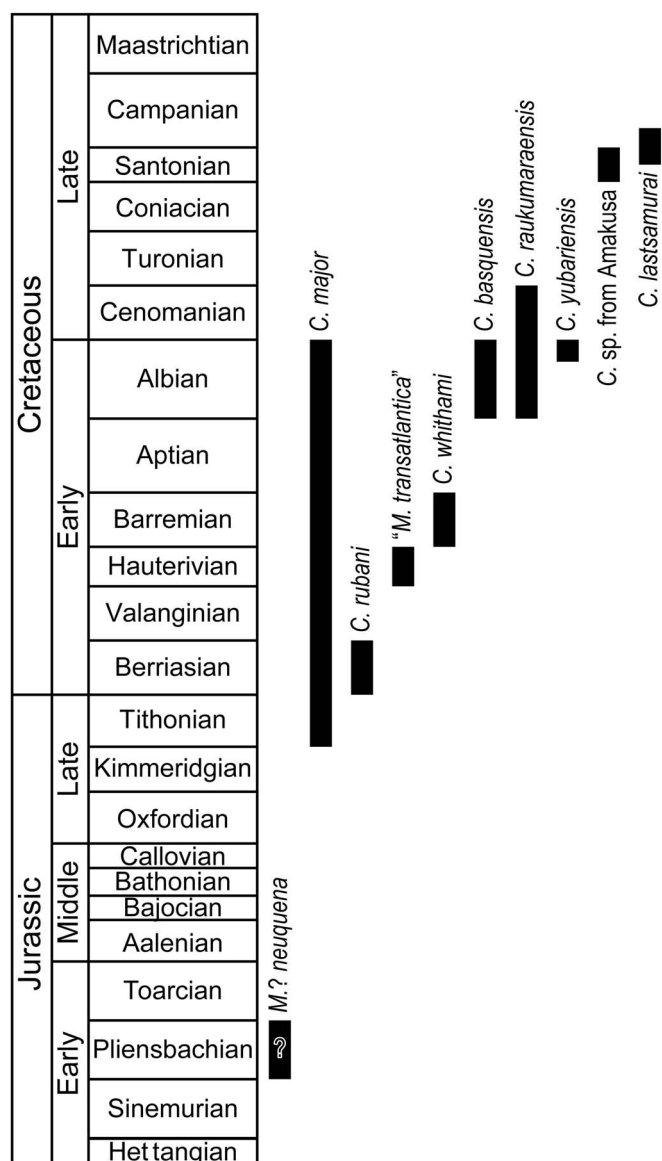


Figure 10. Range chart of *Caspiconcha* species and relatives; note the highest diversity in the Albian.

decrease in sulfide release at methane seeps after the mid-Cretaceous drop in marine sulfate concentrations; fewer sulfides would mean less food for the presumed sulfur-oxidizing symbionts of *Caspiconcha* (Kiel, 2015). An additional or alternative explanation is offered by Hryniewicz et al. (2017b): the decline of *Caspiconcha* coincides with the appearance of large thyasirid bivalves at methane seeps. These infaunal bivalves could potentially have mined the available sulfide produced deep in the sediment so that very little sulfide reached the upper sediment layers that *Caspiconcha* was able to penetrate (Hryniewicz et al., 2017b).

History of seep-inhabiting kalenterids/modiomorphids.—The apparent origin of *Caspiconcha* in the latest Jurassic should be treated cautiously because the fossil record of seep deposits before the late Jurassic is scarce (Campbell, 2006). A possible Early Jurassic species belonging to *Caspiconcha* is *Myoconcha neuquena* Leanza 1940 from the Early Jurassic of Argentina.

Judging from the descriptions and figures of Leanza (1940) and Griffin and Pastorino (2006) and preliminary observations by RGJ and AK, *M. neuquena* possesses an edentulous hinge and a caspiconchiid process, suggesting affiliation to the genus *Caspiconcha*. However, we need further investigations to confirm its taxonomy. Several bivalves found at even older vent and seep deposits were considered as belonging to the modiomorphids and may thus be related to *Caspiconcha* as well. These include a species from a Late Triassic seep deposit in Oregon (Peckmann et al., 2011), large modiomorphid bivalves from Late Triassic seeps in Turkey (Kiel et al., 2017), the large and elongate *Ataviaconcha wendti* Hryniewicz et al., 2017a found in Devonian and Silurian seep deposits in Morocco (Aitken et al., 2002; Hryniewicz et al., 2017a; Jakubowicz et al., 2017), and *Sibaya ivanovi* Little et al., 1999 from a Devonian vent locality in the Ural mountains, Russia (Little et al., 1999). This recurrence of modiomorphid/kalenterid-like bivalves at vent and seep deposits from Silurian through Cretaceous time may imply either that modiomorphid/kalenterid bivalves have repeatedly colonized these environments through Earth's history, or that *Caspiconcha* is the last member of a long-lived vent- and seep-inhabiting lineage among the kalenterids. Whatever the exact relationships among these bivalves are, it remains intriguing that the dimerelloid brachiopods colonized seep (and vent) environments throughout roughly the same time interval, and disappeared just slightly earlier, in the mid-Hauterivian (Early Cretaceous) (Kiel et al., 2014). If *Caspiconcha* and its relatives were indeed chemosymbiotic (cf. Kelly et al., 2000; Jenkins et al., 2013), the apparent long coexistence of dimerelloid brachiopods and chemosymbiotic bivalves contradicts the hypothesis that brachiopods were pushed out of the vent/seep environment by chemosymbiotic bivalves through competitive replacement (cf. Campbell and Bottjer, 1995b).

Implications for the modern chemosynthetic fauna.—There was a considerable confusion about the origin of the vesicomimid bivalves because molecular age estimates indicated an early Cenozoic origin, although three vesicomimid species from Cretaceous sediments in Hokkaido, Japan, were known from the paleontological literature (e.g., Little and Vrijenhoek, 2003; Kiel and Little, 2006). The first to question the vesicomimid affinities of these species were Amano and Kiel (2007), and two of the species were subsequently identified as members of different bivalve families: '*Calyptogena*' sp. from the Albian Ponbetsu seep deposit (Kanie et al., 1993) was described by Kiel et al. (2008) as the solemyid *Acharax mikasaensis* Kiel, Amano, and Jenkins, 2008, and *Vesicomya inflata* Kanie and Nishida, 2000 from large Cenomanian concretions in the Horokonai area (Kanie and Nishida, 2000; Kanie et al., 2000) was redescribed as type species of the new lucinid genus *Ezolucina* Amano et al., 2008. The last of the three alleged Cretaceous vesicomimids, '*Calyptogena*' sp. from the Omagari seep deposit (Hikida et al., 2003) is here described as *Caspiconcha lastsamurai* n. sp. Thus, all three Cretaceous 'vesicomimids' were clearly misidentified and the oldest confirmed fossil occurrence of the Vesicomimidae is *Archivesica* cf. *A. tschudi* (Olsson, 1931) from the Eocene of Washington State, USA (Amano and Kiel, 2007), although subsequent work suggested that it belongs to a different vesicomimid genus (Amano and Kiel, 2012; Amano et al., 2014).

Conclusions

We formally described four new species of seep-restricted genus *Caspiconcha* from late Albian to early Campanian of Spain, New Zealand, and Japan. The augmented fossil record clearly shows that *Caspiconcha* reached its highest diversity and broadest distribution in the Albian, followed by a decrease in diversity, abundance, and geographic range. In the Late Cretaceous, only two species of *Caspiconcha* are known and are geographically restricted to the western Pacific (New Zealand and Japan). The New Zealand record marks the last abundant occurrence of *Caspiconcha*, and so far, only one species of *Caspiconcha* is known to have survived until the Campanian. With the identification of ‘*Calyptogena*’ sp. of Hikida et al. (2003) as a new species of *Caspiconcha*, the alleged last Cretaceous record of the family Vesicomidae has been dismissed.

Acknowledgments

We thank two anonymous referees and editors of the journal for their constructive and helpful comments. RGJ thanks Y. Miyajima (Kyoto University) and K. Sato for helping with fieldwork in Japan; RGJ and AK thank S. Kelly (CASP, University of Cambridge, UK) for access to Greenland *Caspiconcha* collection in Sedgwick Museum; and SK thanks L. Agirrezabala (Universidad del País Vasco, Spain) and J.S. Crampton (GNS Science, New Zealand) for making the fieldwork in Spain and New Zealand possible and enjoyable, and G. Hundertmark (Göttingen) for photography. The research of RGJ was supported by JSPS KAKENHI Grant Number 26287131, 26400500, and 16H05740 and Grant for Program to Disseminate Tenure Tracking System (JST); AK was supported by the research grant no. 2012/07/B/ST10/04189 from National Science Centre, Poland; and SK was supported by the Deutsche Forschungsgemeinschaft through grant Ki802/6-1.

References

- Agirrezabala, L.M., Kiel, S., Blumenberg, M., Schäfer, N., and Reitner, J., 2013, Outcrop analogues of pockmarks and associated methane-seep carbonates: A case study from the Lower Cretaceous (Albian) of the Basque–Cantabrian Basin, western Pyrenees: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 390, p. 94–115.
- Aitken, S.A., Henderson, C.M., Collom, C.J., and Johnston, P.A., 2002, Stratigraphy, paleoecology, and origin of Lower Devonian (Emsian) carbonate mud buildups, Hamar Laghdad, eastern Anti-Atlas, Morocco, Africa: *Bulletin of Canadian Petroleum Geology*, v. 50, p. 217–243.
- Amano, K., and Kiel, S., 2007, Fossil vesicomid bivalves from the North Pacific region: *Veliger*, v. 49, p. 270–293.
- Amano, K., and Kiel, S., 2012, Two Neogene vesicomid species (Bivalvia) from Japan and their biogeographic implications: *Nautilus-Sanibel*, v. 126, p. 79.
- Amano, K., Jenkins, R.G., Kurihara, Y., and Kiel, S., 2008, A new genus for *Vesicomya inflata* Kanie & Nishida, a Lucinid Shell Convergent with that of Vesicomids, from Cretaceous Strata of Hokkaido, Japan: *Veliger*, v. 50, p. 255–262.
- Amano, K., Jenkins, R.G., Ohara, M., and Kiel, S., 2014, Miocene vesicomid species (Bivalvia) from Wakayama in southern Honshu, Japan: *The Nautilus*, v. 128, p. 9–17.
- Ascher, E., 1906, Die Gastropoden, Bivalven und Brachiopoden der Groditscher Schichten: Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, v. 19, p. 135–167.
- Bouchet, P., Rocroi, J.P., Bieler, R., Carter, J.G., and Coan, E.V., 2010, Nomenclator of bivalve families with a classification of bivalve families: *Malacologia*, v. 52, p. 4–172.
- Campbell, K.A., 2006, Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: Past developments and future research directions: *Palaeogeography Palaeoclimatology Palaeoecology*, v. 232, p. 362–407.
- Campbell, K.A., and Bottjer, D.J., 1995a, Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold seep environments: *Geology*, v. 23, p. 321–324.
- Campbell, K.A., and Bottjer, D.J., 1995b, *Peregrinella*: An Early Cretaceous cold-seep-restricted brachiopod: *Paleobiology*, v. 21, p. 461–478.
- Chavan, A., 1954, Les *Pleurophorus* et genres voisins: *Cahiers Géologiques Seyssel*, v. 22, p. 200.
- Chavan, A., 1969, Superfamily Carditacea. Part N, Mollusca 6, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology*: Lawrence, Geological Society of America and University of Kansas Press, p. N543–N548.
- Cox, L.R., et al., 1969, Mollusca 6: Bivalvia, Lawrence, Geological Society of America and University of Kansas Press, *Treatise on Invertebrate Paleontology*, 489 p.
- Dall, W.H., 1889, On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group: *American Journal of Science*, series 3, v. 38, p. 445–462.
- Damborenea, S.E., 2004, Early Jurassic *Kalentera* (Bivalvia) from Argentina and its palaeobiogeographical significance: *Ameghiniana*, v. 41, p. 185–198.
- Fang, Z.-j., and Morris, N.J., 1997, The genus *Pseudosanguinolites* and some modioliform bivalves (mainly Paleozoic): *Palaeoworld*, v. 7, p. 49–74.
- Gabb, W., 1869, Cretaceous Fossils: *Palaeontology of California*, v. 2, section 2, pt. 1, p. 125–205.
- Goedert, J.L., and Kaler, K.L., 1996, A new species of *Abyssochrysois* (Gastropoda: Loxonematoidea) from a middle Eocene cold-seep carbonate in the Humpulips Formation, western Washington: *The Veliger*, v. 39, p. 65–70.
- Gray, J.E., 1854, A revision of the arrangement of the families of bivalve shells (Conchifera): *Annals and Magazine of Natural History*, series 2, v. 13, p. 408–418.
- Griffin, M., and Pastorino, G., 2006, *Madrynomys bruneti* n. gen. and sp. (Bivalvia: ?Modiomorphidae): A Mesozoic survivor in the Tertiary of Patagonia?: *Journal of Paleontology*, v. 80, p. 272–282.
- Grobben, K., 1894, Zur Kenntnis der Morphologie, der Verwandtschaftsverhältnisse und des Systems der Mollusken: *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe*, v. 103, p. 61–86.
- Hautmann, M., 2001, Die Muschelfauna der Nayband-Formation (Obertrias, Nor-Rhät) des östlichen Zentraliran: *Beringeria*, v. 29, p. 1–181.
- Hautmann, M., 2008, Taxonomy and phylogeny of the Triassic bivalve families Mysidiellidae Cox, 1964 and Healeyidae new family: *Journal of Paleontology*, v. 82, p. 555–564.
- Hikida, Y., Suzuki, S., Togo, Y., and Ijiri, A., 2003, An exceptionally well-preserved fossil seep community from the Cretaceous Yezo Group in the Nakagawa area, Hokkaido: *Paleontological Research*, v. 7, p. 329–342.
- Hryniewicz, K., Jakubowicz, M., Belka, Z., Dopieralska, J., and Kaim, A., 2017a, New bivalves from a Middle Devonian methane seep in Morocco: The oldest record of repetitive shell morphologies among some seep bivalve molluscs: *Journal of Systematic Palaeontology*, v. 15, p. 19–41.
- Hryniewicz, K., Amano, K., Jenkins, R.G., and Kiel, S., 2017b, Thyasirid bivalves from Cretaceous and Paleogene cold seeps: *Acta Palaeontologica Polonica*, v. 62, p. 705–728.
- Jakubowicz, M., Hryniewicz, K., and Belka, Z., 2017, Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports* v. 7, p. e14292.
- Jenkins, R.G., and Hikida, Y., 2011, Carbonate sediments microbially induced by anaerobic oxidation of methane in hydrocarbon-seeps, in Tewari, V., and Seckbach, J., eds., *Stromatolites: Interaction of microbes with sediments*, Volume 18: Dordrecht, Springer, p. 591–605.
- Jenkins, R.G., Kaim, A., and Hikida, Y., 2007, Antiquity of the substrate choice among acmaeid limpets from the Late Cretaceous chemosynthesis-based communities: *Acta Palaeontologica Polonica*, v. 52, p. 369–373.
- Jenkins, R.G., Kaim, A., Little, C.T.S., Iba, Y., Tanabe, K., and Campbell, K.A., 2013, Worldwide distribution of the modiomorphid bivalve genus *Caspiconcha* in late Mesozoic hydrocarbon seeps: *Acta Palaeontologica Polonica*, v. 58, p. 357–382.
- Kaim, A., and Schneider, S., 2012, A conch with a collar: Early ontogeny of the enigmatic fossil bivalve *Myoconcha*: *Journal of Paleontology*, v. 86, no. 4, p. 652–658.
- Kaim, A., Jenkins, R.G., and Warén, A., 2008, Provannid and provannid-like gastropods from the Late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda: Abyssochrysoidea): *Zoological Journal of the Linnean Society*, v. 154, p. 421–436.
- Kaim, A., Jenkins, R.G., and Hikida, Y., 2009, Gastropods from Late Cretaceous Omagari and Yasukawa hydrocarbon seep deposits in the Nakagawa area, Hokkaido, Japan: *Acta Palaeontologica Polonica*, v. 54, p. 463–490.

- Kaim, A., Skupien, P., and Jenkins, R.G., 2013, A new Lower Cretaceous hydrocarbon seep locality from the Czech Carpathians and its fauna: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 390, p. 42–51.
- Kaim, A., Jenkins, R.G., Tanabe, K., and Kiel, S., 2014, Mollusks from late Mesozoic seep deposits, chiefly in California: *Zootaxa*, v. 3861, p. 401–440.
- Kanie, Y., and Nishida, T., 2000, New species of chemosynthetic bivalves, *Vesicomya* and *Acharax* from the Cretaceous deposits of northern Hokkaido: Science Report of the Yokosuka City Museum, v. 47, p. 79–84.
- Kanie, Y., Yoshikawa, Y., Sakai, T., and Takahashi, T., 1993, The Cretaceous chemosynthetic cold water-dependent molluscan community discovered from Mikasa City, central Hokkaido: Science Report of the Yokosuka City Museum, v. 41, p. 31–36.
- Kanie, Y., Nishida, T., Kuramochi, T., and Kawashita, Y., 2000, Chemosynthetic bivalve community discovered from the Cretaceous deposits in Horokanai-cho, northwestern Hokkaido: Science Report of the Yokosuka City Museum, v. 47, p. 73–78.
- Kelly, S.R.A., Blanc, E., Price, S.P., and Whitham, A.G., 2000, Early Cretaceous giant bivalves from seep-related limestone mounds, Wollaston Forland, Northeast Greenland, in Harper, E.M., Taylor, J.D., and Crame, J.A., eds., *The Evolutionary Biology of the Bivalvia*, v. Volume 177: London, Geological Society, p. 227–246.
- Kiel, S., 2013, Lucinid bivalves from ancient methane seeps: *Journal of Molluscan Studies*, v. 79, p. 346–363.
- Kiel, S., 2015, Did shifting seawater sulfate concentrations drive the evolution of deep-sea methane-seep ecosystems?: *Proceedings of the Royal Society B: Biological Sciences*, v. 282, no. 1804.
- Kiel, S., and Amano, K., 2013, The earliest bathymodiolin mussels: Evaluation of Eocene and Oligocene taxa from deep-sea methane seep deposits in western Washington State, USA: *Journal of Paleontology*, v. 87, p. 589–602.
- Kiel, S., and Little, C.T.S., 2006, Cold-seep mollusks are older than the general marine mollusk fauna: *Science*, v. 313, p. 1429–1431.
- Kiel, S., and Peckmann, J., 2008, Paleocology and evolutionary significance of an Early Cretaceous *Peregrinella*-dominated hydrocarbon-seep deposit on the Crimean Peninsula: *Palaos*, v. 23, p. 751–759.
- Kiel, S., Amano, K., and Jenkins, R.G., 2008, Bivalves from Cretaceous cold-seep deposits on Hokkaido, Japan: *Acta Palaeontologica Polonica*, v. 53, p. 525–537.
- Kiel, S., Campbell, K.A., and Gaillard, C., 2010, New and little known mollusks from ancient chemosynthetic environments: *Zootaxa*, v. 2390, p. 26–48.
- Kiel, S., Birgel, D., Campbell, K.A., Crampton, J.S., Schiøler, P., and Peckmann, J., 2013, Cretaceous methane-seep deposits from New Zealand and their fauna: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 390, p. 17–34.
- Kiel, S., Glodny, J., Birgel, D., Bulot, L.G., Campbell, K.A., Gaillard, C., Graziano, R., Kaim, A., Lazăr, I., and Sandy, M.R., 2014, The paleoecology, habitats, and stratigraphic range of the enigmatic Cretaceous brachiopod *Peregrinella*: *PLoS One*, v. 9, p. e109260.
- Kiel, S., Krystyn, L., Demirtaş, F., Koşun, E., and Peckmann, J., 2017, Late Triassic mollusk-dominated hydrocarbon-seep deposits from Turkey: *Geology*, v. 45, no. 8, p. 751–754.
- Leanza, A., 1940, *Myoconcha neuquena* n. sp. del Lias de Piedra Pintada en El Neuquén: *Paleontologia*, v. 22, p. 123–131.
- Linnaeus, C., 1758, *Systema naturae* ed. 10: Holmiae, Salvii, 824 p.
- Little, C.T.S., and Vrijenhoek, R.C., 2003, Are hydrothermal vent animals living fossils?: *Trends in Ecology and Evolution*, v. 18, p. 582–588.
- Little, C.T.S., Maslennikov, V.V., Morris, N.J., and Gubanov, A.P., 1999, Two Palaeozoic hydrothermal vent communities from the southern Ural mountains, Russia: *Palaeontology*, v. 42, p. 1043–1078.
- Little, C.T.S., Birgel, D., Boyce, A.J., Crame, J.A., Francis, J.E., Kiel, S., Peckmann, J., Pirrie, D., Rollinson, G.K., and Witts, J.D., 2015, Late Cretaceous (Maastrichtian) shallow water hydrocarbon seeps from Snow Hill and Seymour Islands, James Ross Basin, Antarctica: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 418, p. 213–228.
- Marwick, J., 1953, Divisions and faunas of the Hokonui System (Triassic and Jurassic): *Paleontological Bulletin*, v. 21, p. 1–141.
- Neveškaja, L., 2009, Principles of systematics and the system of bivalves: *Paleontological Journal*, v. 43, p. 1–11.
- Newell, N.D., 1957, Notes on certain primitive heterodont pelecypods: *American Museum Novitates*, v. 1857, p. 1–14.
- Newell, N.D., 1969, Classification of the Bivalvia, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology*, v. Volume 1: Lawrence, Geological Society of America and University of Kansas Press, p. N205–N224.
- Ogihara, S., 2005, The evolution of chemosynthetic biological community at the site of cold-seep carbonate precipitation: *Fossils*, v. 78, p. 40–46. [in Japanese with English abstract].
- Olsson, A.A., 1931, Contributions to the Tertiary paleontology of northern Peru. Part 4. The Peruvian Oligocene: *Bulletins of American Paleontology*, v. 17, p. 97–264.
- Peckmann, J., Kiel, S., Sandy, M.R., Taylor, D.G., and Goedert, J.L., 2011, Mass occurrences of the brachiopod *Halorella* in Late Triassic methane-seep deposits, eastern Oregon: *The Journal of Geology*, v. 119, p. 207–220.
- Sandy, M.R., 2010, Brachiopods from ancient hydrocarbon seeps and hydrothermal vents, in Kiel, S., ed., *The Vent and Seep Biota*, v. Volume 33: Dordrecht, Springer, p. 279–314.
- Sowerby, J., 1823–1825, *The Mineral Conchology of Great Britain*: London, Richard Taylor, Shoe-Lane, 168 p.
- Stanton, T., 1895, Contributions to the Cretaceous paleontology of the Pacific coast: The fauna of the Knoxville beds: *Bulletin of the United States Geological Survey*, v. 133, p. 11–132.
- Takahashi, A., Hirano, H., and Sato, T., 2003, Stratigraphy and fossil assemblage of the Upper Cretaceous in the Teshionakagawa area, Hokkaido, northern Japan: *Journal of the Geological Society of Japan*, v. 109, p. 77–95.
- Takahashi, A., Hikida, Y., Jenkins, R.G., and Tanabe, K., 2007, Stratigraphy and megafauna of the Upper Cretaceous Yezo Supergroup in the Teshionakagawa area, northern Hokkaido, Japan: *Bulletin of the Mikasa City Museum, Natural Science*, v. 11, p. 25–59.
- Waller, T.R., 1990, The evolution of ligament systems in the Bivalvia, in Morton, B., ed., *The Bivalvia - Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge*, Edinburgh, 1986: Hong Kong, Hong Kong University Press, p. 49–71.

Accepted 16 January 2018