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A monospecific assemblage of terebratulide brachiopods in the Upper Cretaceous seep deposits of Omagari, Hokkaido, Japan

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The Campanian (Upper Cretaceous) seep carbonate at Omagari (Hokkaido, Japan) yields a monospecific association of the terebratulide brachiopod *Eucalathis methanophila* Bitner sp. nov. The association is the only occurrence of brachiopods known from the post-Early Cretaceous history of chemosynthesis-based communities. Unlike many earlier rhynchonellide-dominated hydrocarbon seep associations—which disappeared in Aptian times—this association is composed of chlidonophorid terebratulides. It is hypothesised here that large rhynchonellide brachiopods have been outcompeted from chemosynthesis-based associations by large chemosymbiotic bivalves (especially lucinids) and that this seep association containing numerous terebratulide brachiopods originated as a result of immigration from the background fauna settling in a seep that lacked numerous large bivalves but offered some hard substrates for brachiopod attachment. Some living chlidonophorids are known to settle around seep/vent localities or more generally in deep-water hard-substrate settings. We review occurrences of brachiopods in chemosynthesis-based associations and show that brachiopods immigrated repeatedly to seep/vent environments. *Eucalathis methanophila* Bitner sp. nov. represents the oldest and single Mesozoic record of the genus. The new species is similar in ornamentation to three living species, Indo-Pacific *E. murrayi*, eastern Atlantic *E. tuberosa*, and Caribbean *E. cubensis* but differs in having a higher beak and wider loop. Additionally the studied species is nearly twice as large as *E. tuberosa*.

Key words: Brachiopoda, Chlidonophoridae, *Eucalathis*, hydrocarbon seep, chemosynthesis-based community, Campanian, Cretaceous, Mesozoic, Japan.

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Introduction

Although present in the oldest-known Silurian hydrothermal vent deposits (Little et al. 1999b) brachiopods seem to be of decreasing importance in chemosynthesis-based associations through time. After an Early Cretaceous acme of brachiopod occurrences in hydrocarbon seep deposits (Campbell 2006; Kiel and Peckmann 2008) related to wide dispersal of rhynchonellide *Peregrinella* few younger seep/vent localities yield any brachiopod fauna. Moreover, there is no unequivocal report of brachiopod obligate association to chemosynthesis-based communities in Recent hydrothermal vents and hydrocarbon seeps. Herein we summarise published information on brachiopod occurrences in the chemosynthesis-based associations, stressing that the Omagari seep site is the latest-known occurrence of a rich brachiopod association but one that is dominated by chlidonophorid terebratulidines rather than rhynchonellides.

Institutional abbreviations.—UMUT, University Museum, University of Tokyo, Tokyo, Japan; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

Other abbreviations.—L, length; W, width; T, thickness.

Geological setting

All specimens described in this paper came from the Omagari site which yields probably the best researched Cretaceous hydrocarbon seep deposits in Japan (Hikida et al. 2003). The 10-meter-wide seep carbonate body is located on a small islet in the Abeshinai River near the mouth of its tributary Osou-shinai River (Fig. 1). The seep carbonate in Omagari was first mentioned by Hashimoto et al. (1967) who reported a dense assemblage of tube-like trace fossils, which were later identified (Hikida et al. 2003) as possible vestimentiferan worm

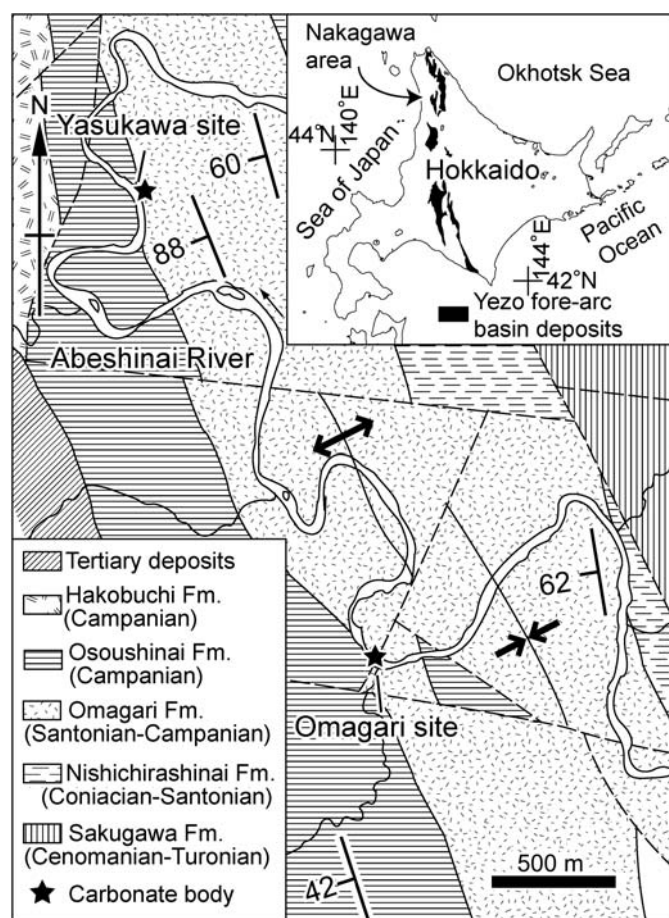


Fig. 1. Geological map of the Nakagawa area, Hokkaido, showing the location of the Omagari site. Modified from Takahashi et al. (2003).

tubes. Hikida et al. (2003) identified some fossils from this locality. Subsequently Kiel et al. (2008) formally described bivalves and Kaim et al. (2008, 2009) gastropods. The islet at Omagari is composed mainly from Campanian (Upper Cretaceous) rocks of two facies: (i) worm-tube boundstone facies and (ii) brecciated facies (Hikida et al. 2003). The former facies consists of solid carbonates containing numerous silicified worm tubes while the other fossils are uncommon. The brecciated facies consists of a mixture of brecciated carbonates and siliciclastics (mudstone to sandstone clasts). All types of rocks in brecciated facies contain numerous fossils but they are easiest to recover from mudstone and siltstone. For more comprehensive description of the locality the reader is referred to Hikida et al. (2003) and Kaim et al. (2009).

Material and methods

The investigated specimens were extracted by wet-sieving (mesh size 0.5 mm) of weakly consolidated mudstone and siltstone clasts of the brecciated facies because of practical reasons. We have not observed any brachiopods in the worm-tube boundstone facies. Although all our specimens are articulated, some are damaged and/or crushed, and most are covered

by carbonate crusts, thus being difficult to clean. The number of examined specimens is 21; however, additional samples are present at Nakagawa Museum of Natural History, Hokkaido, Japan.

The internal morphology was investigated by transverse serial sections of two specimens. The distance between the sections was variable (between 0.04 and 0.1 mm). Subsequently acetate peels have been prepared for each section. For the study of shell ultrastructure, two specimens were embedded in Araldite 2020 resin, cut and polished, then etched with 5% HCl before coating with platinum for observation under a scanning electron microscope. The SEM micrographs were taken in the SEM laboratory of ZPAL using a Philips XL-20 scanning microscope.

Review of the brachiopod occurrences in chemosynthesis based associations

Brachiopods are present in the earliest-known chemosynthesis-based associations containing metazoan animals. The lingulate brachiopod *Pyrodiscus* reported from the Silurian (?Ludlow) of Yaman Kasy, Ural Mountains, Russia (Little et al. 1999b) is the sole inarticulate brachiopod described so far from chemosynthesis-based associations (Table 1). *Septatrypa lantenoisi* is an atrypid brachiopod reported by Barbieri et al. (2004) from Upper Silurian carbonate mound in Morocco. Barbieri et al. (2004) interpreted *Septatrypa*-bearing rocks as hydrocarbon seep deposits, however, later authors (Buggisch and Krumm 2005; Himmler et al. 2008) argued that the reported isotope data indicate methanogenesis rather than methane oxidation which typifies seep environment. The first rhynchonellid brachiopods in chemosynthesis-based associations appear in the Devonian. The Devonian *Dzieduszyckia* is a very large, sturdily ribbed rhynchonellid with a wide but disjunct worldwide distribution. It is known from Poland, Morocco, western America, Russia, Kazakhstan, and China (Campbell and Bottjer 1995b; Sandy 1995; Baliński and Biernat 2003). Campbell and Bottjer (1995b) and Sandy (1995) speculated that *Dzieduszyckia* apparently thrived in chemosynthesis-based associations. Baliński and Biernat (2003) challenged this speculation showing that isotope data from some Moroccan and Polish localities does not meet the criteria for seep environments. However, Baliński and Biernat (2003) measured mainly shell material with admixture of sediment, and—as already pointed out by Campbell (2006)—carbon and oxygen isotopes measured from shell material from hydrocarbon seeps are expected to fall within a range close to normal marine conditions. A relation of *Dzieduszyckia*-bearing deposits from western Meseta of Morocco to hydrocarbon seepage has been confirmed by Peckmann et al. (2007). Remaining localities await critical evaluation. Another rhynchonellid, a medium-sized, ribbed *Ibergirhynchia* has been

Table 1. A list of brachiopods occurring in the chemosynthesis-based associations. (*) Buggisch and Krumm (2005) and Himmler et al. (2008) argued that the reported isotope data from *Septatrypa*-bearing localities indicate methanogenesis rather than methane oxidation which typifies seep environment.

Taxon	Reference	Environment	Locality	Age
Lingulida				
<i>Pyrodiscus lorrainae</i> Little, Maslennikov, Morris, and Gubanov, 1999	Little et al. (1999b)	hot vent	Ural Mountains, Russia	Silurian
Atrypida: Septatrypidae				
<i>Septatrypa lantenoisi</i> (Termier, 1936)	Campbell and Bottjer (1995b), Barbieri et al. (2004)	?cold seep*	Morocco	Upper Silurian
Rhynchonellida: Halorellidae				
<i>Dzieduszyckia kielcensis</i> (Roemer, 1866)	Baliński and Biernat (2003)	?cold seep	Holy Cross Mts., Poland	Famennian
<i>Dzieduszyckia intermedia</i> (Termier, 1936)	Baliński and Biernat (2003)	cold seep	Morocco	Famennian
<i>Dzieduszyckia crassicostata</i> (Termier and Termier, 1948)	Baliński and Biernat (2003)	cold seep	Morocco	Famennian
<i>Dzieduszyckia tenuicostata</i> (Termier, 1936)	Baliński and Biernat (2003)	cold seep	Morocco	Famennian
<i>Dzieduszyckia bashkirica</i> (Tschernyshev, 1887)	Baliński and Biernat (2003)	uncertain	Urals, Kazakhstan, Tadjikistan, China	Famennian
<i>Dzieduszyckia sonora</i> Noll, Dutro, and Beus, 1984	Baliński and Biernat (2003)	barite seep	Nevada and Mexico	Famennian
Rhynchonellida: Peregrinellidae				
<i>Anarhynchia gabbi</i> (Ager, 1968)	Manceñido and Dagys (1992); Sandy (1995, 2001); Stefanoff and Sandy (1998)	?cold seep	California, USA	Lower Jurassic
<i>Anarhynchia</i> cf. <i>gabbi</i> (Ager, 1968)	Little et al. (1999a)	hot vent	California, USA	Pliensbachian, Jurassic
<i>Peregrinella multicarinata</i> (Lamarck, 1819)	Biernat (1957), Thieuloy (1972), Ager et al. (1972), Campbell and Bottjer (1995a, b); Kiel and Peckmann (2008)	cold seep	France, Switzerland, Poland, Czech Rep., Germany, Romania, Italy, Crimea, Caucasus	?Late Berriasian-Hauterivian
<i>Peregrinella silesica</i> (Ascher, 1906)	Ascher (1906)	?cold seep	Carpathians, Czech Rep.	Hauterivian
<i>Peregrinella whitneyi</i> (Gabb, 1869)	Campbell et al. (1993), Campbell and Bottjer (1995 a, b)	cold seep	California, USA	Hauterivian
<i>Peregrinella chisania</i> Sandy and Blodgett, 1996	Sandy and Blodgett (1996)	?cold seep	Alaska, USA	Valanginian-Hauterivian
<i>Peregrinella gongboxueensis</i> Sun, 1986	Sun (1986)	?cold seep	Tibet, China	Valanginian
<i>Peregrinella cheboensis</i> Sun, 1986	Sun (1986)	?cold seep	Tibet, China	Valanginian-Hauterivian
<i>Peregrinella bifurcata</i> Sun, 1986	Sun (1986)	?cold seep	Tibet, China	Valanginian-Hauterivian
<i>Peregrinella baingoinensis</i> Sun, 1986	Sun (1986)	?cold seep	Tibet, China	Valanginian-Hauterivian
<i>Peregrinella dongqoensis</i> Sun, 1986	Sun (1986)	?cold seep	Tibet, China	Valanginian-Hauterivian
<i>Peregrinella</i> sp.	Ortiz-Hernández and Martínez-Reyes (1993)	?cold seep	Mexico	Neocomian-Aptian
Rhynchonellida: Dimerellidae				
<i>Ibergirhynchia contraria</i> (Roemer, 1850)	Gischler et al. (2003)	cold seep	Harz, Germany	Carboniferous
<i>Cooperhynchia schucherti</i> (Stanton, 1895)	Sandy and Campbell (1994)	cold seep	California, USA	Tithonian, Jurassic
Terebratulida: Beecheriidae				
<i>Beecheria</i> sp.	Von Bitter et al. (1990, 1992)	?hot vent	Newfoundland, Canada	Early Carboniferous
Terebratulida: Zeileriidae				
<i>Modestella jeletzkyi</i> Sandy, 1990	Sandy (1990, 1995), Beauchamp and Savard (1992)	cold seep	Arctic Canada	?Albian, Lower Cretaceous
Terebratulida: Chlidonophoridae				
<i>Eucalathis methanophila</i> Bitner sp. nov.	this paper	cold seep	Hokkaido, Japan	Campanian, Upper Cretaceous
Terebratulida: Terebratulidae				
? <i>Liothyrella</i> sp.	Campbell (2006), Campbell et al. (2008)	cold seep	New Zealand	Miocene
Terebratulida: Terebrataliidae				
<i>Coptothyris sinanoensis</i> Kuroda, 1931	Kuroda (1931); Tanaka (1959)	cold seep	Honsiu, Japan	Miocene
Unidentified brachiopod	Majima et al. (2003, 2005)	cold seep	Kyushu, Japan	Pliocene

reported by Gischler et al. (2003) from the Early Carboniferous of Germany. A relation of *Ibergirhynchia*-bearing deposit to hydrocarbon seepage has been confirmed by Peckmann et al. (2001). There are no confirmed records of chemosynthesis-based associations from the Permian and Triassic though Sandy (1995) suggests that some Triassic *Halorella* and *Carapezzia* could be seep-related as they are strikingly similar to Jurassic *Anarhynchia* and *Cooperrhynchia* (see below) respectively and usually occur in isolated carbonate lenses emplaced in otherwise clastic sediments (Sandy 1995, 2001). The Early Jurassic *Peregrinelloidea* from Siberia (Dagys 1968) is very similar and occurs in monospecific associations in carbonate lenses (Sandy 1995). The seep environments for *Halorella*, *Carapezzia*, and *Peregrinelloidea* need critical evaluation and a confirmation from isotope analyses. The brachiopod *Anarhynchia* is known from Pliensbachian (Lower Jurassic) hydrothermal vent deposits of the Franciscan Complex in California (Little et al. 1999a, 2004). The genus has also been recorded from Oregon and Argentina (Mancenido and Dagys 1992; Sandy 1995, 2001; Stefanoff and Sandy 1998) but these localities are not confirmed as seep/vent sites. *Cooperrhynchia* has been reported from Tithonian (Upper Jurassic) seep carbonates in California (Sandy and Campbell 1994).

The Early Cretaceous is a period of ubiquitous occurrences of the rhynchonellide *Peregrinella* in ancient hydrocarbon seep deposits. This brachiopod, as with *Dzieduszyckia*, is characterised by cosmopolitan but disjunct occurrences (Campbell and Bottjer 1995a, b; Sandy 1995; Sandy and Blodgett 1996; Posenato and Morsilli 1999; Kiel and Peckmann 2008). It is known from Alaska (Sandy et al. 1995), US Pacific Coast (Campbell and Bottjer 1995a, b), Mexico (Ortiz-Hernández and Martínez-Reyes 1993; Sandy 1995), Crimea (Kiel and Peckmann 2008), Tibet (Sun 1986), and numerous localities in Europe (Ascher 1906; Biernat 1957; Thieuloy 1972; Posenato and Morsilli 1999; Lazăr et al. 2005). Campbell and Bottjer (1995b) have suggested that *Peregrinella* is an end-member of vent-seep endemic lineages of rhynchonellides (*Dzieduszyckia*–*Ibergirhynchia*–*Peregrinella*), a hypothesis challenged by Baliński and Biernat (2003) who noted that morphological characters of the crura suggest different familial placement.

Terebratulide brachiopods are much less common in the ancient seep deposits. A short-looped brachiopod *Beecheria* has been reported from alleged “low-temperature vent associations” of Lower Carboniferous in Newfoundland (von Bitter et al. 1990, 1992; Sandy 1995). However, the vent nature of these associations is still under debate (Campbell 2006). Another unidentified terebratulide has been reported by Beauchamp and Savard (1992) from a Lower Cretaceous cold seep carbonate in Arctic Canada. The species, named *Modestella jeletzkyi* by Sandy (1990), is the sole occurrence of *Modestella* in seep associations as all the other species of this genus (known mostly from Europe) are not considered to be seep-related (Sandy 1995). Campbell (2006) and Campbell et al. (2008) mentioned a terebratulide ?*Liothyrella* from a possible

Miocene seep deposit in New Zealand. This identification, however, has not been critically evaluated in a taxonomic work.

In Japan brachiopods are known from three hydrocarbon seep localities. The Campanian species in this study has been reported as a “terebratulid brachiopod” by Hikida et al. (2003). A single occurrence of *Coptothyris sinanoensis* in a Miocene carbonate in Nagano Prefecture, later identified as hydrocarbon seep deposit, was described by Kuroda (1931) and listed by Tanaka (1959). Majima et al. (2003, 2005) reported an unidentified brachiopod from a Pliocene locality at Kuge Shrine on Kyushu Island. However, Majima et al. (2005: 89) consider these “...Pliocene brachiopods associated with a cold seep assemblage ... not to be a chemosynthetic species because the brachiopods are rare in the assemblage and have also been collected from the same horizon about 300 m away, where no evidence of a seep is present.”

There are no extant brachiopods that are unequivocally associated with vent/seep environments (Campbell 2006; Peckmann et al. 2007). Some species are recorded in the vicinities (Zezina 2000; Lee et al. 2008) but there is no evidence they are obligatory members of chemosynthesis-based communities. Zezina (2000) reported a number of terebratulide brachiopods living in the vicinity of hydrothermal vents. These include *Terebratulina kiiensis*, *Laqueus blanfordi*, *Macandrevia americana*, *Aneboconcha smithi*, *Nanacalathis atlantica*, and *Abyssothyris* sp. Two other species (*Platidia anomioidea* and *P. concentrica*) were found in a volcanic caldera in the Juan de Fuca Ridge (Zezina 1990). Zezina (2000) noted that several species (*T. kiiensis*, *L. blanfordi*, *M. americana*, *Abyssothyris* sp.) in these locations were represented exclusively by individuals with no mature gonads, i.e., they could not breed there while *A. smithi* is represented only by dwarfed individuals. Lee et al. (2008) recently reported *Melvicalathis macroctena* (Zezina, 1981) attached to basalts and manganese crusts covering rocks in the Southeast Indian Ridge and southeast Pacific but there is no obvious relation of the brachiopods to hydrothermal vents. Lee et al. (2008) suggest that *Melvicalathis macroctena* is a primary opportunistic coloniser of available hard substrates including fresh glassy basalt.

Systematic palaeontology

(by M.A. Bitner)

Phylum Brachiopoda Duméril, 1806

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer, and Popov, 1996

Class Rhynchonellata Williams, Carlson, Brunton, Holmer, and Popov, 1996

Order Terebratulida Waagen, 1883

Suborder Terebratulidina Waagen, 1883

Superfamily Cancellothyridoidea Thomson, 1926

Family Chlidonophoridae Muir-Wood, 1959

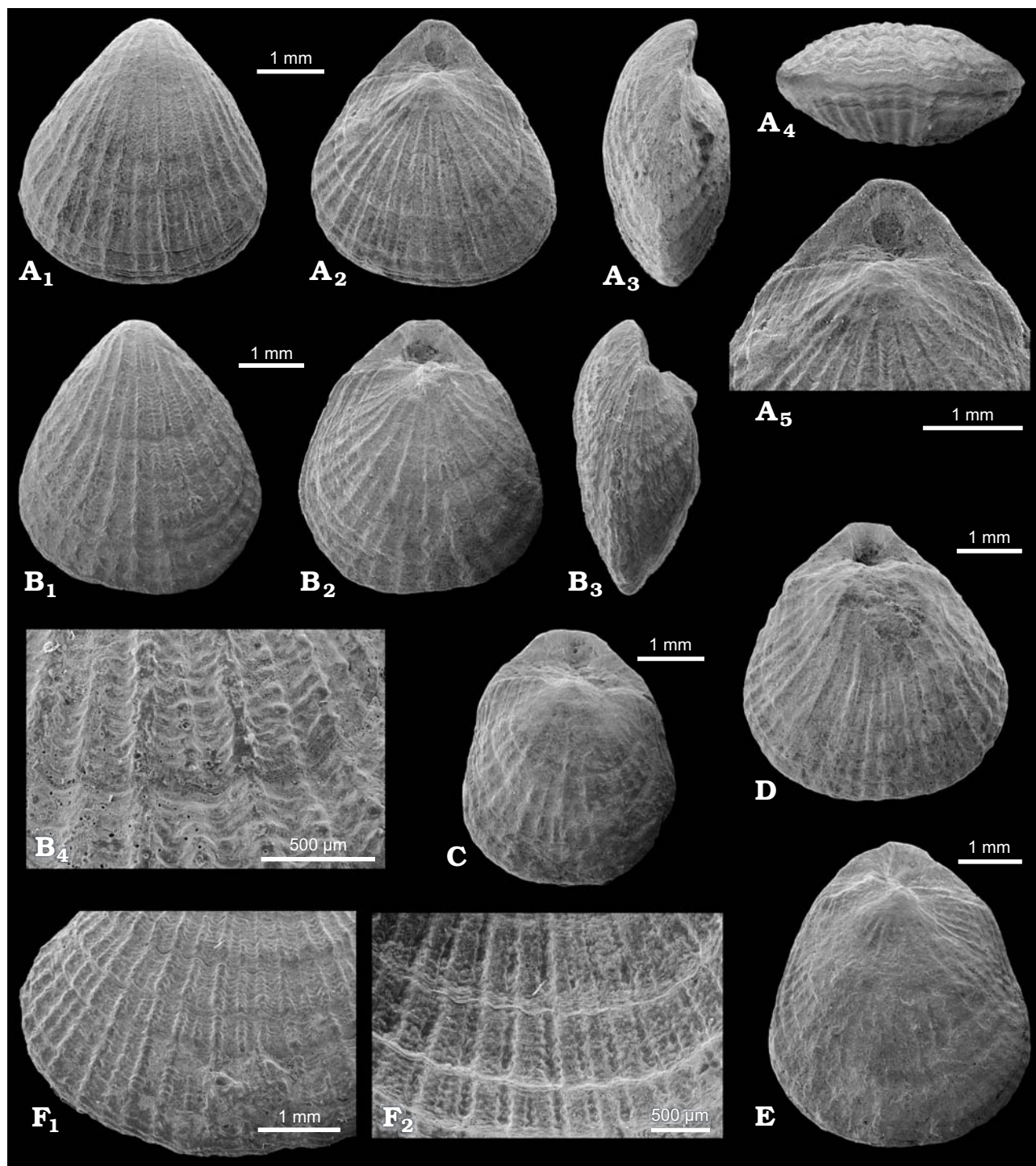


Fig. 2. Terebratulide brachiopod *Eucalathis methanophila* Bitner sp. nov., Campanian, Omagari, Japan. **A.** Holotype, UMUT MB30198, ventral (**A**₁), dorsal (**A**₂), lateral (**A**₃), and anterior (**A**₄) views of complete specimen, enlargement (**A**₅) of the posterior part. **B.** Paratype, UMUT MB30199, ventral (**B**₁), dorsal (**B**₂), and lateral (**B**₃) views of complete specimen, enlargement (**B**₄) of shell surface to show nodular ornament. **C–E.** Paratypes, UMUT MB30200–30202, dorsal views of complete specimens. **F.** UMUT MB30207, shell surface of ventral valve (**F**₁) and enlargement (**F**₂) to show details of ornamentation. All SEM.

Subfamily Eucalathinae Muir-Wood, 1965

Genus *Eucalathis* Fischer and Oehlert, 1890

Type species: *Terebratulina murrayi* Davidson, 1878 by original designation of Fischer and Oehlert (1890: 72); Recent, 28°33'S, 177°50'W, near Kermadec Islands, depth 1080 m (Davidson 1878).

Remarks.—Today *Eucalathis* has a worldwide distribution, being known from the Caribbean, Atlantic, Indian, Pacific, and Antarctic Oceans (Cooper 1973a, b, c, 1977, 1981a, b; Foster 1974; Brunton and Curry 1979; Logan 1983, 1988, 1990, 1998, 2007; Zezina 1985, 1987, 2006; Hiller 1986,

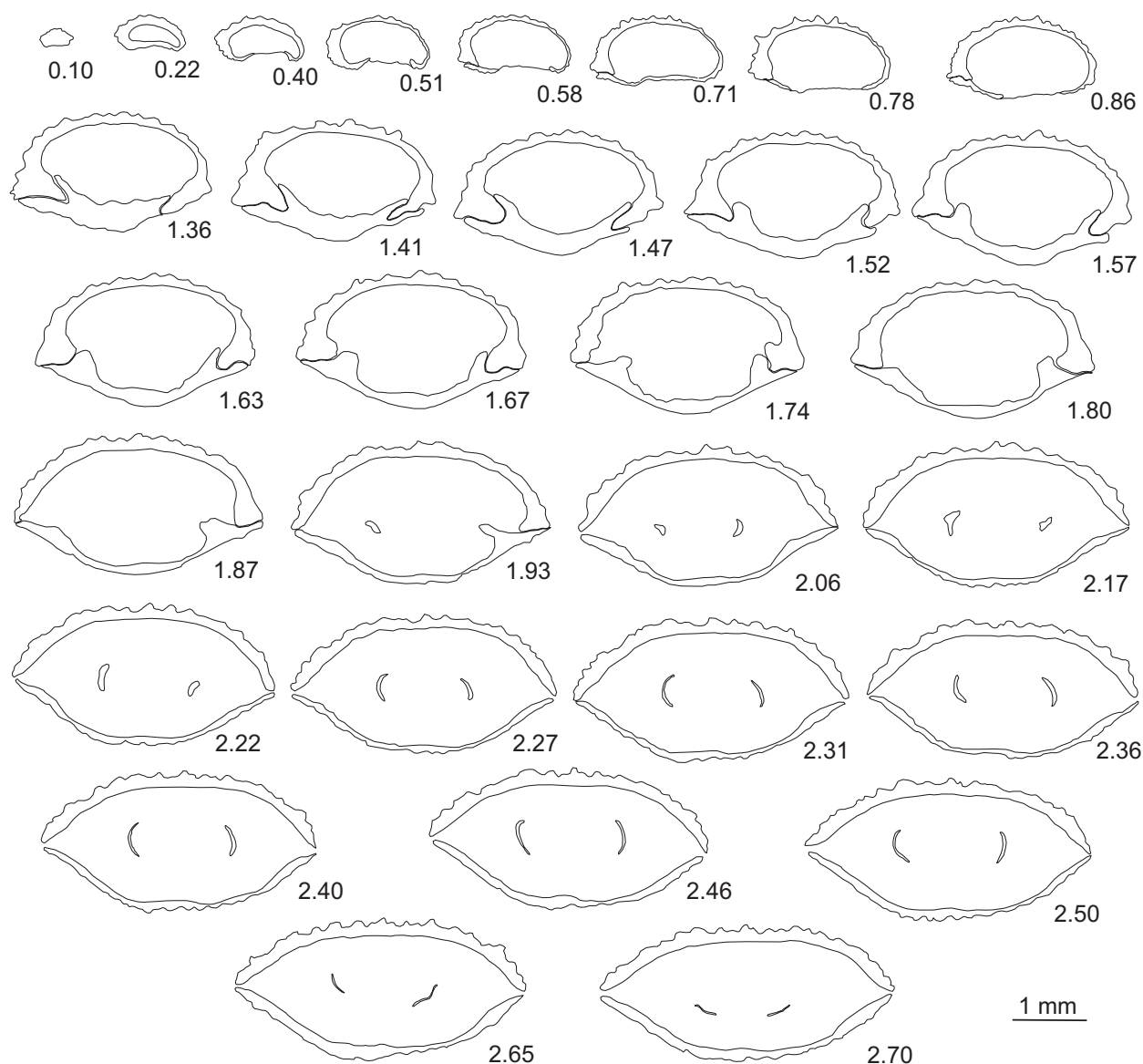


Fig. 3. Transverse serial sections of terebratulide brachiopod *Eucalathis methanophila* Bitner sp. nov. through specimen UMUT MB30203, Campanian, Japan. Original dimensions of the specimens: L = 4.9 mm, W = 4.4 mm, T = 2.0 mm. Numbers indicate distance in mm from the tip of the ventral umbo.

1994; Dawson 1991; Laurin 1997; Gaspard 2003; Álvarez and Emig 2005; Bitner 2006, 2008, 2009). The 13 Recent species assigned to this genus exhibit a wide bathymetric range from 185 to 3870 m (Logan 2007); one deep-water species, *E. macroctena*, included to *Eucalathis* by Zezina (1981), has recently been transferred into a new genus *Melvicalathis* Lee, Lüter, and Zezina, 2008 (Lee et al. 2008). *Melvicalathis* can be easily distinguished from *Eucalathis* by its broad, smooth, triangular in cross-section ribs.

In the fossil record *Eucalathis* is very rare and has been so far reported from the Eocene of Eastern Coast of America (Cooper 1988) and Miocene of Italy (Davidson 1870; Lee et al. 2006). Those fossil species are coarsely ribbed, and thus differ strongly from the specimens described here. Apart from morphological differences, the great stratigraphical gap between the hitherto described *Eucalathis* species and the Late Cretaceous species from Japan justifies the decision to

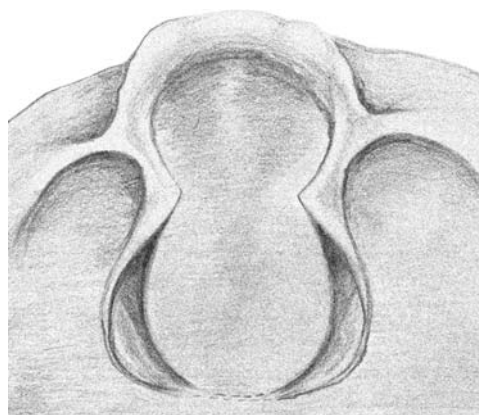


Fig. 4. Reconstruction of internal structures of *Eucalathis methanophila* Bitner sp. nov. based on transverse serial sections (Fig. 3) and 3D digital reconstruction (see at http://app.pan.pl/SOM/app55-Kaim_et_al_SOM.pdf). Drawing by Ewa Widłak-Kaim.

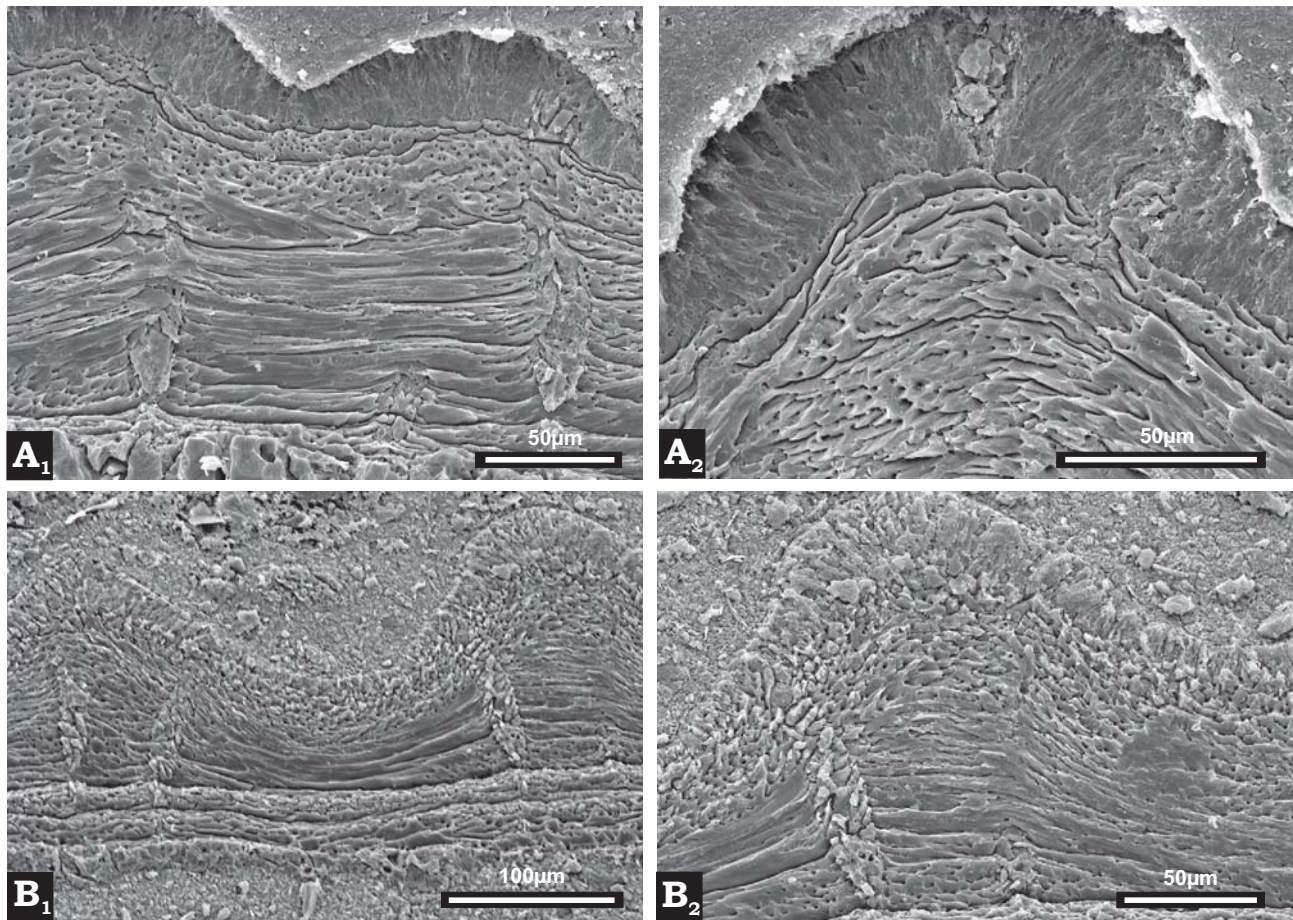


Fig. 5. Terebratulide brachiopod *Eucalathis methanophila* Bitner sp. nov., Campanian, Omagari, Japan. **A.** UMUT MB30197, transverse section of ventral valve, visible fused fibres (A₁), visible boundary of primary and secondary layers (A₂). **B.** UMUT MB30203, ventral valve, transverse sections of the whole shell (B₁), visible boundary between primary and secondary layers, and punctae (B₂). All SEM.

erect a new species. The studied specimens represent not only the first record of *Eucalathis* from Japan but also the oldest occurrence of the genus.

Eucalathis methanophila Bitner sp. nov.

Figs. 2–5.

Etymology: From methane and Latin suffix, *phila*, meaning to like. Refers to its occurrence at the methane seep.

Type material: Holotype: UMUT MB30198 (Fig. 2A₁–A₅), articulated shell; Paratypes: UMUT MB30199–30202 (Fig. 2B–E), articulated shells.

Type locality: Omagari site, Nakagawa area, Northern Hokkaido, Japan. Coordinates 44° 39' 26''N, 144° 2' 25''E.

Type horizon: Hydrocarbon seep deposits of Omagari Formation, Campanian, Upper Cretaceous.

Diagnosis.—*Eucalathis* of medium size with surface ornamented by numerous beaded ribs, high beak with large, oval foramen, anterior commissure rectimarginate, loop wide with subparallel descending branches narrowed anteriorly.

Measurements (in mm).—See Table 2.

Description.—External morphology: Shell small (maximum length 5.7 mm), auriculate, variable in outline from widely subtriangular to elongate oval, with maximum width usually

at two thirds of shell length. Shell biconvex with ventral valve slightly more convex. Shell surface covered with numerous beaded, tuberculate ribs (20–30) which increase in number by intercalations and bifurcations; growth lines distinct (Fig. 2B₄, F₁, F₂). Lateral commissures nearly straight; anterior commissure rectimarginate to incipiently uniplicate. Hinge line wide, slightly curved. Beak relatively high, erect to suberect with sharp, distinct ridges. Foramen large, oval; disjunct deltidial plates form narrow ridges.

Table 2. Measurements of *Eucalathis methanophila* Bitner sp. nov. Abbreviations: L, length, W, width, T, thickness.

Specimen no.	L	W	T	W/L	T/L
UMUT MB30197	5.7	4.9	2.7	0.86	0.47
UMUT MB30198 (holotype)	4.1	3.8	1.95	0.93	0.47
UMUT MB30199 (paratype)	4.3	3.7	1.8	0.86	0.49
UMUT MB30200 (paratype)	4.0	3.2	1.9	0.8	0.47
UMUT MB30201 (paratype)	4.4	4.1	2.2	0.93	0.5
UMUT MB30202 (paratype)	5.2	4.3	2.2	0.83	0.42
UMUT MB30203	4.9	4.4	2.0	0.9	0.41
UMUT MB30204	5.3	4.9	2.4	0.92	0.45
UMUT MB30205	3.2	3.0	1.6	0.93	0.5
UMUT MB30206	3.2	3.1	1.4	0.97	0.44

Internal morphology: Two specimens were sectioned of which the better preserved is figured (Fig. 3). Pedicle collar present. Teeth long, smooth, nearly horizontally inserted into large dental sockets. Inner socket ridges massive, long. No hinge plates observed. Crura short, massive. Loop short and wide with subparallel to slightly divergent descending branches that narrow anteriorly (Fig. 4). Transverse band not preserved in either of the sectioned specimens.

Shell microstructure: Two specimens were studied. The shell is composed of two layers: a primary microgranular layer and a secondary fibrous layer (Fig. 5). In both cases the shell is diagenetically modified, fragmentary fibres of the secondary layer are completely fused (Fig. 5A₁). The primary layer is 27–53 µm thick in the ribs and 12–25 µm in sulci. The secondary layer is 144–205 µm thick in the ribs and 100–114 µm in sulci. The total thickness of the shell is 127 to 241 µm. The punctae are more densely distributed in the rib regions (Fig. 5).

Remarks.—The investigated specimens display, both externally and in a loop character, typical features of the genus *Eucalathis*. This genus was erected for the specimens similar to *Terebratulina* but having disjunct crural processes (Fischer and Oehler 1890); in *Terebratulina* crural processes are united to form a ring. In the ornamentation of the numerous fine ribs the specimens from Japan resemble three living species, Indo-Pacific *E. murrayi* (Davidson, 1878), eastern Atlantic *E. tuberosa* (Jeffreys, 1874), and Caribbean *E. cubensis* Cooper, 1977 but differ in having higher beak and wider loop (Davidson 1878, 1886; Cooper 1977, 1981b; Zvezina 1987). Additionally the studied specimens are nearly twice as large as *E. tuberosa*.

Stratigraphic and geographic range.—Campanian (Upper Cretaceous) seep carbonate at Omagari (Hokkaido, Japan).

Discussion

Brachiopods are known from the chemosynthesis-based associations since Silurian times (Little et al. 1999b) and they were important members from Devonian up to Early Cretaceous constituting at some settings monospecific clusters of numerous individuals (Campbell and Bottjer 1995a, b; Little et al. 1999a; Campbell 2006; Kiel and Peckmann 2008). No Cainozoic fossil and Recent brachiopods are known to be sustained by chemosymbiosis. However, some Devonian (*Dzieduszyckia*) and Early Cretaceous (*Peregrinella*) rhynchonellids attained large sizes at the hydrocarbon seeps as is characteristic of species from other phyla (e.g., molluscs) hosting chemosymbiotic bacteria. Since the demise of *Peregrinella*, brachiopods have become rare elements in the seep/vent environments and nowadays—although still found occasionally nearby—there is no evidence that any brachiopod is an obligatory member of such community. Therefore the occurrence of *Eucalathis methanophila* in the Campanian hydrocarbon seep deposits is surprising. Firstly, it appears in

relatively large numbers in the seep carbonate while it is unknown from ambient strata and, secondly, the brachiopod belongs to the Terebratulida and not to the Rhynchonellida (in contrast to the majority of older taxa). As outlined above, terebratulids are known from occasional occurrences at or near both ancient and modern chemosynthesis-based communities. Nevertheless all Recent examples are considered as “normal” deep water taxa and early colonisers of the rocky (usually basaltic) substrate (Lee et al. 2008). It is worth noting that at least two Recent eucalathines (*Nanacalathis atlantica* and *Melvicalathis macroctena*) are reported from the vicinity of hydrothermal vents (Zvezina 2000; Lee et al. 2008). *Terebratulina tauriniensis* described by Davidson (1870) from a Miocene locality at Gassino near Turin is apparently another species of *Eucalathis*. Although this locality has not been listed as hydrocarbon seep, several outcrops of “Calcarei a *Lucina*” are known from this region. These carbonate deposits have been interpreted by Taviani (1994) as Miocene hydrocarbon seep deposits. *Eucalathis tauriniensis* has been described by Davidson (1870) more than a century before identification of the first hydrocarbon seep faunas and now it is difficult to trace the exact *Eucalathis*-bearing locality of Gassino. Otherwise eucalathines are unknown from the fossil record apart from two occurrences in the Eocene of Eastern Coast of Northern America (Cooper 1988).

All articulate brachiopods are primary suspension feeders collecting their food by a lophophore wedged between two shells. They feed on suspended organic matter and do not possess a functional anus (James et al. 1992). No endosymbiotic interactions have been observed for this group of animals. As mentioned above, some large rhynchonellid brachiopods have been suspected of chemosynthetic metabolism or at least as well adapted to environments typified by high concentrations of reduced chemicals (Campbell et al. 1993; Campbell and Bottjer 1995a, b). The ubiquitous occurrence of *E. methanophila* at Omagari suggests that it was well adapted to a seep environment but its small size makes it unlikely to have hosted any bacterial endosymbionts. Zvezina (2000) suggested that most of the brachiopods in the vicinity of hydrothermal vents were immature and/or dwarfed. The specimens of *E. methanophila* from Omagari are of average size for eucalathines and most of them are seemingly adult specimens. The size of the pedicle foramen suggests that it was functional. Eucalathines, however, are known to possess a number of pedicle shapes. Lee et al. (2008) reported for *Melvicalathis macroctena* short, branched, or brush-like pedicles while Bromley and Surlyk (1973) illustrated *Eucalathis murrayi* with the pedicle divided into rootlets immediately posterior to the pedicle opening. A brachiopod having a short pedicle usually attaches to rocky substrate while brachiopods having branched or brush-like pedicles attach to small hard particles in the loose sediment. Thus *E. methanophila* may have been attached to exhumed seep carbonate, attached to worm tubes projecting above the seafloor, or anchored to sediment around the seep. The seep carbonate normally precipitates subsurface within sediments (Ritger et al.

1987) and there is no direct indication that the carbonate was later exhumed at Omagari seep. Nevertheless, the brecciation events in Omagari seep described by Hikida et al. (2003) may suggest that—at least in some periods—the carbonate could be exhumed due to enhanced/explosive discharge of the methane. Moreover, some carbonate cements, e.g., isopachous rim cements, precipitated around worm tubes which were free of sediment inside (Takahashi et al. 2007). It suggests that the cements precipitated above the sea floor. Last but not least the brachiopods could have attached to the worm tubes, which are extraordinarily common in Omagari while relatively rare in other seep sites in Japan (Jenkins et al. 2007). The presence of these hard substrates could explain why *E. methanophila* is common in Omagari while absent at any other seep sites in the Upper Cretaceous of Hokkaido (AK and RGJ unpublished data).

Campbell and Bottjer (1995a) suggested that the rhynchonellide brachiopods were displaced in chemosynthesis-based associations by chemosymbiotic bivalves at the end of Early Cretaceous. Indeed demise of *Peregrinella* happened around the same time as the onset of the modern, mollusc-dominated seep fauna (Campbell and Bottjer 1995a; Kiel and Little 2006; Kiel and Peckmann 2008). Kiel and Peckmann (2008) have demonstrated that the presence or absence of dominant brachiopods is inversely correlated with the presence or absence of dominant lucinids. They suggested, however, that mass occurrences of thick-shelled brachiopods made it difficult for lucinids and other infaunal bivalves to survive at seep sites (Kiel and Peckmann 2008: 757). We are inclined rather to the suggestion of Campbell and Bottjer (1995a) that inversely, the increasing competition from seep-adapted bivalves (including lucinids)—many of which hosted chemosymbiotic bacteria—might be a plausible explanation of the demise of brachiopods from chemosynthesis based associations. Such an explanation would parallel the general trend in brachiopod decline during Mesozoic times. Numerous authors (Gould and Calloway 1980; Thayer 1985, 1986; Ager 1986) have suggested that after the P-T crisis brachiopods were outcompeted by bivalves in a majority of environments. Still there are some Recent examples where brachiopods successfully coexist with bivalves (Lee 2008).

Large bivalves, especially lucinids are uncommon at Omagari (Kiel et al. 2008) compared to gastropods, for example (Kaim et al. 2009). In this respect the Omagari site is unusual among other Upper Cretaceous and younger seep sites. Scarcity of such bivalves at Omagari might explain the abundant presence of *E. methanophila*. However, it remains unclear why the Omagari seep was settled by terebratulides and not by rhynchonellides. Lee (2008) has shown that rhynchonellides declined more rapidly than terebratulides after Middle Jurassic diversity zenith. By the Cretaceous rhynchonellides were much less common, less ecologically differentiated, and taxonomically diverse than terebratulides and therefore immigration of the latter into Campanian seep communities might be from purely stochastic reasons. This hypothesis might be also supported by the lack of any reports

of rhynchonellides from the vicinity of Recent seep/vent localities. On the other hand, the oldest seep related sediments reported so far from Japan came from Albian (Kaim and Jenkins 2008, Kaim et al. 2009) while the youngest occurrence of *Peregrinella* is recorded from Neocomian–Aptian of Mexico (Ortiz-Hernández and Martínez-Reyes 1993), therefore it remains unknown if *Peregrinella* was present in the vicinity of present-day Japan during the Early Cretaceous times. Geographically closest are the occurrences reported by Sun (1986) from Tibet.

Conclusions

Eucalathis methanophila, as with some other brachiopods associated with hydrocarbon seeps in the geological past, constitutes a monospecific association with molluscs and worm tubes in the Campanian methane seep site at Omagari. Although it still remains disputable if the species was an obligatory member of hydrocarbon seep community, it may have been adapted to thrive in such an extreme environment. *E. methanophila*, unlike most of the earlier brachiopods associated with hydrocarbon seeps, belongs to the Eucalathinae, a subfamily within Terebratulida. Two species of this subfamily are known from the vicinity of hydrothermal vents although they are considered to be deep water opportunists. The occurrence of *E. methanophila* in Omagari may suggest that it was well adapted to environments typified by high concentrations of reduced chemicals. If so it would be the latest record of a brachiopod species closely connected to a chemosynthesis-based association. The increasing importance of chemosymbiont-bearing bivalves at Cretaceous hydrocarbon seeps might be a plausible explanation of the demise of brachiopods from these environments. The presence of numerous brachiopods in Omagari might be related to relatively low abundance of bivalves at this locality and/or presence of numerous worm tubes serving as a source of hard substrate for attachment.

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