Mass occurrence of hokkaidoconchid gastropods in the Upper Jurassic methane seep carbonate from Alexander Island, Antarctica

ANDRZEJ KAIM^{1*} and SIMON R.A. KELLY²

¹Instytut Paleobiologii, Polska Akademia Nauk, ul. Twarda 51/55, 00-818 Warszawa, Poland ²CASP, West Building, 181A Huntingdon Road, Cambridge CB3 0DH, United Kingdom *kaim@twarda.pan.pl

Abstract: The Tithonian (Upper Jurassic) methane seep carbonate of the Gateway Pass Limestone Bed (Alexander Island, Antarctica) yields enormous numbers of the minute gastropod mollusc, *Hokkaidoconcha hignalli* sp. nov. together with an unidentified limpet gastropod and occasional protobranch and lucinid bivalves. This assemblage constitutes one of the most abundant (by means of the specimen number) records of Jurassic chemosynthesis-based communities. The gastropod family Hokkaidoconchidae is extremely common in Cretaceous hydrocarbon seep carbonates from Japan and is known also from Upper Jurassic/Cretaceous hydrocarbon seep carbonates in California. It is an extinct family closely related to modern seep and vent dwelling Provannidae. This is the first confirmed record of this family in the Southern Hemisphere, indicating its surprisingly early and widespread distribution reaching high latitudes.

Received 10 October 2008, accepted 3 December 2008

Key words: Antarctic Peninsula, cold seep, Hokkaidoconchidae, mollusc, Tithonian

Introduction

The research on ancient chemosynthesis-based communities has progressed much in the last few years (e.g. Majima et al. 2005, Campbell 2006, Kiel & Little 2006) and of special interest are the discoveries of Cretaceous seep carbonates from Japan (Hikida et al. 2003, Jenkins et al. 2007a, 2007b, Kaim et al. 2008a, Kiel et al. 2008a) and US Pacific Coast (Kiel et al. 2008c) yielding associations resembling in several aspects the modern hydrocarbon seep communities. It is also noteworthy that the associations described from Cretaceous reptile bones (Kaim et al. 2008b) and sunken driftwood (Kiel et al. 2008b) from Japan are of similar composition. It suggests that already in Cretaceous modern-type chemosynthesis-based the communities were well established and surprisingly uniform in faunal composition. Consequently, hydrocarbon seep faunas from older strata, especially from the Jurassic, are of great importance for deciphering the evolution of chemosynthetic communities. However, such associations are known from a few isolated and distant localities only. The earliest discovered Tithonian localities in California (Charlie Valley, Paskenta, and NW Berryessa) yielded a number of molluscs (Stanton 1895, Easton & Imlay 1955), but their chemosynthetic significance was not realised until much later (Campbell & Bottjer 1991, 1993, Sandy & Campbell 1994). The gastropods from Californian seep carbonates have been recently reviewed in much detail by Kiel et al. (2008c). Gaillard et al. (1992) described an Oxfordian seep carbonate from southern France, illustrating

some lucinid bivalves but they did not mention any gastropods. The Tithonian seep carbonate from Atoll Nunataks Formation of Alexander Island, Antarctica (Kelly 1991, Kelly *et al.* 1995) is another example of Jurassic seep carbonate. This occurrence is of particular interest given its remoteness to any other known Mesozoic chemosynthesis-based associations. Although lithological and taphonomical description supported by critical confirmatory geochemical data was published by Kelly *et al.* (1995) the formal description of the fossils awaited careful palaeontological preparation. Herein we describe the gastropods from the Atoll Nunataks Formation.

Geological setting

The gastropod-bearing seep carbonate unit, formally designated by Kelly *et al.* (1995) as the Gateway Pass Limestone Bed, is located in the upper part of the Atoll Nunataks Formation (Doubleday *et al.* 1993) of the Fossil Bluff Group that is a clastic-filled forearc basin succession. The specimens were collected from Station KG.4209 ($68^{\circ}39'W$, $71^{\circ}38'S$) on Offset Ridge, Alexander Island, Antarctica (Fig. 1). The Gateway Pass Limestone Bed is exposed discontinuously between scree-filled gullies near the northern foot of the crags of Station KG.4209 for about 200 m (Kelly *et al.* 1995). The seep carbonate is composed of calcite-cemented mudstone and sandstone covered by irregular crusts up to 2 m wide and 20 cm thick. The $\delta^{13}C$ isotope values measured from the seep carbonate are very

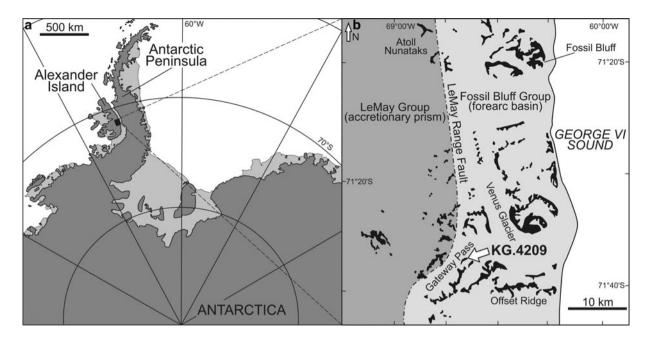


Fig. 1. a. Locality map of Antarctic Peninsula. b. Location of Station KG.4209, Gateway Pass, Alexander Island, Antarctica.

negative and vary from -33.5% to -44.6% PDB (Kelly et al. 1995). The mass aggregations of fauna occurred in the mudstones associated with the crusts (Kelly et al. 1995). Dominant numerically are gastropods (Fig. 2a) with some contribution from large lucinacean and small protobranch bivalves. Kelly et al. (1995) provisionally identified cerithiform and neritiform gastropod shells in the Gateway Limestone Bed. The former are described herein as hokkaidoconchids while the latter could not be confirmed in the material examined. The original aragonitic shells of gastropods have been replaced by nonferroan lowmagnesium calcite spar (Kelly et al. 1995). The palaeolatitude of Alexander Island in the Late Jurassic is estimated as about 60°S by Golonka (2000); however, the terrane model of Vaughan & Storey (2000) places some doubt on any simple palaeolatitude assignment for Alexander Island prior to the mid-Cretaceous. According to Vaughan et al. (2002) the final phase of terrane accretion occurred in late Early Cretaceous.

Material and methods

The Gateway Pass locality was discovered in 1990 and given locality number KG.4209. The same site was revisited in 1992 for which locality number KG.4603 was used. The specimens were collected by S.R.A.K. and deposited in the collection of the British Antarctic Survey (BAS), Cambridge, UK. A part of a slab numbered KG.4603.44 was loaned to A.K. for preparation. The piece of weathered carbonate coquina of about 10 cm in length was split slowly using a hydraulic jawbreaker and the resulting exposed fossils were obtained from the cracked rock. The

specimens and matrix are indurated and do not always part cleanly. The successfully extracted specimens were mounted on stubs, platinum-coated and observed under the Philips XL20 scanning electron microscope (SEM) at the Institute of Paleobiology, Polish Academy of Science, Warsaw, Poland.

Systematic palaeontology

Phylum MOLLUSCA Linné, 1758; Class GASTROPODA Cuvier, 1797 Order CAENOGASTROPODA Cox, 1959 Superfamily Abyssochrysoidea Tomlin, 1927 Family Hokkaidoconchidae Kaim, Jenkins and Warén 2008

Remarks. Hokkaicoconchids have multispiral protoconch which is not decollated, while in provannids the protoconch is always decollated when multispiral. Moreover, the teleoconch of provannids is never as tall as in hokkaidoconchids (Kaim *et al.* 2008a)

Genus Hokkaidoconcha Kaim, Jenkins and Warén 2008 Hokkaidoconcha hignalli sp. nov. Fig. 3d-n

Etymology. The species is named after Martin Hignall (formerly BAS), who was the geological field assistant to S.R.A.K. in the field when the Gateway Pass limestone was discovered in 1990.

Holotype. BAS KG.4603.44C, incomplete adolescent shell with neither protoconch nor aperture (Fig. 3e, g, j-m).

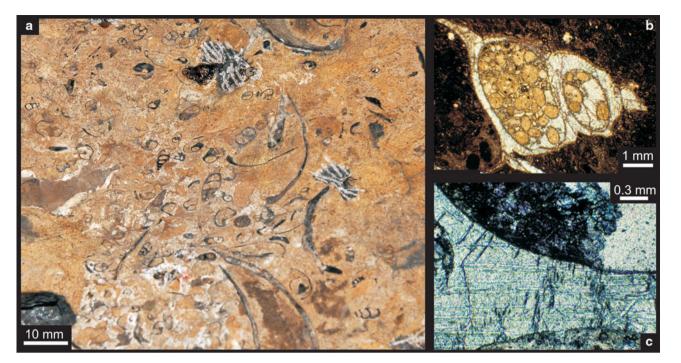


Fig. 2. Gastropod coquina from Upper Jurassic methane seep carbonate from Station KG.4209, Gateway Pass, Alexander Island, Antarctica.
a. A rock slab displaying mass occurrence of hokkaidoconchid gastropods BAS KG.4209.324.
b. Longitudinal cross section of *Hokkaidoconcha hignalli* sp. nov. in mudstone, with inner part of shell having sparry infill. Abundant subspherical/suboval faecal pellets of gastropods clearly shown in contrast to sparry infill, but are also present as completely dark cross-sections within the mudstone.
KG.4209.233.I.
c. Detail from thin section of hokkaidoconchid gastropod showing microborings of probable fungal hyphae penetrating the shell from the interior surface. Their position suggests that infestation was probably post-mortal. KG.4209.233.I

Paratypes. Numerous cross sections on the weathered rock surfaces in the collection at BAS, and on thin sections. Eight specimens were extracted from the rock matrix. Holotype (BAS KG.4603.44C) and two paratypes are illustrated (BAS KG.4603.44B and BAS KG.4603.44D; Fig. 3d, h, i and Fig. 3f & n respectively).

Locality. Station KG.4209 ($68^{\circ}39'W$, $71^{\circ}38'S$) on Offset Ridge, Alexander Island, Antarctica.

Age. Tithonian (Upper Jurassic) Gateway Pass Limestone Bed, Atoll Nunataks Formation, Fossil Bluff Group (Kelly *et al.* 1995).

Diagnosis. Shell is of tall, cylindrical cerithioid shape. Apical whorls are ornamented with strong axial ribs, stronger in the adapical part and fading away in the abapical direction. Later in ontogeny axial ornamentation disappears. Spiral ornamentation is absent. Growth lines are orthocline except the last whorl where they are opisthocyrt. Adapical part of the whorl bears a narrow ramp. There is no clear demarcation of the basal surface.

Description. The shell protoconch is unknown. Initial teleoconch whorls are ornamented with 10-12 sturdy and blunt orthocline axial ribs. The ribs fade away on the

third-fourth preserved whorl. The height of holotype with five whorls is 10.1 mm and its width is 5.1 mm. The aperture is not preserved.

Remarks. We classify the species under consideration as a hokkaidonchid based principally on the gross morphology and mass occurrence in seep carbonates rather than on well-established phylogeny. Such dense occurrence is typical for hokkaidoconchids (and also provannids) in the Cretaceous methane seep deposits of Hokkaido, Japan (Kaim et al. 2008a). However, in case of H. hignalli we cannot confirm its generic attribution because we do not have specimens with protoconch preserved at our disposal. Nevertheless, the specimens described herein are most similar to the specimens of Hokkaidoconcha tehamaensis described by Kiel et al. (2008c) from the Tithonian locality at Paskenta in California. However, the latter species is ornamented by opisthocline rather than orthocline axial ribs and usually (but not always) also possesses fine spiral threads. The axial ribs of H. tehamaensis, similar to those on H. hignalli, are strongest on upper part of whorl and may disappear completely on lower half. Growth lines of H. tehamaensis are strongly prosocyrt unlike the ones of H. hignalli, which are orthocline first and then bent into opisthocline in the upper part of the flank. Similar features are observed in some specimens identified by Kiel et al.

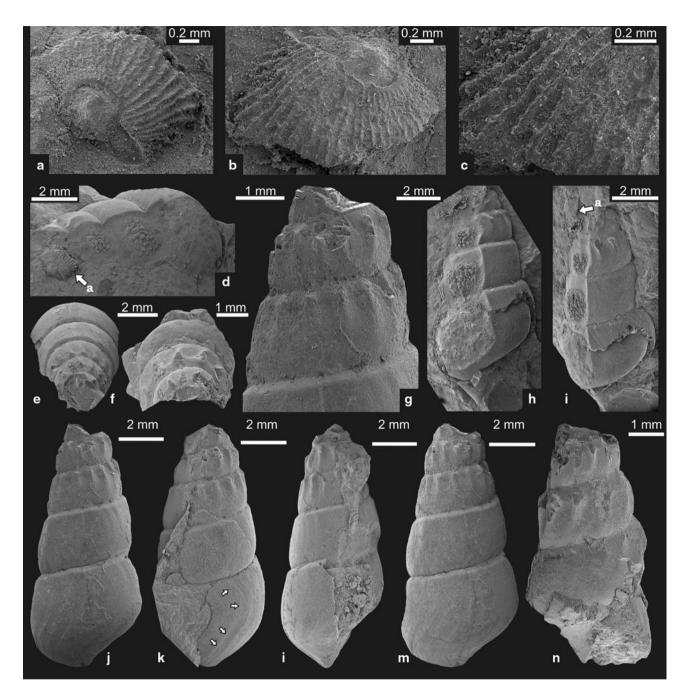


Fig. 3. a-c. Unidentified limpet gastropod BAS KG.4603.44A. d-n. Abyssochrysoid gastropod *Hokkaidoconcha hignalli* sp. nov.
d, h, i. Specimen BAS KG.4603.44B; the arrows on d and i show location of the limpet from Fig. 3a-c. e, g, j-m, the arrows on k show the opisthocyrtic growth lines. Holotype BAS KG.4603.44C. f, n. Specimen BAS KG.4603.44D. Note faecal pellets visible on 3d, h, i & 1.

(2008c: fig. 5K) as *Abyssochrysos? giganteum* Kiel, Campbell, Elder and Little, 2008. The latter species may also belong to Hokkaidoconchidae but again it cannot be confirmed without knowledge of the protoconch morphology.

Gastropoda indet. Fig. 3a-c

Material. The single limpet shell (BAS KG.4603.44A; Fig. 3a-c) is partially exposed in the rock matrix.

Locality. Station KG.4209 (68°39'W, 71°38'S) on Offset Ridge, Alexander Island, Antarctica.

Age. Tithonian (Upper Jurassic) Gateway Limestone Bed, Atoll Nunataks Formation, Fossil Bluff Group (Kelly *et al.* 1995).

Description. An irregular limpet shell, with apex eroded, is partially covered by rock matrix. The shell is 1.1 mm high

and 1.8 mm long. The apex is located about one-third of the shell length in its anterior/posterior extent. The surface is ornamented by numerous ribs, which are triangular in cross-section. There are 26 radial ribs on the visible half of the shell. All ribs are primaries, and there are no secondaries visible on the exposed part. The ribs widen toward the aperture. Interior shell features are unknown.

Remarks. This shell may belong to one of several groups of gastropods having convergent external morphology of the limpet shells. Without knowledge of the protoconch and internal surface we prefer to leave this shell in open nomenclature. Similar irregular shells are known from Patellogastropoda, Neomphalina, Cocculinidae, and Hipponicidae. Less probable are vetigastropods, capulids, siphonariids, and amathinids. Among taxa known from chemosynthesis-based communities similar irregular shell is possessed by the neomphalid *Symmetrocapulus* McLean, 1990. However, this similarity might be purely superficial.

Discussion

The laminated crusts of Gateway Pass Limestone Bed were originally identified as stromatolites (Kelly 1991) and consequently reinterpreted as methane-seep carbonates based on peculiar growth pattern, and even more importantly, on their geochemical signature (Kelly et al. 1995). The crusts would appear to have been deep water bacterial mats which lined the seep openings. The bacterial crusts probably provided the food source for the grazing hokkaidoconchid and other gastropods. Associated with the mudstones and the sediment filled shells are abundant faecal pellets (Kelly et al. 1995: text-fig. 6D). These are about 1 mm diameter and subspherical in shape (Fig. 2b & Fig. 3d, h, i, 1). They are typical of those made by gastropods. Despite the few protobranch bivalves present (Kelly et al. 1995, fig. 6C), which are known to be active deposit feeders, the sediment appears not to have been significantly reworked by sediment and detritus-feeding fauna, thus the gastropod faecal pellets have survived. The few large lucinid bivalves were living deeply within the sediment, and were collecting nutrient largely from the symbiotic bacteria on modified gills (Taylor & Glover 2000).

Provannids, the Recent counterparts of hokkaidoconchids, are known from both vents and seeps, as well as from various organic substrates in the deep sea (Kaim *et al.* 2008a). Large provannid genera *Ifremeria* and *Alviniconcha* are vent-specialized and they derive their nourishment largely from endosymbiotic bacteria (Suzuki *et al.* 2006). Species of two other genera (*Desbruyeresia* and *Provanna*) are much smaller and they apparently obtain their nourishment from grazing (Warén & Bouchet 1993). It seems to be sound arguing that hokkaidoconchids had a life style similar to the smaller species of Provannidae.

We could not find any specimens of brachiopod *Peregrinella* which are extremely common in many Late Jurassic–Early Cretaceous seep sites (see e.g. Kiel & Peckmann 2008). As suggested by Kiel & Peckmann (2008) *Peregrinella* and lucinds were mutually exclusive at the methane seeps. *Peregrinella* most commonly accompanied by modiomorphid *Caspiconcha* and/or abyssochrysoid *Paskentana* as documented is from several North American and European seep sites (Kiel & Peckmann 2008). The fauna from Gateway Pass Limestone Bed represents another type of association dominated by lucinid bivalves and hokkaidoconchid gastropods. Similar associations are known from US Pacific Coast (Kiel *et al.* 2008c) and Japan (Kaim *et al.* 2008a).

Conclusions

The Tithonian (Upper Jurassic) Gateway Pass Limestone Bed preserves the only known Mesozoic methane seep association from the Southern Hemisphere. The most abundant are high-spired gastropods identified by Kelly et al. (1995) as cerithiforms described here as probable hokkaidoconchids. Their mass occurrence together with a limpet gastropod and lucinid bivalves strongly resembles those of the Cretaceous hydrocarbon seep assemblage at Kanajirisawa in Hokkaido, Japan (Kaim et al. 2008a). Such gastropod assemblages are also relatively common in the Cretaceous plesiosaur bone (Kaim et al. 2008b), sunken wood (Kiel et al. 2008b), and other hydrocarbon seep associations from Japan and from the Pacific Coast of the USA (Kiel et al. 2008c). This suggests strongly that already in the Late Jurassic this type of community was well developed and widespread throughout the world oceans (Kaim et al. 2008a: table 1) reaching high austral latitudes by Tithonian. The large distance between Antarctic and North Pacific localities strongly suggests that the association of provannid/hokkaidoconchid gastropods with chemoautotrophy-based communities have originated well before latest Jurassic. Hokkaidochid-lucinid associations stand probably in opposition to Peregrinelladominated associations as recently suggested by Kiel & Peckmann (2008).

Acknowledgements

The material was collected during the Natural Environment Research Council (NERC) supported Mesozoic Forearc Basin Dynamics project conducted by the British Antarctic Survey (BAS) under the leadership of David Macdonald (formerly BAS, now Aberdeen University). Martin Hignall and Nick Lewis (formerly BAS) assisted S.R.A.K. in collecting the samples in 1990 and 1992 respectively. J. Alistair Crame, Mike Tabecki and Alex Tate are thanked for access to the BAS Collections. Anders Warén (Naturhistoriska Riksmuseet, Stockholm, Sweden) is acknowledged for comment on the gastropods described herein. Robert G. Jenkins (University of Yokohama, Japan) is acknowledged for assistance in Cambridge and critical reading the early draft of this paper. J. Alistair Crame and Steffen Kiel are acknowledged for their thoughtful reviews.

References

- CAMPBELL, K.A. 2006. Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: past developments and future research directions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232, 362–407.
- CAMPBELL, K.A. & BOTTJER, D.J. 1991. Enigmatic limestones and associated faunas in the Great Valley Sequence (Jurassic–Cretaceous) of California. *Geological Society of America, Abstracts with Programs*, 23, 10.
- CAMPBELL, K.A. & BOTTJER, D.J. 1993. Fossil cold seeps (Jurassic–Pliocene) along the convergent margin of western North America. *National Geographic Research and Exploration*, 9, 326–343.
- DOUBLEDAY, P.A.D., MACDONALD, D.I.M. & NELL, P.A.R. 1993. Sedimentology and structure of the trench-slope to forearc basin transition in the Mesozoic of Alexander Island, Antarctica. *Geological Magazine*, **130**, 737–754.
- EASTON, W.H. & IMLAY, R.W. 1955. Upper Jurassic fossil localities in Franciscan and Knoxville formations in southern California. *The American Association of Petroleum Geologists Bulletin*, **39**, 2236–2340.
- GAILLARD, C., RIO, M., ROLIN, Y. & ROUX, M. 1992. Fossil chemosynthetic communities related to vents or seeps in sedimentary basins: the pseudobioherms of southeastern France compared to other world examples. *Palaios*, 7, 451–465.
- GOLONKA, J. 2000. Cambrian-Neogene: plate tectonic maps. Kraków: Wydawnictwa Uniwersytetu Jagiellońskiego, 125 pp.
- HIKIDA, Y., SUZUKI, S., TOGO, Y. & JIRI, A. 2003. An exceptionally wellpreserved fossil seep community from the Cretaceous Yezo Group in the Nakagawa area, Hokkaido, northern Japan. *Paleontological Research*, 7, 329–342.
- JENKINS, R.G., KAIM, A. & HIKIDA, Y. 2007a. Antiquity of the substrate choice among acmaeid limpets from Late Cretaceous chemosynthesisbased communities. *Acta Palaeontologica Polonica*, **52**, 369–373.
- JENKINS, R.G., KAIM, A., HIKIDA, Y. & TANABE, K. 2007b. Methane flux dependent lateral faunal changes in a Late Cretaceous chemosymbiotic assemblage from the Nakagawa area of Hokkaido, Japan. *Geobiology*, 5, 127–139.
- KAIM, A., JENKINS, R.G. & WARÉN, A. 2008a. 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*, **154**, 421–436.
- KAIM, A., KOBAYASHI, Y., ECHIZENYA, H., JENKINS, R.G. & TANABE, K. 2008b. Chemosynthesis-based associations on Cretaceous plesiosaurid carcasses. *Acta Palaeontologica Polonica*, 53, 97–104.
- KELLY, S.R.A. 1991. Antarctic stromatolites from the Late Jurassic of Alexander Island. *Palaeontological Association Newsletter*, **12**, 12.

- KELLY, S.R.A., DITCHFIELD, P.W., DOUBLEDAY, P.A. & MARSHALL, J.D. 1995. An Upper Jurassic methane-seep limestone from the Fossil Bluff Group Forearc Basin of Alexander Island, Antarctica. *Journal of Sedimentary Research*, A65, 274–282.
- KIEL, S. & LITTLE, C.T.S. 2006. Cold-seep mollusks are older than the general marine mollusk fauna. *Science*, **313**, 1429–1431.
- KIEL, S. & PECKMANN, J. 2008. Paleoecology and evolutionary significance of an Early Cretaceous *Peregrinella*-dominated hydrocarbon-seep deposit on the Crimean Peninsula. *Palaios*, 23, 751–759.
- KIEL, S., AMANO, K. & JENKINS, R.G. 2008a. Bivalves from Cretaceous coldseep deposits on Hokkaido, Japan. *Acta Palaeontologica Polonica*, 53, 525–537.
- KIEL, S., AMANO, K., HIKIDA, Y. & JENKINS, R.G. 2008b. Wood-fall associations from Late Cretaceous deep-water sediments of Hokkaido, Japan. *Lethaia*, 10.1111/j.1502-3931.2008.00105.x.
- KIEL, S., CAMPBELL, K.A., ELDER, W.P. & LITTLE, C.T.S. 2008c. Jurassic and Cretaceous gastropods from hydrocarbon seeps in forearc basin and accretionary prism settings, California. *Acta Palaeontologica Polonica*, 53, 679–703.
- MAJIMA, R., NOBUHARA, T. & KITAZAKI, T. 2005. Review of fossil chemosynthetic assemblages in Japan. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 227, 86–123.
- McLEAN, J.H. 1990. A new genus and species of neomphalid limpet from Mariana vents with a review of current understanding of the relationships among Neomphalacea and Peltospiracea. *Nautilus*, 104, 77–86.
- SANDY, M.R. & CAMPBELL, K.A. 1994. A new rhynchonellid brachiopod genus from Tithonian (Upper Jurassic) cold-seep deposits of California and its paleoenvironmental setting. *Journal of Paleontology*, 68, 1243–1252.
- STANTON, T.W. 1895. Contributions to the Cretaceous paleontology of the Pacific coast: the fauna of the Knoxville beds. *Bulletin of the United States Geological Survey*, **133**, 1–132.
- SUZUKI, Y., KOJIMA, S., SASAKI, T., SUZUKI, M., UTSUMI, T., WATANABE, H., URAKAWA, H., TSUCHIDA, S., NUNOURA, T., HIRAYAMA, H., TAKAI, K., NEALSON, K.H. & HORIKOSHI, K. 2006. Host-symbiont relationships in hydrothermal vent gastropods of the genus *Alviniconcha* from the southwest Pacific. *Applied and Environmental Microbiology*, **72**, 1388–1393.
- TAYLOR, J.D. & GLOVER, E.A. 2000. Functional anatomy, chemosymbiosis and evolution of the Lucinidae. In HARPER, E.M., TAYLOR, J.D. & CRAME, J.A., eds. The evolutionary biology of the Bivalvia. Geological Society, London, Special Publication, 177, 207–255.
- VAUGHAN, A.P.M. & STOREY, B.C. 2000. The eastern Palmer Land shear zone: a new terrane accretion model for the Mesozoic development of the Antarctic Peninsula. *Journal of the Geological Society*, 157, 1243–1256.
- VAUGHAN, A.P.M., PANKHURST, R.J. & FANNING, C.M. 2002. A mid-Cretaceous age for the Palmer Land event, Antarctic Peninsula: implications for terrane accretion timing and Gondwana palaeolatitudes. *Journal of the Geological Society*, **159**, 113–116.
- WARÉN, A. & BOUCHET, P. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta*, 22, 1–90.