

# A new Late Pliocene large provannid gastropod associated with hydrothermal venting at Kane Megamullion, Mid-Atlantic Ridge

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## Abstract

A new gastropod, *Kaneconcha knorri* gen et sp. nov., was found in marlstone dredged from the surface of Adam Dome at Kane Megamullion on the flank of the Mid-Atlantic Ridge in an area of former hydrothermal activity. The snail is interpreted as a large provannid similar to the chemosymbiotic genera *Ifremeria* and *Alviniconcha*. This is the first record of presumably chemosymbiotic provannids from the Atlantic Ocean and also the first fossil record of such large provannids associated with hydrothermal venting. Extant *Alviniconcha* and *Ifremeria* are endemic to hydrothermal vents in the Pacific and Indian oceans. *Kaneconcha* differs from *Ifremeria* in having no umbilicus and a posterior notch, and it differs from *Alviniconcha* in having the profile of the whorl slightly flattened and having no callus on the inner lip. A dark layer covering the *Kaneconcha* shell is interpreted here as a fossilized periostracum. The shell/periostracum interface shows fungal traces attributed to the ichnospecies *Saccomorpha clava*. We hypothesize that large chemosymbiotic provannids (i.e., *Kaneconcha*, *Ifremeria*, and *Alviniconcha*) form a clade that possibly diverged from remaining provannids in the Late Jurassic, with the Late Jurassic/Early Cretaceous *Paskentana* being an early member.

## Introduction

Hydrothermal venting has been observed and investigated along the axes of mid-ocean ridges (MORs) for more than three decades (e.g., Rona, 1984). The majority of known vents expel high-temperature (>300°C) fluids in basalt-hosted environments and are associated with precipitation of polymetallic sulfides. At faster-spreading ridges these vents typically occur along the neovolcanic zone, while at slow-spreading ridges they also are commonly associated with faults and fractures outside this zone but within the MOR rift valley (German and Von Damm, 2003). Low-temperature (<100°C) venting from basaltic basement is thought to be much more widespread, both within and outside MOR rift valleys (German and Von Damm, 2003); it can be either localized or diffuse, and it is often associated with precipitation of Fe- and Mn oxyhydroxides. In addition, low-temperature fluids can emanate from fractures in serpentinized-peridotite basement, constructing edifices composed of calcite, aragonite, and brucite (e.g., the Lost City vents at Atlantis Massif near 30°N on the Mid-Atlantic Ridge; Kelley *et al.* 2001).

Hydrothermal vents are well known for having unusual biological communities that are based on chemosynthetic processes. Taxonomic diversity at vents is basically similar in a majority of communities worldwide, although variations in composition of the populations are discernible between particular basins and even oceans (Desbruyères *et al.* 2006). For example, Atlantic vents are dominated by mussels and swarms of shrimps while Pacific vents are dominated by large provannid gastropods, mussels, and siboglinid tube and alvinellid worms. Indian Ocean vent communities appear to have a mixture of these assemblages. The most characteristic animals thriving in hydrothermal vent ecosystems are polychaetes and molluscs (see e.g. Desbruyères *et al.* 2006). Among the molluscs, gastropods and bivalves are the most abundant in numbers and also the most diversified taxonomically. Gastropods are probably the most species-rich group of vent animals (more than 100 species identified in 50 genera), and they are also the best known group in terms of distribution and zoogeography (Desbruyères *et al.* 2006). Within the entire Atlantic Ocean, all but one major group of vent gastropods are present, although the populations are generally sparse. It appears, however, that generic gastropod diversity at the Mid-Atlantic Ridge is somewhat impoverished (or is underestimated) because there are only 15 genera reported from Mid-Atlantic Ridge vents while, for example, the East Pacific Rise has 24 genera. The most striking feature of the Mid-Atlantic Ridge gastropod distribution is the total absence of the family Provannidae, even though its species are known from Caribbean and West African hydrocarbon seeps (Warén & Bouchet 2009). Therefore the finding of large fossil provannid gastropods in deposits that accumulated in a zone of venting that was once active at the Mid-Atlantic Ridge axis is interesting in both paleogeographical and evolutionary aspects.

In the present paper we focus on description and interpretation of large gastropods that appear to have been associated with venting of hydrothermal fluids at Kane Megamullion when it was at or near the axis of the Mid-Atlantic Ridge. The megamullion lies just south of Kane Fracture Zone on the west flank of the Mid-Atlantic Ridge near 23°30'N (Fig. 1). This gastropod is unique in two ways: 1) It is the first reported occurrence of a large provannid gastropod in the Atlantic Ocean, and 2) it is the first reported, fossil occurrence of vent-related gastropods found off-axis in any ocean basin. To provide context for our descriptions, we summarize below the geological setting and evidence for hydrothermal venting at Kane Megamullion.

### **Geological Setting of Kane Megamullion**

Kane Megamullion (Fig. 1) is an oceanic core complex, originally formed by very long-lived slip (~1-2 m.y.) on a single normal or 'detachment' fault in the west wall of the Mid-Atlantic Ridge rift valley. Because of the unusually long duration of fault slip, the footwall of the detachment rolled over to maintain isostasy, and it formed the dome-shaped megamullion. The detachment fault surface caps the megamullion (Fig. 2) and has characteristic corrugations (mullion structures) that are parallel to the slip direction and have amplitudes up to several hundred meters (Tucholke *et al.* 1998).

Kane Megamullion now lies between about 30 and 55 km off-axis and is developed in crust that dates from 3.3 Ma (the age of the ‘breakaway’ where the detachment fault originally nucleated) to the fault termination at 2.1 Ma (the seafloor trace of the contact between the footwall and hanging wall of the now-inactive fault) (Figs. 1 and 2). The detachment fault surface is cut by two major sets of high-angle, west-facing normal faults (East and West faults) that developed in response to bending stresses as the footwall was exhumed and rolled over. These faults divide the megamullion into a series of domes as labelled in Fig. 1. Sampling of the detachment surface and the interior of the footwall where it is exposed in the high-angle fault scarps and in slump scars has been accomplished both by dredging and by use of the remotely operated vehicle (ROV) Jason. The samples show that the footwall consists primarily of gabbros and mantle peridotites (Dick *et al.*, 2008). A notable exception occurs at Adam Dome, where West Fault exposes an upward transition from gabbros to sheeted diabase dikes.

Manifestations of low-temperature hydrothermal venting were observed in all but one dive made by ROV Jason at several places across the surface of Kane Megamullion (stars, Fig. 1). Visual indications of venting appear in two forms: 1) cemented mounds of mixed rock debris and Mn-Fe-rich sediment, and 2) cemented, slabby sedimentary layers that also are Mn- and Fe-rich (Tucholke *et al.*, 2007). Geochemical analyses of a variety of Fe-Mn-rich sediment samples recovered by ROV Jason show a clear signature of low-temperature hydrothermal venting, although in some other samples the enrichment is hydrogenous, i.e., precipitated from seawater (B.E. Tucholke, S. Humprihs and H.J.B. Dick, manuscript in preparation).

The cemented debris mounds range from conical to elongate or ridge-like and are up to ~8 meters high, with flank slopes of ca. 30° to near-vertical. Compositions of the mounds range from nearly pure rock debris (primarily basalt, but also occasional gabbro and serpentinite) to polymict breccia, commonly cemented together by Fe-Mn-rich sediment. Some mounds contain nearly pure, Fe-Mn-rich sediment that shows flow structures resembling basalt pillows. The mounds are thought to have been produced where point-source, low-temperature fluid venting occurred through the hanging wall close to the seafloor trace of the detachment fault when it was active at the Mid-Atlantic Ridge axis (dashed arrow, Fig. 2) (Tucholke *et al.* 2007). The fluids are thought to have cemented the hanging-wall debris and affixed it to the emerging footwall while the surrounding unconsolidated debris wasted away down the sloping fault surface.

Slabby, Fe-Mn-rich sedimentary layers occur on the flanks or at the bases of mounds and also on relatively smooth seafloor. In the latter case, the slabs are sometimes cracked in linear to polygonal patterns, with upturned ridges produced at the cracks.

The predominantly sedimentary mounds, as well as the cemented and cracked slabs, may have formed in association with diffuse venting of low-temperature fluids through the footwall as it was exhumed and fractured in response to extensional bending stresses during rollover.

It is notable that no hydrothermal sulfides have been found at Kane Megamullion, and

there consequently is no existing evidence for high-temperature venting there. However, it is entirely possible that such venting did occur and has yet to be discovered.

### **Geological Context of Sampled Gastropods**

The gastropods that we describe here were sampled by dredging (haul number Knorr 180-2-28) from seafloor that dates to Late Pliocene on the east flank of Adam Dome (Figs. 1 and 2). According to seafloor magnetic-anomaly interpretations of Dick *et al.* (2008), crust at this location lies at chron 2An.1n, indicating an age of ~2.6-3.0 Ma on the Gradstein *et al.* (2004) time scale. The east flank of Adam Dome is part of the original detachment-fault surface that was uplifted and rotated eastward when West Fault was formed (Fig. 2). There was no ROV Jason dive to document hydrothermal features at the dredge location. However, hydrothermal features were identified on the detachment surface farther upslope near the crest of the dome (star, Figs. 1 and 2). In addition, the broad distribution of hydrothermal features noted in Fig. 1 suggests that hydrothermal effects probably occur across most of the detachment surface, including the area of the dredge site.

Dredge Knorr 180-2-28 recovered primarily peridotite with lesser amounts of gabbro, but it also yielded 5.5 kg of marlstone that contained the gastropods (Fig. 3). The marlstone is a clayey foram-nannofossil micrite. It contains abundant *Orbulina* and occasional small mineral and basalt grains typically less than 1 mm in size. Unlike slabby carbonates that are more typical of the observed hydrothermal deposits on Kane Megamullion, these marlstones show no unusual Fe-Mn enrichment and they are relatively uniform rather than layered. Thus they seem not to have been deposited directly at a vent location, but it is unknown how far removed they may have been from a vent site.

The question arises as to whether the gastropods were associated with venting at the axis of the Mid-Atlantic Ridge at the time that Kane Megamullion was formed, or with later venting that occurred off-axis. Nannofossils in sediment taken from within the aperture of one of the specimens date to Late Pliocene Zone NN16b (M.-P. Aubry, written comm., 2010), or about 2.5 to 2.8 Ma on the time scale of Gradstein *et al.* (2004). This is the same age as the underlying crust, and it indicates that the gastropods lived in association with hydrothermal venting that occurred either on or very close to the axis of the Mid-Atlantic Ridge in Late Pliocene time.

The gastropods occur mostly as shell fragments, although one nearly complete specimen was recovered (Fig. 3). After the larger, more intact specimens were recognized in the dredge samples (Fig. 3E), careful dissection of the marlstones recovered additional fragments. All the shells are literally paper-thin, and during extraction they were coated with a thin layer of glue in order to prevent cracking and disintegration. In all, six incomplete gastropods plus one nearly complete specimen (Fig. 3) were extracted, and they probably represent the same number of individuals.

### **Institutional abbreviations**

SMNH, Swedish Museum of Natural History, Stockholm, Sweden; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

### **Systematic palaeontology**

Phylum **Mollusca** Linnaeus 1758

Class **Gastropoda** Cuvier 1797

Order **Caenogastropoda** Cox, 1959

Superfamily **Abyssochrysoidea** Tomlin, 1927

Family **Provannidae** Warén & Ponder, 1991

Genus *Kaneconcha* nov.

**Derivation of name.** After Kane Megamullion, the type locality, and Latin *concha*, shell.

**Type species.** *Kaneconcha knorri* sp. nov., by monotypy.

**Diagnosis.** As for the species.

*Kaneconcha knorri* sp. nov.

(Fig. 3)

**Diagnosis.** Rounded globose shell of moderate size. Lateral flank slightly flattened with evenly rounded demarcation from shell base. Maximum shell diameter at flank-base demarcation. Suture weakly incised. Blunt spiral ribs evenly distributed. Dense prosocline enhanced growth lines. Aperture with shallow anterior notch.

**Derivation of name.** After the name of the research ship R/V Knorr, from which dredge-haul 180-2-28 recovered the type material from seafloor on the flank of the Mid-Atlantic Ridge.

**Holotype.** ZPAL Ga.16/1 (Fig. 3), an almost complete shell with no protoconch.

**Type locality.** Atlantic Ocean, Kane Megamullion, east flank of Adam Dome. Coordinates: 23° 23' N, 45° 23' W. Water depth: 3293-2827 m.

**Type horizon.** Marlstone bed sampled by dredging, Knorr dredge number 180-2-28, Late Pliocene.

**Other material.** Six incomplete specimens (ZPAL Ga.16/2-7) from marlstones of the same dredge haul as the holotype.

**Description.** Protoconch unknown. Shell moderately large, globose, with lateral flank slightly flattened, and with high expansion rate. Shell thin, composed of two layers. Inner layer milky white, external layer dark brown. Both layers re-calcified so the original

microstructure could not be observed. In some places there are traces of bioerosion between inner and outer layers, infilled by a substance of the same colour and mineralogy as the outer layer. Ornamentation consists of blunt spiral ribs evenly distributed over lateral flank and the base and prosocline-enhanced growth lines. There are six spiral ribs on lateral flank and five on the base. The base is not clearly demarcated from the lateral flank. Aperture teardrop-shaped with shallow anterior notch. No callus on the inner and outer lips.

**Dimensions.** The holotype is 32 mm high and 34.5 mm wide. The shell wall is approx. 200  $\mu\text{m}$  thick in the apertural region of the fully grown specimen. The inner white layer is about 175  $\mu\text{m}$  thick while the outer dark brown layer is about 25  $\mu\text{m}$  thick.

**Remarks.** *Kaneconcha* has a quite unique shell morphology. The only similar known gastropod is *Ifremeria*, which has some similarity in the shape and sculpture of the basal surface. *Ifremeria* is one of two large Recent provannids (i.e., *Ifremeria* and *Alviniconcha*) that host symbiotic chemoautotrophic bacteria and are endemic to high-temperature hydrothermal vents. The mineralized part of the shell of these Recent gastropods is very thin, thinner than the external organic layer, the periostracum, towards the outer lip. During desiccation their shells crack into several pieces due to tension created when the organic and mineral layers shrink differentially. Thus their shells are usually kept in alcohol, and adult *Alviniconcha* and *Ifremeria* shells illustrated in the literature (e.g., Okutani & Ohta 1988; Bouchet & Warén 1991; Warén & Bouchet 1993) are covered by the thick periostracum. Juveniles of *Alviniconcha* are usually ornamented by one or two spiral keels that disappear later during the ontogeny, and adult shells are smooth or they show weakly visible spiral lines. Small specimens of *Ifremeria* are heavily ornamented with numerous spiral ribs equipped with blunt nodes. Later in ontogeny the ornaments largely disappear and only weakly visible spiral lines remain (Warén & Bouchet 1993, Fig. 4 herein). The adult *Ifremeria* possesses, however, a well developed spiral ridge near the apical suture, which is manifested as a narrow indentation on the outer lip and a groove on the inner surface of the shell. The adult shell of *Ifremeria* also possesses a shallow umbilicus that is absent at the juvenile stage. Both *Ifremeria* and *Alviniconcha* have an indistinct anterior canal. When compared to these two genera, our adult/adolescent *Kaneconcha* is similar in having a globose shell outline, weakly expressed spiral ornamentation, a very thin shell, and a shallow anterior notch. It differs from *Ifremeria* in having no umbilicus and posterior notch and from *Alviniconcha* in having the profile of the whorls slightly flattened (*Alviniconcha* has the shell evenly rounded) and in having no callus on the inner lip. It seems that *Kaneconcha* (Fig. 3) is more similar to *Ifremeria* (Fig. 4) than to *Alviniconcha*, especially in the organization of corrugated growth lines in the siphonal region of its aperture.

Among fossil gastropods, the most similar are Late Jurassic-Early Cretaceous *Paskentana* (Kiel *et al.* 2008, 2010) and Oligocene *Elmira* (Cooke 1919; Kiel & Peckmann 2007) from hydrocarbon seep deposits in California and Cuba, respectively. *Kaneconcha* differs from *Paskentana* in having higher expansion rate and the maximum shell diameter at the flank-base demarcation, while in *Paskentana* maximum diameter is gained in the middle portion of the lateral flank. *Kaneconcha* differs from *Elmira* in

having a slightly flattened lateral flank while *Elmira* is evenly rounded and its shell is much thicker. We feel that that Provannidae is the best assignment for *Kaneconcha*, although we do not know the protoconch of the new gastropod, which could have helped this identification.

### **The dark layer as possible fossilized periostracum.**

The new gastropod possesses a dark brown layer (Fig. 5C, D) that is interpreted here as a fossilized periostracum. The periostracum in shelly organisms (e.g., molluscs and brachiopods) is a protective layer, composed of proteins, that reduces dissolution of the mineral shell by chemical agents, bioeroders, and epizoans (e.g., Bottjer 1981). The large species of provannids are known to possess an extremely thick periostracum that protects the thin mineral shell. In *Ifremeria nautilei* Bouchet & Warén, 1991 the periostracum might be nearly twice as thick as the mineral shell (Fig. 5B). The species of *Alviniconcha*, in addition to a thick periostracum attached directly to the shell, also possesses abundant periostracal hairs (Fig. 5A). The organic periostracum is rarely preserved in fossil specimens although there are some reports of such preservation in specimens from geological epochs ranging back to Cambrian (e.g., Singh 1979, Biernat and Baliński 1982, Butterfield 2003). The fossil occurrences still require critical evaluation, but that task is beyond the scope of this paper.

The fossil shells of *Kaneconcha* are composed of two distinct layers (Fig. 5C, D). The milky white layer is interpreted here as the calcareous layer while the dark brown layer is interpreted as a fossilized periostracum. The dark layer is thinner than the periostraca known from Recent shells of *Ifremeria* and *Alviniconcha*. Possibly the organic periostracum shrunk during fossilization. A fragment of a dissected shell shows that the periostracum-shell interface was settled by bioeroders (Fig. 5D). The shell surface is bored by numerous sack-shaped cavities resembling the ichnospecies *Saccomorpha clava* Radtke, 1991 attributed to marine endolithic fungi (Golubic *et al.* 2005; Wisshak *et al.* 2008). The cavities are partially infilled by calcareous material that is visually identical to the overlying dark layer. The “sack” interiors are hollow. These features strongly suggest that the organic membranes of the borers were re-calcified at the same time as the organic periostracum.

### **Evolutionary context of *Kaneconcha***

Provannidae is a group of gastropods that thrive in chemoautotrophy-based communities. The various species of *Provanna* occur at hydrothermal vents, hydrocarbon seeps, vertebrate falls and sunken driftwood (Warén & Bouchet 1986, 1993, 2001, 2009; Okutani & Ohta 1988; Bouchet and Warén, 1991; Warén & Ponder 1991; Lewis & Marshall 1996; Sasaki *et al.* 2005; Johnson *et al.* 2010). *Cordesia* is known from seeps and sunken wood, and *Rubyspira* is restricted to whale falls. *Ifremeria*, *Alviniconcha* and Recent *Desbruyeresia* are known exclusively from hydrothermal vents, but only the former two are known to host chemosymbiotic bacteria in their gills. *Ifremeria* harbours thiotrophic  $\gamma$ -Proteobacteria (Suzuki *et al.* 2006; Dubilier *et al.* 2008) while *Alviniconcha* is known to harbour thiotrophic  $\gamma$ - and  $\epsilon$ -Proteobacteria. Moreover, Borowski *et al.*

(2002) suggest that thiotrophic and methanotrophic symbionts co-occur in *Ifremeria* from vents in the north-Fiji back arc basin (see also Dubilier *et al.* 2008). Hosting large quantities of symbiotic bacteria apparently caused a change in shell morphology from high-spired in the majority of provannids to a fast-expanding littorinimorph that characterizes the large provannids *Ifremeria* and *Alviniconcha*. Much of the shell volume of these provannids is used to accommodate the hypertrophied gill. Based on this observation, we believe that *Kaneconcha* was also dependent on symbiotic bacteria for its nourishment.

The small and high-spired provannids and their ancestor/sister group Hokkaidoconchidae are well documented from Late Cretaceous hydrocarbon seep deposits (Kaim *et al.* 2008a, 2009) and are also known from coeval plesiosaur falls (Kaim *et al.* 2008b) and sunken driftwood (Kiel *et al.* 2009). However, the large provannids have not been found in the fossil record thus far, although a connection between provannids and Late Jurassic-Early Cretaceous *Paskentana* (which have relatively large shells) has been proposed by Kiel *et al.* (2008), supported by a finding of a single provannid-like protoconch associated with mass accumulation of *Paskentana* shells. The idea of an early origin and radiation of provannid gastropods has recently been reinforced by a description of the new provannid *Rubyspira* found on whale falls off California (Johnson *et al.* 2010). Conchologically, *Rubyspira* is strikingly similar to the Early Cretaceous provannid *Atresius* known from hydrocarbon seep deposits on the US Pacific Coast (Kiel *et al.* 2008). Although *Paskentana*-like gastropods are not known from numerous Late Cretaceous chemoautotrophy-based associations in Japan (Kaim *et al.* 2008a, b, 2009; Kiel *et al.* 2009) or from numerous Cenozoic ones worldwide (e.g. Majima *et al.* 2005, Campbell 2006), it has to be stressed that the majority of the Cenozoic localities represent hydrocarbon seeps and very few are hydrothermal vent deposits (Little 2002; Little & Vrijenhoek 2003; Majima *et al.* 2005, Campbell 2006). In this context our finding of *Kaneconcha*, allegedly representing large chemosymbiotic provannids in a Late Pliocene hydrothermal setting, might suggest that this group of gastropods was restricted to vents by Cenozoic time. We do not suggest that *Paskentana* is a direct ancestor of the *Ifremeria/Alviniconcha/Kaneconcha* clade. However, the molecular clock estimates calculated by Johnson *et al.* (2010) seem to suggest a Mesozoic origin of large symbiont-bearing provannids, which were suggested to have diverged from the *Provanna* and *Desbruyeresia/Rubyspira/Abyssochrysos* clades by the Early Cretaceous. It is also worth keeping in mind that species of *Paskentana* are known from seeps only, and no modern seep-dependent snails are known to have symbiotic bacteria (AW unpublished).

### **Palaeogeography and palaeoenvironment of provannids**

Known occurrences of the two Recent chemosymbiotic provannids are restricted to the Pacific and Indian oceans (Fig. 6). *Alviniconcha* occurs in Lau Basin, Fiji Basin, Manus Basin, Mariana Trough (all in the Pacific Ocean) and in the vicinity of Rodriguez Triple Junction (Indian Ocean). *Ifremeria* has been found only in the Pacific in Lau Basin, Fiji Basin, and Manus Basin. The remaining known provannids are not chemosymbiotic and are high-spired; they currently occur worldwide although they are



uncommon in the Atlantic Ocean. Of these forms, *Provanna* is known from Caribbean and Gulf-of-Mexico cold seeps and probably sunken wood (Warén & Ponder 1991), while *Cordesia* is known from cold seeps off the mouth of the Congo River (Warén & Bouchet 2009) and also from a single larva collected over the Mid-Atlantic Ridge off West Africa (Bouchet & Warén 1994; Warén & Bouchet 2009).

To date, no Recent provannids of either chemosymbiotic or other species have been reported from areas of hydrothermal venting on the Mid-Atlantic Ridge. It remains unclear whether this absence is a real phenomenon or is an artifact of insufficient sampling. However, the finding at Kane Megamullion of the Late Pliocene *Kaneconcha*, assumed to be a provannid with symbionts, indicates that chemosymbiotic provannids were present in the Atlantic Ocean in the past, and it suggests that they may still occur there.

The palaeoenvironment of the *Kaneconcha* occurrence and the nature of the gastropods' symbionts is uncertain. The related *Alviniconcha* and *Ifremeria* are both associated with hot vents, whereas all known hydrothermal activity at Kane Megamullion was low-temperature. It would appear either that the occurrence of hot vents at the megamullion has been missed (not at all unlikely) or that the *Kaneconcha* symbionts were iron- and manganese-oxidizing forms (although such symbioses are so far unknown among gastropods). In addition, or perhaps alternately, *Kaneconcha* could have harboured methanotrophic symbionts as has been suggested by Dubilier *et al.* (2008) for some *Ifremeria nautilei* from North Fuji Basin. As previously noted, a substantial portion of the basement at Kane Megamullion is serpentinized peridotite, and methane generated by the process of serpentinization (e.g., Charlou *et al.* 1998) and degassed from the basement could have supported methanotrophs. More speculatively, hydrogen-oxidizing bacteria might have formed symbioses with the gastropods, since hydrogen is also an abundant product of the serpentinization reaction; as yet, however, there is no evidence to support such an association. Irrespective of these considerations, it is worth noting that there are no Recent gastropods known to host chemosymbiotic bacteria from cold seeps or food falls. All previously reported (and some yet undescribed, AW unpublished data) chemosymbiotic gastropods live around hot vents.

## Conclusions

A new large gastropod has been found in Upper Pliocene sediments dredged from Kane Megamullion on the west flank of the Mid-Atlantic Ridge, where there are common morphological and geochemical manifestations of former low-temperature hydrothermal venting. The new gastropod, here named *Kaneconcha knorri*, is interpreted as being related to the large, inflated genera of Provannidae, *Ifremeria* and *Alviniconcha*, that are associated with high-temperature hydrothermal venting in the Pacific and Indian Oceans. This finding constitutes the first reported occurrence of large provannid gastropods in the Atlantic Ocean and also the first reported fossil occurrence of large gastropods formerly associated with ridge-axis hydrothermal venting in any ocean basin. The fact that Cenozoic large provannids are known only from hot-vent environments suggests that *Kaneconcha* was also a hot-vent form, even though no hot-vent deposits have been

identified thus far at Kane Megamullion. Alternately, the chemoautotrophic symbionts in *Kaneconcha* may have been iron- or manganese-oxidizing, or even methanotrophs that thrived on methane released by serpentinization of the underlying peridotite basement. The molecular clock estimation for the time of divergence of large chemosymbiotic and other provannids (Johnson *et al.* 2010) may support an interpretation that *Paskentana*, an extinct gastropod from Late Jurassic/Early Cretaceous hydrocarbon seeps, could also belong to the clade of chemosymbiotic provannids. This in turn would be consistent with the idea that a *Paskentana-Kaneconcha-Alvinoconcha>Ifremeria* clade is an ancient group of Provannidae that separated from the other provannids as early as Late Jurassic.

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Figure captions:

**Figure 1.** Bathymetric map of Kane Megamullion showing the location of Knorr 180-2 Dredge 28 (marked in red) that collected gastropods within marlstones from Adam Dome. Depths are in meters at a 100 m contour interval. High-angle, west-dipping faults that dissect the megamullion surface are indicated by ticked lines. Blue lines show tracks of ROV Jason dives and stars locate observed manifestations of former low-temperature hydrothermal venting as discussed in the text. The dashed line in the lower part of the map shows the location of the upper cross-section in Fig. 2. The inset gives the location of Kane Megamullion in the North Atlantic Ocean.

**Figure 2.** Cross-sections showing simplified structural elements of Kane Megamullion (top; no vertical exaggeration) and its position (darker shade, bottom, at 5x vertical exaggeration) in relation to the present axis of the Mid-Atlantic Ridge. In the top panel, approximate seafloor exposure and subsurface trend of the detachment fault surface is shown as a bold line; this surface is interrupted by high-angle, west-dipping normal faults that have eroded in their upper parts and are covered by talus in their lower parts. The dashed arrow near the termination shows how hydrothermal fluids moving up the detachment fault are thought to have vented through the lip of the hanging wall when the fault was active at the axis of the Mid-Atlantic Ridge in Late Pliocene time. Positions of hydrothermal features (stars) and Knorr Dredge 180-2 are shown. All interpreted normal faults are indicated as having true dips of 45°-50° in the subsurface. Location of the upper profile is shown in Fig. 1.

**Figure 3.** *Kaneconcha knorri* gen et sp. nov. from Adam Dome, Kane Megamullion, Mid-Atlantic Ridge; Late Pliocene. **A-D.** Holotype (ZPAL Ga.16/1) in lateral (A), apertural (B), umbilical (C), and apical (D) views. **E.** Shipboard photo of the marlstone sample hosting holotype ZPAL Ga.16/1 (right) and specimen ZPAL Ga.16/2 (left).

**Figure 4.** Recent shell (SMNH 99607) of *Ifremeria nautiliei* Bouchet and Warén, 1991

from Manus Basin in lateral (A), apertural (B), umbilical (C), and apical (D) views.

**Figure 5.** Cross sections through shells of large provannids. **A.** Recent *Alviniconcha hessleri* Okutani & Ohta, 1988. **B.** Recent *Ifremeria nautili* Bouchet and Warén, 1991. **C.** Late Pliocene *Kaneconcha knorri* gen. et sp. nov. **D.** SEM image of a *K. knorri* cross section etched with 1% HCl for 7 min. Note ichnospecies *Saccomorpha clava* Radtke, 1991 at the shell/periostracum interface.

**Figure 6.** Geographic distribution of Recent and fossil provannid and provannid-like gastropods. Data compiled from the literature and SMNH collections.

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23°40'N

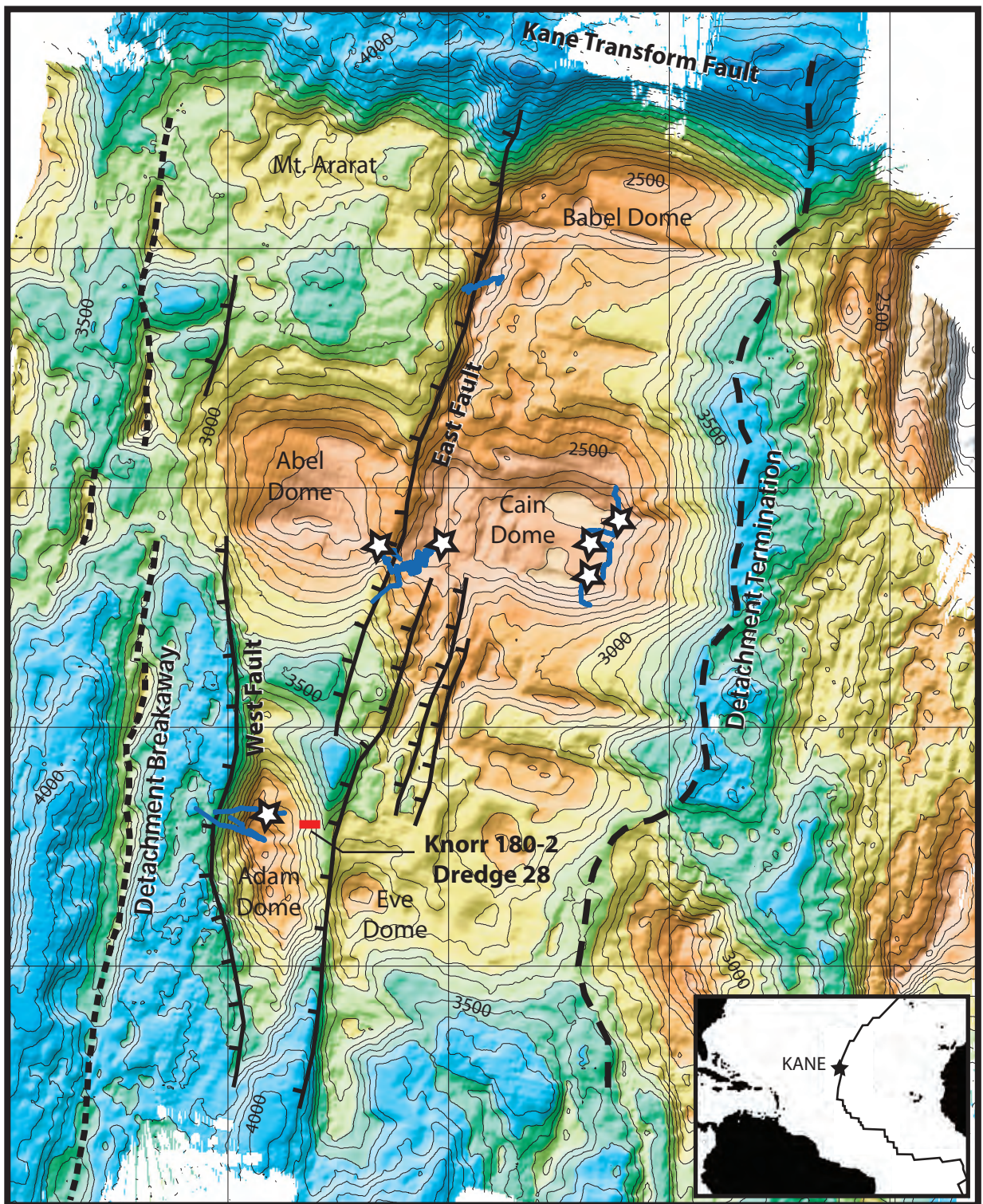
23°35'N

23°30'N

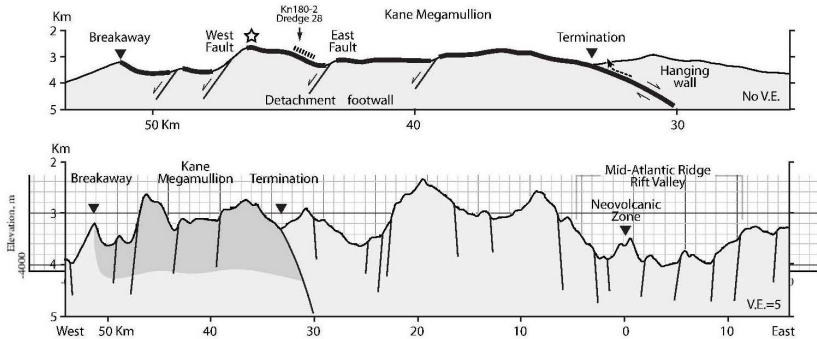
23°25'N

23°20'N

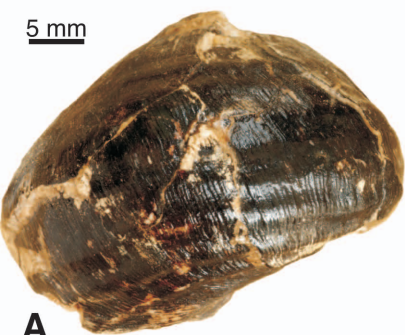
23°15'N





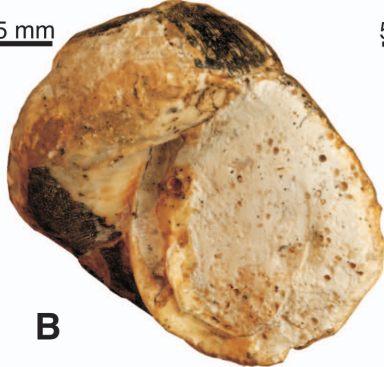


5 mm



**A**

5 mm



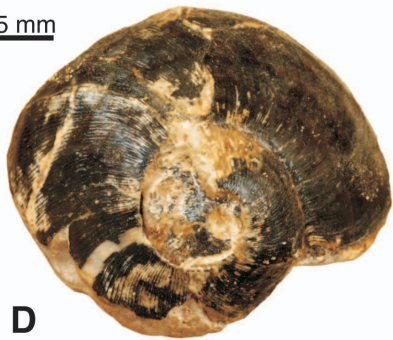
**B**

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**C**

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**D**

5 mm



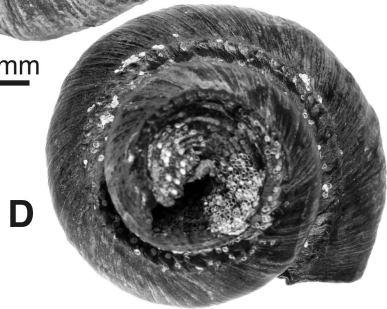
**E**

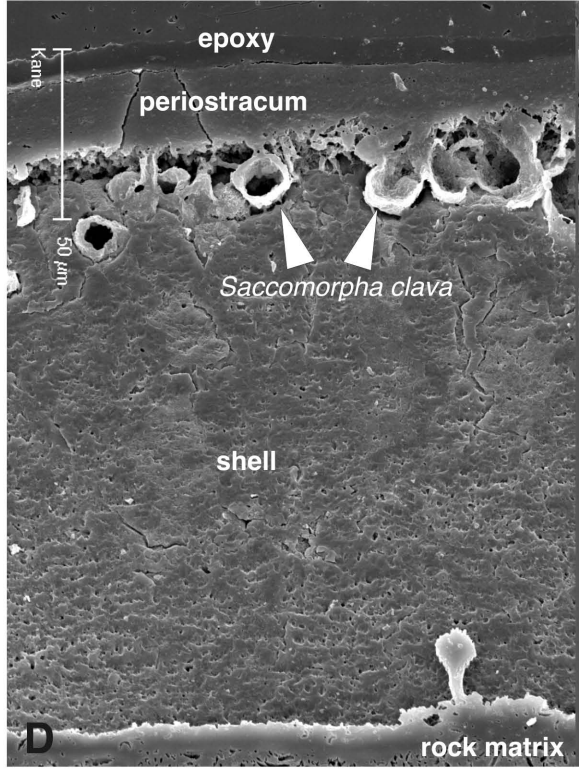
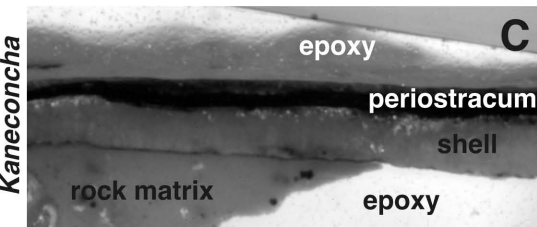
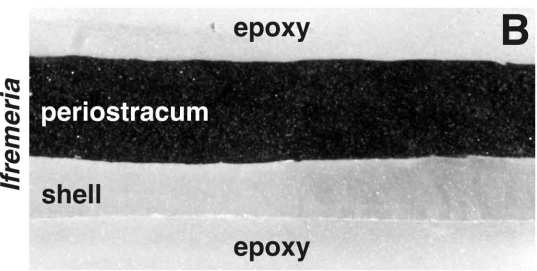
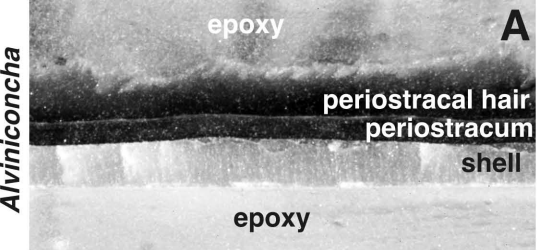


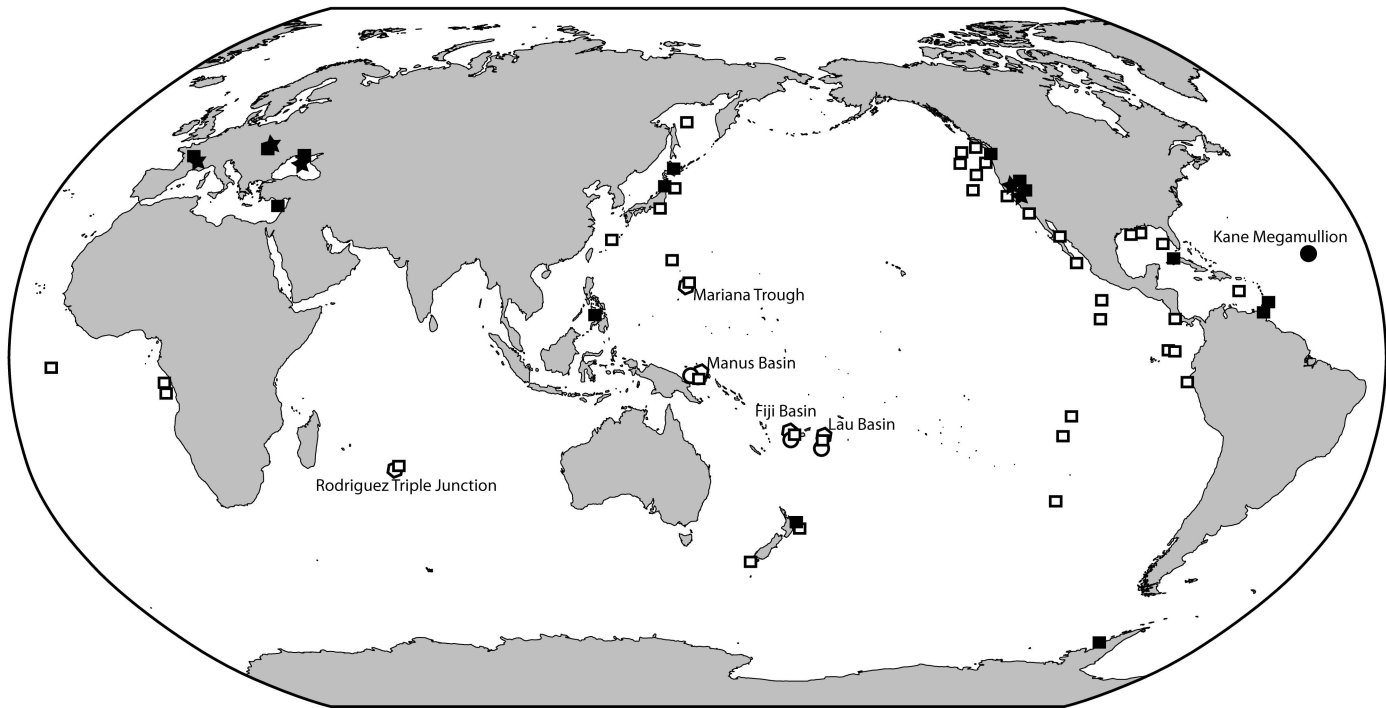
10 mm



10 mm







Recent chemosymbiotic provannids

○ *Alviniconcha*

○ *Ifremeria*

Fossil allegedly chemosymbiotic provannids and provannid like gastropods

● *Kaneconcha*

★ *Paskentana*

Other Recent provannids

□ *Provanna, Desbruyeresia, Cordesia, Rubyspira*

Other fossil provannids and provannid like gastropods

■ *Provanna, Desbruyeresia, Hokkaidoconcha, Atresius*

1000 Kilometers Parallel scale at 0° north 0° east

1000 Kilometers Parallel scale at 30° north 0° east

1000 Kilometers Parallel scale at 60° north 0° east