

Provannid and provannid-like gastropods from the Late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda: Abysochrysoidea)

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A fauna of provannid and provannid-like shells is described from Upper Cretaceous seep carbonates in Hokkaido, Japan. We describe two new provannid species, *Provanna tappuensis* sp. nov. and *Desbruyeresia kanajirisawensis* sp. nov., with preserved protoconchs of unquestionable provannid type with decollate apex. This material confirms the occurrence of Provannidae as early as the Middle Cenomanian. We also describe *Hokkaidoconcha* gen. nov. and a new family *Hokkaidoconchidae* fam. nov., with two named species, *H. hikidai* sp. nov. and *H. tanabei* sp. nov. Hokkaidoconchidae are possibly related to the Provannidae, judging from a similar, but not decollate larval shell, although the juvenile teleoconch whorls differ in being of a general cerithimorph appearance and the details of the aperture are unknown. Furthermore, we review the published fossil record of Provannidae and Abysochrysidae, and we consider that in those older than the Eocene, there is no evidence preserved that unequivocally supports a position there. The Jurassic *Acanthostrophia acanthica* from Italy seems to be the oldest known record of Abysochrysidae, and the most reliable occurrence of the family, older than from the Miocene. Other fossil, pre-Miocene species that have been classified in the Abysochrysidae are provisionally referred to Hokkaidoconchidae. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 154, 421–436.

ADDITIONAL KEYWORDS: Abysochrysidae – Hokkaidoconchide – chemosynthesis-based community – protoconch – decollation.

INTRODUCTION

Although Recent vent and seep communities have been explored to a relatively large extent since their discovery (Lonsdale, 1977; Corliss *et al.*, 1979; Paull *et al.*, 1984; Suess *et al.*, 1985), their fossil record remains poorly known and therefore the historical development of chemosynthesis-based communities is still of debate (Campbell & Bottjer, 1995; Little & Vrijenhoek, 2003; Kiel & Little, 2006). Serious difficulties in deciphering the evolution of chemoautotrophy-based communities are caused by

poor preservation of the fossils found in the ancient hot vents and cold seeps. In the case of fossil gastropods, common animals in such communities (Warén & Bouchet, 2001), a substantial part of the phylogenetic information comes from the protoconch, which is small and fragile. Even in Recent gastropods from chemoautotrophy-based communities the protoconchs are rarely preserved. Owing to extensive teleoconch simplification and convergence, often without knowledge of its protoconch or details of the aperture, it is difficult to decide what higher-level taxonomic group the examined fossil represents. The provannid–abysochrysid–cerithiid quandary from Mesozoic hot vents and cold seeps provides a good example of this

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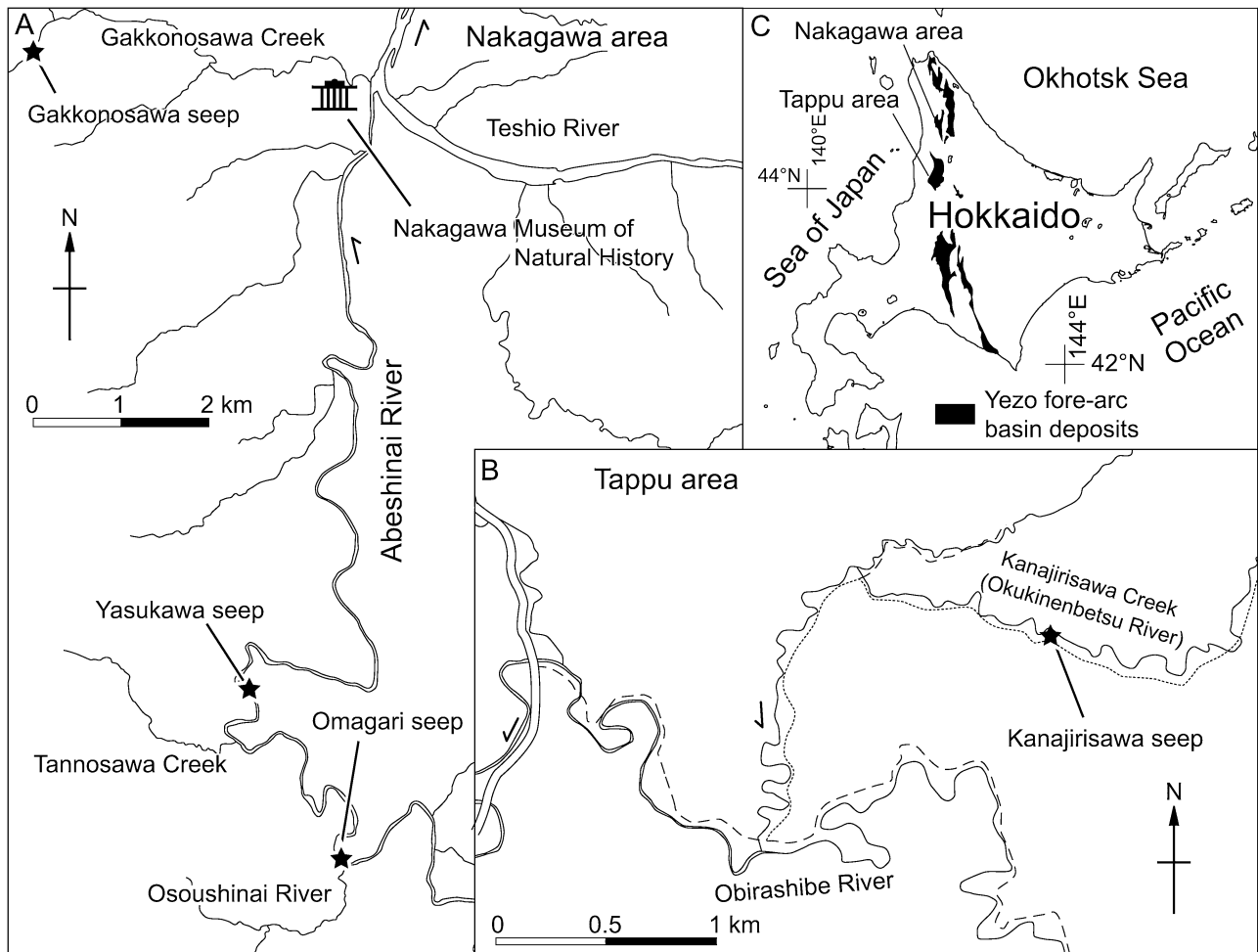


Figure 1. Sketch map of the provannid-bearing localities discussed in the text. A, Nakagawa area. B, Tappu area. C, Hokkaido of Japan with Cretaceous Yezo fore-arc basin deposits indicated.

(e.g. Little *et al.*, 1998; Little, 2002; Campbell, 2006). Newly discovered and well-preserved material from Late Cretaceous seep carbonates of Hokkaido Island (Japan) suggests that some cerithioid-type shells reported from Mesozoic hot vents and cold seeps worldwide may actually represent provannids; most of them, however, are less well preserved and herein are referred to the new family Hokkaidoconchidae based on similarities in the teleoconch. The latter may or may not be a sister group of both Provannidae and Abyssochrysidae. Some of these species may even belong to the Cerithioidea.

GEOLOGICAL SETTING, MATERIAL AND METHODS

The gastropod shells analysed here came from four Upper Cretaceous localities in Hokkaido Island, Japan (Fig. 1). The material is deposited at the

University Museum, University of Tokyo, Tokyo, Japan (abbreviated UMUT).

KANAJIRISAWA

The localized carbonates at Kanajirisawa in the Tappu area (Fig. 1) were ascribed a Middle Cenomanian age by Tanabe *et al.* (1977) and Asai & Hirano (1990). Subsequently, they were interpreted by Kanie *et al.* (1996) as methane seep deposits. The carbonate bodies at Kanajirisawa have strongly negative carbon isotopic compositions as low as -43.5‰ vs. PDB and archaeal biomarkers, e.g. PMI, with extremely negative carbon isotopic compositions as low as -115‰ vs. PDB (R.G.J., unpubl. data). The light isotope of carbon indicates that the latter originated from methane (e.g. Peckmann & Thiel, 2004). This geochemical evidence strongly supports the interpretations of Kanie & Kuramochi (1996) and Kanie *et al.* (1996).

Kanie & Kuramochi (1996) and Kanie *et al.* (1996) described several bivalves from this locality but none of the gastropods. Our specimens were obtained by field collecting from the weathered rock surfaces as well as by dissolving bulk carbonate samples in organic (acetic and formic) acids and partially also in hydrochloric acid. The residue sediment yielded an abundant gastropod and bivalve fauna and moderately common but poorly preserved worm tubes (probably vestimentiferan). The gastropods at Kanajirisawa are small and silicified. The most common gastropods are provannids (about 90% of all specimens) with some contribution from elongated and laterally compressed limpets (most probably pectinodontine-type acmaeids) and very few vetigastropods; these will be described elsewhere.

The early diagenetic silicification has preserved remarkable detail of fine protoconch ornamentation. Such preservation has allowed the description of two new species of Provannidae and one new species of Hokkaidoconchidae fam. nov. (see Taxonomy below). Another species (Fig. 2F, J, R and 'Kanajirisawa provannid' under family Provannidae) of hokkaidoconchid remains undescribed because of poor quality and scarcity of material.

YASUKAWA

The Yasukawa locality (Nakagawa area, see Fig. 1) consists of intercalations of mudstones and sandstones with several methane-influenced carbonate bodies (the four largest ones numbered A–D) distributed over a few tens of metres (see details in Jenkins *et al.*, 2007b). The Yasukawa locality deposits have assigned a Campanian age (Takahashi, Hirano & Sato, 2003; Jenkins *et al.*, 2007b). The gastropods were field collected or extracted by washing the mudstone on a sieve (mesh size 0.5 mm) in hot water with detergent. Most specimens retain their original mineralogy although tiny elements (including protoconchs) are usually worn.

The gastropods were found both in the carbonate bodies and in the surrounding mudstone. The provannids (see 'Yasukawa provannid') are relatively rare and poorly preserved. Much more common is *Hokkaidoconcha hikidai* gen. et sp. nov., which is present in both types of rock. At carbonate bodies B and C this species is the dominating gastropod.

OMAGARI

The locality on the small islet in the Abeshinai River at Omagari (Nakagawa area) has the best described and best known Cretaceous methane-influenced carbonate deposits in Japan. The locality provided us with numerous and relatively well-preserved fossils

including a number of gastropods, bivalves, worm (allegedly vestimentiferan) tubes, brachiopods and decapods (Hikida *et al.*, 2003; Jenkins, Kaim & Hikida, 2007a). The age of the Omagari deposit is considered to be Campanian (Takahashi *et al.*, 2003; Jenkins *et al.*, 2007b). The gastropods from there came both from field collecting and from washing of the sediment in the same way as for the Yasukawa samples. Provannids were not previously reported from this locality. A few specimens are preserved with original calcareous layers but are usually very incomplete (see 'Omagari provannid'). Hokkaidoconchids are unknown from Omagari thus far.

GAKKONOSAWA

The age of this locality in the Nakagawa area (Fig. 1) is uncertain as the seep carbonate is exposed in a boulder that has been extracted from its original place by fluvial erosion. Based on a comparison with other seep-carbonate localities in the area it appears to be of Campanian age. A more detailed description of the locality will be given elsewhere. The locality produced a few silicified specimens of gastropods from seep carbonate with abundant worm (probably vestimentiferan) tubes. We found two specimens of provannids, one of which has the microornamentation of the teleoconch well preserved (see 'Gakkonosawa provannid', Fig. 3H).

DESCRIPTIONS OF SPECIES AND SYSTEMATICS

PHYLUM MOLLUSCA LINNÉ, 1758

CLASS GASTROPODA CUVIER, 1797

ORDER CAENOGASTROPODA COX, 1959

SUPERFAMILY ABYSOCHRYSOIDEA TOMLIN, 1927

Remarks: To facilitate bookkeeping, we include Abyssochrysoidea Tomlin, 1927, Provannidae Warén & Ponder, 1991 and Hokkaidoconchidae fam. nov. in the same superfamily.

FAMILY PROVANNIDAE WARÉN & PONDER, 1991

GENUS *PROVANNA* DALL, 1918

Type species: *Trichotropis (Provanna) lomana* Dall, 1918. Recent; US Pacific Coast.

***PROVANNA TAPPUENSIS* SP. NOV.**

(FIGS 2K–M, O, Q, 3C)

Derivation of name: After the town of Tappu, located close to the type locality.

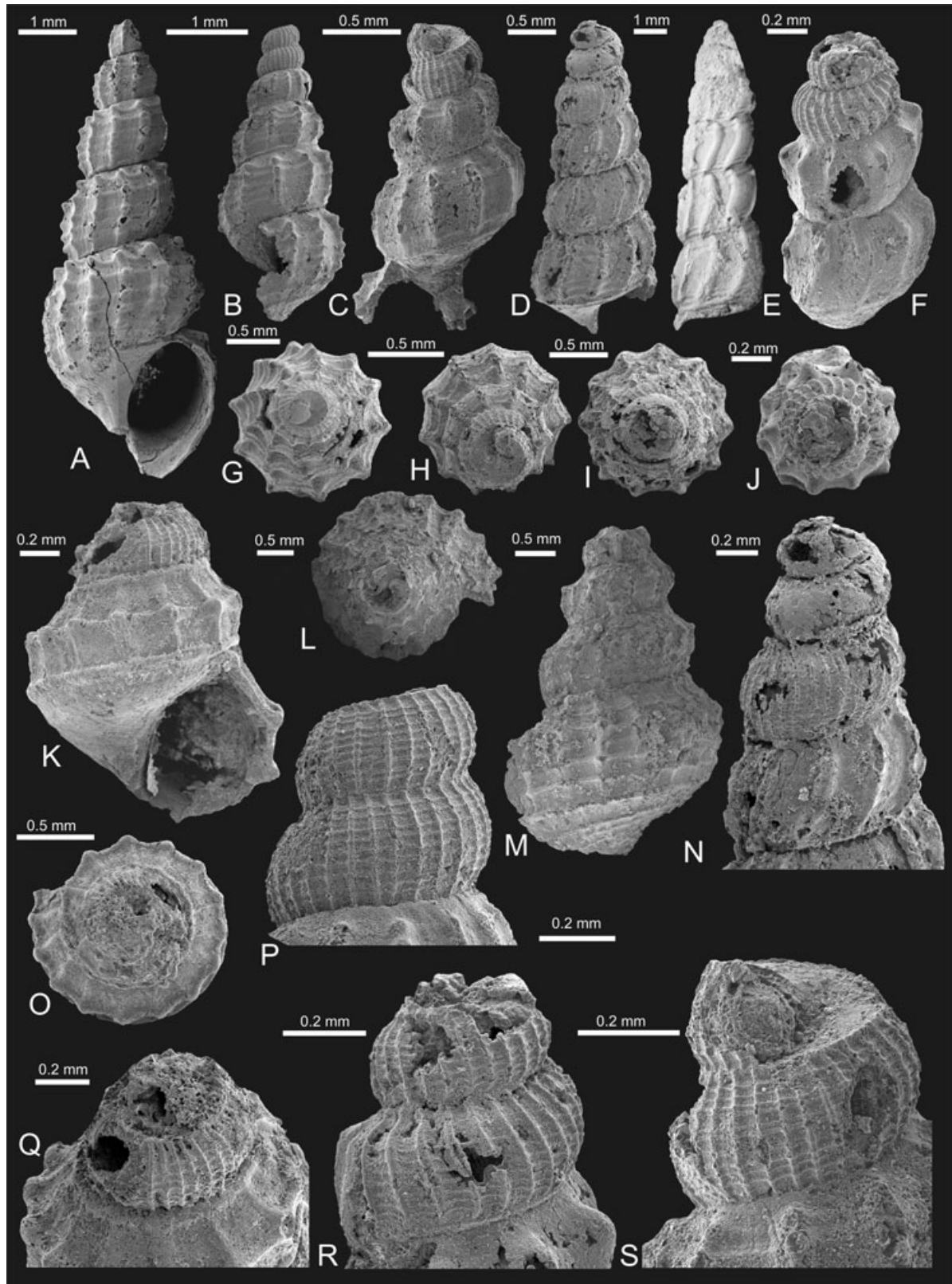


Figure 2. Cenomanian (early Late Cretaceous) provannids and hokkaidoconchids from Kanajirisawa, Tappu area, Hokkaido, Japan. A, *Desbruyeresia kanajirisawensis* sp. nov. Adult or adolescent specimen (holotype) UMUT MM29355. B, G, *P. D. kanajirisawensis*. Juvenile UMUT MM29356 with part of protoconch preserved. B, lateral view; G, apical view; P, close up of the protoconch. C, H, S, *D. kanajirisawensis*. Juvenile UMUT MM29357 with part of protoconch preserved; note that the missing part is broken off but not worn. C, lateral view; H, apical view; S, close-up of the protoconch. D, I, N, *Hokkaidoconcha tanabei* gen nov., sp. nov. Juvenile specimen UMUT MM29360 (holotype). D, lateral view; I, apical view; N, close-up of the apex. E, *H. tanabei*. Adolescent specimen UMUT MM29392 in lateral view. F, J, R, *Kanajirisawa hokkaidoconchid* sp. indet., juvenile specimen UMUT MM29361. F, lateral view; J, apical view; R, close-up of the protoconch. K, O, Q, *Provanna tappuensis* sp. nov. Juvenile UMUT MM29358 (paratype). K, lateral view; O, apical view; Q, close-up of the protoconch. L, M, *P. tappuensis*. Adolescent UMUT MM29359 (holotype). L, apical view, M, lateral view.

Type material: UMUT MM29359 (holotype), adolescent shell with no protoconch; UMUT MM29358 (paratype), juvenile shell with protoconch.

Type locality: Kanajirisawa Creek, Tappu area, Hokkaido, Japan.

Type horizon: Middle Cenomanian (Late Cretaceous) carbonate seep deposits.

Description: Shell (Fig. 2M) sturdily built, of medium size and rissoid-like shape, with strong axial and spiral sculpture. Protoconch (Fig. 2K–L) decollate; top remaining 1+ larval whorl filled with a calcareous plug (Fig. 2L); maximum diameter 0.65 mm; sculptured with about 20–30 (estimate) orthocline axial ribs of uniform strength from suture to suture; and about nine much less prominent spiral cords. Initial teleoconch whorl with one strong median and two, supra- and infra-sutural spiral ribs which form strong nodes and a reticulate pattern with the axial ribs (c. 15 per whorl). With increasing size the number of spiral ribs increases to about five (plus about five on the basal surface), the reticulation becomes less pronounced and the whorls evenly rounded instead of medially keeled. Columella straight. Peristome and siphonal canal (if any) not preserved.

Dimensions: Holotype (UMUT MM29359): maximum shell height 3.88 mm, diameter 2.57 mm. Paratype (UMUT MM29358): maximum height of incomplete protoconch 0.35 mm, diameter 0.65 mm.

Remarks: The teleoconch is quite similar to several Recent species of *Provanna*, but all modern species of *Provanna* have a paucispiral protoconch. It may, however, be assumed that the early members of *Provanna* had a planktotrophic development, or that *Desbruyeresia*, with such development, is a branch of *Provanna* that has retained planktotrophy. The larval shell of *P. tappuensis* resembles that of *Desbruyeresia kanajirisawensis* sp. nov. (see below) but has slightly stronger axial ribs and the whorls more convex. The

teleoconch of *P. tappuensis* is much less elongate and has an angulation on the juvenile whorls whereas the shell of *D. kanajirisawensis* is strongly elongate and the juvenile whorls are not angulated.

GENUS *DESBRUYERESIA* WARÉN & BOUCHET, 1993

Type species: *Desbruyeresia spinosa* Warén & Bouchet, 1993. Recent; North Fiji Basin.

***DESBRUYERESIA KANAJIRISAWENSIS* SP. NOV.**

(FIGS 2A–C, G, H, P, S, 3A)

Derivation of name: After the type locality.

Type material: UMUT MM29355 (holotype), adult or adolescent shell; UMUT MM29356 (paratype), juvenile shell with decollate protoconch preserved; UMUT MM29357 (paratype), another juvenile shell with protoconch.

Type locality: Kanajirisawa Creek, Tappu area, Hokkaido, Japan.

Type horizon: Middle Cenomanian (Late Cretaceous) carbonate seep deposits.

Description: Shell (Fig. 2A) of medium size and melanoid in shape with strong axial and spiral sculpture. The protoconch is decollated; the top of the second larval whorl is filled with a calcareous plug (Fig. 2S). Protoconch clearly demarcated from teleoconch; whorls ornamented by c. 24–26 orthocline axial ribs and 9–10 weaker spiral ribs (Fig. 2B, C, G, H, P, S). Initial teleoconch whorl with five spiral ribs which form weak and progressively stronger nodes and a reticulate pattern with the sturdy axial ribs (c. 13 per whorl). Number of spiral cords constant during ontogeny. Whorls angulated at most apical rib. Nodes at most apical ribs more pointed and directed obliquely toward apex. Suture moderately incised and whorls moderately convex. Growth lines distinct. Base rounded, not clearly demarcated from lateral flank.

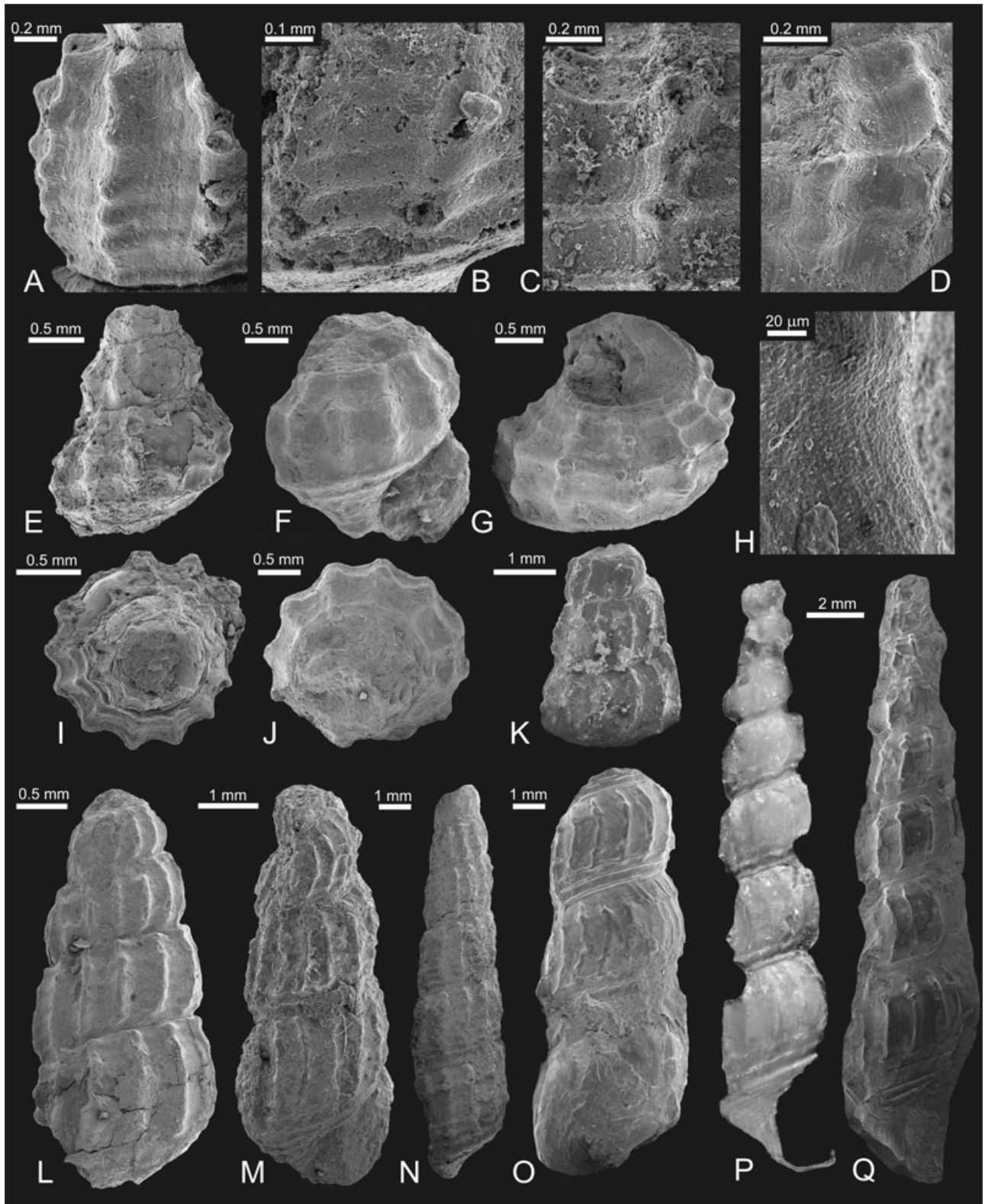


Figure 3. Late Cretaceous provannids and hokkaidoconchids from Hokkaido, Japan. A, *Desbruyeresia kanajirisawensis* sp. nov., UMUT MM29355 (holotype), Cenomanian adult or adolescent specimen from Kanajirisawa, Tappu area; details of ornamentation. B, *Hokkaidoconcha tanabei* gen. nov., sp. nov., UMUT MM29360 (holotype), Cenomanian juvenile specimen from Kanajirisawa, Tappu area; details of ornamentation. C, *Provanna tappuensis* sp. nov., Cenomanian adolescent individual UMUT MM29359 from Kanajirisawa, Tappu area; details of ornamentation. D, E, I, Yasukawa provannid, juvenile Campanian UMUT MM29363 from Yasukawa, Nakagawa area. D, details of ornamentation; E, lateral view; I, apical view. F, J, Omagari provannid, Campanian UMUT MM29362 from Omagari, Nakagawa area. F, lateral view; J, apical view. G, H, Gakkonosawa provannid, Campanian UMUT MM29364 from Gakkonosawa, Nakagawa area. G, lateral view; H, details of ornamentation. K–Q, *Hokkaidoconcha hikidai* from Campanian of Yasukawa, Nakagawa area. K, juvenile UMUT MM29386 in lateral view. L, flattened juvenile UMUT MM29387 in lateral view. M, flattened juvenile UMUT MM29388 in lateral view. N, adolescent individual UMUT MM29389 in lateral view. O, adult UMUT MM29390 in lateral view, juvenile whorls missing. P, Q, adult UMUT MM29391 (holotype) in lateral view. P, light microscopy; Q, SEM.

Axial ribs weaker on base; only spiral ribs and growth lines distinct there. Aperture not fully preserved but apparently rounded with no trace of siphonal channel or notch.

Dimensions: Holotype (UMUT MM29355) composed of five whorls: maximum shell height 7.8 mm, diameter 3.0 mm. Paratype (UMUT MM29356): maximum height of decollated protoconch 0.62 mm, diameter 0.55 mm.

Remarks: This species is the most common gastropod in the Kanajirisawa locality. The teleoconch of *D. kanajirisawensis* is reminiscent of the Recent *Desbruyeresia melanioides* Warén & Bouchet, 1993, which, by contrast, has only three spiral ribs. The protoconch is of typical provannid multispiral type both in the pattern of ornamentation and decollation (compare Warén & Bouchet, 1993: fig. 44C–E and Fig. 4A, B, E herein).

UNNAMED PROVANNID SPECIES

Yasukawa provannid (Fig. 3D, E, I): The provannids at Yasukawa are poorly preserved and no protoconch has been found for these specimens. The best preserved specimen (UMUT MM29363) is a juvenile teleoconch composed of three whorls, but lacking an aperture, as usual. The terminal whorl, the best preserved one, is ornamented by two median spiral ribs and an additional weaker one in the apical portion of the whorl. It has a generalized *Provanna*-like appearance and resembles the Omagari provannid. The difference in ornamentation might be caused by different ontogenetic stage and/or preservation. The specimens are considered to be too poorly preserved to be named.

Gakkonosawa provannid (Fig. 3G, H): The provannid from Gakkonosawa is represented by two specimens. The better preserved specimen (UMUT MM29364)

consists of one teleoconch whorl with no protoconch preserved. The teleoconch is ornamented by three sturdy spiral ribs. The two on the medial part of the whorl are stronger and the one on the apical part is weaker. At the intersections with the sturdy orthocline axial ribs there are blunt but distinct nodes. Moreover, the shell surface is ornamented by an irregular micropattern (Fig. 3H), as is frequently the case in modern species of *Provanna*. The provannid from Gakkonosawa is similar to provannids from Omagari and Yasukawa and differs mainly by more sturdy ornamentation, which may be intraspecific variability.

Omagari provannid (Fig. 3F, J): The best preserved provannid from Omagari (UMUT MM29362) consists of about one teleoconch whorl lacking the protoconch. The shell is ornamented by orthocline sturdy axial ribs and two small weaker spiral ribs with blunt nodes at the intersections. The preserved part of the shell strongly resembles the early whorls of the Recent *Provanna buccinoides* Warén & Bouchet, 1993 from off Fiji (compare Warén & Bouchet, 1993: fig. 54B) but fragmentary preservation excludes any further identification.

FAMILY HOKKAIIDOCONCHIDAE FAM. NOV.

Type genus: *Hokkaidoconcha* gen. nov. (see below)

Included genera: *Hokkaidoconcha* and possibly also *Humptulipsia* described by Kiel (2008).

Description: Protoconch (when multispiral) ornamented with strong axial and weaker spiral ribs; apex not decollated. Teleoconch is of tall, cylindrical cerithioid shape, ornamented with axial and spiral ribs. Spiral ribs commonly wide and blunt. Early teleoconch whorls may be reminiscent of some cerithioids and cerithiopsids. Base is usually demarcated with angulation and prominent spiral rib.

Remarks: Hokkaidoconchidae differ from Protorculidae in having convex base; from Provannidae in having multispiral (non-decollate) protoconch and large, strongly elongated teleoconch; from Abysochrysidae in having multispiral protoconch and more complex sculpture. We introduce this new family not as a result of any well-supported phylogeny, but merely as a convenient place to store the elongate, cerithioid-like fossil seep species until their phylogeny is better known from better preserved material. This should facilitate future research.

No modern species can be recognized as related to the species here referred to Hokkaidoconchidae. Possibly these species constitute the end of their lineage. However, this may be an error, owing to the fact that no complete aperture is known.

Stratigraphic range: Cenomanian to Campanian, Late Cretaceous (or possibly Middle Jurassic to Oligocene).

GENUS *HOKKAIODOCONCHA* GEN. NOV.

Derivation of name: After Hokkaido, the northernmost island of Japan and latin *concha*, shell.

Type species: *Hokkaidoconcha tanabei* sp. nov.

Description: Protoconch multispiral and ornamented with numerous co-labral ribs and finer spiral threads. Teleoconch is of tall, cylindrical cerithioid shape; apical whorls ornamented with strong axial ribs and weak spiral cords. Later in ontogeny spiral ornamentation disappears except immediately above the suture. Basal surface demarcated by strong spiral rib.

Remarks: The protoconch of *Hokkaidoconcha* resembles the provannid multispiral protoconch, but in Provannidae the larval shell is always decollated when multispiral. Moreover, the teleoconch of provannid species is never as cylindrical or tall as it is in *Hokkaidoconcha*. This elongate shell shape is more characteristic for *Abysochrysos*, but all known species of that genus have a lecithotrophic-type protoconch. *Acanthostrophia* Conti & Fischer, 1984 (Middle Jurassic), another genus of similar shell shape, until now within Protorculidae (Nützel, 1998), has a strongly elongate teleoconch but its teleoconch is ornamented by a row of nodes and axial ribs, more like *Abysochrysos*. The larval shell of *Acanthostrophia* is imperfectly described and poorly preserved, hampering comparisons; however, based on similarities in the teleoconch we consider Abysochrysidae to be a more likely home for it (see Abysochrysidae).

It is possible that some Cretaceous species from the US Pacific Coast identified as *Hypsipleura* and/or

abysochrysid (Stanton, 1895; Campbell & Bottjer, 1993; Campbell, Carlson & Bottjer, 1993) may belong to Hokkaidoconchidae, but they are too poorly preserved to classify.

HOKKAIODOCONCHA TANABEI SP. NOV.

(FIGS 2D, E, I, N, 3B)

Derivation of name: In honour of Professor Kazushige Tanabe, who discovered the carbonate seep deposits at Kanajirisawa.

Type material: UMUT MM29360 (holotype), juvenile shell with protoconch. UMUT MM29392 (paratype), adolescent shell with no protoconch.

Type locality: Kanajirisawa Creek, Tappu area, Hokkaido, Japan.

Type horizon: Middle Cenomanian (Late Cretaceous) carbonate seep deposits.

Description: Shell (Fig. 2D, E) of tall, cylindrical cerithioid shape. Protoconch (Fig. 2N) multispiral and ornamented with 30–32 axial ribs and 15–20 weaker spiral cords on its basal 1.5 whorls. Remaining about two apical whorls too corroded to provide details. Initial teleoconch whorls ornamented with 10–12 sturdy and blunt opisthocytic axial ribs and eight broad and flat spiral ridges, with very narrow interspaces. Later in ontogeny spiral ornamentation present only close to suture. Axial ribs sturdier on adult/adolescent shells. Peristome and siphonal canal (if any) not preserved.

Dimensions: Holotype (UMUT MM29360): maximum shell height 3.31 mm, diameter 1.34 mm; protoconch: maximum height 1.08 mm, diameter 0.80 mm. Paratype (UMUT MM29392): maximum shell height 9 mm, diameter 2.85 mm.

Remarks: The ornament of the protoconch of *H. tanabei*, consisting of the opisthocytic axial ribs and weaker spiral ribs, resembles the ornamentation of provannid protoconchs (compare Warén & Bouchet, 1993: fig. 44C–E and Fig. 4A, B, E herein); the latter, however, always have a decollated tip to the protoconch (when multispiral) and orthocline axial ribs. The teleoconch of *H. tanabei* also differs from the ornamentation we know from Recent provannids.

HOKKAIODOCONCHA HIKIDAI SP. NOV. (FIG. 3K–Q)

Derivation of name: In honour of Dr Yoshinori Hikida, for work on chemoautotrophy-based associations in the Nakagawa area.

Type material: UMUT MM29391 (holotype), adult or adolescent shell, and five paratypes, UMUT MM29386–29390.

Type locality: Yasukawa locality, Nakagawa area, Hokkaido, Japan.

Type horizon: Campanian (Late Cretaceous) carbonate seep deposits.

Description: Shell (Fig. 3P, Q) of tall, cylindrical cerithioid shape. Protoconch unknown. Shell of the best preserved specimen (UMUT MM29391, holotype) consists of eight strongly elongated whorls, still embedded in carbonate rock matrix (Fig. 3P, Q). Most juvenile part poorly preserved with strong axial ribs and weaker spiral ridges. Whorls are weakly convex; ornamentation changes during ontogeny; basally only 1–2 spiral ridges remain just above suture. Eleven to 13 sturdy opisthocyrtic axial ribs sometimes more, sometimes less co-labral; start at the most apical part of whorl and continue to spiral rib(s) just above suture and disappear. Sutural rib(s) form first one(s) of a series of 9–10 ridges ornamenting base of last whorl. Axial ribs ornamented by blunt nodes in their most apical and basal portions, apparently remnants of intersections with weak spiral ridges on early teleoconch. The juvenile UMUT MM29389 is also of tall, cylindrical cerithioid shape and ornamented by axial ribs and spiral ridges, later spiral ridges at medial part of the lateral flank weaken and finally disappear (Fig. 3N). Apical spiral ridge strongest, produces weak nodes at intersections with axial ornamentation; also visible on some other juvenile specimens (e.g. UMUT MM29387; Fig. 3L) although these are laterally flattened. Aperture is not fully preserved, but seemingly the shell had no siphonal channel or notch (Fig. 3P).

Dimensions: Holotype (UMUT MM29391): maximum shell height 20.36 mm, diameter 4.54 mm.

Remarks: Shells of *H. hikidai* are relatively common in the Yasukawa methane seep, but they are incompletely preserved. The specimens from mudstones are usually flattened and fragmented while the specimens from the seep-carbonate underwent re-crystallization that commonly distorts the outer surface and the apex of the shells. Therefore, we could not find any protoconch of this gastropod and it is also difficult to find specimens with a well-preserved teleoconch. The teleoconch of juvenile shells strongly resembles some of the Mesozoic cerithioids, e.g. *Cryptaulax* and *Cirsocerithium* (compare Kaim, 2004 and Kiel, 2006a, respectively) and without the adolescent portion of the shell and a complete aperture, it is

difficult to classify such a gastropod appropriately. *H. hikidai* differs from *H. tanabei* in having two strong spiral ribs on the abapical part of the shell flank and these ribs are not crossed by axial ribs. The spiral ribs of juveniles are narrow with wide interspaces in *H. hikidai* whereas they are widely blunt with very narrow interspaces in *H. tanabei*.

UNNAMED HOKKAIDOCONCHID SPECIES

Kanajirisawa hokkaidoconchid sp. indet. (Fig. 2F, J, R): This species is represented by a tiny specimen (UMUT MM29361) consisting of two protoconch and two teleoconch whorls. The whole shell is 1.65 mm high and 0.77 mm broad. The protoconch is 0.63 mm high and 0.59 mm broad. The whorls of the protoconch are more convex than any provannid protoconch described thus far. The axial ribs are sturdy and sigmoid and stronger than those of *H. tanabei*. The spiral ribs on the protoconch follow the pattern known from the provannids and hokkaidoconchids. The teleoconch is ornamented exclusively by slightly opisthocyrtic, sturdy and shouldered ribs, strongly protruding in their apical quarter. No spiral ribs are present.

DISCUSSION

PROVANNIDAE

The family Provannidae includes four described genera, three of which are restricted to hydrothermal vent environments (*Desbruyeresia*, *Alviniconcha* and *Ifremeria*). The latter two genera contain large, specialized vent species deriving their nourishment largely from endosymbiotic bacteria (Suzuki *et al.*, 2006). This mode of life is expressed in the shell morphology by expansion of the whorls in these gastropods, apparently an adaptation to contain the hypertrophied gills with bacterial symbionts (Warén & Bouchet, 1993). *Desbruyeresia* contains a few smaller (6–9 mm) species also restricted to vents, especially spots often called warm seeps. They obtain their nourishment from grazing (Warén & Bouchet, 1993). The genus *Provanna* is richly represented in both seeps and vents, as well as on various organic substrates in the deep sea. There are 13 Recent species described and almost as many undescribed. Species of *Provanna* are bacterial and detritus grazers. Their shell varies in sculptural detail and it is also very plastic in particular species (see e.g. Warén & Bouchet, 1986; Squires, 1995). They have a fairly large larval shell of about 1.0–1.5 whorls, usually with the last half whorl sculptured by close-set uniform axial riblets. The earlier part may or may not have a finely granular sculpture (Fig. 4C). The teleoconch is ornamented by spiral and axial ribs

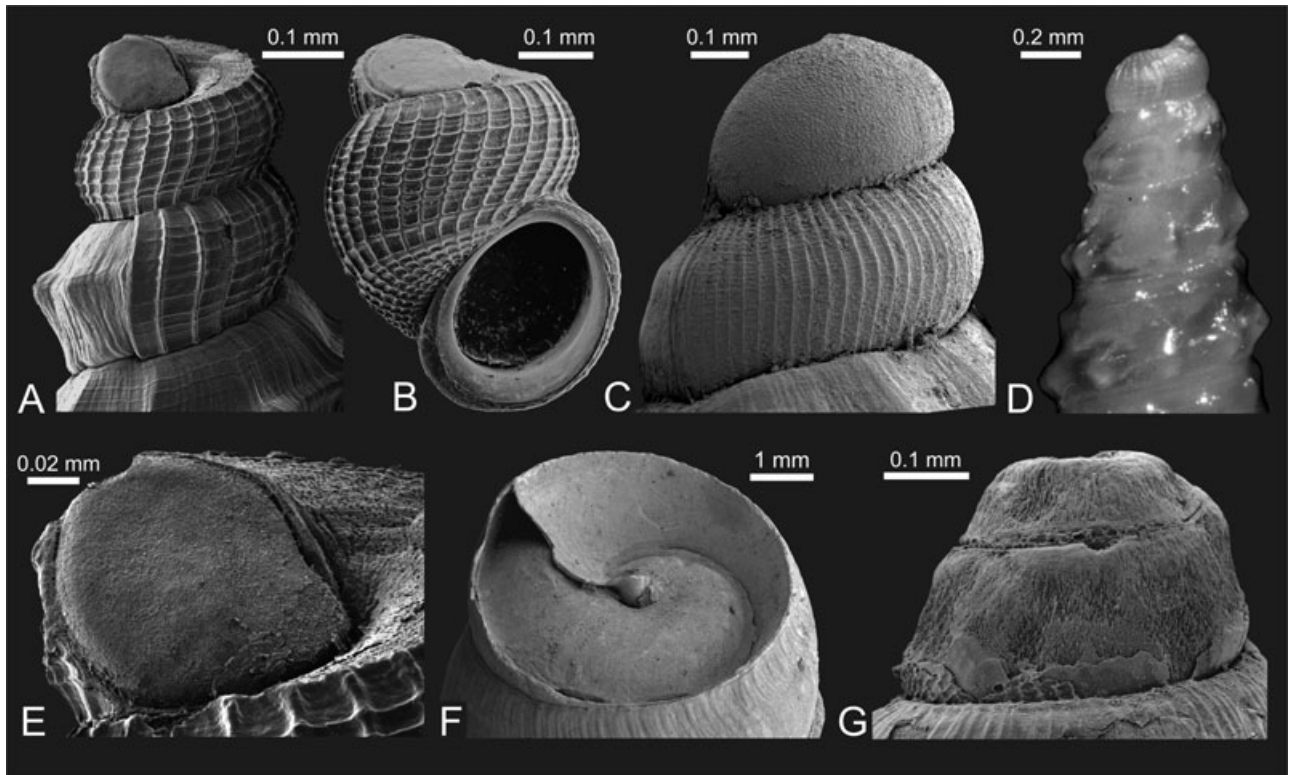


Figure 4. Juvenile Recent Provannidae and Abysochrysidae (A–D) and patterns of shell decollation and preservation (E–F). A, E, *Desbruyeresia spinosa* Warén & Bouchet, 1993 from North Fiji Basin (specimen illustrated also in Warén & Bouchet, 1993: fig. 44D). A, decollate protoconch; E, details of decollation; note no signs of shell abrasion on the protoconch edges B, decollated protoconch of *Alviniconcha hessleri* Okutani & Ohta, 1988 from north Fiji Basin (specimen illustrated also in Warén & Bouchet, 1993: fig. 44C). C, paucispiral protoconch of *Provanna segonzaci* Warén & Ponder, 1991 from Lau Basin. D, *Abysochrysos* sp. from off New Caledonia; note axial ribs and spiral riblets at the beginning of paucispiral protoconch. F, decollation pattern of terrestrial gastropod *Rumina decollata* Linné, 1758. G, typical pattern of in-vivo apex erosion in *Phymorhynchus* sp. shell from the Lucky Strike site on the Mid-Atlantic Ridge; note shell surface abrasion but no sign of decollation.

similar to cerithioids, but the sculptural details are less distinct or demarcated than in cerithioids, sometimes to such an extent that the shell is smooth in a few species (e.g. *P. laevis* Warén & Ponder, 1991, *P. glabra* Okutani, Tsuchida & Fujikura, 1992, and *P. variabilis* Warén & Bouchet, 1986). Some Recent species of *Provanna* have parts of the shell covered by a very fine, granular microsculpture (similar to Fig. 3H). Species of *Desbruyeresia* have a more elongate shell and without knowledge of the planktotrophic-type protoconch, some are easy to misidentify as *Provanna*.

Most of the known provannids belong to the genus *Provanna*. The larval development of these species has not been described, but *Provanna lomana* (Dall, 1918) deposits numerous small eggs in the egg capsule. A few of these develop into viable embryos which devour the others (adelphophagy; A.W., unpubl. data). It is not known if the young specimens leave

the capsule in a crawling or swimming stage, although swimming seems likely because larvae are regularly retrieved in sedimentation traps at the East Pacific Rise (A.W., unpubl. data). The presence of numerous very small granulae on the shell also points towards a planktonic dispersal phase; gastropod species with no planktonic dispersal stage tend to have a coarser sculpture on the protoconch (A.W., unpubl. data).

A different type of larval shell is present in the provannid genera *Desbruyeresia*, *Ifremeria* and *Alviniconcha* (Fig. 4A, B, E). This consists of about 1.5–1.7 whorls and is neatly sculptured with numerous orthocline ribs and finer spiral threads. The crucial feature is, however, that the apical whorls are persistently missing (Fig. 4A, B, E) and the most apical part of the remaining whorls is neatly plugged by a calcareous filling (Fig. 4E) in these provannids. The land-snail *Rumina decollata* (Linné, 1758), known for

its ability to detach its apical whorls, has a very similar septum or filling (Kat, 1981; Fig. 4F herein). The lack of apical whorls in these provannids is not the result of the corrosive effect of seawater as is commonly seen in other gastropods with planktotrophic development (see corroded protoconch of Recent *Phymorhynchus* sp. on Fig. 4G and Cenomanian *H. tanabei* on Fig. 2D, I, N), as all edges and surfaces of the larval whorls are untouched by corrosion for some time after settling. It is likely that this type of larval shell is a result of planktotrophic development as the egg size of *Alviniconcha*, *Ifremeria* and *Desbruyeresia* is about $120 \times 150 \mu\text{m}$ and the decollated larval shells $350\text{--}450 \mu\text{m}$, a difference too large to be explained by the normal size difference between larva and egg, c. 1.3 \times . This, however, needs to be confirmed, for example by examination of hatching larvae. *Ifremeria* even broods its larvae in a modified posterior pedal gland at least up to the trochophore stage (A.W., unpubl. data).

Uncertainty regarding planktotrophy does not reduce the value of this highly unusual type of protoconch as a synapomorphy of three genera of Provannidae. The similarity in sculpture to the last whorl of the protoconch of species of *Provanna* indicates that this protoconch is the result of a change in type of development, from assumed planktotrophy to lecithotrophy and adelphophagy, and it can be assumed that the ancestors of modern *Provanna* had similar protoconchs to *Desbruyeresia*, *Ifremeria* and *Alviniconcha*.

The difference between *Provanna* and *Desbruyeresia* was originally assumed to be lack of a pallial tentacle in *Desbruyeresia* (Warén & Bouchet, 1993), but this tentacle has since been found in better preserved specimens (A.W., unpubl. data). The remaining difference then is the more slender and *Melania*-like shell of *Desbruyeresia* plus possibly the type of larval development.

Recent research on pre-Eocene chemoautotrophy-based associations has resulted in several reports of fossil alleged provannids (Table 1). However, none of them was sufficiently well preserved to allow safe conclusions about systematic position. The oldest reported provannid-like gastropods are from Tithonian–Albian (Upper Jurassic to Lower Cretaceous) sequences of the US Pacific Coast. These presumed ‘provannids’ listed by Campbell (2006) require better preserved specimens to determine if they may be Hokkaidoconchidae or some other group.

The best preserved shells of the possible Cretaceous provannids described thus far are those from Turonian–Campanian hot vent deposits on Cyprus (Little *et al.*, 1998, 1999; Little, 2002). The specimen illustrated by Little *et al.* (1999: fig. 2G) and identified therein as ‘cerithioid gastropod B from Kinousa’

is lacking the protoconch and aperture, but the axial and spiral ornamentation as well as the shell shape resemble *Desbruyeresia kanajirisawensis* described herein (Figs 2A–C, G, H, P, S, 3A). The other specimen (Little *et al.*, 1999: fig. 2H), identified as ‘cerithioid gastropod A from Memi’ is more problematic. It is rather poorly preserved and somewhat similar to the extinct cerithiid genus *Cryptaulax*. Nevertheless, it cannot be excluded that these species are provannids. To use them as an indication of a Cretaceous occurrence of Provannidae, however, is speculative.

Another alleged provannid has been described by Bandel & Kiel (2000) as *Desbruyeresia antiqua* from the Campanian (Upper Cretaceous) of Spain. The sole specimen came from an olisthostrome containing a mixture of gastropods from different settings (Kiel & Bandel, 2001); therefore the original environment of *D. antiqua* remains uncertain and no connection to a chemoautotrophy-based association has been established. The protoconch of this specimen is poorly illustrated but the authors have stated (Bandel & Kiel, 2000: 213) that the protoconch ornament of this specimen ‘... consists of simple collabral axial ribs and a fine pattern of spiral ribs between them’ (not visible to us in their SEM pictures). This protoconch, however, is not decollated and is more reminiscent of several species of *Cosmocerithium* (?Eumetulidae; see Kaim, 2004 figs 39–42 and Guzhov 2004 figs 10–11) and/or *Vatopsis* (?Eumetulidae; see, for example, *V. ewae* and *V. nuetzeli*; Kaim 2004: figs 37, 38).

The Palaeocene provannids mentioned by Schwartz *et al.* (2003) from California are questionable as the single specimen they illustrated (Schwartz *et al.*, 2003: fig. 5g) is much more similar to species of Aporrhaidae (compare similar aporrhoids in Kaim, 2004: fig. 137).

The earliest safe record of *Provanna* was until now known from the Eocene–Oligocene (*Provanna antiqua* Squires, 1995; Peckmann *et al.*, 2002; Gill *et al.*, 2005; Kiel, 2006b); subsequent fossil provannids are more abundant but are known mostly from North America and the Caribbean (Goedert & Campbell, 1995; Squires, 1995; Gill *et al.*, 2005; Kiel, 2006b; see also Table 1). Two seemingly safe records of *Provanna* from Miocene whale falls are known from Japan (Amano & Little, 2005, Amano, Little & Inoue 2007).

Pseudonina bellardii (Michelotti, 1847) was reviewed by Bertolaso & Palazzi (1994). It is a European Miocene–Pliocene species found associated with specimens of Xylophagidae, Teredinidae and *Idas* (Mytilidae), and therefore was assumed to be living on sunken drift wood. It was later (Bouchet *et al.*, 2005) transferred to Provannidae, which remains disputable given that its protoconch is not decollated and the character-rich globose teleoconch differs from all known provannids.

Table 1. Fossil and Recent Provannidae, Hokkaidoconchidae and Abysochrysidae compiled from the literature

Taxon	Reference(s)	Family	Environment	Locality	Age
Hokkaidoconchidae					
<i>Hokkaidoconcha tanabei</i> sp. nov.	This paper	Hokkaidoconchidae	Cold seep	Kanajirisawa, Japan	Cenomanian
<i>Hokkaidoconcha hikidai</i> sp. nov.	This paper	Hokkaidoconchidae	Cold seep	Yasukawa, Japan	Campanian
<i>Hypsipleura</i> spp., <i>Cerithium</i> spp. (review needed)	Stanton, 1895; Campbell & Bottjer, 1993; Campbell, <i>et al.</i> 1993	?Hokkaidoconchidae	Cold seep	Paskenta, California, USA	Tithonian
<i>Abysochrysos thiteuloy</i> (Macotay, 1980)*	Kiel & Little, 2006	?Hokkaidoconchidae	Cold seep	France	Hauterivian
Zygopleurid sp. A	Gill <i>et al.</i> , 2005	?Hokkaidoconchidae	Cold seep	Belleplaine, Barbados	Eocene
Zygopleurid sp. B	Gill <i>et al.</i> , 2005	?Hokkaidoconchidae	Cold seep	Frizers, Barbados	Eocene
<i>Abysochrysos</i> sp.	Kugler <i>et al.</i> , 1984; Gill <i>et al.</i> , 2005	?Hokkaidoconchidae	Cold seep	Frizers, Barbados	Eocene
<i>Abysochrysos raii</i> Goedert & Kaler, 1996†	Goedert & Kaler, 1996	?Hokkaidoconchidae	Cold seep	Washington State	Eocene
<i>Desbruyeresia antiqua</i> Bandel & Kiel, 2000	Bandel & Kiel, 2000	?Hokkaidoconchidae	?Normal	Torallola, Spain	Campanian
Kanajirisawa hokkaidoconchid sp. indet.	This paper	?Hokkaidoconchidae	Cold seep	Kanajirisawa, Japan	Cenomanian
Abysochrysidae					
<i>Abysochrysos melvilli</i> (Schepman, 1909)	Ladd, 1977	Abysochrysidae	Normal	Fiji	Miocene
<i>Acanthostrophia acanthica</i> Conti & Fischer, 1984	Conti & Fischer, 1984	?Abysochrysidae	?Normal	Case Canepine, Italy	Bajocian
Provannidae					
<i>Desbruyeresia kanajirisawensis</i> sp. nov.	This paper	Provannidae	Cold seep	Kanajirisawa, Japan	Cenomanian
<i>Provanna tappuensis</i> sp. nov. Cerithioid B (provannid)	This paper Little <i>et al.</i> , 1999	Provannidae Provannidae	Cold seep Hot vent	Kanajirisawa, Japan Kinouza, Cyprus	Cenomanian Turonian/ Campanian
Yasukawa provannid	This paper	Provannidae	Cold seep	Yasukawa, Japan	Campanian
Omagari provannid	This paper	Provannidae	Cold seep	Omagari, Japan	Campanian
Gakkonosawa provannid	This paper	Provannidae	Cold seep	Gakkonosawa, Japan	Campanian
<i>Provanna antiqua</i> Squires, 1995	Squires, 1995; Kiel, 2006b	Provannidae	Cold seep	Washington State, USA	Oligocene/ Eocene
<i>Provanna</i> sp.	Amano & Little, 2005	Provannidae	Whale fall	Shosanbetsu, Japan	Miocene
<i>Provanna?</i> sp.	Amano <i>et al.</i> , 2007	Provannidae	Whale fall	Rekifune, Japan	Miocene
Provannid	Gill <i>et al.</i> , 2005	Provannidae	Cold seep	Freeman's Bay, Trinidad	Miocene
Cerithioid A (probably provannid)	Little <i>et al.</i> , 1999	?Provannidae	Hot vent	Memi, Cyprus	Turonian/ Campanian

*Species described by Macotay (1980), probably *nomen nudum*.†Designated as the type species of a new genus *Humtulpisia* (Kiel, 2008).
Some taxa are included tentatively pending taxonomic revision.

ABYSSOCHRYSIDAE VS. HOKKAIODOCONCHIDAE

In the Recent deep-sea, abyssochrysid s constitute a small and very uniform group, one genus with six species (see Houbrick, 1979; Bouchet, 1991; Killeen & Oliver, 2000), which are known from Brazil, West and South Africa, Oman and Indonesia. All described species have a smooth, lecithotrophic larval shell, but one, undescribed species from deep water off New Caledonia has a brown, lecithotrophic and multispiral protoconch of two whorls, similar to that of *Provanna* (Fig. 4D), presumably indicating an ancestry from species with an axially ribbed multispiral protoconch. Fossil protoconchs of *Abyssochrysos* are unknown thus far, unless *Acanthostrophia* belongs here as suggested herein.

None of the Recent abyssochrysid s is reported to be a member of a chemoautotrophy-based community and, like McArthur & Tunnicliffe (1998), we believe that they do not belong to vent-seep faunas.

The fossil record of abyssochrysid s is scanty (Table 1) and disputable. The Miocene counterpart of *Abyssochrysos melvilli* (Schepman, 1909) was reported from Fiji (Ladd, 1977, Houbrick, 1979), from non-seep deep-sea deposits.

The Middle Jurassic *Acanthostrophia acanthica* Conti & Fischer, 1984 was described from Case Cane-pine (Umbria, Italy) as a member of the Zygopleuridae, and was then transferred to Protorculidae by Nützel (1998). Its strongly elongated teleoconch and squareish aperture with no trace of a canal displays good similarity to *Abyssochrysos* and *Hokkaidoconcha*. *Acanthostrophia* seems to have a multispiral, axially ribbed protoconch but little detail is available from the figures provided by Conti & Fischer (1984) and it is uncertain if it is plankto- or lecithotrophic. Based on the similarity in shell shape we consider Abyssochrysidae to be a better place for *Acanthostrophia*.

There are several reports of assumed pre-Miocene abyssochrysid s found in chemoautotrophy-based associations (Table 1). We consider these to be possible hokkaidoconchid s rather than abyssochrysid s. These records include Eocene 'abyssochrysid s' from Barbados (Kugler, Jung & Saunders, 1984; Gill *et al.*, 2005) and possibly also the records from the US Pacific Coast (Goedert & Kaler, 1996; Kiel, 2008) of the same age; in both cases these animals were from cold seeps. Assignment of the latter two to Hokkaidoconchidae, however, remains questionable pending material with preserved protoconchs.

Some Mesozoic (Late Jurassic to Early Cretaceous) gastropods from the US Pacific Coast (Stanton, 1895; Campbell & Bottjer, 1993; Campbell *et al.*, 1993) were described as species of *Hypsipleura* or *Cerithium*. This material is pending revision, but some may belong to Hokkaidoconchidae.

A possible hokkaidoconchid (or at least related to the genus) has been described by Kiel (2008) and is known also from the Early Cretaceous of France (Lemoine *et al.*, 1982; Kiel & Little, 2006).

CERITHIOIDEA

Cerithioid s range far back in the fossil record, possibly to the Late Triassic (Bandel, 1993; Nützel, Hamedani & Senowbari-Daryan, 2003). They constitute one of the most common groups of caenogastropods in Jurassic and Cretaceous outer shelf deposits (Kaim, 2004; Bandel, 2006; Gründel & Kaim, 2006). The shell of some Mesozoic cerithioid s, referred to as Cryptaulacidae by Gründel (1976), is characterized by elongate shape with strong spiral and axial ribs usually forming nodes at the intersections. Cryptaulacid protoconchs are easy to recognize owing to their squat shape, two strong spiral ribs and general absence of axial sculpture (e.g. see Kaim, 2004). Additionally, the protoconch may be ornamented by a pattern of microtubercles. These, however, are usually restricted to the apical part of the protoconch (including the embryonic shell) and the surface of the spiral ribs. Most of the Recent cerithioid s have additional elongated nodes of varying shape and distribution on their protoconchs (e.g. Houbrick, 1992).

Modern chemosynthetic faunas contain only a few cerithiid gastropods: *Lirobittium* has been recorded from seeps off California by Levin *et al.* (2000) and *Bittium s.l.* from sunken wood in the tropical Pacific of the Philippines and Vanuatu (A.W., unpubl. data). There are no reliable records of cerithioid s from fossil hot vents and cold seeps. According to sperm morphology studies of Healy (1990a, b, 1992, 2000) the relationship of abyssochrysid s and provannid s to cerithiid s is rather distant. The same results were obtained by Colgan *et al.* (2007) from a multi-gene study of relationships within the Caenogastropoda.

CONCLUSIONS

The Cretaceous methane seeps from Hokkaido shed some light on the evolution of chemoautotrophy-based communities. There are faunistic similarities to Recent communities (Provannidae, some limpets) but there are also differences such as the presence of *Hokkaidoconcha* (not known from the Recent). The silicified gastropods from Kanajirisawa, with a decol-lated protoconch, provide good support for the occurrence of Provannidae in the Late Cretaceous and they constitute the oldest (Middle Cenomanian) reliable records of the Provannidae. This association provided also relatively well-preserved specimens of gastropods having some features shared by Provannidae and Abyssochrysidae. For these gastropods we describe

a new genus *Hokkaidoconcha* gen. nov. and family Hokkaidoconchidae fam. nov. We interpret the abyssochrysid-like Jurassic *Acanthostrophia acanthica* Conti & Fischer, 1982 (not from chemoautotrophic environments) as a possible member of Abyssochrysidae, but we cannot confirm the presence of Abyssochrysidae in fossil seeps and vents.

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