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New gastropods from deep-sea hydrocarbon seeps off West Africa

Anders Warén^{a,*}, Philippe Bouchet^b^a Swedish Museum of Natural History, Box 50007, SE-10405 Stockholm, Sweden^b Muséum National d'Histoire Naturelle, CP 51, 57 rue Cuvier, F-75231 Paris Cedex 05, France

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ABSTRACT

Thirteen new species of gastropods are described from the Zairov 1–2 and Biozaire 1–3 cruises to the methane seeps off the Congo River: Patellogastropoda: *Paralepetopsis sasakii* sp. nov. (Neolepetopsidae); Cocculiniformia: *Pyropelta oluae* sp. nov. and *P. sibuetae* sp. nov. (Pyropeltidae); *Tentaoculus granulatus* sp. nov. (Pseudococculinidae); Neomphalina: *Leptogyra costellata* sp. nov. (Family uncertain); Vetigastropoda: *Puncturella similis* sp. nov. (Fissurellidae); *Lepetodrilus shannonae* sp. nov. (Lepetodrilidae); Caenogastropoda: *Provanna reticulata* sp. nov. and *P. chevalieri* sp. nov., *Cordesia provannoides* gen. et sp. nov. (Provannidae); *Phymorhynchus coseli* sp. nov. and *P. cingulata* sp. nov. (Conidae); Heterobranchia: *Hyalogyrina rissoella* sp. nov. (Hyalogyrinidae). All species except *T. granulatus* (from a settlement trap) belong to groups known from cold seeps and the entire seep fauna here is new to science. Biogeographical affinity of this gastropod fauna is to the West Atlantic seeps, not to the Mediterranean seeps or Mid-Atlantic vents. Fragments of the autecology of the species are presented. The evolution of the seep gastropod fauna is briefly discussed and a continuous immigration of taxa is supported. The oldest verified occurrences of modern taxa in the seeps date back to Cenomanian (Cretaceous) time, while some taxa seem not to appear until very late Tertiary.

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1. Introduction

The interest in chemosynthetic environments, hydrothermal vents and various types of seeps has remained at a high level, ever since the discovery of vents in 1977 (Ballard, 1977; Lonsdale, 1977) and the subsequent preliminary description of this ecosystem (Corliss et al., 1979). Only a few years later the first hydrocarbon seep localities were described from off Florida (Paull et al., 1984) and the Gulf of Mexico (Brooks et al., 1985). In less than 30 years these environments have become fairly well known, much better than the surrounding deep-sea. The basic features of the vent and seep faunas, their ecology and relations to the micro-organisms utilizing chemically bound energy in geologically derived effluents were summarized by Van Dover (2000) and their fauna by Desbruyères et al. (2006). By contrast, accumulations on the deep-sea floor of biogenic substrates produced elsewhere where energy is more easily available constitute another type of chemosynthetic

Abbreviations: aspi, Aspirateur, suction sampler; CL, Carottier à lame, a push corer with closing mechanism, covering a rectangular surface of 10 cm × 20 cm; CP, Chalut à perche, beam trawl; C-P, critical-point dried; CT, Carottier tube, push (tube) corer, diameter 5.3 cm; GBT, Grande boîte ROV, large transport container; MAC, Module Autonome de Colonisation, colonization set-up; MNHN, Muséum National d'Histoire Naturelle, Paris; panier, ROV basket, smaller transport containers; PI, principal investigator; PL, Plongée, dive; Radular teeth, 0—central tooth, 1–5—lateral teeth, m1—first marginal teeth; ROV, remotely operated vehicle; SMNH, Swedish Museum of Natural History, Stockholm

* Corresponding author.

E-mail address: anders.waren@nrm.se (A. Warén).

environment that has received much less interest. Attention to the fauna living on biogenic substrates started simultaneously with the discovery of vents (Turner, 1973, 1977; Wolff, 1979), and subsequently remained confined to the taxonomical literature (Marshall, 1983, 1985–1988, 1998; Dell, 1987; Hasegawa, 1997) until the discovery of spectacular whale carcasses (Smith et al., 1989; Rouse et al., 2004; Haag, 2005; Braby et al., 2007). The faunal relations between wood-, seep-, and vent faunas was pointed out early (Warén and Bouchet, 1993) but have recently become more generally acknowledged (Distel et al., 2000; Kiel and Goedert, 2006).

In this paper, we describe 12 new species of gastropods found during ecological surveys carried out off the mouth of the Congo River on the African west coast, and an additional species caught in settlement traps in the vicinity.

In order to better set this fauna in its context, we regularly refer to related species, also from hydrothermal vents and biogenic substrates. Much of this is still unpublished, but a combined review of seep- and hydrothermal gastropods is under preparation.

2. Material examined and methods

2.1. Sampling data

All specimens were sorted out from samples taken by the Zairov 1–2 and the Biozaire 1–3 expeditions, by the Ifremer

laboratory “Environnement Profond” (Deep-Sea Environment). Preliminary identifications were supplied to the Ifremer laboratory by R. von Cosel MNHN and the specimens were forwarded to the first author for description of the new species.

Expedition data:

Zairov 1–2, 05 Dec. 2000–02 Jan. 2001; ROV Victor dives 70–76, PIs H. Ondreas and B. Savoye, Ifremer.

Biozaire 1, 03 Jan.–15 Jan. 2001, ROV Victor PL 77–83, PI M. Sibuet, Ifremer.

Biozaire 2, 15 Nov.–04 Dec. 2001, ROV Victor PL 138–148, PI M. Sibuet, Ifremer.

Biozaire 3, 12 Dec. 2003–10 Jan. 2004, only beam-trawl (Chalut a Perche), CP 10–CP 24, PI A. Khripounoff, Ifremer.

Samples were mainly taken with suction samplers (aspi), push corers (CT, CL), or with the manipulator arms of the ROV. Many specimens were collected as epifauna but fell off after their substrate was deposited in the storage containers (panier and GBT) of the ROV Victor.

In addition to the dives with ROV Victor, a series of hauls with a 5 m wide beam trawl (CP) were done during Biozaire 3; CP 20 across the Regab site and six more in the immediate surroundings. The gastropods of these trawls have been identified partly only. Those species that are normal for deep-sea bottoms were not included, only those that have or may be suspected to have affinity to chemosynthetic environments are included (Table 1).

One new species and four very young gastropods were obtained in settlement traps, baited with organic material and

glass sand Module Autonome de Colonisation (MAC); Desbruyères et al., 1980). These were situated some distance south of the dive sites (Fig. 1.)

MAC5/68-ZA, 07°19.720'S, 011°29.470'E, 1303 m depth.

MAC5/76-ZA, 07°19.03'S, 011°30.45'E, 1255 m depth.

MAC6/94-ZA, 07°19.500'S, 011°29.250'E, 1307 m depth.

MAC7/103-ZC, 07°40.32'S, 010°01.14'E, 3993 m depth.

Metadata concerning the cruises are archived in the Biocean database (Fabri et al., 2006) and available on Internet (www.ifremer.fr/biocean).

A summary of all identifications and how the specimens were collected is appended in Table 2.

2.2. Locality descriptions

The material collected during the ROV dives comes from the following four sites (Fig. 1):

Diapir site. 06°35.0'S, 10°24.5'E, 2300 m depth. PL 138. Three pockmarks and carbonate concretions with no visible seepage. Black concretion, with *Lepetodrilus* and three clams.

Guiness site. 01°34.5'S, 008°32.5'E, 600 m. PL 83, 148. Two pockmarks with bacterial mats and clam beds.

Mps 1-Congo site. 05°28.0'S, 010°57.5'E, 1500 m. PL 71. An area with pockmarks, and clam debris; no visible seepage.

Regab site. 05°48.0'S, 009°42.5'E, 3150 m. PLs 74, 75, 81, 82, 145–147. A large cluster of pockmarks with methane seeps and

Table 1
Trawling during Biozaire 3.

Trawl number	<i>Paralepetopsis sasakii</i>	<i>Calliotropis</i> sp.	<i>Bathybela</i> aff. <i>tenellunum</i>	<i>Phymorhynchus coseli</i>	<i>Phymorhynchus cingulatus</i>	<i>Gymnobela</i> aff. <i>aquilarum</i>	<i>Provanna reticulata</i>	Depth	Latitude °S	Longitude °E
CP 10			(1)					3956	05 51.10	008 21.51
CP 18		(2)	1					3142	05 48.15	009 43.91
CP 19		(3)	1					3184	05 48.07	009 41.61
CP 20	20	9	9	37	3	6	570	3113	05 46.89	009 44.66
CP 21		(3)	(1)					3130	05 47.50	009 43.80
CP 22		(2)	1					3121	05 46.97	009 44.18
CP 23		(2)	(2)					3147	05 45.92	009 43.99

Numbers in parentheses refer to empty shells.

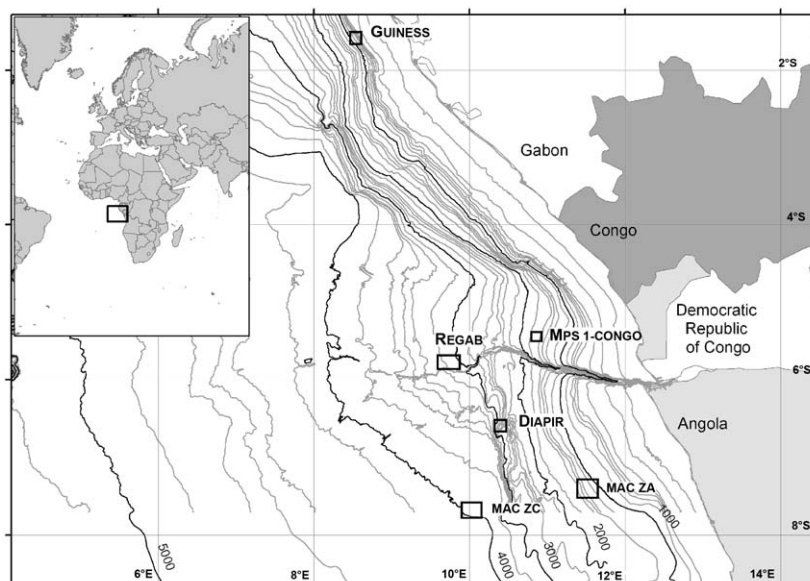


Fig. 1. Map of sites. MAC ZA and MAC ZC are settlement traps.

Table 2
List of specimens examined and collecting data.

ROV Victor dive number and collecting effort	<i>Paralepetopsis sasakii</i>	<i>Pyropelta oluae</i>	<i>Pyropelta sibuetae</i>	<i>Tentaoculus granulatus</i>	<i>Leptogyra costellata</i>	<i>Puncturella similes</i>	<i>Lepetodrilus shannonae</i>	<i>Cordesia provannoides</i>	<i>Provanna reticulata</i>	<i>Provanna chevalieri</i>	<i>Phymorhynchus coseli</i>	<i>Phymorhynchus cingulata</i>	<i>Hyalogyrina rissoella</i>	Locality
71-panier A	Juv								2 juv					Mps 1-Congo/1450
74-panier02	3								1					Regab/3150
75 on black smoker Éch 2									6		1			Regab/3150
75-panier A	6j								9					Regab/3150
75-panier C ^a							1 L		1					Regab/3150
81	17													Regab/3150
81-CL01					1				1				6	Regab/3150
81-aspi01	1								13				200	Regab/3150
81-aspi03									2					Regab/3150
81-GBT01	3							1						Regab/3150
82-aspi04													50	Regab/3150
82-aspi05													1	Regab/3150
82-aspi06									11				1	Regab/3150
82-GBT01	4									3				Regab/3150
82-GBT02										3				Regab/3150
83-aspi02									5					Guiness/750
83-aspi04	3													Guiness/750
138-panier								1						Diapir/2300
145-GBT01												1		Regab/3150
146-aspi01	1						1		11				2	Regab/3150
146-aspi02									26	1				Regab/3150
146-Aspi03	25						56		12	15				Regab/3150
146-GBT01	6								101	3				Regab/3150
146-GBT02	5						37		42					Regab/3150
146-panier02	37	3			1		61		46	5			9	Regab/3150
146-CT04							1		2					Regab/3150
146-CL08 0–1 cm													2	Regab/3150

147-aspi01			3			Regab/3150	
147-aspi03	1		3	125		450	Regab/3150
147-aspi05				67	1 ec	50	Regab/3150
147-Aspi08					1		Regab/3150
147-GBT01	2		1	5			Regab/3150
147-GBT02	6		1				Regab/3150
147-panier/GBT03	8		1	9			Regab/3150
147-panier			8	15		11	Regab/3150
147-CL2 (5–10 cm) 1 mm	1						Regab/3150
148-GBT01	6	6					Guinness/750
148-GBT02	3	1					Guinness/750
148-GBT-03	4						Guinness/750
148-Panier			3				Guinness/750
148-CL07 (0–10 cm)						15	Guinness/750
MAC5/68-ZA		1					1255
MAC5/77-ZA					3L ^b		1255
MAC6/94-ZA		1					1307
MAC7/103-ZC					1Y ^b		3993
CP20	20			570	44 ^c	3	Regab/3113

Numbers in parenthesis refer to empty shells.

ec—egg capsule; L—larvae; Y—young specimen.

^a A single cocculiniform shell, probably young and not identified.

^b Indicates uncertain identification.

^c Many empty shells not included.

rich fauna of tube worms, mussels, clams and shrimps (Komai and Segonzac, 2005; Ondreas et al., 2005; Gay et al., 2006; Olu-Le Roy et al., 2007).

2.3. Preservation and working methods

All material was originally preserved in 4% formalin and later transferred to 70–80% ethanol. It has therefore been difficult to use the material for molecular analyses. The treatment of the specimens follows Warén and Bouchet (2001) and Geiger et al. (2007). Shell morphology is described with indications of right–left and lower–higher as seen on the figures. The preparation of patellogastropod radulae for SEM necessitated some testing to obtain good results since neolepetopsid radulae seem unusually sensitive to alkaline and oxidizing agents (sodium hydroxide and commercial bleach \approx 5% sodium hypochlorite). Radulae were dissected out from large limpets and cleaned in diluted bleach; for small specimens the whole body was soaked. We tested various concentrations of bleach and found the result to be variable, depending on the state of preservation, but frozen and alcohol stored specimens were most sensitive, those preserved in formalin most resistant. Dilutions of the commercial bleach 1:1–1:5 immediately destroyed the teeth. At 1:25 a radula sac could be rinsed clean by spraying water into a bowl containing the

radula after 10 min–1 h. This state can be recognized by the tissues breaking up and becoming transparent. Prolonged storage at this concentration destroyed the teeth and cusps were falling off. At a dilution of 1:50 the cleaning took 2 h; at a dilution 1:100, 8–16 h and after 2 days in bleach 1:100 the radula was more or less destroyed. A specimen of *Bathyacmaea* (Pectinodontidae, Patellogastropoda) was starting to loose its teeth in exposed places after 10 min in bleach 1:25. Commercial bleach varies in oxidizing potential, why it is advised to start with specimens that can be replaced, when starting with a new supply bottle.

The gastropod material including primary type specimens is stored in MNHN, some paratypes and vouchers are in SMNH.

3. Species descriptions

Class Gastropoda

The family arrangement and nomenclature follow Bouchet et al. (2005).

Subclass Patellogastropoda

3.1. Family Neolepetopsidae McLean, 1990

Genus *Paralepetopsis* McLean, 1990

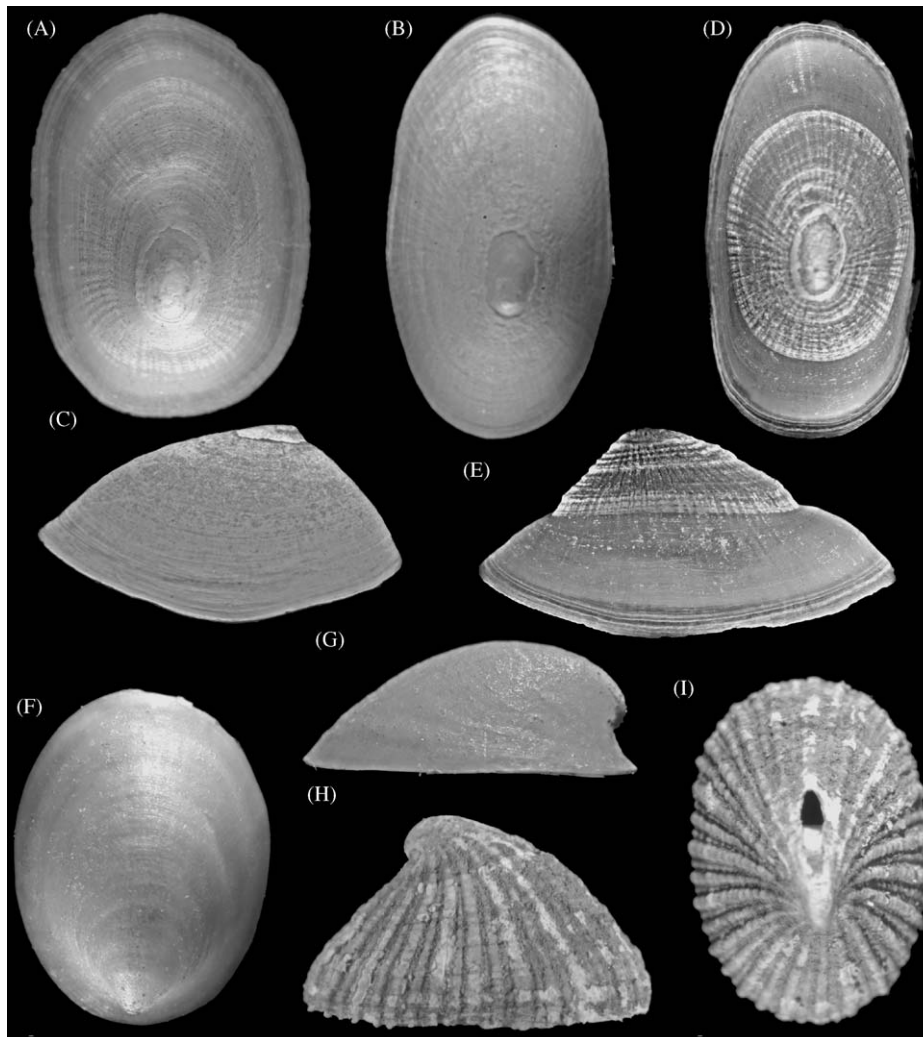


Fig. 2. (A–E) *Paralepetopsis sasakii*. (A) Flat specimen (from mussels), 11 mm. (B, C) Concave base (from tube worm), 10 mm. (D) E Holotype, 12.1 mm shell length. (F, G) *Lepetodrilus shannonae*, 5.3 mm shell length. (H, I) *Puncturella similis*, holotype, 5.9 mm shell length.

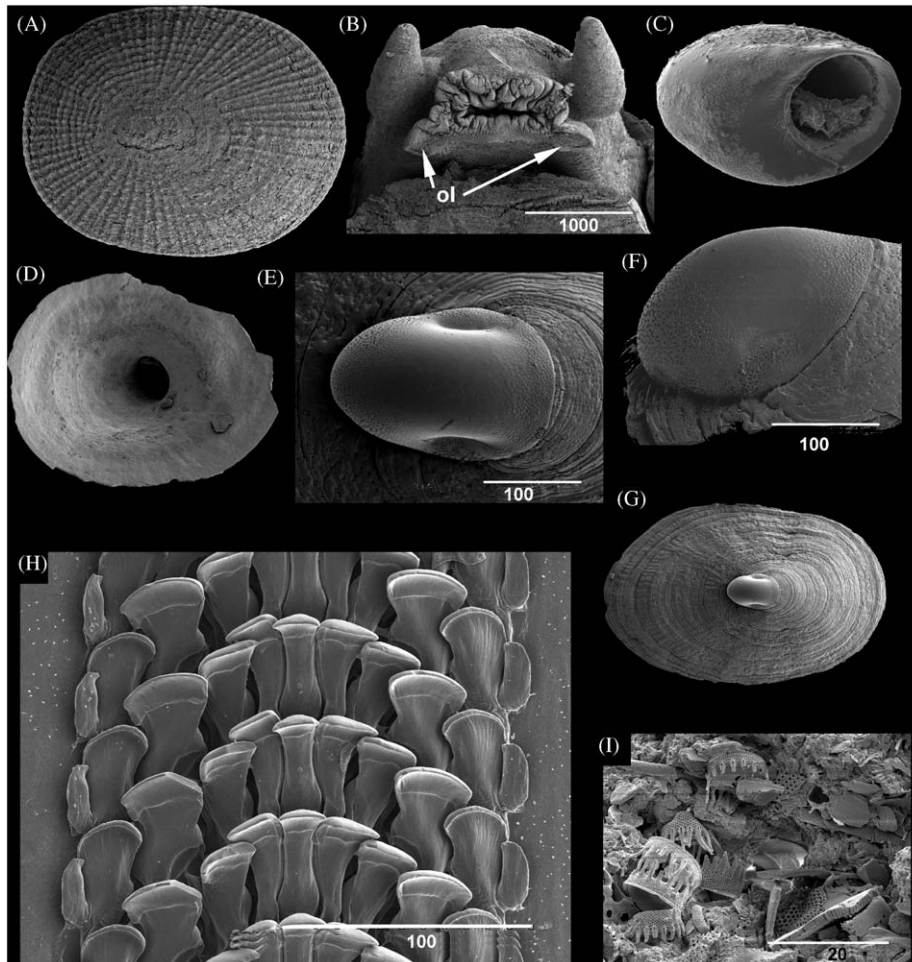


Fig. 3. *Paralepetopsis sasakii*. (A) Flat specimen, normal sculpture, shell length 7.8 mm. (B) Head; anterior end of foot cut to better show oral lappets (ol). (C) Protoconch, shell length 0.24 mm (broken off from shell, internal thickening visible on outer lip). (D) Young shell, ventral view, before sealing connection to protoconch; shell length 0.57 mm. (E, F) Larval shell *in situ*, dorsal and lateral view. (G) Young specimen, shell length 1.32 mm. (H) Radula. (I) Gut content with diatom tests and calcareous particles. Scale lines in μm .

Type species: *P. floridensis* McLean, 1990; sulphide seeps at the Florida Escarpment.

Paralepetopsis sasakii sp. nov.
(Figs. 2A–E, 3A–I)

Type material: Holotype MNHN 20042 and 12 paratypes MNHN 20043, 12 paratypes SMNH #7195.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth [PL146, GBT01].

Material examined: Ca 150 specimens, for details see Table 2.

Distribution: Only known from Regab, MPS 1-Congo, Guinea in 750–3150 m depth.

Etymology: Named after Takenori Sasaki, The University of Tokyo, an old friend and specialist of vent and seep faunas and limpets.

Description: *Shell* (Figs. 2A–E, 3A) of normal size for genus, up to 13 mm long, sturdy, and with rough surface. Shape variable according to substrate; slender and tall with concave basal surface when living on tubes (Figs. 2B–E); lower and broader with flat basal surface when living on mussels (Fig. 3A, 13G). Occasional specimens change substrate and shell shape (Holotype, Fig. 2D–E). Protoconch (Figs. 3C, E, F) largest diameter (= length) ca 240–250 μm ; sculptured by sharply impressed pits on early parts and close to outer lip; at 0.5–0.8 mm shell length sealed from teleoconch by septum. Apex of teleoconch situated at anterior

1/2–1/3 of shell and has lost all detail by corrosion at size of 1.5–2 mm. Anterior surface of shell slightly convex in profile, as is posterior one. Periostracum thin and colourless, hardly noticeable. Outer layer of shell semitransparent, slightly brownish or whitish and rough. Thick medium layer perfectly transparent, followed by an inner, thin, white, chalky and thin layer with concentric pattern, easily peeling. Sculpture (Fig. 3A) of numerous radial ribs, increasing in number with size, and concentric growth lines, together producing a reticulate and scaly appearance.

Dimensions. Maximum shell length 13 mm, diameter of holotype 12.1 mm.

Soft parts (Fig. 3B). The external morphology agrees well with the original description of the genus and Fretter's (1990) more detailed account.

Radula (Fig. 3(H)) formula 5–C–5, roughly of same length as shell or slightly longer, slender, not much mineralized, cusps amber coloured; bases and shafts interlocking. Recently formed part lacks mineralized reinforcement and teeth are soft. Central tooth well developed with simple, rounded, chisel-like cutting edge; shaft basally broader and flattened, with narrow antero-lateral ridge at each side. First lateral tooth of similar shape, slightly broader, base more tapering; with single lateral, more sturdy and curved lateral ridge. Second lateral similar to first. Third lateral tooth ("pluricuspid tooth" *sensu* McLean, 1990) slightly larger and much more sturdily built; with long and

antero-laterally drawn out bases. Fourth lateral without apical mineralization, more scale-like with broad, recurved apical part. Fifth lateral scale-like, apically pointed, half as long as fourth one.

Remarks: *Paralepetopsis sasakii* differs from *P. floridensis* McLean, 1990 and *P. ferrugivora* Warén and Bouchet, 2001 (from the Florida Escarpment seeps and Mid-Atlantic Ridge respectively) in having rounded cutting edges on the central and lateral teeth instead of truncated ones (cf. Warén and Bouchet, 2001: Figs. 2e, f), and by having a shell with more distinct radial sculpture. *Paralepetopsis floridensis*, furthermore, has an almost smooth protoconch; the pits are very indistinct, even in perfect specimens; the protoconch of *P. ferrugivora* is not known.

The shell varies in shape according to the substrate. Specimens from tubes are higher, more slender and the ends of the shell are “lifted” to fit the tubes; specimens living on mussels (Fig. 13G) are broader and have a flat shell base. This could easily give an impression of two species, but the specimen chosen as holotype (Figs. 2D, E) started its life with a flat base and when half-grown, it changed to the more slender shape. We interpret this as a change of substrate from mussels to tubes.

The intestine contains grey to white granular calcareous matter (Fig. 3I). This seems to be the coating of most hard surfaces, which is scratched off together with its bacterial inhabitants and masses of diatom tests. Crustacean remains, polychaete skins, and mud were also found. *Paralepetopsis sasakii* was figured in situ on mussels by (Komai and Segonzac (2005): Fig. 14C). From this and the gut content it can be concluded that it crawls around on hard surfaces such as shells (Fig. 12G) and worm tubes, grazing sediment and bacterial growth.

Subclass Cocculiniformia

3.2. Family Pyropeltidae McLean and Haszprunar, 1987

Genus *Pyropelta* McLean and Haszprunar, 1987.

Type species: *Pyropelta musaica* McLean and Haszprunar, 1987, hydrothermal vents at the Juan de Fuca Ridge.

Remarks: The genus *Pyropelta* is so far known from vents, seeps and whale-falls, some undescribed tropical cocculiniform species from wood falls indicate a closer relationship to the family Pseudococculinidae than previously assumed.

Two new species are described below, one more shallow and one deep. They differ from each other in shell shape; *P. sibuetae* being flatter and having a longer cusp on the innermost marginal tooth, which in *P. oluae* resembles a so-called latero-marginal plate. *Pyropelta sibuetae* also seems to live under different conditions than other species of *Pyropelta* usually do, since its shell surface is not as destroyed by corrosion as is common in the genus and obvious in *P. oluae*. At least one additional, undescribed species of *Pyropelta* is known from seeps in the Gulf of Mexico and the Florida Escarpment (E. Cordes, C. Van Dover, pers. comm.), but the genus is not known from the Mid-Atlantic Ridge.

Corrosion similar to that in *Pyropelta oluae* is sometimes seen in other deep-sea limpets, but then the pattern is different and consists of holes in the original surface, like in *P. sibuetae*, not terraced from the apex as in *P. oluae*.

Pyropelta sibuetae sp. nov.

(Figs. 4A–F, 13B–D)

Type material: Holotype MNHN 20044 and 5 paratypes MNHN 20045, 1 paratype SMNH #7186.

Type locality: Guinness Site, 01°34.45'S, 008°32.49'E, 750 m depth [PL 148, GBT01].

Material examined: 7 specimens, for details see Table 2.

Distribution: Only known from the type locality.

Etymology: Named after Myriam Sibuet, Ifremer, an esteemed colleague in deep-sea biology for more than thirty years.

Description: *Shell* (Figs. 4B–D, 13B–D) of normal size for genus, up to 4 mm long, fragile, almost smooth to terraced by corrosion. Shape almost round, slightly longer than wide; height slightly less than 1/3 of length; anterior and posterior surfaces straight in profile. Protoconch not known. The apex is situated well behind the center in young specimens, perfectly central in adult ones. Periostracum thin and colourless, only visible close to margin. Original sculpture (before corrosion) only very fine growth lines, hardly visible without SEM (Fig. 4C).

Dimensions. Maximum shell length ca 4 mm, diameter of holotype 3.8 mm.

Soft parts (Figs. 4A, 13D) occupy most of shell (Fig. 13D). Foot almost round with indistinct propodium and a pair of posterior epipodial tentacles. Head with low perioral ridge and short, equally developed cephalic tentacles, of which right one has a ciliated sperm tract continuing backwards on neck (Fig. 4E). Ca 15 gill leaflets in anterior half of right pallial furrow.

Radula (Fig. 4F) formula ca 30–4–C–4–ca 30, roughly of 1/3 of shell length. Central tooth poorly developed and lacks apical part, posterior end notched. 1st to 3rd lateral teeth of uniform shape, but 1st has a broader base; 4th is more slender and twisted; apical plates with smooth edges except the outer side of 4th lateral which is finely serrated. Innermost marginal tooth similar to subsequent ones but larger, especially basal part; outer marginals gradually more slender laterally; outermost ones flat with simple, hand-shaped, membranous apical part.

Remarks: See under generic heading.

Pyropelta oluae sp. nov.

(Figs. 4G–J)

Type material: Holotype MNHN 20046 and 2 paratypes MNHN 20047.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth [PL 146, panier 02].

Material examined: Only known from the type material.

Distribution: Only known from the type locality.

Etymology: Named after Karine Olu-Le Roy, distinguished explorer of seep biology at Ifremer.

Description: *Shell* (Figs. 4I, J) of normal size for genus, up to 4 mm long; fragile, and with surface terraced by corrosion. Shape almost round, slightly longer than wide, height about 2/5 of length; anterior surface slightly convex to straight, posterior one convex in profile. Protoconch not known. The apex is situated just behind the center. Periostracum thin and colourless, only visible close to margin. Original sculpture not visible anywhere.

Dimensions. Maximum shell length ca 4 mm, diameter of holotype 3.9 mm.

Soft parts. No specimen was well enough preserved to allow C-P drying but no difference from *P. sibuetae* was noticed at examination under a stereo-microscope.

Radula (Figs. 4G, H) formula ca 30–4–C–4–ca 30, roughly of 1/4 of shell length. Central tooth poorly developed and lacks apical part; posterior end evenly curved or notched. 1st to 3rd lateral teeth of similar shape but 1st with broader base; 4th more slender and twisted; apical plates with smooth edges except outer side of 4th lateral which is finely serrated. Innermost marginal, a low plate without shaft, only postero-lateral cusp with one main and a few smaller denticles on each side. Marginals gradually more slender laterally; outermost ones flat with simple, hand-shaped apical part.

Remarks: See under generic heading.

3.3. Family Pseudococculinidae Hickman, 1983

Genus *Tentaoculus* Moskalev, 1976

Type species: *Tentaoculus perlucida* Moskalev, 1976, 300–450 m depth, off New Guinea.

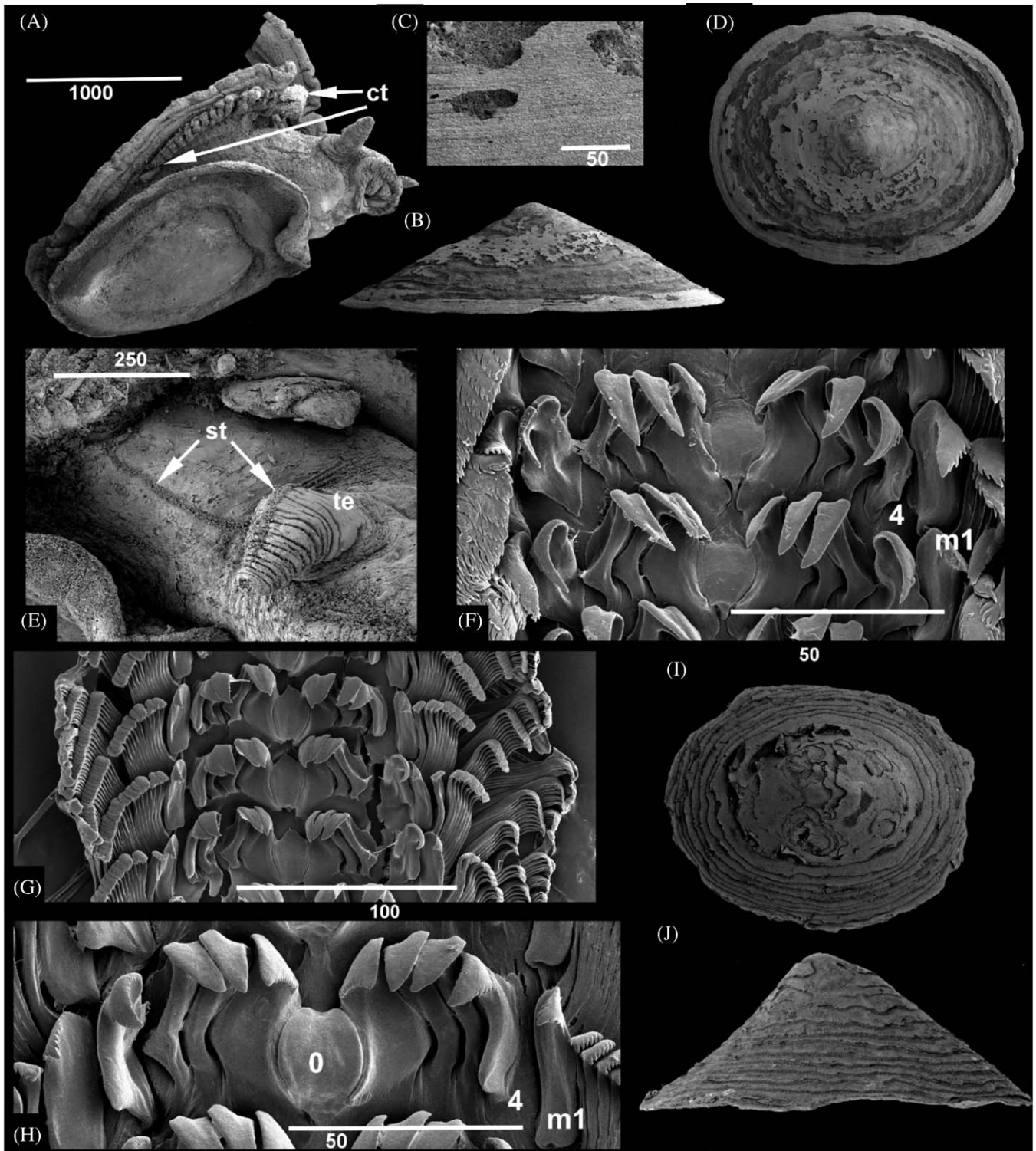


Fig. 4. *Pyropelta* spp. (A–F) *P. sibuetae*. (A) C–P dried body. (B–D) Shell of same specimen, length 3.4 mm, with detail of sculpture and corrosion (also in Fig. 12B). (E) Right side of head with sperm tract on neck and cephalic tentacle. (F) Radula (a successful preparation would have shown marginal teeth as in G). (G–H) *P. oluae*. (G–H) Radula. (I, J) Shell, shell length 3.7 mm. Scale lines in μm . ct—ctenidium; st—sperm tract; te—cephalic tentacle.

Remarks: No details are known about the ecology of the type species. A few additional species have been described from anomuran carapaces and sunken seaweed. Moskalev's (1976) description was not very detailed and the protoconch sculpture was not mentioned or figured. Marshall's (1986) use of the name was more or less based only on the distinctive radula (pers.

comm.), with a large and well developed 1st lateral tooth, equipped with apical denticles. Marshall's (1986) new species also had an internal septum, absent in *T. granulatus*, and not mentioned by Moskalev in the original description.

Tentaoculus granulatus sp. nov.
(Figs. 5A–H)

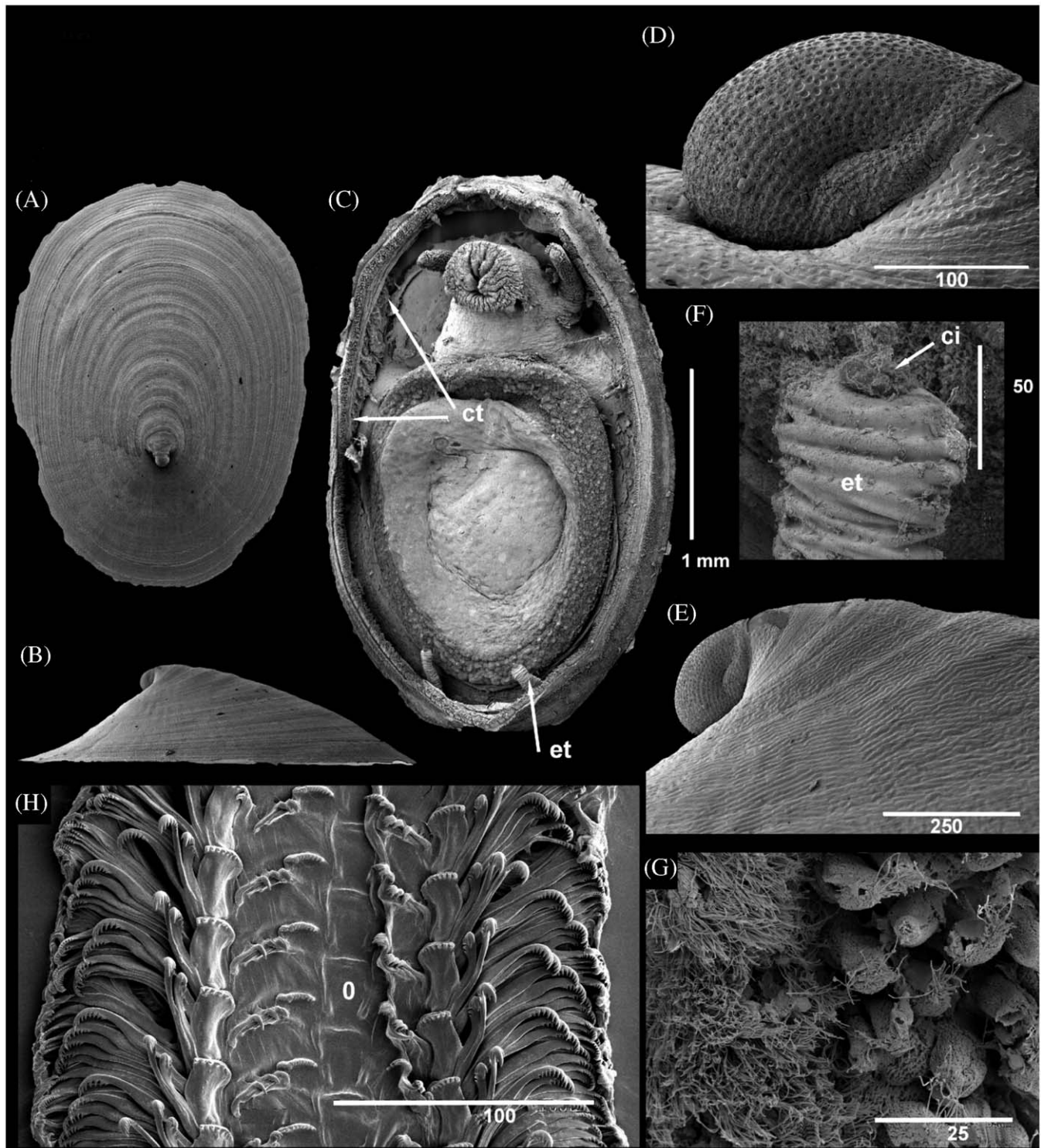


Fig. 5. *Tentaoculus granulatus*. (A, B, D, E, H) Holotype, length 3.8 mm (posterior margin missing). (C, F, G) C-P dried paratype. (C) Body removed from shell, ventral view. (D, E) Larval shell and apex. (F) End of epipodial tentacle with ciliary tuft. (G) Sensory papillae and more dorsal ciliation on inside of pallial skirt. (H) Radula. Scale lines in μm . 0—central tooth; 4—4th lateral tooth; ci—ciliary tuft; ct—ctenidium; et—epipodial tentacle.

Type material: Holotype MNHN 20048, 1 paratype SMNH #7187.

Type locality: Off Angola, 07°19.500'S, 011°29.250'E, 1307 m depth, [MAC6/94-ZA].

Material examined: 2 specimens from the MAC ZA sites, for details see Table 2.

Distribution: Only known from the type material.

Etymology: Latin adjective *granulatus*, -a, -um, meaning granular referring to the appearance of the shell surface.

Description: *Shell* (Figs. 5A–E) large for genus, 3.7 mm (estimated) long, fragile with a combination of concentric and granular sculpture. Shape regularly ovate with apex just in front of posterior 1/3; 3.8 times as long as high. Protoconch (Fig. 5D) largest diameter (= length) ca 230–240 μm ; sculptured by

spirally arranged pits, diameter 2–6 µm; initial part with lateral bulge at each side. Anterior surface of shell slightly convex in profile, posterior one, weakly concave. Periostracum thin and colourless, hardly noticeable. Teleoconch sculpture starts with pits similar to those of protoconch, gradually transforming to produce small concentrically arranged ridges which with increasing size become less conspicuous when incremental lines dominate.

Dimensions. Maximum shell length >3.7 mm (holotype).

Soft parts (Figs. 5C, F, G). Body small, occupies roughly 2/3 of shell diameter in preserved specimens. Foot small and round, equipped with a pair of simple, posteriorly placed epipodial tentacles (Fig. 5F). Head with small oral disc and a pair of cylindrical tentacles; right cephalic tentacle with external ciliated sperm tract continuing along neck to pallial cavity. Right, anterior 1/2–1/5 of inside of pallial skirt with series of gill leaflets; inside of pallial margin and cephalic tentacles covered by sensory papillae (Fig. 5G).

Radula (Fig. 5(H)) formula ca 20–4–C–4–ca 20, length roughly 1/5 of shell length, broad, delicately built. Central tooth a low plate with posterior transverse ridge. 1st lateral sturdily built, long and triangular with apical cutting edge, one main denticle at outer corner, 7 more central, smaller and 6 much smaller outer denticles. 2nd to 4th laterals much more slender, claw-like with apical denticulated cusp. Innermost marginal broad and sturdily built with 8 apical denticles. Consecutive marginals claw-like with apical denticulation.

Remarks: *Tentaoculus granulatus* resembles *T. eritmeta* (Verrill, 1884) (see McLean and Harasewych, 1995) from 2600 m depth, off New Jersey (US), but that species has a more slender and higher shell with internal septum; it is known from shells only.

Subclass Vetigastropoda

3.4. Family Fissurellidae Fleming, 1822

Genus *Puncturella* Lowe, 1827

Type species: *Patella noachina* Linné, 1771, Europe.

Remarks: The genus *Puncturella* includes a few intertidal to bathyal species inhabiting rocks, shells and other hard surfaces. Three species have been described from vent localities: *P. parvinobilis* Okutani et al., 1993 and *P. rimaizenaensis* Okutani et al., 1993, both off Japan and *P. solis* Beck, 1996 from Edison Seamount off Lihir Islands. Of these species, *P. parvinobilis* and the new species described below, are quite similar to the type species. McLean and Geiger (1998) described three more fissurellids related to the genus *Fissurisepta*, from the vicinity of vents, but since they all were found as single specimen and have not been found again in vent environments they were probably occasional guests to chemosynthetic environments.

Puncturella similis sp. nov. (Figs. 2(H, I, 6H–J))

Type material: Holotype MNHN 20049 and 1 paratype MNHN 20050, 1 paratype SMNH #7184.

Type locality: Guinness site, 01°34.45'S, 008°32.49'E, 750 m [PL 148, panier].

Material examined: The type material.

Distribution: Only known from the type locality.

Etymology: Latin adjective, *similis*-similar, with reference to its resemblance to *P. noachina*.

Description: *Shell* (Figs. 2H, I) of normal size and shape for genus, ca 6 mm long, sturdy, with a rough surface. Protoconch not known, corroded. Anterior surface of shell evenly convex in profile, posterior one flatter. Periostracum thick and light brown.

Sculpture consists of ca 30 primary radial ribs with 1–2 secondary ones intercalated between primaries. Scale-like growth lines give ribs a file-like appearance. Internal septum, foramen and apex similar to those of *P. noachina*.

Dimensions. Maximum shell length 5.9 mm (holotype).

Soft parts (Figs. 6H, I). Normal for genus; 5 small medially placed, one large posterior and one large anterior epipodial tentacles (not ciliated). Eye lobes large; eyes absent. One tapering and ciliated neck tentacle behind right cephalic tentacle (Fig. 6I).

Radula (Fig. 6J) ca 10 times as long as wide, slightly shorter than half length of shell, rhipidoglossate, similar to *P. noachina* but more delicate. Innermost marginal tooth without complete shaft.

Remarks: *Puncturella similis* resembles *P. noachina* (see Fretter and Graham, 1976; McLean and Geiger, 1998) but differs in having a finer sculpture of about 30 radial primary ribs alternating with secondary ribs of half their size, while *P. noachina* has ca 20–25 primary ribs and scattered, much smaller secondary ribs. Furthermore, *P. noachina* has eight epipodial tentacles of more uniform size along each side of the foot and well developed eyes.

3.5. Family Lepetodrilidae McLean, 1988

Remarks: Results from DNA investigations (Geiger and Thacker, 2006; Kano, 2008; S. Johnson, pers. comm.) suggest that the Lepetodrilidae, the Gorgoleptidae, and the vent slit limpets (Temnocinclinae, Sutulizoninae [Scissurellidae] and Clypeosectidae [Fissurelloidea]), form a monophyletic group as suggested by Warén and Bouchet (2001) and Bouchet et al. (2005), based on protoconch morphology and radular ontogeny. Lepetodriolea may be a sister group to Scissurelloidea or, more likely, end up within the Scissurelloidea.

Genus *Lepetodrilus* McLean, 1988

Type species: *L. pustulosus* McLean, 1988, hydrothermal vents, Galapagos Rift.

Remarks: The species of *Lepetodrilus* form a morphologically uniform group with only slight disparity in shell, gill, penial, epipodial and radular morphology. Some are difficult to identify and cryptic species are common (Craddock et al., 1997; Johnson et al., 2006), also cases where detailed examination of external characters has failed to reveal differences, especially among the species similar to *L. elevatus* from the East Pacific Rise (Matabos et al., 2007) and the western Pacific.

The species of *Lepetodrilus* often totally dominate the gastropod fauna of the vents at the EPR and MAR. Two species from the North Pacific vents have evolved bacterial symbiosis and cultivate filamentous bacteria on the gill (Johnson et al., 2006; Bates, 2007).

The genus was not previously known from cold seeps (Warén and Bouchet, 2001), but five undescribed species are now known, two off Costa Rica, one in the Gulf of Mexico, one at the Florida Escarpment (AW, unpubl.), and the fifth one is described below. As far as known, they are not as numerically dominating in the gastropod fauna of the seeps, as in vents.

One of the species from Costa Rica, the Gulf of Mexico species and the West African species described below, form a group of very similar species that can be recognized by the shell shape which is more evenly rounded in profile and by the presence of a pallial penis in the two latter. The species from off Costa Rica is a female, so the type of penis is unknown.

Lepetodrilus shannonae sp. nov. (Figs. 2F, G, 6A–F, 7A–F)



Fig. 6. Details of soft parts. (A–F) *Leptodrilus shannonae*. (A) Female, head; buccal mass and radula partly everted. (B) Epipodial tentacle, dorsal view. (C) Male, neck lobe, ventral view; lobe partly detached from neck. (D, E) Radula, central tooth enlarged. (F) Stomach content of calcareous particles and diatom tests. (G) *Leptogyra costellata*, operculum (damaged), diameter 0.56 mm. (H–J) *Puncturella similis*. (H) C-P dried body, ventral view. (I) Detail of right side of head with cephalic tentacle, eye lobe and neck tentacle. (J) Radula, outermost lateral teeth removed on right side. el—eye lobe; et—epipodial tentacle; nl—neck lobe; nt—neck tentacle; te—cephalic tentacle. Scale lines in μm .

Type material: Holotype (a male) MNHN 20051 and 19 paratypes MNHN 20052, 27 paratypes SMNH #7185.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth [PL 146, aspi 3].

Material examined: Ca 160 specimens, for details see Table 2.

Distribution: Only known from the Regab and Diapir sites.

Etymology: Named after Shannon Johnson, Monterey Bay Aquarium Research Institute, a co-worker during cruises and of invaluable help to AW for understanding the Lepetodrilidae.

Description: *Shell* (Figs. 2F, G) of medium size for genus, 4–7 mm long, brownish–greenish, rather sturdy, ovate and of elevated limpet shape with initial part close to, but inside shell margin; largest width at anterior 1/3. Protoconch corroded in all specimens; teleoconch with about one tightly coiled whorl of rapidly increasing diameter, lacks a columellar shelf. Whole shell covered by tough, brownish–greenish periostracum, folded across shell margin and spanning about 1/12 of width of aperture (across calcareous peristome). Sculpture consists of indistinct, low, close-set concentric and rounded ridges (Fig. 7C), separated by interspaces of similar width, most distinct at mid part of shell, more indistinct towards margin and apex in adult specimens. Muscle scars distinct, equally developed on both sides, reach anterior 1/4 of shell and cross posterior part of shell as narrow line.

Dimensions. Maximum shell length 7.9 mm; holotype, a male of 6.1 mm length.

Soft parts (Figs. 6A–C, 7D–H). Foot rounded, anteriorly somewhat truncated, with distinctly set off propodium; posterior half of foot surrounded by an epipodial ridge with a broad, 3-fingered, flap-like posterior epipodial tentacle on each side at posterior 1/3 (Fig. 6B); no anterior epipodial tentacle. No notch in ridge between epipodial tentacles. Pallial margin bilobed, with inner crenulated lobe demarcated by a deep fissure where the periostracum is produced. Single inconspicuous retractile pallial tentacle in the pallial margin, at level of right cephalic tentacle. Shortly posterior to pallial tentacle emerges a fleshy, gutter-like process (Fig. 7G) with wrinkled interior and apical row of 10 µm long papillae (Fig. 7H) and a single slightly larger papilla at its outer edge. Head large and broad (Figs. 7D, E); postero-laterally widened, with very short snout; and apical–ventral mouth. Cephalic tentacles conical, slightly longer than snout in preserved specimens; left one abutting a small eye-lobe, right one (Figs. 6A, C) abutting a larger eye-lobe and a flap-like neck fold of similar size and shape in males and females. Sensory papilla on right, ventral part of neck (Fig. 7E). Gill (Fig. 7F) not hypertrophied, bipectinate throughout its length; dorsal leaflets low and ridge-like; efferent axis attached for 1/4 of its length, afferent one for 2/3. Sensory bursicles present. Right gill rudimentary (Fig. 7F); only 3–4 ciliated ridges remain. Ventral leaflets up to 0.5 mm long in large specimen, slightly more than 30 in number. Rectum inconspicuous. Pallial part of gonoduct, to the right of the rectum and fused to it.

Radula (Figs. 6D, E) rhipidoglossate, formula ca 40–5–C–5–ca 40, normal for the genus. Central tooth very low and of almost degenerated appearance. First lateral tooth with coarsely and unevenly denticulate edge. Second to outermost lateral teeth, with long apical plate; in second lateral both sides smooth, in third outer side finely serrated, in fourth one coarsely serrated, and in fifth one, inner side with 5–7, outer with 5 larger apical and 5 smaller, more basal denticles. Marginals start as rather sturdy, tall teeth with interlocking shafts and serrated, triangular, apical plate, then gradually transform into tall, narrow, tightly stacked laminar structures with simple, serrated, ovate apical plate directed 45° sideways from longitudinal axis of radula (and shaft) by a subapical flexure of shaft; outer side of shaft with conspicuous spine at base of apical plate.

Jaws consisting of numerous, unusually thin and slender prismatic elements.

Remarks: The gutter-like pallial structure is previously not known in Lepetodrilidae. It is unquestionably of pallial origin. The terminal papillae resemble the pallial margin papillae; but they are one tenth the size and lack the apical cilia of the sensory papillae typical for vetigastropods and in a slightly modified shape present in juvenile *Lepetodrilus*; therefore we do not believe them to be homologous, but new structures associated with the function of the appendage.

Four specimens were sexed by light staining with carm alum, which accentuates the appearance of the gonad; long acicular lobes in the male; uniformly granular in females. Ten more were sexed without staining. No questionable specimens were found and although the males often are smaller than the females, there is no indication of hermaphroditism, and the appendage is found only in males.

The function of the male pallial appendage is uncertain since *L. shannonae* already has a neck fold, which has been interpreted as a penis (Fretter, 1988; McLean, 1988; Bates, 2007) but in *L. shannonae* it is of the same size in females and males, while in other species there is a conspicuous sexual dimorphism (Fretter, 1988). Furthermore, the neck fold has a function to transport food from the gill (Bates, 2007).

The most parsimonious guess for a function is a newly formed penis since it is absent in females, while the neck lobe manages food transport only. Novel penial structures are also present in the lepetodrilid genus *Gorgoleptis*, whose species have a cephalic penis with internal vas deferens (Fretter, 1988) and are frequent in vetigastropods in general (Kano, 2008).

The content of the gut consists of a mixture of sediment, organic material, calcareous crusts, and numerous diatom tests (Fig. 6F).

Subclass Neomphalina

3.6. Family uncertain

Genus *Leptogyra* Bush, 1897

Type species: *Leptogyra verrilli* Bush, 1897, off Delaware, 2195 m.

Remarks: Warén and Bouchet (1989, 1993) mentioned the similarity in radula between *Leptogyra* and *Helicrenion* and the similar protoconchs of some neomphalines and *Leptogyra*; Haszprunar and Kiel, (2005) also mentioned non-conclusive similarities in anatomy and shell structure between some species of Neomphalina and the genera *Leptogyra* and *Leptogyropsis* Marshall, 1988. Kano (2008) has confirmed this in a study based on three genes. This slightly enlarged concept of Neomphalina does, however, not explain the relations to other gastropods. In molecular studies (Colgan et al., 2000; Geiger and Thacker, 2006; Kano, 2008) the group ends up outside the Vetigastropoda.

Species of *Leptogyra* normally live on sunken driftwood (Marshall, 1988), but an undescribed species, very similar to *Leptogyra costellata*, is known from the Blake Ridge seep (Van Dover, pers. comm.; Van Dover et al., 2003) and *Leptogyra inflata* Warén and Bouchet, 1993 lives in vents in the Lau Basin.

Two additional genera are normally placed close to *Leptogyra*, *Xyleptogyra* Marshall, 1988 with an extra left cephalic tentacle as in *Leptogyra*, and *Leptogyropsis* Marshall, 1988, which lacks this extra tentacle. None of these genera is especially similar to *L. costellata* in radular characters, but the shell characters of *L. costellata* are very similar to *L. verrilli*.

Leptogyra costellata sp. nov.

(Figs. 6H, 8A–D)

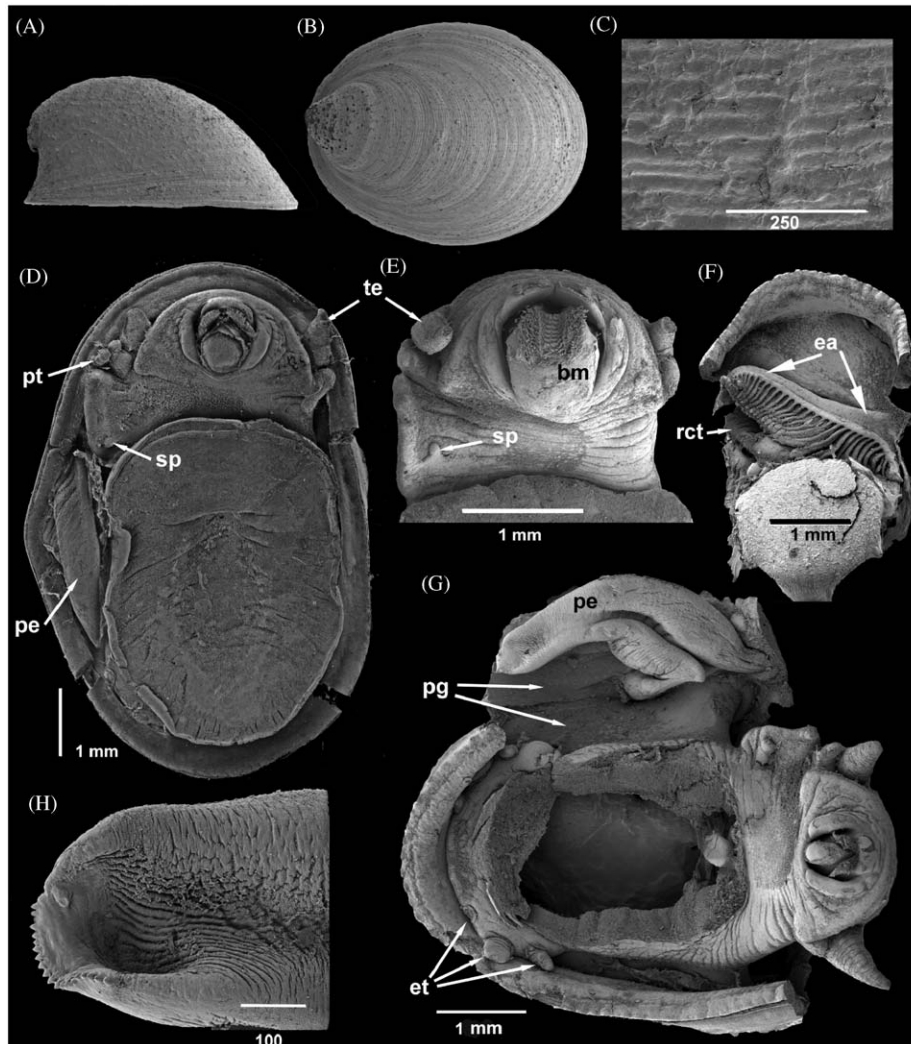


Fig. 7. *Lepetodrilus shannonae*. (A–C) Shell, length 6.3 mm and detail of sculpture. (D) Male, ventral view. (E) Ventral view of head, anterior end of foot removed to show sensory papillus. (F) Ventral view of pallial cavity with ctenidium in situ. (G) Male, foot and viscera removed, pallial skirt bent laterally to expose penis. (H) Tip of penis. Scale lines in μm unless otherwise stated. Bm—buccal mass; ea—efferent axis; et—epipodial tentacle; pe—penis; pg—pallial groove; pt—pallial tentacle; rct—right ctenidium; sp—sensory papillus; te—cephalic tentacle.

Type material: Holotype MNHN 20053, 1 paratype SMNH #7182.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth [PL 81, CL01, 5–10 cm below surface].

Material examined: 2 specimens, for details see Table 2.

Distribution: Only known from the Regab site.

Etymology: Latin, adjective, *costellatus* –a –um, meaning with riblets, referring to the sculpture of the shell.

Description: *Shell* (Figs. 8A–C) small for genus, estimated diameter ca 2 mm (broken), sturdy, fairly tall-spined. Protoconch (Fig. 8A) with 2/3 of a whorl, largest diameter ca 230 μm ; initial part covered by a fine and irregular net-sculpture, last 1/4 whorl smooth. Periostracum thin and colourless, hardly noticeable. Sculpture consists of incised, indistinct spiral lines, more distinct on last whorl and eight in number, often interrupted by smooth areas; and prosocline, sigmoid, raised growth lines, more distinct on last half whorl. Umbilicus wide with 3–4 low spiral ridges inside.

Dimensions. Uncertain, both specimens damaged; holotype 0.98 mm diameter; paratype 1.9 mm.

Soft parts. Not examined in detail. One epipodial tentacle at midpoint of large, flat foot confirmed.

Radula (Fig. 8D). Rhipidoglossate, formula ca 20–4–C–4–ca 20, 6–7 times as long as broad. Central tooth flat, membranous, with

recurved apical part equipped with 7–9 denticles. 1st lateral tooth similar to central, 3rd lateral tooth more claw-like; 2nd one intermediate; 4th lateral tooth twice as high as 3rd, and more sturdily built with several apical cusps. Ca 20 marginals, gradually smaller towards outer margin.

Operculum (Fig. 6H). Very thin, round, multispiral, with subcentral nucleus and short growth edge.

Remarks: *Leptogyra costellata* differs from the West Atlantic type species *L. verrilli* (Marshall, 1988, Fig. 2A–C) by having distinct, oblique axial ribs. The paratype is larger than the holotype, but its sculpture is less well preserved. The holotype is supposed to have been taken 5–10 cm down in the sediment but this is unlikely since the species of *Leptogyra* normally live on firm substrates, pieces of wood and shells. The large flat foot suggests that it can crawl also on top of the mud, but certainly not infaunally. Attempts were made to extract the soft parts from the paratype, but the foot broke off from the head and visceral mass.

Subclass Caenogastropoda

3.7. Family Provannidae Warén and Ponder, 1991

Remarks: Species of Provannidae occur on wood falls and in chemosynthetic environments (Warén and Bouchet, 2001;

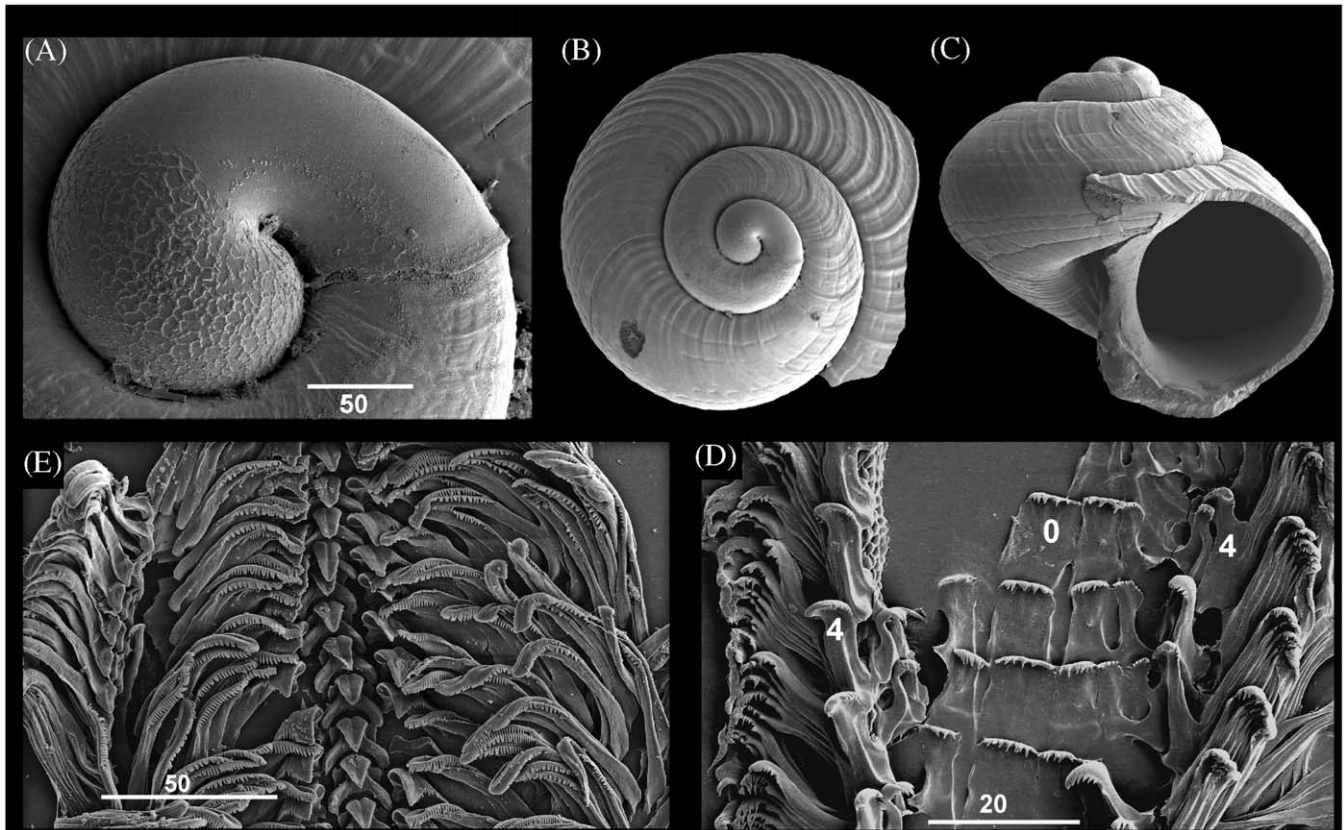


Fig. 8. (A–D) *Leptogyra costellata*. (A) Protoconch. (B, C) Shell, height 0.86 mm. (D) Radula. (E) *Hyalogyrina rissoella*, Radula. Scale lines in μm .

Desbruyères et al., 2006). Their relations to other caenogastropods are uncertain, but anatomical features (Warén and Ponder, 1991) and sperm characters (Healy, 1990, 2000) support relations to both Littorinidae and Abysochrysidae; relations to Littorinidae were supported by Colgan et al. (2007), a study based on several genes, but not including Abysochrysidae. We here describe a new genus that substantiates the relations to the Abysochrysidae.

Genus *Provanna* Dall, 1918

Type species: *Trichotropis* (?) (*Provanna*) *lomana* Dall, 1918, deep water off southern California at or close to seeps.

Remarks: More than a dozen species have been described, two of them from Atlantic seeps, *P. admetoides* Warén and Ponder, 1991, west of Florida in ca 625 m, and *P. sculpta* Warén and Ponder, 1991, off Louisiana in about 500–800 m. The genus has not been found on the Mid-Atlantic Ridge.

Provanna reticulata sp. nov.
(Figs. 9C, D, 10I–L)

Type material: Holotype MNHN 20054 and ca 300 paratypes MNHN 20055, ca 250 paratypes SMNH #7173.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth [CP 20].

Material examined: Ca 1000 specimens, for details see Table 2.

Distribution: Known from Regab, Guinness and MPS 1-Congo sites, 750–3150 m.

Etymology: Latin adjective *reticulatus*, *a*, *um*—reticulate, referring to the sculpture of the shell.

Description: *Shell* (Figs. 9C, D, 10I) of average to large size for genus, 10–14 mm high (estimated, no adult specimen has more than 1.5–2.5 whorls left), broad, with almost round aperture,

dominating spiral- and less-prominent axial sculpture and tough brownish–greenish periostracum. Protoconch (Fig. 10J), intact only in very small specimens, <2.5 mm, Fig. 10I) 0.6 mm high with ca 1.5 whorls; initial part finely granulated, gradually going over to numerous sharp ribs, ca 18 on last quarter-whorl, crossed by ca 25 spiral cords of half the size of the riblets, together forming a uniformly reticulate sculpture. Teleoconch sculpture starts with 3 spiral ridges of which more basal one is infrasutural. Adult specimens sometimes have one spiral ridge intercalated between the two apical ones and usually 2–3 additional basal ones. Axial ribs of variable strength, vary in number, 10–20 on the last whorl and form distinct nodules at intersections with spiral ridges. Columella covered by distinct parietal callus. Aperture evenly rounded except its upper and lower corners. Siphonal canal indicated by very short and shallow depression and distinct twist of columella.

Soft parts normal for the genus (Warén and Ponder, 1991) with short, stubby tentacles; large snout with ventro-apical mouth; large and fleshy foot with a distinct lateral groove paralleling the edge of the sole; single pallial tentacle present.

Operculum (Fig. 10K) with nucleus at 27% of its height and 1.3 times as high as broad. No conspicuous muscle attachments.

Radula (Fig. 10L) taenioglossate, long and slender, 4–5 mm long and 0.2–0.3 mm broad in an average size specimen; central tooth broad with a single cusp; laterals tall and narrow, with main cusp, 2 inner and 3–4 outer cusps; both marginals of same size and shape, with numerous apical, and a series of smaller lateral denticles; apical denticles 50% more numerous on outer marginal tooth. Jaw thin and membranous, only a cuticle lining.

Remarks: *Provanna reticulata* was figured in situ by Komai and Segonzac (2005): Fig. 14B).

Provanna chevalieri sp. nov.
(Figs. 9A, B, 10E–H)

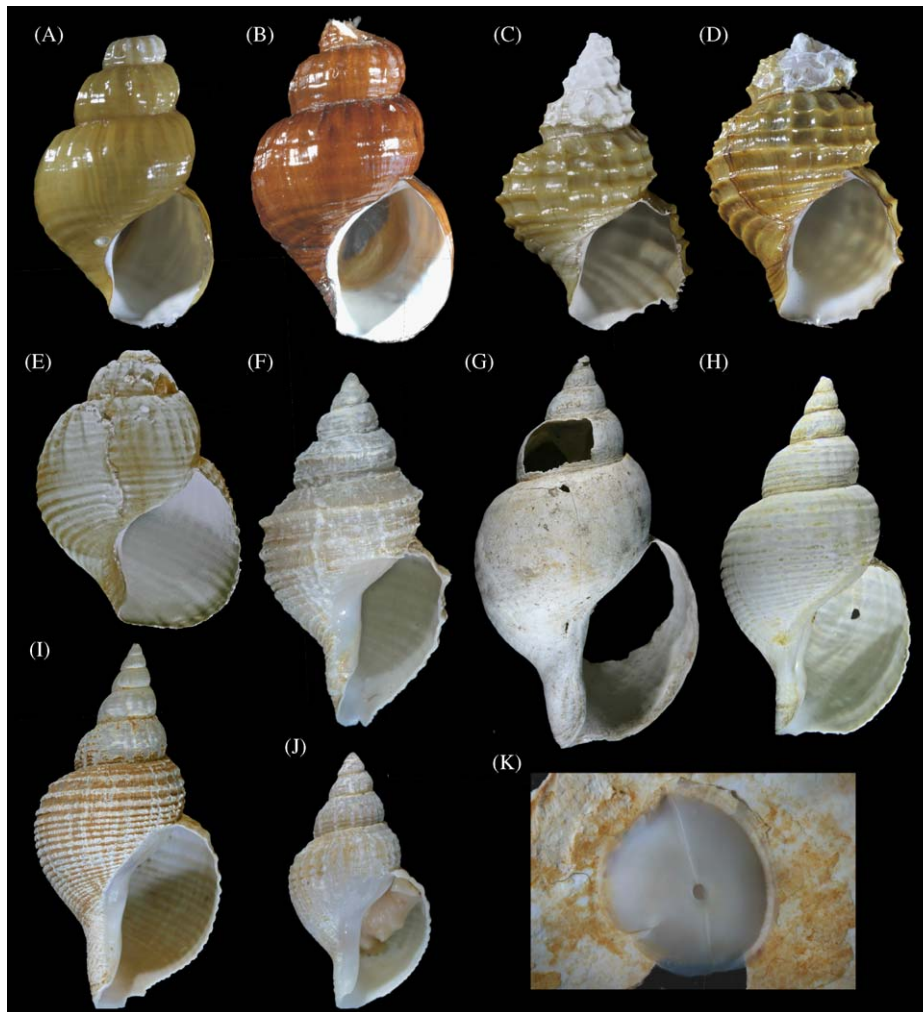


Fig. 9. (A, B) *Provanna chevalieri*, paratype and holotype, 10.1 and 11.5 mm shell height. (C) D *P. reticulata*, paratype and holotype, 8.8 and 11.5 mm shell height. (E) *Cordesia provannoides*, holotype, shell height 10.5 mm. (F) *Phymorhynchus cingulatus*, holotype, shell height 25.9 mm. (G–K) *P. coseli*. (G) Large shell, 65 mm. (H) Holotype, 64 mm. (I, J) Immature specimens 44 and 14.8 mm. (K) Egg capsule assumed to belong to *P. coseli*, 7.5 mm diameter.

Type material: Holotype MNHN 20056, 1 paratype MNHN 20057 and 1 paratype SMNH #7181.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth [PL 146, GBT 01].

Material examined: 24 specimens from Regab, for detail see Table 2.

Distribution: Only known from Regab.

Etymology: This new species is named after Christian Chevalier, currently Portfolio Manager of Exploration Asia with Total Company. Back in 1999, as Exploration Manager with Elf, he noticed specimens of seep-associated molluscs (including the present new *Provanna*) during environmental surveys carried out by Elf on the Congo-Angola margin, recognized their importance, and consulted us on their biological significance.

Description: *Shell* (Figs. 9A, B) of normal size and shape for genus, 8–11.5 mm high, sturdy, with smooth surface. Protoconch not known. Periostracum thick brown or yellowish, shiny. Teleoconch sculpture consists of ca 20 indistinct axial ribs per whorl, crossed by more indistinct spiral ridges of similar width. 3–4 spiral ridges at, or just below periphery of whorls. Axial ribs better developed apically, disappear on base. Aperture rounded-ovate; columella distinctly protruding at short but distinct siphonal canal.

Dimensions. Maximum shell length 11.5 mm (holotype).

Soft parts. The external morphology agrees well with *P. reticulata* and other species of *Provanna*.

Radula (Figs. 10F–H), taenioglossate, 15 times as long as wide. Outer marginals (Fig. 10H) with ca 18, inner ones with ca 13, apical denticles. Laterals with 4–5 denticles, of which 2nd from inner side is twice as large as any other. Central tooth well developed with sturdy anterior supports and a smooth cutting edge.

Remarks: *Provanna chevalieri* differs from *P. reticulata* in having mainly axial sculpture of rounded ribs, while *P. reticulata* has about as strong axial as spiral sculpture.

Cordesia gen. nov.

Type species: *Cordesia provannoides* sp. nov.

Etymology: Named after Erik Cordes, then at Pennsylvania State University, who found this interesting genus in the Gulf of Mexico.

Diagnosis: Similar to *Provanna* but male with a cylindrical penis; two right pallial tentacles, lower one much smaller.

Remarks: This new genus differs from known provannids in possessing a penis. The larval shell agrees with known provannids with planktotrophic larval development in being dehiscent and sealed with a calcareous plug (cf. Kaim et al., 2008). The foot has a well developed longitudinal groove along the sides and there is a large annulated pallial tentacle at the right corner of the pallial margin. The radula is long and slender with the characteristic tall

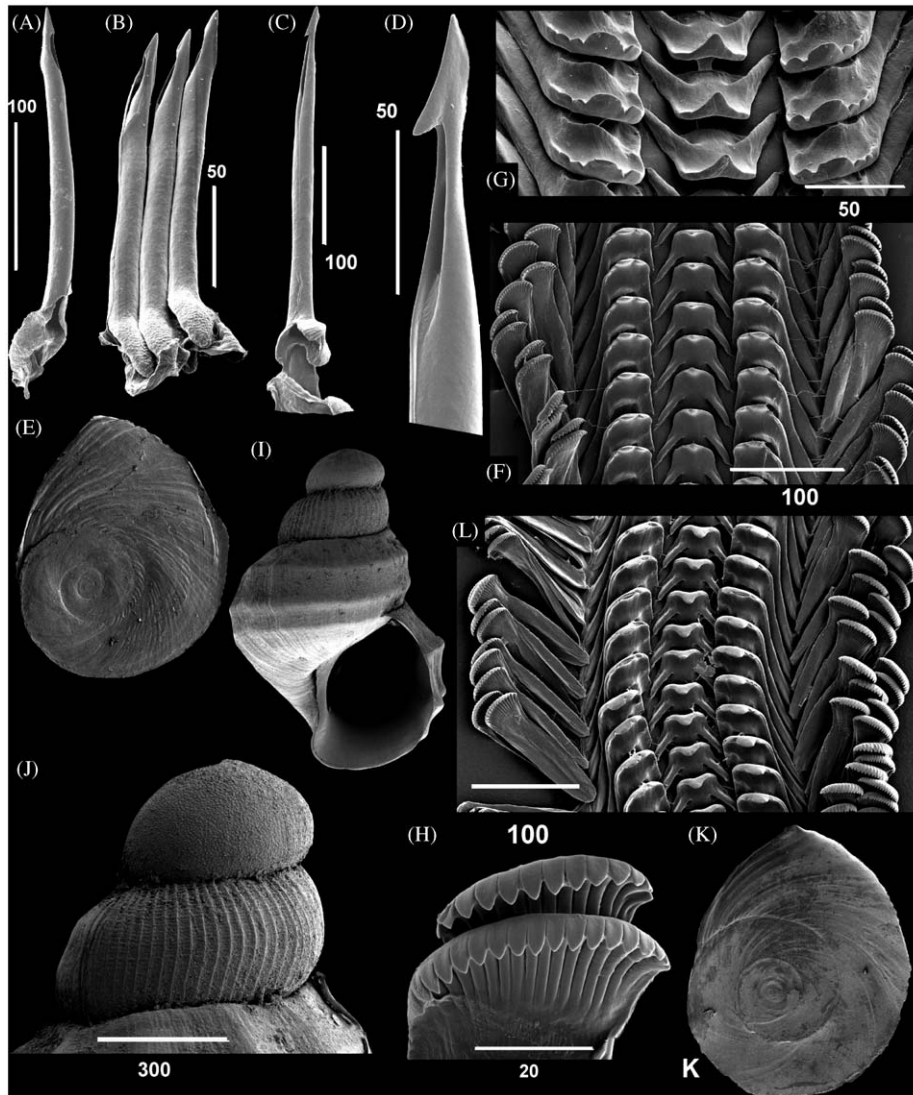


Fig. 10. (A–D) *Phymorhynchus* spp., radular teeth. (A) *P. cingulatus*. (B) *P. coseli*, young, 14.8 mm (specimen in Fig. 8F). (C, D) *P. coseli*, adult. (E–H) *Provanna chevalieri*. (E) Operculum, max. diameter 4.8 mm. (F–H) Radula. (G) Radula, posterior view to show lateral teeth. (H) Detail of marginal teeth, more lateral one in front. (I–L) *P. reticulata*. (I) Young specimen, height 1.6 mm. (J) Detail of apex. (K) Operculum, diameter 3.7 mm. (L) Radula. Scale lines in μm .

and flat marginal teeth. There seems thus to be no question about including *Cordesia* in Provannidae. The question whether the penis is plesiomorphic and lost in other Provannidae, or an autapomorphy, can only be speculated over at present. The presence of a second, much smaller pallial tentacle seems not to have been mentioned for any caenogastropod, and can only be compared to *Abyssochrysos* (Abyssochrysoidea) which has a similar arrangement of pallial tentacles and penis (erroneously described by Houbriek, 1979; his figured specimen is a female and at least *Abyssochrysos brasilianum* Bouchet, 1991 has a penis similar to *Cordesia*, in addition to the two pallial tentacles). This opens the questions of whether *Cordesia* is an abyssochrysid; or if the Provannidae should be included in the Abyssochrysoidea. We favour a third option, that the penis is a plesiomorphic feature and has been lost in other provannids. For this alternative speaks the similarity in radular features between *Cordesia* and provannids, the fact that no abyssochrysid is known from chemosynthetic environments, and that abyssochrysoidea are carnivores or parasites, judging from gut content (AW unpubl. obs.), not grazers as plesiomorphic provannids and *Cordesia*.

A single shell of a possible second species of *Cordesia* was recently found on a submerged log in the Philippines, in a depth of

a few hundred meters. “*Fossarus*” *cereus* Watson, 1880 from 2500 m depth north of Australia has never been properly classified, the shell is damaged and the soft parts of the holotype and unique specimen seem to have been eaten by a beetle. The shell does, however, show some superficial similarity to *Cordesia*.

Cordesia provannoides sp. nov.

(Figs. 9E, 11A–F)

Type material: Holotype MNHN 20058, 1 paratype SMNH #7182.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth, [PL 81, GBT01]

Material examined: The holotype and one specimen from Alvin dive 3916, West Florida Escarpment, 26°02.39'N, 84°55.09'W, 3304 m depth; one specimen, south of Puerto Rico, 14°50'N, 67°20'W, 4956–5005 m depth (Indian River Coastal Zone Museum 065:02748, see also Bouchet and Warén, 1994 Fig. 5.1B).

Distribution: Seeps off Congo and Florida.

Etymology: Named after Erik Cordes, to whom we owe many thanks for sharing his gastropods from the Gulf of Mexico and Florida Escarpment.

Description. *Shell* (Fig. 9E) of normal size for provannids, short and broad with weak spiral and axial sculpture and a large

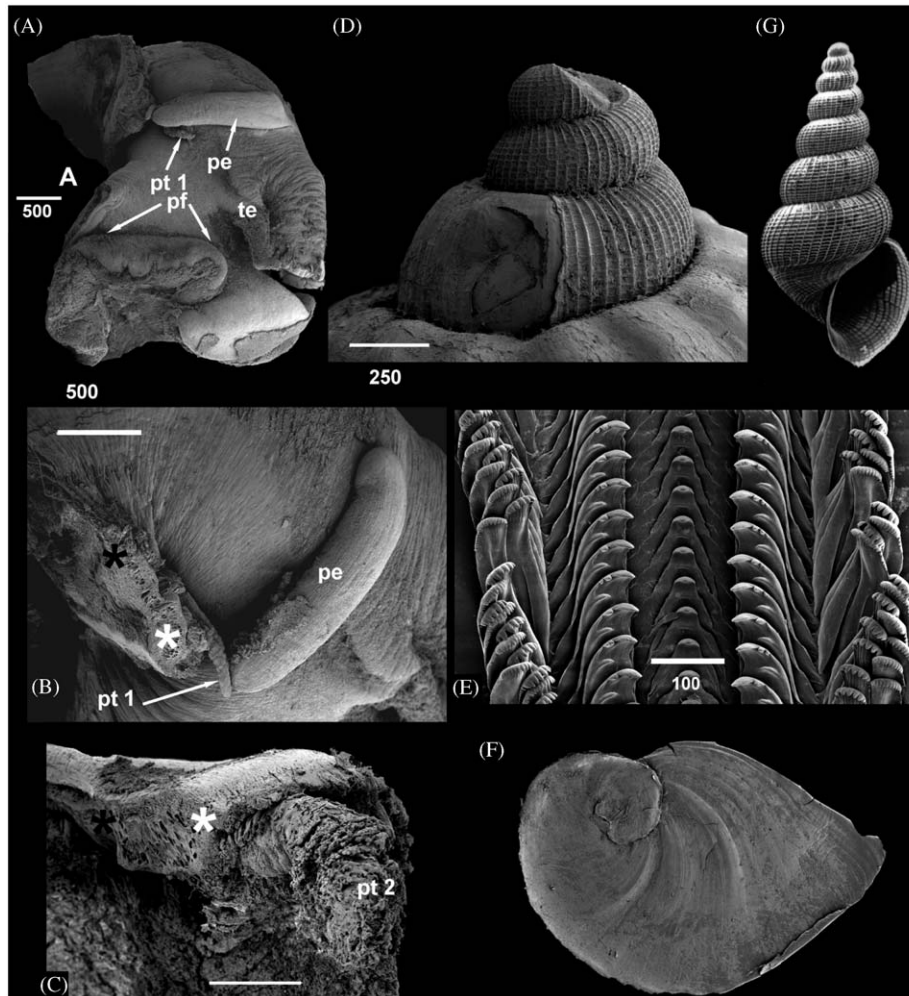


Fig. 11. *Cordesia provannoides*. (A) Head-foot, right side; pallial skirt removed, epithelium peeled. (B) Penis. (C) Pallial skirt, right corner; * fits with * in fig. (B). (D) Apex with protoconch. (E) Radula. (F) Operculum, maximum diameter 4.2 mm. (G) "Richter's larva" from surface plankton off West Africa; height 2.0 mm. Scale lines in μm . pe—penis; pf—pedal fold; pt 1, pt 2—pallial tentacles; te—cephalic tentacles.

aperture with distinct, short siphonal canal. Protoconch (Fig. 11D) maximum diameter ca 0.75 mm, visible height 0.85 mm, consisting of 2 whorls sculptured with ca 13 sharp and narrow spiral cords and 50 stronger axial ribs. Initial part dehiscent and sealed with a calcareous plug. Teleoconch (holotype) with 3+ whorls of rapidly increasing diameter; evenly rounded, connected by a distinct but shallow suture, sculptured by 7–8 spiral cords at end of penultimate whorl and 8–9, more distinct ones on basal surface of body whorl; intersected at close to right angle by 20–25, slightly higher axial ribs, ending above basal surface. Aperture large, constituting slightly less than 60% of shell height; peristome drawn out and expanded in lower right part. Columella with distinct callus demarcated by a shallow furrow, curved to the right and forwards in its lower part.

Dimensions. Height of holotype 10.5 mm.

Soft parts (Figs. 11A–C). Holotype, a male (gonad not examined); histology poorly preserved and all epithelia peeling. Head-foot of normal provannid appearance with a large, slightly tapering snout; stout cylindrical cephalic tentacles with indistinct lateral bulge as only remain of an eye lobe. Lower part of foot demarcated by a furrow parallel to edge of the sole. Propodium large, well demarcated. Pallial cavity deep, with a series of at least 25–30 gill leaflets occupying most of its width. Osphradium simple, with series of indistinct bulges, parallel to left edge of gill. Pallial margin simple, indistinctly bilobed. Small tapering pallial

tentacle present at right corner of pallial cavity, inserted shortly behind pallial margin, close to back; second pallial tentacle 3 × as thick, attached dorsally and anteriorly to smaller one. Male with well developed, cylindrical penis, attached behind and between bases of cephalic tentacles.

Operculum (Fig. 11F) thin, yellowish, paucispiral with distinct growth lines; width 2/3 of height, nucleus at 20–25% of height.

Radula (Fig. 11E) taenioglossate, long, and narrow. Central tooth shield-shaped; apical part distinctly set off with small denticle; base expanded and lacking supporting ridges. Lateral tooth sturdy and narrow with an apical cusp, 1 abutting denticle on its central and 2 on its lateral side, followed by a strong denticle, well below. Marginals long and robust with a basal supporting ridge along central margin, apically and laterally equipped with a series of denticles, twice as large and half in number on inner marginal.

Remarks: The description above is based on two specimens, the West African holotype which seems to be adult but lacks the protoconch, and the Floridian ones which is half-grown, but has a well preserved protoconch. Since we have seen no distinguishing characters we treat them under the same name. The description of the soft parts is based on the seemingly adult holotype.

Kaim et al. (2008) discussed the morphology of the protoconch in *Ifremeria*, *Alviniconcha* and *Desbruyeresia* (all Provannidae) and concluded that the larval development is planktotrophic and that the veligers discard the apical whorls and seal the lower two

whorls with a calcareous plug. Based on protoconch morphology a similar behaviour can be assumed for the larvae of *Cordesia*.

The substrate of *Cordesia provannoides* from south of Puerto Rico was not recorded but there is a possibility that it was living on wood. Some species of *Provanna* have been recorded from both wood and seeps (Warén and Bouchet, 2001).

We have earlier (Bouchet and Warén 1994, p. 103, Fig. 5.1A; this paper Fig. 10G) illustrated a gastropod larva taken by Dr. G. Richter during Cruise 51 of R.V. Meteor in February 1979, 50–100 m below surface at 01°39.7'S, 22°00.1'W (off West Africa), over 4570 m of water. At the time we had left the identification open as no described gastropod had a matching protoconch, but we had matched it with an undescribed benthic juvenile gastropod from south of Puerto Rico and noted that it was "nearest to the Provannidae and Abyssochrysidae". It now seems that the larva corresponds to *Cordesia provannoides*, or a very similar species. At that time we took the occurrence of this provannid larva in surface water as evidence of larval migration to

more shallow water, and possible capability of long distance (trans-Atlantic) dispersal with surface currents.

3.8. Family Conidae Fleming, 1822

Genus *Phymorhynchus* Dall, 1908

Type species: *Pleurotomella (Phymorhynchus) castanea* Dall, 1908; by original designation; deep water east of Galapagos.

Remarks: The genus can be recognized by the large rhynchodeum, large size, presence of mainly spiral sculpture and total absence of subsutural (anal) sinus in the shell (also in very small specimens). The species from hydrothermal vents and seeps are all quite similar to each other, more so than to any of the species from non-vent/seep environments that we have examined (Bouchet and Warén, 1980; Warén and Bouchet, 2001; Desbruyères et al., 2006 and unpublished) or those described by Dall (1908). The species from the ambient deep-sea have more developed axial

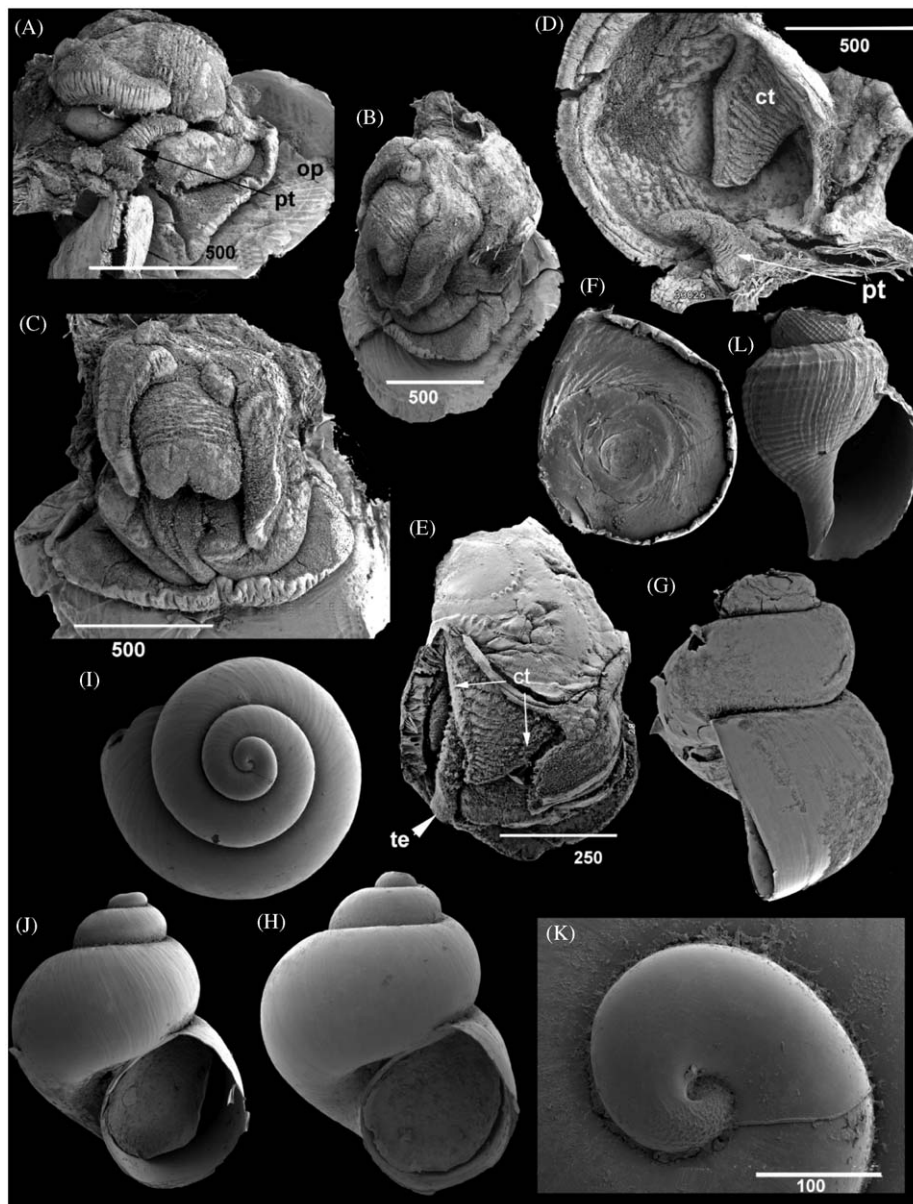


Fig. 12. (A–K) *Hyalogyrina rissoella*. (A–C) Head-foot seen from the right, left and front. (D) Pallial skirt. (E) Head-foot, pallial skirt removed to show ctenidium. (F) Operculum, maximum diameter 1.5 mm. (G–H) Large specimens, 2.9 mm and 3 mm. (I–J) Specimens with complete apex, 1.2 mm and 2.0 mm. (K) Larval shell. L *Phymorhynchus* sp., very young specimen, MAC 7/103-ZC, height 2.0 mm. Scale lines in μm . ct—ctenidium; op—operculum; pt—pallial tentacle; te—cephalic tentacle.

ribs and the spiral cords are more distinctly differentiated in size, the adapical spirals being stronger and separated by wider interspaces than the abapical ones.

A specimen of *Phymorhynchus* sp. from the EPR had eaten *Neomphalus fretterae* (Warén and Bouchet, 1989), and several specimens of *P. ovatus* from the MAR had remains of *Bathymodiolus* and worm-shaped animals in their oesophagus (Warén and Bouchet, 2001). *Phymorhynchus cingulatus* (below) had fragments of polychaetes in its oesophagus.

No protoconchs identifiable as belonging to the new species below have been available, but one juvenile specimen of *Phymorhynchus*-type with slightly more than one teleoconch whorl and remains of the protoconch (Fig. 12L) was found in a settlement trap, MAC7/103-ZC. It may belong to another species of Conoidea, many of which have very similar protoconchs, but it has no trace of anal sinus as is present in most conids. Three conid larval shells with no teleoconch and even less safe identification were found in MAC5/76-ZA.

Phymorhynchus cingulatus sp. nov.

(Figs. 9F, 10A)

Type material: Holotype MNHN 20059, 1 paratype MNHN 20060 and 1 paratype SMNH #5052.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth [CP 20].

Material examined: Only the type material.

Distribution: 2 specimens and one shell from the type locality.

Etymology: Latin adjective *cingulatus* –a, –um, with bands, referring to the spiral sculpture.

Description: *Shell* (Figs. 9F) of medium size, white, fragile, fusiform, with mainly spiral sculpture, thin, brown periostracum, and rounded aperture. Apex and protoconch not known in detail, due to corrosion. Teleoconch originally with 4–4.5 whorls (estimated) of slowly increasing diameter. Sculpture consists of 2 primary spiral keels above suture, 1 slightly weaker at suture, and 6 still weaker below this (on body whorl), and in addition 1–4 secondary ridges intercalated between keels. No trace of sculpture remains on apical whorls because of corrosion. Keels prominent and sharp, much more narrow than interstices, lack secondary spiral micro-sculpture. Incremental sculpture consists of numerous irregular, weak lines and scattered stronger scars. Outermost layer of shell and periostracum worn off or corroded, except on last two whorls. Whorls evenly convex, suture very shallow. Aperture high and elongate, outer lip not thickened; in profile unusually straight and without trace of labial sinus. Siphonal canal long, and slender, well set off and gutter-like.

Dimensions. Height of holotype 25.9 mm (largest specimen).

Soft parts. Normal for the genus with a large rhynchodeum.

Radula (Fig. 10A) toxoglossate, normal for the genus, but lacking barb.

Remarks: The oesophagus of the holotype (used for radular preparation) contained several polychaete fragments with bristles but only capillary setae with no good structures for identification (F. Pleijel, pers. comm).

Phymorhynchus cingulatus belongs to a species group within *Phymorhynchus* characterized by having 2–3 strong spiral keels. At the Mid-Atlantic Ridge there is *P. carinatus* Warén and Bouchet, 2001; at the Florida Escarpment and the Gulf of Mexico, the Rodriguez Triple Junction and the Southern part of the East Pacific Rise three additional undescribed species. This grouping should be tested by molecular characters to clarify the relation to *Phymorhynchus* s.str., but the absence of a radular barb is a character in addition to shell morphology, that supports it.

Phymorhynchus coseli sp. nov.

(Figs. 9G–K, 10B–D, 12L)

Type material: Holotype MNHN 20061, 33 paratypes MNHN 20062, 11 paratypes SMNH #5054.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m depth [PL 75, on a “black smoker”].

Material examined: 47 specimens, and many shells, see Table 2 for details.

Distribution: Only known from the type locality.

Etymology: Named after Rudo von Cosel (Frankfurt and Paris), companion on many mollusc workshops, who made the initial identifications of the molluscs from the Zairov 1–2 and Biozaire 1–3 cruises.

Description: *Shell* (Figs. 9G–J) large, white, fragile, buccinoid, with uniform spiral sculpture, brown periostracum, and rounded aperture. Apex and protoconch not known in detail (but see Fig. 12L). Teleoconch originally with 5.5 ± 0.5 whorls of rapidly increasing diameter, sculptured by spiral cords, 18 on last whorl close to outer lip, 5–6 on penultimate, and 4 on antepenultimate whorl. Apically no trace of sculpture remains because of corrosion. Cords evenly rounded, much broader than the interstices, engraved with 15–20 fine, undulating lines, and increase in prominence towards apical part of whorls. Incremental sculpture visible mainly on last half whorl of shell and consists of numerous irregular, weak lines and scattered stronger scars. Outermost layer of shell and brownish periostracum are usually worn off or corroded all over, except sometimes in the interspaces between ribs and close to lip. Whorls evenly convex; suture shallow. Aperture high and elongate, outer lip not thickened, in profile unusually straight and without a trace of a labial sinus. Siphonal canal very short; lower part of outer lip projects below end of columella.

Radula toxoglossate (Figs. 10B–D) with well developed barb. Young specimens (Fig. 10B) lack the barb.

Dimensions. Height of holotype 64 mm, largest shell 72 mm (estimated).

Soft parts. As described for the genus (Sysoev and Kantor, 1995; Warén and Bouchet, 2001).

Remarks: *Phymorhynchus coseli* closely resembles specimens of an unnamed species of *Phymorhynchus* from the Gulf of Mexico, Florida Escarpment and Blake Ridge seeps, but the whorls are slightly more convex in *P. coseli*, most apparent at the aperture, where the outer lip forms an almost right angle to the preceding whorl; in the west Atlantic species the angle is larger and the aperture more slender.

A single large egg capsule was found in PL 147, attached to a piece of shell (Fig. 9(K)). Among the gastropods from Regab it is most likely to have been deposited by *P. coseli*.

Subclass Heterobranchia

3.9. Family Hyalogyrinidae Warén and Bouchet, 1993

Remarks: Several species of this family live in the vents and seeps, on sunken wood and whale-falls in temperate to tropical areas from the Aleutian seeps to off New Zealand (Marshall, 1988; Warén et al., 1996; Warén and Bouchet, 2001; Braby et al., 2007; AW unpublished). They have been found in sediment samples, on rocks, and on mats of blue-green algae. At a whale-fall off Monterey (California) bacterial mats were seen to be covered by thousands of individuals (AW unpubl. obs.). The gut is filled with sediment. Two Mediterranean species were described from an old amphora and from a submarine cave (Warén et al., 1996).

Ponder (in Bouchet et al., 2005) placed Hyalogyrinidae in the Valvatoidea and thus in the “lower heterobranchs” (sensu Ponder, 1991), a position supported by the heterostrophic protoconch, the sculpture of its initial whorl and the very unusual structure of the jaw. This placement is seemingly contradicted by the rhipidoglossate radular type. The radular sac is, however, not

bilobed at the initial part (as is normal among vetigastropods, see Ponder and Lindberg, 1997). This radular type is shared by *Hyalogyrina*, *Hyalogyra* and *Xenoskenea* among the heterobranchs (see Warén et al., 1993).

Genus *Hyalogyrina* Marshall, 1988

Type species: *H. expansa* Marshall, 1988; on sunken, bathyal driftwood off New Zealand.

Remarks: In addition to the described species, we have examined undescribed ones from various vent, seep and wood-fall localities in the Pacific. A fossil species was recently mentioned from a latest Oligocene to earliest Miocene wood-fall in the state of Washington (Kiel and Goedert, 2006), but the protoconch differs from all known recent species of *Hyalogyrina* in having most of the initial whorl covered by an irregular net-sculpture and Kiel and Goedert (2007) named it *Xylodiscula okutanii*.

The type of larval development of the species of *Hyalogyrina* is unknown since no egg masses are known and, although the initial whorl is very small, the absence of a demarcated protoconch 1 prohibits direct comparisons to planktotrophic species with a multispiral protoconch.

Hyalogyrina rissoella sp. nov.

(Figs. 8E, 12A–K)

Type material: Holotype MNHN 20063 and ca 400 paratypes MNHN 20064, 50 paratypes in SMNH #7203.

Type locality: Regab site, 05°48.0'S, 009°42.5'E, 3150 m, depth [PL 147, aspi 03].

Material examined: Ca 725 specimens, for details see Table 2.

Distribution: Only known from Regab and Guinness sites.

Etymology: “rissoella”, Latin, diminutive of *Rissoa*, from its resemblance to species of family Rissoellidae; used as a noun in apposition.

Description: *Shell* (Fig. 12G, H) of normal size for genus, tall-globular, rather fragile, smooth, slightly yellowish beige due to soft parts and transparency of shell, with very thin, slightly iridescent periostracum. Protoconch (Fig. 12(K)) with about 0.8 whorls, diameter ca 240–250 µm, with very small initial part sculptured by small, crowded pits, 4–5 µm in diameter, to some extent spirally arranged and fused. Where this sculpture ends, diameter starts to increase rapidly and shell becomes perfectly smooth. Outer lip of protoconch slightly constricted; width of whorl 3 times width of whorl where sculpture stops. Teleoconch with about 2.5 whorls in a 1.5 mm specimen; precise number in adults not known because larger specimens have lost apex by corrosion. Suture deep, whorls not very firmly adjoined, shell almost perfectly smooth, incremental lines barely visible on last whorl. Umbilical slit quite oblique, its width corresponds to 1/12 of shell diameter. Peristome prosocline, more tangential than radial, not thickened, and not indented, only flattened by preceding whorl. Cross section of whorls more D-shaped than circular.

Dimensions. Maximum height ca 3.2 mm holotype 1.6 mm.

Soft parts (Fig. 12A–E). Foot large, broad and flat, posteriorly rounded, anteriorly shallowly bilobed, lacking demarcated propodium. Low epipodial ridge starts at anterior part of operculum, continues forwards and reaches base of cephalic tentacles. No epipodial tentacles. Cephalic tentacles about as long as snout in preserved specimens, covered by cilia, more densely towards the tip; smooth at base, connected by small skin fold across base of snout. Right tentacle with low, dorsal bulge at its basal 1/5; in another specimen two bulges at left side of right tentacle. Left

cephalic tentacle with bulge at right side. Snout almost cylindrical, strongly transversally folded, slightly expanded and ciliated distally, with apical–ventral mouth. Pallial cavity rather deep, half a whorl. Bipectinate gill attached only at basal part, behind ctenidial leaflets, no real leaflets, but ca 15 low, ciliated ridges on each side. Gill situated just in front of intestinal coils. Pallial margin distinctly thickened, with densely ciliated tentacle (Figs. 12A, D) at its right corner. Inner, posterior half of pallial cavity partly occupied by invaginated pallial roof, with a loop of intestine. Stomach and intestine contain grey sediment; faecal rod is partly split by a deep longitudinal furrow.

Operculum (Fig. 12F). Transparent, colourless, round, multi-spiral, with distinct growth lines and central nucleus; width of the last whorl, at growth zone, corresponds to 1/5 of diameter.

Radula (Fig. 8E) rhipidoglossate, formula ca 15–1–C–1–ca 15; 0.3 mm long, 3 times as long as broad, with ca 17 transverse rows, with marginal teeth folded across laterals and central. Central tooth low and broad with projecting lateral supports, a triangular, finely serrated apical plate and distinct “wings” behind the lateral support. Lateral tooth low and broad, its central half forms triangular plate with finely serrated central side and a more coarsely denticulated outer side with irregularly scattered larger denticles. Its lateral half is simple, and lacks dentation. First marginal flattened, with a dorsal regular comb of small denticles, an apical finely serrated truncation and equally fine ventral serration; basal 2/3 of length lacks serration. Second marginal longer, more slender and both sides of apical half denticulated. Laterally, teeth become slightly shorter, more slender, and loose denticles. General overviews of seep ecology and biogeography were given by Sibuet Olu-Le Roy, 2002 and Sibuet and Olu 1998.

Jaw. Not seen.

Remarks: *Hyalogyrina rissoella* differs from other hyalogyrinids in being comparatively tall-spined and of a *Rissoella*-like shape, and by having two central-basal bulges on the right cephalic tentacle and a single on the left one. The bulges are present also in half-grown specimens.

4. Discussion and conclusions

4.1. Gastropod fauna

This is listed above and summarized in Table 2. In addition to these, three species obtained by trawling during Biozaire 3 (Table 1) may have some seep affinity and are briefly mentioned here, to draw attention to them as possible seep-favoured species:

Calliotropis sp. (Fig. 13E, Seguenzioidea, family Calliotropidae (Kano et al., in press). Species of the closely related genus *Bathybembix* are common on methane bottoms off the North American West Coast (Sahling, 1997; AW unpublished) and the related genus *Amberleya* was common in Upper Jurassic to Lower Cretaceous seep deposits (Kiel et al., 2008).

Bathybela aff. *tenellunum* (Locard, 1897) (Fig. 13A, Conidae) and *Gymnobela* aff. *aquilarum* (Watson, 1881) (Fig. 13F, Conidae). A similar species has been found frequently at seeps in the Gulf of Mexico (AW unpubl.).

One of the new species, *Tentaoculus granulatus*, is probably not seep related, but it is included since it belongs to a group, Pseudococculinidae, favoured by biogenic substrates. That leaves 12 “seep species”, represented by almost 2000 specimens, a low diversity for bathyal environments, but an above average number of species for seeps.



Fig. 13. (A) *Bathybela* cf. *tenellum*, CP 23, 49.5 mm; only in trawls. (B–D) *Pyropelta sibuetae*. (B) Paratype, 3.8 mm. (C, D) Holotype, 4.3 mm. (E) *Calliotropis* sp., CP 21, 25.5 mm, only in trawls. (F) *Gymnobela* aff. *aquilarum*, CP 20, 26 mm. (G) Mussel bank at Regab with *Bathymodiolus* sp. and the shrimp *Alvinocaris muricola*. White limpets are *Paralepetopsis sasaki*; Red arrows indicate *Provanna reticulata*; blue ones *Lepetodrilus shannonae*.

Table 3

Nearby records of gastropods, related to West African seep species.

W African seeps	Florida esc. seeps ^a	Caribbean seeps ^b	MAR 14–38°N ^c	MAR 04°S ^d	Blake Ridge ^e	Habitat of genus
<i>Paralepetopsis sasakii</i>	<i>P. floridensis</i>	<i>P. sp.</i>	<i>P. ferrugivora</i>	<i>P. sp.</i>	Not known	Seeps and vents
<i>Pyropelta oluae</i>	<i>P. sp.</i>	<i>P. sp.</i>	Not known	Not known	Not known	Seeps and vents
<i>P. sibuetae</i>						
<i>Tentaoculus granulatus</i>						Biogenic substrates ^f
<i>Puncturella similis</i>	Not known	<i>P. sp.</i>	Not known	Not known	Not known	Seeps, vents, rocks, shells
<i>Lepetodrilus shannonae</i>	L. sp. nov.	<i>L. aff. shannonae</i>	<i>L. atlanticus</i>	<i>L. sp. nov.</i>	Not known	Seeps and vents
<i>Cordesia provannoides</i>	C. provannoides	Not known	Not known	Not known	Not known	
<i>Provanna reticulata</i>	Not known	<i>P. 2 spp.</i>	Not known	Not known	Not known	Wood, vents, seeps, whale-falls
<i>P. chevalieri</i>						
<i>Phymorhynchus coseli</i>	<i>P. sp. nov.</i>	<i>P. sp. nov.</i>	<i>P. 2 spp.</i>	Not known	<i>P. sp. nov.</i>	Seeps, vents, ambient sea
<i>Phymorhynchus cingulatus</i>	P. aff. cingulatus	P. aff. cingulatus	<i>P. carinatus</i>	Not known	Not known	Seeps, vents, ambient sea
<i>Leptogyra costellata</i>	Not known	Not known	Not known	Not known	L. sp. nov.	Wood, vents, seeps, caves
<i>Hyalogyrina rissoella</i>	Not known	Not known	Not known	Not known	Not known	Wood, vents, seeps, whale-falls

Species in bold are remarkably similar to their West African counterparts.

^a Unpublished material from C. Van Dover and E. Cordes.^b Unpublished material from E. Cordes.^c Warén and Bouchet (2001).^d Based on unpublished records, courtesy Dr. O. Giere and Meteor cruise M68/1.^e Unpublished material from Van Dover et al. (2003).^f Species of *Tentaoculus* are known from a variety of biogenic substrates, wood and crab carapaces (Marshall 1986).

4.2. Biogeography

The gastropod fauna explored by the Biozaire program is a fairly typical and quite species-rich seep fauna as also indicated by published and unpublished information on other taxa: Vestimentifera (Andersen et al., 2004) mussels (*Bathymodiolus* 2 spp.) and clams (*Calyptogena* 4 spp.) (von Cosel pers comm); vent-seep shrimps *Alvinocaris muricola* Williams, 1988 (Ramirez-Lldora and Segonzac, 2006); squat lobster *Munidopsis geyeri* Pequegnat and Pequegnat, 1970 (Macpherson and Segonzac, 2005) and synaptid holthurians (Ramirez-Lldora and Segonzac, 2006). None of the gastropods described above break this pattern. All genera are known from seeps and/or vents, except *Tentaoculus*, which is an occasional guest in the settlement trap.

The shrimp *Alvinocaris muricola* occurs at West African seeps as well as in the Caribbean and the vestimentiferan *Escarpiia laminata* from the Gulf of Mexico seeps is evidently very close to *E. southwardae* Andersen et al., 2004 from the Gulf of Guinea (Ramirez-Lldora and Segonzac, submitted). Two species of *Bathymodiolus* show very close affinity to West Atlantic seep populations (Olu-Le Roy et al., 2008) and the gastropods follow this pattern, with 4 species having their nearest known relatives at West Atlantic seeps (Table 3). More species may follow this pattern of relationship, but their detailed relations are less obvious from morphological characters and need genetic investigation.

The Mediterranean seeps in the Olimpi and Anixamander areas (Olu-Le Roy et al., 2004) and those off Cádiz in the nearby Atlantic (L. Genio, pers. comm.) have a very different fauna, with only two gastropod genera shared with other vent or seep localities. One is *Lurifax*, known from New Zealand seeps (Lewis and Marshall, 1996), Mid-Tertiary cold seeps in Washington State, the MAR (Warén and Bouchet, 2001) and Japanese vents (Sasaki and Okutani, 2005). The other genus is *Hyalogyrina*, with several species also known from biogenic substrates. Most other species, like *Putzeysia* (Seguenzioidea) and *Clelandella* (Trochidae) belong to northeast Atlantic or Mediterranean radiations and contribute to an impression of a restricted recruitment and recent evolution.

The more closely situated Mid-Atlantic ridge (see Table 3) shows little faunal affinity, not more than more distant vent localities like the East Pacific Rise or the Indian Ocean vents at Rodriguez Triple Junction (Desbruyères et al., 2006; AW unpubl.).

4.3. Ecology

Gut content was examined in *Paralepetopsis sasakii*, *Lepetodrilus shannonae*, *Provanna reticulata* and *Hyalogyrina rissoella*. These species are grazers, scraping off bacterial film and detritus from both soft and hard surfaces. In *Paralepetosis* and *Lepetodrilus* the gut is often to a large extent filled with calcareous material and diatom tests (Figs. 3I, 6F). This is also our experience from other seep localities, while in vents non-calcareous minerals dominate and diatoms are almost absent. *Hyalogyrina* occurred in hundreds in PL147, aspi 3 and PL 81, aspi 3; this genus is often common on bacterial mats. Because of the scarcity of specimens *Puncturella*, *Tentaoculus*, *Cordesia*, and *Leptogyra* were not examined, but they can also be assumed to be grazers like related species. One of the three specimens of *Phymorhynchus* that were examined for a radula, was found to have eaten polychaetes, but both species can be assumed to be predatory and feed on other gastropods, polychaetes, mussels, and carrion (Warén and Bouchet, 2001).

No gastropods from the West African seeps exhibit any striking reduction of the alimentary system or hypertrophy of the gill, usually a good indication of more advanced symbiosis with bacteria, but this is not known from any gastropod from hydrocarbon- or sulphide seeps, only in hydrothermal vents.

4.4. Reproduction and dispersal

The type of larval development is not known with certainty for *Hyalogyrina rissoella*, but the other species except *Phymorhynchus* spp. and *Cordesia provannoides* have lecithotrophic larval development, presumably with a planktonic dispersal phase. The latter is uncertain for *Provanna*. This is not strikingly reflected in the distribution since three out of four planktotrophs seem to be endemic to the African seeps.

4.5. Evolution of the seep fauna

A more detailed discussion of the evolution will have to wait for a broader review of the seep faunas worldwide (Warén, in prep), but two recent papers need some comments. Geiger and Thacker (2006) suggested that the group Neomphalina colonized the chemosynthetic environments during the middle of the Triassic, based on molecular studies, but what their results

actually suggest is that Neomphalina is a sister group to Cocculinidae and Vetigastropoda that may have been separated since the Triassic, but Geiger and Thacker gave no evidence that Neomphalina lived in chemosynthetic environments at the time of divergence.

Kaim et al. (2008) unambiguously show the presence of several species of Provannidae in Japanese Middle Cenomanian (Cretaceous, ca 94 my bp) cold seeps. A few other gastropods similar to modern ones were present in the same deposits (notably tubicolous limpets), while much of the seep gastropod fauna from that time cannot easily be related to modern taxa (Kiel et al., 2008). Most modern seep taxa have not been found at all, or only in comparatively young fossil seeps (Buccinidae, Conidae; Warén and Bouchet, 2001; Kiel and Little, 2006; Kiel, 2006). This supports the view of Warén and Bouchet (1993, 2001) that there has been a continuous inflow of taxa to the seeps accompanying the evolution in shallow water and subsequent extinction of old inhabitants. The time when the oldest surviving groups spread to seeps cannot, at present, be determined based on known fossil deposits due to poor preservation of the fossils, but Kaim et al.'s (2008) report gives hope for tracing the taxa further back in time.

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References

- Andersen, A.C., Hourdez, S., Marie, B., Jollivet, D., Lallier, F.H., Sibuet, M., 2004. *Escarpia southwardae* sp. nov., a new species of vestimentiferan tubeworm (Annelida, Siboglinidae) from West African cold seeps. Canadian Journal of Zoology 82, 980–999.
- Ballard, R.D., 1977. Notes on a major oceanographic find. Oceanus 20, 35–44.
- Bates, A.E., 2007. Feeding strategy, morphological specialization, and presence of bacterial epibionts in lepetodrilid gastropods from hydrothermal vents. Marine Ecology Progress Series 347, 87–99.
- Bouchet, P., 1991. New records and new species of *Abyssochrysis* (Mollusca, Caenogastropoda). Journal of Natural History 25, 305–313.
- Bouchet, P., Warén, A., 1980. Revision of the North-East Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). Journal of Molluscan Studies Supplement 8, 1–119.
- Bouchet, P., Warén, A., 1994. Ontogenetic migration and dispersal of deep-sea gastropod larvae. In: Eckelbarger, K.J., Young, C. (Eds.), Reproduction, Larval Biology and Recruitment in the Deep-Sea Benthos. Columbia University Press, New York, pp. 98–117.
- Bouchet, P., Rocroi, J.-P., Fryda, J., Hausdorf, B., Ponder, W., Valdés, Á., Warén, A., 2005. Classification and nomenclator of gastropod families. Malacologia 47, 1–397.
- Braby, C.E., Rouse, G.W., Johnson, S.B., Jones, W.J., Vrijenhoek, R.C., 2007. Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. Deep-Sea Research I 54, 1773–1791.
- Brooks, J.M., Kennicut II, M.C., Fay, R.R., 1985. Hydrates, oil seepage and chemosynthetic ecosystems on the Gulf of Mexico slope. EOS, Transactions of the American Geophysical Union 66, 105.
- Colgan, D.J., Ponder, W.F., Egger, P.E., 2000. Gastropod evolutionary rates and phylogenetic relationships assessed using partial 28S rDNA and Histone H3 sequences. Zoologica Scripta 29, 29–63.
- Colgan, D.J., Ponder, W.F., Beacham, E., Macaranas, J., 2007. Molecular phylogenetics of Caenogastropoda (Gastropoda: Mollusca). Molecular Phylogenetics and Evolution 42, 717–737.
- Corliss, J.B., Dymond, J., Gordon, L.I., Edmond, J.M., von Herzen, R.P., Ballard, R.D., Green, K.G., Williams, D., Bainbridge, A., Crane, K., Van Andel, T.H., 1979. Submarine thermal springs on the Galápagos rift. Science 203, 1073–1083.
- Craddock, C., Lutz, R.A., Vrijenhoek, R.C., 1997. Patterns of dispersal and larval development of archaeogastropod limpets at hydrothermal vents in the eastern Pacific. Journal of Experimental Marine Biology and Ecology 210, 37–51.
- Dall, W.H., 1908. Report on the dredging operations off the west coast of Central America... The Mollusca and the Brachiopoda. Bulletin of the Museum of Comparative Zoology 43, 205–487.
- Dell, R.K., 1987. Mollusca of the family Mytilidae (Bivalvia) associated with organic remains from deep water of New Zealand, with revisions of the genera *Adipicola* Dautzenberg, 1927 and *Idasola* Iredale, 1915. Records, National Museum of New Zealand 3, 17–36.
- Desbruyères, D., Bervas, J.Y., Khripounoff, A., 1980. Un cas de colonisation rapide d'un sédiment profond. Oceanologica Acta 3, 285–291.
- Desbruyères, D., Segonzac, M., Bright, M., 2006. Handbook of deep-sea hydrothermal vent fauna. Denisia 18, 1–544.
- Distel, D.L., Baco, A.R., Chuang, E., Morill, W., Cavanaugh, C., Smith, C.R., 2000. Do mussels take wooden steps to deep-sea vents. Nature 403, 725–726.
- Fabri, M.-C., Galerou, J., Larou, M., Maudire, G., 2006. Combining the Biocean database for deep-sea benthic data and online Ocean Biogeographic Information System. Marine Ecology Progress Series 316, 215–224.
- Fretter, V., 1988. New archaeogastropod limpets from hydrothermal vents; superfamily Lepetodrilacea. II. Anatomy. Philosophical Transactions of the Royal Society of London B 318, 33–82.
- Fretter, V., 1990. The anatomy of some new archaeogastropod limpets (Order Patellogastropoda, Suborder Lepetopsina) from hydrothermal vents. Journal of Zoology, London 222, 529–555.
- Fretter, V., Graham, A., 1976. The prosobranch molluscs of Great Britain and Denmark. Part 1. Journal of Molluscan Studies Supplement 3, 39–100.
- Gay, A., Lopez, M., Ondreas, H., Charlou, J.L., Sermondadaz, G., Cochonot, P., 2006. Seafloor facies related to upward methane flux within a giant pockmark of the Lower Congo Basin. Marine Geology 226, 81–95.
- Geiger, D., Marshall, B.A., Ponder, W.F., Sasaki, T., Warén, A., 2007. Techniques for collecting, handling, preparing, storing and examining small molluscan specimens. Molluscan Research 27, 1–50.
- Geiger, D.L., Thacker, C.E., 2006. Molecular phylogeny of basal gastropods (Vetigastropoda) shows stochastic colonization of chemosynthetic habitats at least from the mid Triassic. Cahiers de Biologie Marine 47, 343–346.
- Haag, A., 2005. Marine biology: Whale fall (News feature). Nature 433, 566–567.
- Hasegawa, K., 1997. Sunken-wood associated gastropods collected from Suruga Bay, Pacific side of the Central Honshu, Japan, with descriptions of 12 new species. National Science Museum Monographs Tokyo 12, 59–123.
- Haszprunar, G., Kiel, S., 2005. *Leptogyra* and *Leptogyropsis*: two wood-inhabiting neomphaloid gastropods. In: Hydrothermal Vent and Seep Biology Symposium, La Jolla, CA, 2005, Abstracts, p. 163.
- Healy, J.M., 1990. Taxonomic affinities of the deep-sea genus *Provanna*: new evidence from sperm structure. Journal of Molluscan Studies 56, 119–122.
- Healy, J.M., 2000. Mollusca: relict taxa. In: Jamieson, B.G.M. (Ed.), Reproductive Biology of Invertebrates, Part B, Progress in Male Gamete Ultrastructure and Phylogeny, vol. 9. Wiley, Chichester, pp. 21–79.
- Houbrick, R.S., 1979. Classification and systematic relationships of the Abyssochrysidae, a relict family of bathyal snails (Prosobranchia: Gastropoda). Smithsonian Contributions to Zoology 290, 1–21.
- Johnson, S.B., Young, C.R., Jones, W.J., Warén, A., Vrijenhoek, R.C., 2006. Migration, isolation and speciation of hydrothermal vent limpets (Gastropoda: Lepetodrilidae) across the Blanco Transformation Fault. Biological Bulletin 210, 140–157.
- Kaim, A., Jenkins, R.G., Warén, A., 2008. Provannid and provannid-like gastropods from the late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda, Abyssochrysoidea). Zoological Journal of the Linnean Society 154, 421–436.
- Kano, Y., 2008. Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitat. Zoologica Scripta 37, 1–21.

- Kano, Y., Chikyu, E., Warén, A. Morphological, ecological, and molecular characterisation of the enigmatic planispiral snail *Adeuomphalus* (Vetigastropoda: Seguenzioidea). *Journal of Molluscan Studies*, in press.
- Kiel, S., 2006. New records and species of molluscs from Tertiary cold-seep carbonates in Washington State, USA. *Journal of Paleontology* 80, 121–137.
- Kiel, S., Campbell, K.A., Elder, W.P., Little, C.T.S., 2008. Jurassic and Cretaceous gastropods from hydrocarbon seeps in forearc basin and accretionary prism settings, California. *Acta Palaeontologica Polonica* 53, 679–703.
- Kiel, S., Goedert, J.L., 2007. New mollusks associated with biogenic substrates in Early Cenozoic deep-water sediment of Washington State. *Acta Palaeontologica Polonica* 52, 41–52.
- Kiel, S., Little, C.T.S., 2006. Cold seep mollusks are older than general marine mollusk fauna. *Science* 313, 1429–1431.
- Kiel, S., Goedert, J.L., 2006. Deep-sea food bonanzas: early cenozoic whale-fall communities resemble wood-fall rather than seep-communities. *Proceedings of the Royal Society B* 273, 2625–2631.
- Komai, T., Segonzac, M., 2005. A revision of the genus *Alvinocaris* Williams and Chace (Crustacea: Decapoda: Caridea: Alvinocarididae), with descriptions of a new genus and a new species of *Alvinocaris*. *Journal of Natural History* 39, 1111–1175.
- Lewis, K.B., Marshall, B., 1996. Seep faunas and other indicators of methane-rich dewatering on New Zealand convergent margins. *New Zealand Journal of Geology and Geophysics* 39, 181–200.
- Lonsdale, P., 1977. Clustering of suspension feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centres. *Deep-Sea Research* 24, 857–863.
- Macpherson, E., Segonzac, M., 2005. Species of the genus *Munidopsis* (Crustacea, Decapoda, Galatheididae) from the deep Atlantic Ocean, including cold-seep and hydrothermal vent areas. *Zootaxa* 1095, 1–60.
- Marshall, B.A., 1983. The family Cocculinellidae (Mollusca: Gastropoda) in New Zealand. *Records, National Museum of New Zealand* 2, 139–143.
- Marshall, B.A., 1985. Recent and tertiary deep-sea limpets of the genus *Pectinodonta* Dall (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12, 273–282.
- Marshall, B.A., 1986. Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12, 505–546.
- Marshall, B.A., 1987. Osteopeltidae (Mollusca: Gastropoda): a new family of limpets associated with whale bone in the deep-sea. *Journal of Molluscan Studies* 83, 121–127.
- Marshall, B.A., 1988. Skeneidae, Vitrinellidae, and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History* 22, 949–1004.
- Marshall, B.A., 1998. A new deep-sea limpet of the genus *Pectinodonta* Dall, 1882 from New Zealand and new distribution records for *P. aupouria* and *P. morioria* Marshall, 1985. *The Nautilus* 112, 52–57.
- Matabos, M., Thiebaut, E., Le Guen, D., Sadosky, F., Jollivet, D., Bonhomme, F., 2007. Geographic clines and stepping-stone patterns detected along the East Pacific Rise in the vetigastropod *Lepetodrilus elevatus* reflect species crypticism. *Marine Biology* 153, 545–563.
- McLean, J.H., 1988. New archaeogastropod limpets from hydrothermal vents: superfamily Lepetodrilacea. I. Systematic descriptions. *Philosophical Transactions of the Royal Society of London B* 319, 1–32.
- McLean, J.H., 1990. Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. *Journal of Zoology, London* 222, 485–528.
- McLean, J.H., Geiger, D.L., 1998. New genera and species having the *Fissurisepta* shell form, with a generic level phylogenetic analysis (Gastropoda: Fissurididae). *Contributions in Science, Los Angeles County Museum of Natural History* 475, 1–32.
- McLean, J.H., Harasewych, M.G., 1995. Review of western Atlantic species of cocculinid and pseudococculinid limpets with descriptions of new species (Gastropoda: Cocculiniformia). *Contributions in Science, Natural History Museum of Los Angeles County* 453, 1–33.
- Moskalev, L.I., 1976. Concerning the generic diagnostics of the Cocculinidae (Gastropoda Prosobranchia). *Trudy Instituta Okeanologii im. P.P. Shirsova* 99, 59–70, 246. (in Russian).
- Okutani, T., Fujikura, K., Sasaki, T., 1993. New taxa and new distribution records of deep-sea gastropods collected from or near chemosynthetic communities in the Japanese waters. *Bulletin of the National Science Museum, Tokyo Series A* 19 (4), 123–143.
- Olu-Le Roy, K., Caprais, J.-C., Fifis, A., Fabri, M.-C., Galéron, J., Budzhinsky, H., Le Menach, K., Khirpounoff, A., Ondréas, H., Sibuet, M., 2007. Cold-seep assemblages on a giant pockmark off West Africa: spatial patterns and environmental control. *Marine Ecology* 28, 115–130.
- Olu-Le Roy, K., Cosel, R., von Hourdez, S., Carney, S.L., Jollivet, D., 2008. Amphiatlantic cold-seep *Bathymodiolus* species complexes across the Equatorial belt. *Deep-Sea Research I* 54, 1890–1911.
- Olu-Le Roy, K., Sibuet, M., Fiala-Médioni, F., Gofas, S., Salas, C., Mariotti, A., Foucher, J.-P., Woodside, J., 2004. Cold-seep communities in the deep Eastern Mediterranean Sea: composition, symbiosis and spatial distribution on mud volcanoes. *Deep-Sea Research* 51, 1915–1936.
- Ondreas, O., Olu, K., Fouquet, Y., Charlou, J.-L., Gay, A., Dennielou, B., Donval, J.-P., Fifis, A., Nadalig, T., Cochonat, P., Cauquil, E., Bourillet, J.-F., Le Moigne, M., Sibuet, M., 2005. ROV study of a giant pockmark on the Gabon continental margin. *Geo-Marine Letters* 25, 281–292.
- Paull, C.K., Hecker, B., Neumann, A.C., Hook, J., Corso, W., Freeman-Lynde, R., Commeau, R., Golubic, S., Curry, J., 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science* 226, 965–967.
- Ponder, W.F., Lindberg, D.R., 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society* 119, 83–265.
- Ponder, W.F., 1991. Marine valvatoidean gastropods—implications for early heterobranch phylogeny. *Journal of Molluscan Studies* 57, 21–32.
- Ramirez-Llodra, E., Segonzac, M., 2006. Reproductive biology of *Alvinocaris muricola* (Decapoda: Caridea: Alvinocarididae) from cold seeps in the Congo Basin. *Journal of the Marine Biological Association, UK* 86, 1347–1356.
- Rouse, G.W., Goffredi, S.K., Vrijenhoek, R.C., 2004. *Osedax*, bone-eating marine worms with dwarf males. *Science* 305, 668–671.
- Sahling, H., 1997. Untersuchungen an cold seep assoziierten Organismen im NE-Pazifik. *Diplomarbeit der Christian Albrechts Universität*, pp. vii+89pp.
- Sasaki, T., Okutani, T., 2005. A new species of *Lurifax* (Gastropoda: Heterobranchia: Orbitestellidae) from Sumisu Caldera, Southern Japan. *Venus* 63, 121–124.
- Sibuet, M., Olu, K., 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold seep communities at active and passive margins. *Deep-Sea Research* 45 (1–3), 517–567.
- Sibuet, M., Olu-Le Roy, K., 2002. Cold seep communities on continental margins: structure and quantitative distribution relative to geological and fluid venting patterns. In: Weffer, G., Billett, D., Hebbeln, D., Jørgensen, B.B., Van Weering, T.J. (Eds.), *Ocean Margin System*. Springer, Berlin, pp. 235–251.
- Smith, C.R., Kukert, H., Wheatcroft, R.A., Jumars, P.A., Deming, J.W., 1989. Vent fauna on whale remains. *Nature* 34, 127–128.
- Sysoev, A.V., Kantor, Y.I., 1995. Two new species of *Phymorhynchus* (Gastropoda, Conoidea, Conidae) from the hydrothermal vents. *Ruthenica* 5, 17–26.
- Turner, R.D., 1973. Wood-boring bivalves, opportunistic species in the deep-sea. *Science* 180, 1377–1379.
- Turner, R.D., 1977. Wood, mollusks and deep-sea food chains. *Bulletins of the American Malacology Union* 213, 13–19.
- Van Dover, C.L., 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton University Press, Princeton, NJ, 424pp.
- Van Dover, C.L., Aharon, P., Bernhard, J.M., Caylor, E., Doerries, M., Flickinger, W., Gilhooly, W., Goffredi, S.K., Knick, K.E., Macko, S.A., Rapoport, S., Raulfs, E.C., Ruppel, C., Salerno, J.L., Seitz, R.D., Sen Gupta, B.K., Shank, T., Turnipseed, M., Vrijenhoek, R., 2003. Blake Ridge methane seeps: characterization of a soft-sediment, chemosynthetically based ecosystem. *Deep-Sea Research I* 50, 281–300.
- Warén, A., Bouchet, P., 1989. New gastropods from East Pacific hydrothermal vents. *Zoologica Scripta* 18, 67–102.
- 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.
- Warén, A., Bouchet, P., 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. *The Veliger* 44, 116–231.
- Warén, A., Carozza, F., Rocchini, R., 1996. Description of two new species of Hyalogyrinidae (Gastropoda, Heterobranchia) from the Mediterranean. *Bollettino Malacologico* 32, 57–66.
- Warén, A., Gofas, S., Schander, C., 1993. Systematic position of three European heterobranch gastropods. *The Veliger* 36, 1–15.
- Warén, A., Ponder, W.F., 1991. New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam. n. (Caenogastropoda). *Zoologica Scripta* 20, 27–56.
- Wolff, T., 1979. Macrofaunal utilization of plant remains in the deep-sea. *Sarsia* 64, 117–136.