Chapter 7
Gastropods from Recent Hot Vents and Cold Seeps: Systematics, Diversity and Life Strategies

Takenori Sasaki, Anders Warén, Yasunori Kano, Takashi Okutani, and Katsunori Fujikura

Contents

T. Sasaki (✉)
The University Museum, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo, 113-0033, Japan
e-mail: sasaki@um.u-tokyo.ac.jp

A. Warén
Swedish Museum of Natural History, Box 50007, SE-10405 Stockholm, Sweden

Y. Kano
Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan

T. Okutani and K. Fujikura
Japan Agency for Marine-Earth Science and Technology, 2-15 Natsushima, Yokosuka 237-0061, Japan

S. Kiel (ed.), *The Vent and Seep Biota*, Topics in Geobiology 33,
DOI 10.1007/978-90-481-9572-5_7, © Springer Science+Business Media B.V. 2010

7.1 Introduction

Since the first discovery of hydrothermal vents at the Galapagos Spreading Center in 1977, gastropods have gained considerable attention as a major constituent of the chemosynthesis-based biological communities, especially the colonies of large species like *Alviniconcha*, *Ifremeria* and *Lepetodrilus*, or morphologically strange ones like the scaly-foot snail. Various types of symbiotic relations to bacteria have broadened the interest in them. During more than 30 years numerous vent and seep biotopes have been found mainly in temperate seas, but recently hydrothermal vents off Jan Mayen in the North Atlantic at 80°N and cold seeps off Norway between 67°N and 70°N (Haakon Mosby Mud Volcano) with chemosynthesis-based fauna (see Warén and Bouchet 2001; Desbruyères et al. 2006: 516–517 for map). Biology of these vent/seep organisms is still in an early state of exploration; much of what is known is summarized in the monographs by Van Dover (2000) and Desbruyères et al. (2006). Vent/seep taxa have also been a major target in research on higher phylogeny and systematics of gastropods. Several new families were established in the 1980s, based on seemingly "great differences" in morphology.

In this review, we attempt to provide a brief overview of the phylogeny, anatomical organization (Appendix 7.1), protoconch morphology (Appendix 7.2), and biology for taxonomic groups, supplemented by an exhaustive bibliography. We also compiled a list of species described until 2009 (Appendix 7.3), which is an updated version from Warén and Bouchet (2001). Still new taxa are regularly found at new sites or by refined methods of investigation, and a set of more than 50 species is under description. At this point the great surprises are rare and many of the former new "vent families" have been recognized as parts of others. Among gastropods the greatest enigma is the Neomphalina, a group of three families that defies all attempts to classify it with or in other subgroups of Gastropoda, especially molecular attempts. The survey is arranged systematically following Bouchet et al. (2005) except for some part. The systematics of Trochoidea and Seguenzioidea were updated, following recent phylogenetic analyses (Kano 2008; Williams et al. 2008; Kano et al. 2009). Neomphalina is treated as a seventh clade in addition to Patellogastropoda, Vetigastropoda, Cocculiniformia (mainly Cocculinidae), Neritimorpha, Caenogastropoda and Heterobranchia.

The following abbreviations are used for institutions. IFREMER – Institut français de recherche pour l'exploitation de la mer; JAMSTEC – Japan Agency for Marine-Earth Science and Technology; NSMT – National Museum of Nature and Science, Tokyo (formerly National Science Museum, Tokyo); SMNH – Swedish Museum of Natural History; UMUT – The University Museum, The University of Tokyo.

7.2 Groups of Vent/Seep-Associated Gastropods

It is not always obvious which species are seep and vent-associated. Often a large majority of the organisms in a seep or vent belong to a small number of species which do not occur in the periphery but congregate on chimneys or in seepages.

Many of these are endemic to vents, even at genus and occasionally at higher taxonomic level. Other species are regularly found also in other biotopes, but they occur in much larger densities in chemosynthetic environments. Such species are common in cold seeps, rare in hot vents but may also be favoured by food falls. We term them vent- or seep favoured. However, sometimes species do not want to follow human classifications or categorizations; *Lepetodrilus corrugatus* from the Endeavour Ridge, probably the best known locality for vent faunas, is obviously a vent-seep species like its 26 congeners (Johnson et al. 2008) but is known from a single specimen only. No more specimens have been found among hundreds of thousands of specimens of *Lepetodrilus* from all kinds of environments at the Ridge (V. Tunnicliffe, personal communication, 2007).

7.2.1 Clade Patellogastropoda

This clade is currently composed of seven families, Patellidae, Nacellidae, Neolepetopsidae, Lepetidae, Lottiidae, and Eoacmaeidae (Fig. 7.1) (see Nakano and Ozawa 2007: fig. 3; Lindberg 2008). Of these, Neolepetopsidae and Pectinodontidae (= ‘Acmaeidae’) have independently adapted to vents and seeps. Both feed by grazing with a very long radula. Fertilization is external, and larval development is lecithotrophic. All species lack a copulatory organ, a prostate gland and a receptaculum seminis. The protoconch is symmetrical and consists of an almost complete but poorly visible coil. It is difficult to find the protoconch, since it is rapidly corroded and specimens smaller than a millimeter are needed.

Family Neolepetopsidae (Fig. 7.1a)

This family consists of ten described species in three genera (see Appendix 7.3; McLean 2008). They are mostly vent/seep-endemic, but *Neolepetopsis nicolasensis* and *Paralepetopsis clementensis* were described from whale carcasses off California (McLean 2008). The Neolepetopsidae was originally proposed as an independent suborder Lepetopsina based on two characters, the articulation of radular teeth and non-mineralized radula (McLean 1990b). In a molecular phylogenetic analysis by Harasewych and McArthur (2000), *Eulepetopsis* and *Paralepetopsis* form a clade which is closest to *Acmaea mitra*, a shallow water species of the family Lottiidae. The shells are characterized by foliated structure (McLean 1990b, pl. VIII, fig. h; Kiel 2004). The base of the shell is flat in most species, but in some species it adjusts to the substratum. For example, the holotype of *Neolepetopsis gordensis* has a low apex and flat apertural margin in lateral view, but one of paratypes is laterally compressed, and its apertural margin is convex in lateral view (McLean 1990b: pl. 1, 2008: fig. 1a–b). These types occur on bivalves and tubes of Vestimentifera respectively and may give an impression of distinct species. Occasionally one can find specimens that have changed habitat, which is reflected in the shell.

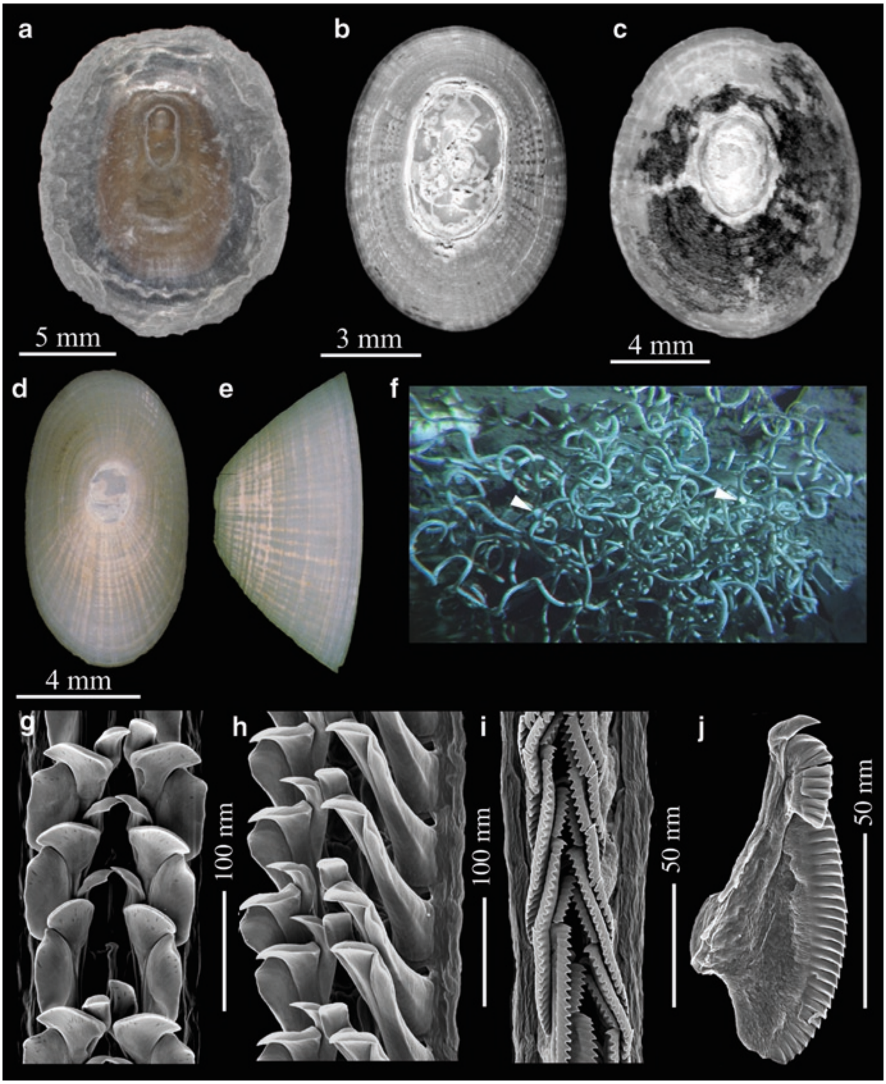

Fig. 7.1 Patellogastropoda. (**a**) *Eulepetopsis vitrea* McLean 1990b. SMNH 43437, East Pacific Rise, 9°N, 2,517 m, vent. (**b**) *Bathyacmaea subnipponica* Sasaki et al. 2003. Holotype UMUT RM27959. Ryuyo Canyon, Nankai Trough, Japan, 1,100 m, seep. (**c**) H. *Bathyacmaea tertia* Sasaki et al. 2003. Holotype, UMUT RM27955. North Knoll of Iheya Ridge, Okinawa Trough, Japan, 969 m, vent. (**d–f**) *Serradonta vestimentifericola* Okutani et al. 1992. (**d–e**) Holotype NSMT-Mo 69643. Off Hatsushima, Sagami Bay, Japan, 1,110–1,200 m, seep. (**f**) Habitat on vestimentiferan tubes. *Hyper-Dolphin* Dive 528, off Hatsushima, 1,095 m. (**g**) *Bathyacmaea secunda* Okutani et al. 1993. Paratype UMUT RM 29199. (**i–j**) Radula of *Serradonta kanesunosensis* Sasaki et al. 2003. Holotype, UMUT RM27961. Kanesunose Bank, Nankai Trough, Japan, 322 m, seep (a: Photo taken by T. Sasaki at SMNH; b–c, h–j: Sasaki et al. 2003; f: Sasaki et al. 2007; g: Sasaki et al. 2006a)

Neolepetopsids lack a gill and the gas exchange is restricted to the surface of the pallial cavity. The radula is formulated as 2-3-1-3-2 and characterized by a well-developed rachidian tooth, pluricuspid outermost lateral teeth, and two broad and scale like marginal teeth (Warén and Bouchet 2001: fig. 2). The radular teeth were formerly believed to be non-minelarized (McLean 1990b) but revealed to be a misinterpretation. Cruz and Farina (2005) reported that the radula of *P. ferrugivora* has a similar elemental composition to those of other patellogastropods having dark-colored, well-mineralized radular teeth. However, the iron oxide in *P. ferrugivora* is amorphous unlike shallow-water patellogastropods showing crystlline phases (Cruz and Farina 2005). Our experience is that these radulae are even more sensitive to chemical cleaning than other patellogastropods and it is only the anterior part that is fully mineralised. McLean's SEM photos show the immature radula. Other striking characters of the family include the absence of osphradia, the absence of basal plates in radula, and posteriorly torted esophagus. Oral lappets which might be related to feeding are present in *Eulepetopsis vitrea* (Fretter 1990: fig. 2), *Paralepetopsis sasakii* (Warén and Bouchet 2009: fig. 3) and *Paralepetopsis ferrugivora* (Warén and Bouchet 2001: fig. 4a).

Warén and Bouchet (2001) reported that the gut is usually filled with ferruginous crusts (Warén and Bouchet 2001: 123 for *Eulepetopsis vitrea*; 125 for *Paralepetopsis ferrugivora*). Nematodes and ciliate fragments are also found in the intestine of *Paralepetopsis ferrugivora* (Warén et al. in Desbruyères et al. 2006: 85). *Paralepetopsis sasakii* had its gut full of calcareous fragments and diatom tests (Warén and Bouchet 2009). *Eulepetopsis vitrea* and *Paralepetopsis floridensis* are gonochoristic and their eggs are heavily yolked and large (Gustafson and Lutz 1994: 88). Larval development of neolepetopsids is lecithotrophic with a planktonic dispersal stage (Warén et al. in Desbruyères et al. 2006: 83–85) on the basis of egg size and protoconch morphology. The protoconch is symmetrical in all patellogastropods including *E. vitrea* (McLean 1990b: pl. VII) and *P. floridensis* (McLean 1990b: pl. X).

Family Pectinodontidae ("Acmaeidae")(Fig. 7.1b–j)

The Pectinodontidae has frequently been classified in the Acmaeidae (e.g. Sasaki et al. 2003), but the type species of genus *Acmaea*, *A. mitra,* formed a clade with *Niveotectura pallida* within the Lottiidae (Nakano and Ozawa 2007), and much of this classification is in a state of limbo. To avoid misunderstandings and unnecessary changes forth and back we use Pectinodontidae. The family contains three genera, *Bathyacmaea* and *Serradonta* from vents or seeps and *Pectinodonta* from sunken wood (Fig. 7.1b–j).

1. Genus *Bathyacmaea* (Figs. 7.1b–c, g–h): Five species (see Appendix 7.3) are known from the western Pacific (and an unnamed species from seeps off Costa Rica). The habitat is either vents or seeps and attached to rocks and shells of

other molluscs. The shell of *Bathyacmaea* is characterized by three layers of semi-foliated structure of the shell (Fuchigami and Sasaki 2005). Radula morphology is strange among gastropods: the teeth are long and spoon-like with cusps at the top, and robust basal plates (e.g. Okutani et al. 1992: figs. 10–11, 1993: figs. 18–19; Sasaki et al. 2003: figs. 5–7). Sexes are separate. Their mode of reproduction is unknown, but external fertilization is plausible as in other patellogastropods. The protoconch has not been found.

2. Genus *Serradonta* (Fig. 7.1d–f, i–j): This genus is represented by two species from seeps in Japan. The shell is elongate, laterally compressed, and its apertural margin is convex in lateral view. This morphology allows the shell to fit a tube-shaped substrate. A similar shell morphology is also known in Late Cretaceous fossil species (Jenkins et al. 2007a, b), but also in the genera *Paralepetopsis* and *Neolepetopsis*. Species of *Serradonta* are similar to those of *Bathyacmaea* in pale shells with a finely reticulate sculpture, but their distinction is unmistakable in radular morphology. The radular teeth of *Serradonta* consist of two longitudinal rows of composite teeth, paralleling the wood-eating genus *Pectinodonta* (Okutani et al. 1992: figs. 5–6; Sasaki et al. 2003: fig. 8). The habitat is restricted to the surface of vestimentiferan tubes in *S. vestimentifericola* (Sasaki et al. 2007), but unknown for *S. kanesunosensis*. Protoconch and eggs have not been observed.

7.2.2 Clade Vetigastropoda

The phylogeny of Vetigastropoda remains contentious (Williams and Ozawa 2006; Williams et al. 2008; Kano 2008, Kano et al., 2009) (Figs. 7.2, 7.3, 7.4, and 7.5). Geiger and Thacker (2006) and Geiger et al. (2008) define Vetigastropoda to encompass Cocculiniformia and Neomphalina, based on the shared presence of bursicles in the gills of the latter hot-vent taxa with Vetigastropoda in a strict sense (Sasaki 1998), although conflicting phylogenetic relationships have been suggested for the three groups (e.g. Ponder and Lindberg 1997; McArthur and Harasewych 2003; Aktipis et al. 2008). On the other hand, the monophyly of Vetigastropoda *s.s.* (including Pleurotomarioidea, Haliotoidea, Scissurelloidea, Fissurelloidea, Lepetodriloidea, Lepetelloidea, Seguenzioidea, Phasianelloidea, Angarioidea and Trochoidea) is well supported by both morphological and molecular characters, except perhaps the inclusion of Pleurotomaroidea which lack sensory bursicles in the gill leaflets and sensory papillae on any part of the head-foot, as well as having an enigmatic radula. Molecular evidence, however, supports this concept. The internal relationship of the clade is far from resolved. Recent phylogenetic analyses demonstrate that fundamental revision is needed for the classification of superfamilies and families currently assigned to Trochoidea (Williams and Ozawa 2006; Williams et al. 2008) and Seguenzioidea (Kano 2008; Kano et al. 2009). Some species from

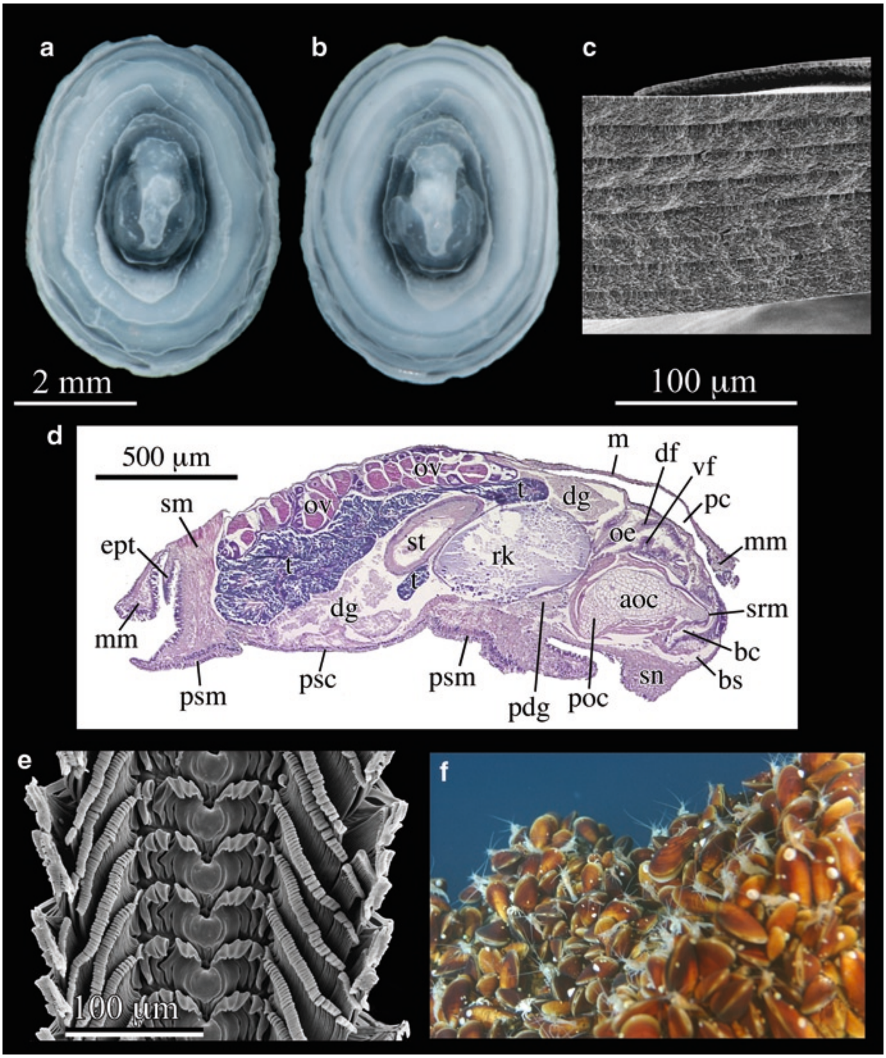

Fig. 7.2 Pyropeltidae. *Pyropelta ryukyuensis* Sasaki et al. 2008. (**a**) Exterior of shell. (**b**) Interior of shell (a–b, Holotype UMUT RM29412). (**c**) Vertical section of shell. (**d**) Longitudinal section of animal. (**e**) Radula. Hatoma Knoll, Okinawa Trough, 1,451 m, vent. (**f**) Habitat on *Bathymodiolus platifrons*. Hatoma Knoll, ca. 1,480 m. *Shinkai 2000* Dive 1361. Abbreviations: aoc, anterior odontophoral cartilage; bc, buccal cavity; bs, buccal sinus; df, dorsal fold of oesophagus; dg, digestive glands; e, oesophagus; ept, epipodial tentacle; i, intestine; m, mantle; mm, mantle margin; ov, ovary; pc, pallial cavity; pdg, pedal ganglion; poc, posterior odontophoral cartilage; psc, central part of pedal sole; psm, marginal part of pedal sole; sm, shell muscle; sn, snout; srm, subradular membrane; st, stomach; t, testis; vf, ventral fold of oesophagus. A color plate of this figure can be found in Appendix I (Plate 14) (a–f: Sasaki et al. 2008)

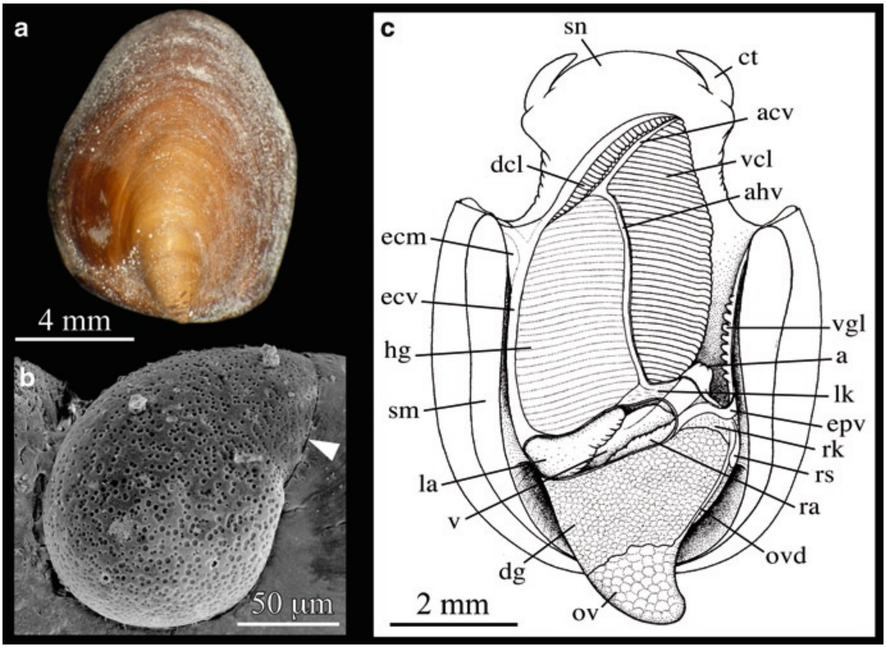

Fig. 7.3 Lepetodrilidae. (**a–c**) *Lepetodrilus nux* (Okutani et al. 1993). (**a**) Dorsal view of shell. Holotype, NSMT-Mo 69972, Izena Hole, Okinawa Trough, 1,340 m, vent. (**b**) Protoconch. *Arrowhead* indicates the boundary between the protoconch and the teleoconch. UMUT RM 27967. North Knoll of Iheya Ridge, Okinawa Trough, 1,390 m, vent. (**c**) Animal with most part of mantle removed. Abbreviations: a, anus; acv, afferent ctenidial sinus; ahv, afferent hypobranchial sinus; ct, cephalic tentacle; dg, digestive gland; ecm, efferent ctenidial membrane; ecv, efferent ctenidial sinus; epv, efferent pallial sinus; hg, hypobranchial gland; la, left auricle; lk, left kidney; ov, ovary; ovd, oviduct; ra, right auricle; rk, right kidney; rs, seminal receptacle; sm, shell muscle; sn, snout; v, ventricle; vcl, ventral ctenidial lamellae; vgl, vestigial gill leaflets (a: Sasaki et al. 2005; b: Sasaki et al. 2003; c. Sasaki 1998)

vent/seep environments are in indeterminate systematic positions among other vetigastropods (e.g. *Sahlingia xandaros*).

Superfamily Fissurelloidea

Family Fissurellidae

The family is highly diversified in shallow-water environment (Geiger et al. 2008), but only seven species are known from vents/seeps in the genera *Clathrosepta*, *Cornisepta* and *Puncturella* (see Appendix 7.3). The biology is poorly known for deep-sea species. This family is not a common member of vent/seep communities.

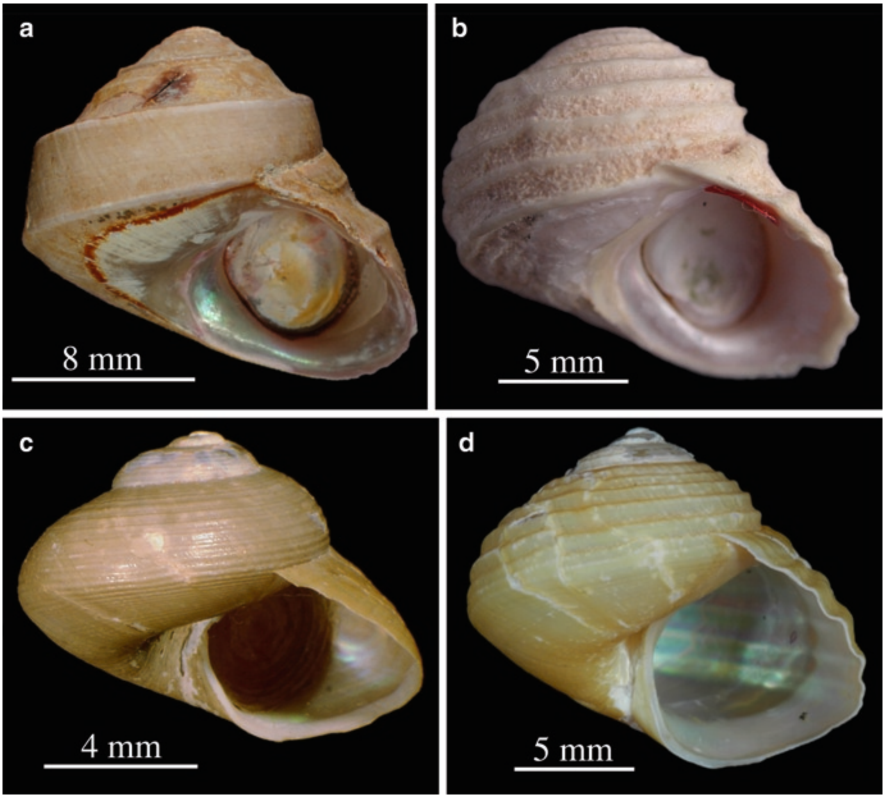

Fig. 7.4 Collonidae (a–b) and Turbinidae (c–d). (**a**) *Cantrainea macleani* Warén and Bouchet 1993. SMNH21179. Gulf of Mexico, off Louisiana, 546 m, hydrocarbon seep. (**b**) *Cantrainea jamsteci* (Okutani and Fujikura 1990). Holotype, NSMT-Mo 66235. Minami Ensei Knoll, Okinawa Trough, 720 m, vent. (**c**) *Margarites shinkai* Okutani et al. 1992. Holotype, NSMT-Mo 69635. Off Hatsushima, Sagami Bay, 1,110–1,200 m, seep. (**d**) *Margarites ryukyuensis* Okutani et al. 2000. Holotype, UMUT RM27884. North Knoll of Iheya Ridge, Okinawa Trough, 968 m, vent (a: Photo taken by T. Sasaki at SMNH; c–d: Sasaki et al. 2005)

Superfamily Lepetelloidea

Family Pyropeltidae (Fig. 7.2, Plate 14)

The family was established for a single genus *Pyropelta* currently contains seven species from northeastern, northwestern and southwestern Pacific (see Appendix 7.3; also McLean 1992b). Four of seven species are vent-endemic, but two species, *P. musaica* and *P. corymba* were collected also from whale bone and/or seeps in addition to vents (McLean 1992b; Smith and Baco 2003: table 6). *Pyropelta corymba* and *P. ryukyuensis* were found to attach to the shells of *Provanna* spp. (Warén and Bouchet 2001: fig. 6) and *Bathymodiolus* (Fig. 7.2f), respectively. *Pyropelta*

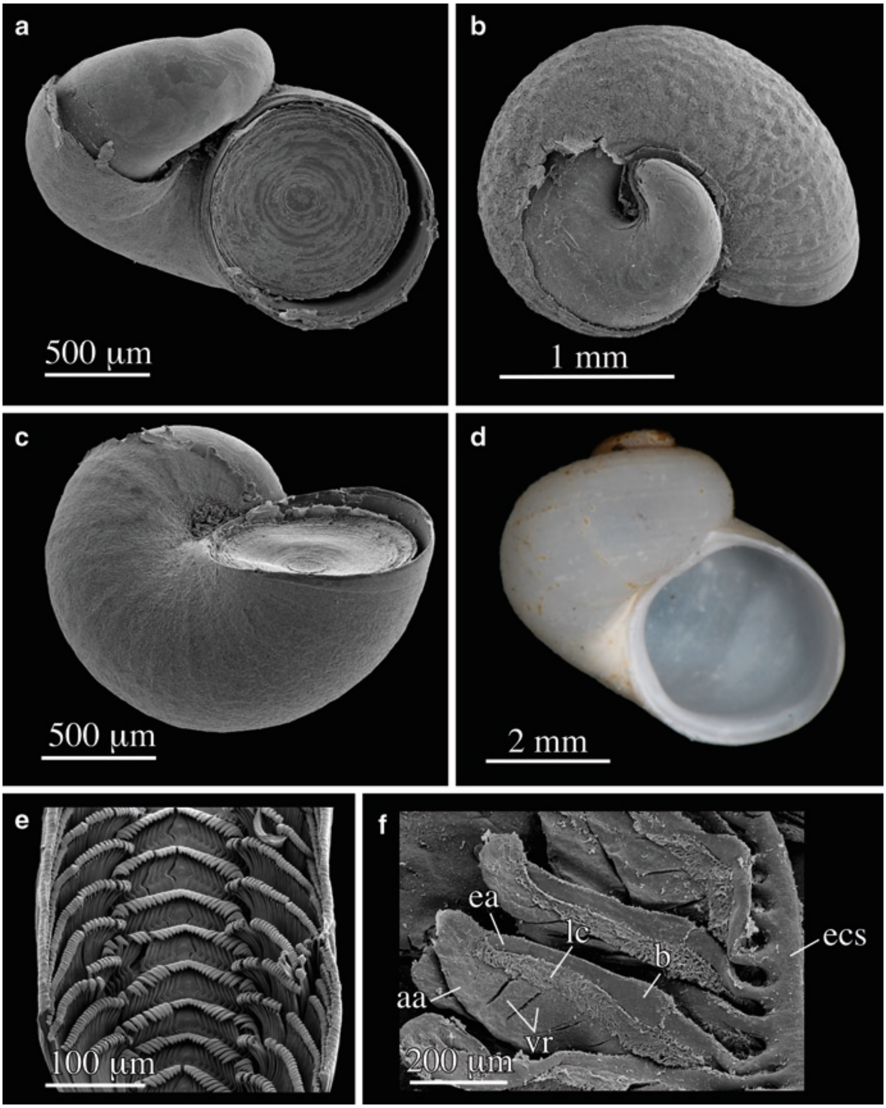

Fig. 7.5 Skeneinae, Turbinidae. (**a–c**) *Bruciella wareni* Okutani et al. 2004. Kairei Field, Indian Ocean, 2,434 m, vent. (**a**) Apertural view of Holotype. UMUT RM28666. (**b**) Apical view. Paratype, UMUT RM28668. (**c**) Basal view. Paratype, UMUT RM28669. (**d–f**) *Iheyaspira lequios* Okutani et al. 2000. North Knoll of Iheya Ridge, Okinawa Trough, Japan, ca. 1,000 m, vent. (**d**) Shell of holotype. (**e**) Radula. (**f**) Ctenidium. Abbreviations: aa, afferent ctenidial axis; b, bursicle; ea, efferent ctenidial axis; ecs, efferent ctenidial sinus; lc, lateral cilia; vr, vertical ridge of ctenidial lamella. (d, f) Holotype, UMUT RM27887. (e) Paratype, UMUT RM27888. (a–c: Okutani et al. 2004; d: Sasaki et al. 2005; e–f: Okutani et al. 2000)

wakefieldi McLean 1992 is known only from whale bones. *Pyropelta* has several distinctive conchological characters among gastropods (Sasaki et al. 2008: 314), including irregular surface sculpture, several repeated layers of homogeneous and prismatic structures (Fig. 7.2c), the myostracum exposed exterior by corrosion, the microtubes penetrating the myostracum, the shell growth front deeply inside of the interior away from the shell margin. Sequential secretion of shell layers might be adaptive in the deep sea, where shell corrosion is more extensive than in shallow-water environments. The repetitive thin prismatic layers are a useful character to identify fossil pyropeltids (Kiel 2006: fig. 3).

The main food source of *Pyropelta* are bacteria (Warén et al. in Desbruyères et al. 2006: 93) which are scraped with a rhipidoglossate radula (Fig. 7.2d). All species examined are hermaphroditic with separate testis and ovary (Fig. 7.2d). The right cephalic tentacle of male is modified into a copulatory organ (McLean and Haszprunar 1987), and the spermatozoa are conveyed along the neck with ciliary tract (Warén and Bouchet 2009: fig. 7.4e). The eggs have the vitelline layer which is one of characters restricted to Vetigastropoda. Larval development is lecithotrophic with planktonic dispersal stage (Warén et al. Desbruyères et al. 2006: 93).

Family Pseudococculinidae

The Pseudococculinidae are rare in vents and seeps, and there are only a few records (see Appendix 7.3). Most species of the family live on sunken wood (e.g. Marshall 1986). Some species of the Pseudococculinidae have a concentric shell sculpture similar to that of *Pyropelta* (e.g. McLean 1988b, 1991; McLean and Harasewych 1995). However, the single known study on the shell microstructure of Pseudococculindae (Lindberg and Hedegaard 1996: fig. 12) did not show the repetition of microstructual units. The Pseudococculinidae and Pyropeltidae are clearly separated by radular morphology (e.g. Warén and Bouchet 2009: figs. 4–5).

Superfamily Lepetodriloidea

Family Lepetodrilidae (Fig. 7.3)

The family currently comprises four genera: *Lepetodrilus*, *Gorgoleptis*, *Clypeosectus*, and *Pseudorimula*. *Gorgoleptis* was originally given an independent family status (Gorgoleptidae: McLean 1988a), and the latter two genera were united as the Clypeosectidae (McLean 1989b). However, these were later transferred into this family by Warén and Bouchet (2001: 155). Molecular phylogenetic data support the closeness of *Clypeosectus* and *Pseudorimula* to *Lepetodrilus* (Warén et al. 2003; Johnson et al. 2008). *Lepetodrilus* and *Gorgoleptis* share many similar characters, as they were originally defined as Lepetodriloidea: Diagnostic characters of these are: non-papillate tentacles, a single left ctenidium which is bipectinate at the anterior free tip but monopectinate posteriorly, a single left hypobranchial gland, the gonad discharging through the right kidney, the vas deferens functioning as the seminal vesicle, the prostate, the receptaculum seminis, a ciliated genital groove in female (see Sasaki 1998: 215). On the other hand, *Lepetodrilus* and *Gorgoleptis* are distinguished by the configuration of shell muscles, the presence or absence of operculum, the elaboration of epipodial tentacles, and the structure and position of the penis. In *Gorgoleptis*, all species keep the operculum until just below the maximum size (Warén and Bouchet 2001: 154).

1. Genus *Pseudorimula*: The shell of the genus has an obliquely elongate slit which is finally closed at the margin. No operculum is retained after metamorphosis. In *P. midatlantica*, the shell is frequently encrusted with bacterially precipitated iron and manganese oxides (Warén and Bouchet 2001: 156). Male has the prostate gland (Haszprunar 1989a: 7, fig. 9C) but lack a penis and seminal groove. Femals lack a receptaculum seminis (Haszprunar 1989a: 8). Development is without planktotrophic stage (Warén et al. in Desbruyères et al. 2006: 91).
2. Genus *Clypeosectus:* This genus also has an oblique slit in the shell, but it is not closed at the margin. No operculum is retained after metamorhosis. Reproductive system differs from that of *Pseudorimula*. In male the proximal vas deferens functions as a seminal vesicle. The prostate gland is present around the urinogenital opening (Haszprunar 1989a: 7, fig. 5B). The oviduct is connected to the renopericardial duct and also to the right kidney; female has an isolated receptaculum seminis opening at the right side of the pallial cavity (Haszprunar 1989a: figs. 3C, 4B). The eggs are yolky and large (maximum diameter 200 μm: Haszpruar 1989a: 7; Gustafson and Lutz 1994: 87). *C. curvus* is a specialist grazer on folliculinid ciliates (Bergquist et al. 2007). The protoconch of *C. delectus* was figured by McLean (1989b: fig. 9C, F).
3. Genus *Gorgoleptis*: The genus (three species) is a rare group confined to vents of East Pacific Rise (Warén and Bouchet 2001: appendix 2). The shell of the genus has no slit. The operculum is small, multispiral and positioned at the posterior side of the foot. Anatomically the genus is diagnosed by a pair of separate shell muscle attachments, long epidpodial tentacles whose number is five on the left and four on the right, the penis developed from the left side of the snout. The male has a prominent prostate gland; female lacks a receptaculum seminis (Fretter 1988). Larval development is lecithotrophic with planktonic dispersal stage (Warén et al. in Desbruyères et al. 2006: 87).
4. Genus *Lepetodrilus* (Fig. 7.3): The genus exhibits the highest diversty among vent/seep-associated gastropods. There are 14 described species: 10 species are distributed in the East Pacific, four in the West Pacific, and a single species on the Mid-Atlantic Ridge and in the West African seeps. Johnson et al. (2008) barcoded 16 species or 19 DNA types, but recognised six more of which no material was available for barcoding. The shell is limpet-shaped with a posterior apex, and without a slit. At microscopic level the shell consists of three layers: outermost prismatic, middle crossed-lamellar and innermost prismatic layers, among which the middle layer is prominently thick (Hunt 1992: figs. 4–8). Diagnostic characters of *Lepetodrilus* include the horseshoe-shaped shell muscle attachment, the lack of an operculum in adults, and three pairs of short epipodial tentacles

(Sasaki 1998: 215). The penis has a deep seminal groove near the base of the right cephalic tentacles when present. The penis is prominent or absent, depending on species or individuals. In *L. shannonae* it there is no penial difference between male and female, but the male has what seems to be a newly evolved penis of pallial origin.

Lepetodrilus have two different ways of feeding: ciliary feeding and grazing. Morphologically, ciliary feeding is correlated with enlargement of frontal and abfrontal ciliary pads at the tip of ctenidial lamellae (Bates 2007a: fig. 10). Limén et al. (2007: fig. 2) confirmed that food particles were collected by cilia at the same time as chemoautotrophic bacteria are cultivated on the gill. Rejected food particles are expelled as pseudofeces (Johnson et al. 2006: fig. 4G). Grazing is suggested by wear of radular teeth (Bates 2007a: 94) and inclusion of mineral particles in the gut. Among species of *Lepetodrilus*, there is variability in the relative size of the radula and stomach: the differences probably represent the degree of dependence on grazing and suspension feeding. Filamentous episymbiotic bacteria are farmed on the ctenidium, transported along the neck region, and ingested, as was found in food particles (Beck 1993: pl. 5, fig. 5, *L. schrolli*; Johnson et al. 2006: fig. 4H, L. *L. gordensis*; Bates 2007a: fig. 9A, 2007b: fig. 2, *L. fucensis*). Stable carbon and nitrogen isotopic composition also indicated that epibiotic bacteria on the ctenidium are used for nutrition (Levesque et al. 2006).

Species from the East Pacific Rise have been most intensively analyzed at population level with molecular characters (especailly COI gene of mtDNA). Johnson et al. (2006) revealed that northern and southern lineages of formerly called *L. fucensis* are distinct species. A new species *L. gordensis* was proposed for a lineage from Gorda Ridge and Escanaba Trough, and *L. fucensis* sensu stricto is confined to the Explorer and Juan de Fuca ridge systems. Morphologically *L. gordensis* lacks a sensory neck papilla and has a more tightly coiled teleoconch. Similarly Matabos et al. (2007) demonstrated the presence of distinct lineages in *L. elevatus* from 13°N to 9°50′N and from 9°50′N to 17°S (Matabos et al. 2008: fig. 5). Divergence time of these southern and northern lineages was estimated to be 11.6 Ma by Plouviez et al. (2009). Johnson et al. (2008) barcoded *Lepetodrilus* species, using 1,000 base pairs of COI gene, and revealed five cryptic species along the EPR, of which up to three occurred sympatrically.

Two cases of predation have been reported for *Lepetodrilus*. *Buccinum thermophilum* is a predator of *L. elevatus* (Voight and Sigwart 2007) [possibly *L. fucensis,* not *L. elevatus*], and the octopod *Graneledone boreopacifica* for *L. fucensis* (Voight 2000a). The shell is damaged in the former species, and the shell fragments were found in the gut of the predator in the latter species.

Lepetodrilus are generally gonochoristic and exert internal fertilization. The female have an isolated receptaculum seminis on the right side; the male has the prostate (Fretter 1988; Sasaki 1998). The male has a penis with a seminal furrow on the right side of the head in *L. fucensis* (Johnson et al. 2006: fig. 4B; Bates 2007a: fig. 8D; Kelly and Metaxas 2007: fig. 3e) and in *L. gordensis* (Johnson et al. 2006: fig. 4H). McLean (1993) reported that a penis was absent in *L. elevatus* from Mariana Trough. Warén and Bouchet (2001: 154) also noted that most males of

Lepetodrilus from North Fiji Basin lack a penis, although some individuals will develop it. *Lepetodrilus fucensis* was confirmed to form euspermatozoa only (Hodgson et al. 1997). Elongate head (nucleus) and flagellum (Hodgson et al. 1997: fig. 4, ant-aquasperm type) are suggestive of fertilization within the pallial cavity rather than of ect-aquasperm type which is typical of species conducting external fertilization (Hodgson et al. 1997: 94). Development is probably through free-swimming lecithotrophic larvae with a planktonic period (Warén et al. in Desbruyères et al. 2006: 88). The protoconch has been illustrated for several species (Table 7.2). Growth rate of *L. fucensis* from Juan de Fuca Ridge is 0.4 cm per year (Kelly and Metaxas 2008: table 7). Reproduction starts at 3.8 (male) and 3.9 (female) mm in shell length in *L. fucensis* (Kelly and Metaxas 2007). Histological condition of the gonad indicates gametogenesis is continuous, and reproduction is asynchronous in *L. fucensis* (Kelly and Metaxas 2007).

Family Sutilizonidae

The family was originally classified as a part of Scissurellidae: *Temnocinclis* and *Temnozaga* in Temnocinclinae and *Sutilizona* in Sutilizoninae (McLean 1989b). Warén and Bouchet (2001) recognized the family Sutilizonidae for these groups, but they are likely to end up in the Lepetodrilidae as indicated by similarities in the protoconch. The family has a limpet-shaped shell, asymmetrical in *Sutilizona* or nearly symmetrical in *Temnocinclis* and *Temnozaga*, with a long slit and selenizone, a multispiral operculum, paired monopectinate ctenidia, non-papillate cephalic and epipodial tentacles. The number of epipodial tentacles varies among genera. The anatomy of *Temnocinclis euripes*, *Temnozaga parilis*, and *Sutilizona theca* was described by Haszprunar (1989a: 3–5). All species are gonochoristic. The ovary contains large yolky eggs, and the oviduct is ciliated and non-glandular. The male lacks a penis. In *S. theca* all stages of sperm development except ripe spermatozoa were observed (Haszprunar 1989a: 5). The gonoduct has a common opening with the right kidney. Eggs are large (200 µm in maximum) and exhibit all stages of development in *S. theca* (Haszprunar 1989a: 5). The above anatomical features indicate that spawning is continuous, and fertilization is likely to occur in the female mantle cavity (Gustafson and Lutz 1994: 82). The protoconch of *S. theca* (McLean 1989b: fig. 4F) has dense pits and spiral ridges, very similar or identical to that in Lepetodrilidae, an indication of close relations. The larval development is lecithotrophic with planktonic dispersal stage (Warén et al. in Desbruyères et al. 2006: 98–100).

Superfamily Seguenzioidea

Family uncertain

The Seguenzioidea was recently redefined to include the Cataegidae, Chilodontidae, Calliotropidae, Seguenziidae, and skeneimorph genera (e.g. *Adeuomphaus*, *Xyloskenea* and *Ventsia*) of uncertain familial assignment (Kano 2008; Kano et al. 2009).

The genus *Adeuomphalus* is characterized by a planispiral shell with axial lamellae, monopectinate gill, and anteriorly bifurcated foot with a pair of epipodial sense organs and epipodial tentacles (Warén and Bouchet 2001: 132; Kano et al. 2009). Among seven recent and a single fossil species of the genus, three species were collected near hydrothermal vents (see Appendix 7.3) together with carnivorous sponges. A parasitic mode of life was suggested by the absence of radulae as in other parasitic gastropods and a tubular snout (Kano et al. 2009). *Ventsia tricarinata* has been assigned to the Skeneidae, but anatomical characters are similar to those of *Adeuomphalus* (Kano et al. 2009: 414). Especially, the possession of the seminal receptacle suggests the inclusion of the genus in the Seguenzioidea (Kunze et al. 2008; Kano et al. 2009), and DNA also suggests its affinity to the Seguenzioidea (Kano 2008).

Family Seguenziidae

Bathymargarites symplector is similar to *Margarites* in shell form, but strikingly different in having "penis" which is modified from the right neck lobe (Warén and Bouchet 1989: 87). The reproduction is therefore not considered to be external. The eyes are present at bases of cephalic tentacles with pigmented part of variable shape (Warén and Bouchet 1989). Feeding is by grazing on a surface layer of detritus. Stomach content consists of mineral particles and fragments of various organisms (Warén et al. in Desbruyères et al. 2006: 101). Larval development is lecithotrophic with planktonic dispersal stage (Warén et al. in Desbruyères et al. 2006: 101).

Superfamily Trochoidea

Traditional classification recognized only three families, namely Trochidae, Turbinidae and Skeneidae, in this superfamily (Hickman and McLean 1990). However, recent phylogenetic studies have revealed the traditional Trochoidea to be polyphyletic (Williams and Ozawa 2006; Kano 2008; Williams et al. 2008). Some of the traditional trochoideans have been transferred to Seguenzioidea (Kano 2008, Kano et al. 2009) as well as to the newly established Angarioidea and Phasianelloidea. The redefined Trochoidea comprises five families including Trochidae, Turbinidae, Solariellidae, Calliostomatidae and Liotiidae (Williams et al. 2008). This is probably not the final edition, since some basal groups show a tendency of jumping back and forth depending on the selection of species.

Family Turbinidae (Fig. 7.4c, d)

Williams et al. (2008) classified this trochoid family into five subfamilies, namely Turbininae, Prisogasterinae, Margaritinae, Tegulinae and Skeneinae. Vent/seep endemic turbinids belong to either Margaritinae or Skeneinae. Members of the genus *Margarites* (Fig. 7.4c–d) are common in shallow subtidal zones, but also known from vents and seeps. *Margarites shinkai* lives on muddy bottom in the seep-associated *Calyptogena* bed, together with *Provanna* species (Sasaki et al. 2007).

The subfamily Skeneinae (Fig. 7.5) had been treated as an independent family in Trochoidea (e.g. Hickman and McLean 1990). However, recent anatomical and molecular studies have revealed that 'Skeneidae' was a miscellany of little-known minute vetigastropods, often mixed up even with neomphalines, caenogastropods and heterobranchs (Heß et al. 2008; Kano 2008; Kunze et al. 2008; Kano et al. 2009; see below). The type genus *Skenea* and several similar genera have been classified in the family Turbinidae based on the phylogenetic position of a morphologically similar genus, *Protolira* (Warén et al. 2003) and *Dillwynella* (Kano 2008; Williams et al. 2008). The anatomy of the type species of *Skenea*, *S. serpuloides*, was described by Kunze et al. (2008). Probable members of Skeneinae from vent/seep environments include *Protolira* and *Bruceiella* (Fig. 7.5a–c), possibly also *Fucaria* and *Iheyaspira* (Fig. 7.5d).

In the genus *Fucaria*, food consists of detritus from the sea bottom as is suggested by gut contents. Larval development lecithotrophic with planktonic dispersal stage (Warén et al. in Desbruyères et al. 2006: 95). *Protolira thorvaldssoni* lives at vents and also on whale bones from which the species was originally described. Food consists of the detrital surface layer of the sea bottom. Species of *Skenea* and the closely related vent genus *Protolira* have a propodial penis, assumed internal fertilization and are hermaphrodites (Warén 1992; Warén and Bouchet 1993). Larval development lecithotrophic with planktonic dispersal stage (Warén et al. in Desbruyères et al. 2006: 97).

Family Colloniidae (Fig. 7.4a, b)

Phasianelloidea was recently established by Williams et al. (2008) for Phasianellidae and Colloniidae solely based on the topology of their multi-gene phylogeny. The two families had been classified in Turbinidae of Trochoidea at subfamilial rank (Phasianellinae and Colloniinae), based on opercular, shell and radular characters (e.g. Hickman and McLean 1990; Bouchet et al. 2005). However, the traditional 'Turbinidae' classification or species with calcareous opercula has been rejected by nuclear rRNA gene data but the conclusions are not consistent and some details seem unlikely (Williams and Ozawa 2006; Kano 2008; Williams et al. 2008). Future anatomical studies are needed to morphologically explore the clade. Vent/seep collonids are represented by the members of the genus *Cantrainea* only. Their shells (Fig. 7.4a–b) are thick for deep-sea gastropods, and opercula are also heavily calcified. There are four known species from vents and seeps (see also Appendix 7.3): *C. macleani* from off Louisiana (Warén and Bouchet 1993: 8; 2001: 132); *C. jamsteci* and *C. nuda* are both from off Ryukyu Islands, Japan; *C. panamense* off Chile.

7.2.3 Clade Neomphalina

The term Neomphalida (e.g. Heß et al. 2008) has also been used for this group, but it is a younger name (Fig. 7.6, Plate 15). The phylogenetic position of this clade is still uncertain regarding the status within or outside Vetigastropoda (Heß et al. 2008: 399). For example, anatomical characters indicate the inclusion of the Neomphalina ("hot-vent taxa") in the Vetigastropoda (Aktipis et al. 2008: figs. 9.3), but a combined analysis of morphological and molecular characters was considered to support relations to the Cocculinidae (Aktipis et al. 2008: figs. 9.4–9.7). Molecular phylogeny by Geiger and Thacker (2006) was interpreted to show that the Neomphalina are basal to vetigastropods. The morphological characterization is difficult due to an unusually great variation in morphology, with a number of misleading apomorphies but the monophyly is supported by molecular phylogeny (Kano and Warén in prep) as well as a mosaic pattern of plesiomorphies. The presence of shell pores (Batten 1984, *Neomphalus fretterae*; Warén and Bouchet 1993: 35, fig. 27B–D, *Ctenopelta porifera*; Heß et al. 2008: fig. 8, *Leptogyra* and *Leptogyropsis*; Kiel and Goedert 2007: fossil *Leptogyra* from the Eocene) had been regarded as one of putative shared characters but most neomphalins lack pores. The Neomphalina is the last mollusc group above the family level, considered endemic to chemosynthetic environments but it is now known from food-falls, seeps and vents (Kano 2008, Warén and Bouchet 2009). All species have a protoconch with no trace of planktotrophy, and a planktonic dispersal phase can be assumed since larvae of several species were retrieved in plankton traps during the French ATOS and HOPE programs on the EPR (Warén unpubl., see also Mills et al. 2007). Two types of protoconch morphology occur: a plesiomorphic one with a fine net-sculpture, especially on the initial part (Melanodrymiidae and Neomphalidae) and a strongly bent type with prominent spiral ridges in the Peltospiridae.

Family Melanodrymiidae (Fig. 7.6e)

The genus *Melanodrymia* had been assigned either Peltospiridae or Neomphalidae, but redefined as the type genus of Melanodrymiidae based on both anatomy and molecular phylogeny (Salvini-Plawen and Steiner 1996). The genera *Leptogyra*, *Xyleptogyra* and *Leptogyropsis* were also transferred from the Skeneidae to this family (Heß et al. 2008). Molecular evidence (but not all morphology) supports the monophyly of the family (Heß et al. 2008). The anatomy of *Melanodrymia aurantiaca* was described by Haszprunar (1989b). The presence of spermatophore was mentioned for *Melanodrymia* sp. ("rust covered") by Warén and Bouchet (2001: 161). They found lanceolate objects attached to the posterior part of the pallial cavity. The food of *Melanodrymia* consists of the detrital surface layer of the bottom (Warén et al. in Desbruyères et al. 2006: 106)

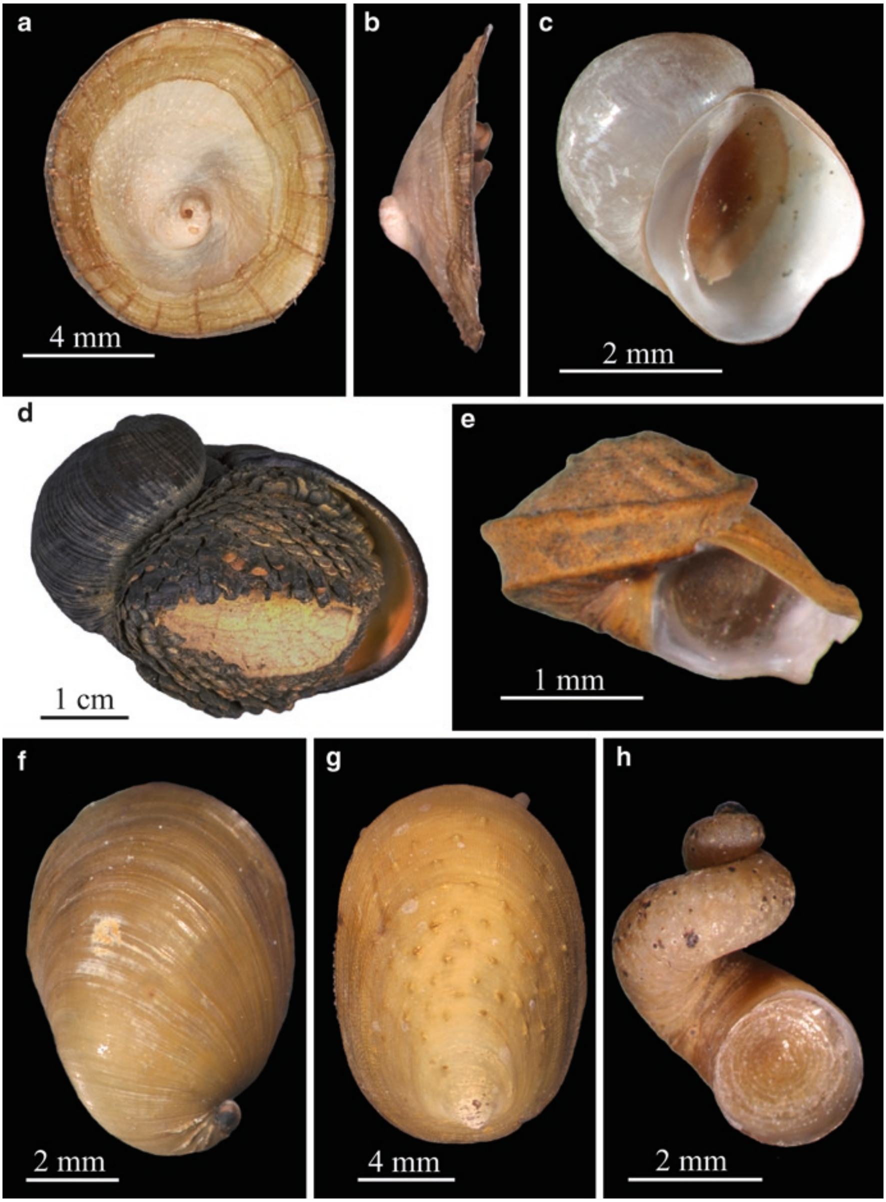

Fig. 7.6 Neomphalina. (**a–b**) *Neomphalus fretterae* McLean 1981. SMNH43346. East Pacific Rise, 13°N, 2,630 m, vent. (**c**) *Cyathermia naticoides* Warén and Bouchet 1989. SMNH21160. East Pacific Rise, 13°N, 2,630 m, vent. (**d**) Scaly-foot gastropod. Kairei Field, Indian Ocean, 2,422 m, vent. UMUT RM30208. (**e**) *Melanodrymia aurantiaca* Hickman 1984. SMNH43311, East Pacific Rise, 13°N, 2,632 m, vent. (**f**) *Peltospira operculata* McLean 1989. SMNH43168. East Pacific Rise, 13°N, 2,649 m, vent. (**g**) *Nodopelta heminoda* McLean 1989. SMNH43316. East Pacific Rise, 13°N, 2,630 m, vent. (**h**) *Pachydermia laevis* Warén and Bouchet 1989. SMNH43130. East Pacific Rise, 13°N, 2,650 m, vent. A color plate of this figure can be found in Appendix I (Plate 15). (a–b, e–h: Photo taken by T. Sasaki at SMNH)

Family Neomphalidae (Fig. 7.6a–c)

The family currently encompasses six genera: *Cyathermia, Lacunoides, Neomphalus, Planorbidella, Solutigyra* and *Symmetromphalus*. Familial assignment is not always consistent among past studies. For example, Cyathermiidae McLean 1990a was once proposed for *Cyathermia*; *Melanodrymia* currently in the Melanodrymiidae was contained in this family (Warén and Bouchet 2001) due to similarities in the protoconch. *Planorbidella* and *Pachydermia* were transferred from the Peltospiridae to the Neomphalidae, based on the similarities to *Neomphalus* in the protoconch (Warén and Bouchet 2001: 157), but *Pachydermia* was assigned to the Peltospiridae based on molecular phylogenetic tree (Heß et al. 2008). The family is with a couple of uncertain exceptions endemic to hydrothermal vent environments (e.g. *Retiskenea*).

The shell form is extremely variable among different genera: limpet-shaped (*Neomphalus fretterae*: Fig. 7.6f and *Symmetromphalus*), naticiform (*Cyathermia*: Fig. 7.6h), and high-spired with disjunct whorls (*Pachydermia*: Fig. 7.6d). The shells of other genera are *Velutina*-like or skeneimorph. Some species have characteristic conchological characters. *Cyathermia naticoides* has a deep notch at basal side of the outer lip (Fig. 7.6h). Its function is uncertain, but possibly used to increase the exposure of the gill to the sea water. The shell of *Neomphalus fretterae* (and some others) is penetrated by numerous pores (Batten 1984: fig. 12). Young stages of *Neomphalus fretterae* strikingly resemble *Cyathermia naticoides* (Warén and Bouchet 1989: 69). Sexual size dimorphism is known in *Pachydermia laevis* (Warén and Bouchet 1989: 80) and *Neomphalus fretterae*. McLean (1981) mentioned a 15% difference in maximum size of sexes in *Neomphalus*. The operculum is also variable among the family. In limpet like genera, a small operculum persists in subadult *Symmetromphalus* (Beck 1992a: pl. 4, fig. 2). In *Neomphalus*, the operculum is lost at a size of a few millimeter. Spirally coiled species retain a complete multisprial operculum.

The anatomy of the Neomphalidae is mainly described for *Neomphalus fretterae* by Fretter et al. (1981) and also for *Symmetromphalus* by Beck (1992a). Supposed general characters of the family are: a long neck, the epipodial tentacles along the posterior side of the foot, the male gonoduct with the prostate, and an open seminal groove in the left cephalic tentacle (see also Warén and Bouchet 2001 for *Lacunoides* and *Cyathermia*). Fertilization is likely to occur internally within the female oviduct (*Neomphalus*: Fretter et al. 1981). The anatomy of *Pachydermia laevis* was described by Israelsson (1998). The configuration of the shell muscle is often supposed to be of high value in taxonomic ranking, but the muscle is crescent-shaped in *Neomphalus* and symmetrically paired in *Symmetromphalus.* Filter feeding predominates in the limpet species while grazing may be the only way in species with a small gill like *Pachydermia*, judging from the relative size of the radula. *Cyathermia* uses the ctenidium for filter feeding and also grazes on bacterial growth on tube worms (Warén and Bouchet 1989: 71). Development is inferred to be non-planktotrophic from protoconch morphologies and dimensions (Gustafson and Lutz 1994: 83).

Family Peltospiridae (Fig. 7.6f–h)

The family is composed of nine described genera: *Ctenopelta, Depressigyra, Echinopelta, Hirtopelta, Lirapex, Nodopelta, Pachydermia, Peltospira* and *Rhynchopelta*. *Solutigyra* were originally assigned to this family (Warén and Bouchet 1989: 82) but later transferred to the Neomphalidae (Warén and Bouchet 2001). Current knowledge on anatomy is mainly based on *Rhynchopelta, Nodopelta, Echinopelta, Hirtopelta and Peltospira* (Fretter 1989). Shell form varies greatly in the family, from symmetrically limpet-like (*Echinopelta*, *Nodopelta* and *Rhynchopleta*), haliotiform limpet-like (*Ctenopelta* and *Hirtopelta*), to skeneiform (*Depressigyra*, *Lirapex*). In the genus *Peltospira*, the shell is variable from depressed haliotiform (*P. operculata*) to inflated *Vanikoro*-like shape (*P. smaragdina*). The shell sculpture is also variable: The surface is characteristically ornamented by spirally arranged small tubercles (*Ctenopelta*), sparsely scattered spines or tubercles in (*Echinopelta, Hirtopelta* and *Nodopelta*), commarginal elements (*Peltospira, Rhynchopelta*, and *Lirapex*), or nearly smooth (*Depressigyra*). The shell microstructure has not sufficiently been examined for the family. In *Ctenopelta porifera*, the shell has two different types of pores which consist of macropores (30–70 μm in diameter) and micropores (2–3 μm in diameter) (Warén and Bouchet 1993: 35, fig. 27B–D). The operculum is present in spirally coiled forms (*Depressigyra* and *Lirapex*). In limpet forms, the operculum is absent in most species, but present at the posterior end of the foot in *Hirtopelta* (Fretter 1989: fig. 16, *H. hirta*; Beck 2002: fig. 8, *H. tufari*). In the genus *Peltospira*, the operculum is present in *P. operculata* (McLean 1989a: figs. 4, 6; Fretter 1989: fig. 9), lost in *P. smaragdina* before reaching 1 mm (Warén and Bouchet 2001: 168) and also absent in adult in *P. delicata*.

Some species are confirmed or presumed to have ecological association with bacteria. *Hirtopelta tufari* possess bacteria in bacteriocytes of the ctenidium (Beck 2002: figs. 12–15). In *Ctenopelta porifera* tubular spiny shell sculpture and the setae of the foot might be related to bacterial symbioses (Warén and Bouchet 1993: 33). Sexes are separate, and females are larger than males in *Ctenopelta porifera* (Warén et al. in Desbruyères et al. 2006: 117). In *Rhyncopelta concentrica*, internal fertilization is suggested by filiform spermatozoa (introsperm) (Hodgson et al. 2009).

Family Peltospiridae: Scaly foot gastropod (Fig. 7.6d)

The 'Scaly foot gastropod' was discovered from the bases of black-smoker chimneys in the Kairei vent field at Rodriguez Triple Junction in the Indian Ocean (Warén et al. 2003). The species has not yet been named but will be taxonomically described by Anders Warén. It is nearly sedentary and firmly attached to rocks. The shell is rounded, swollen, and covered with thick black periostracum. The animal lacks the operculum, but the sclerites on the side of the foot function like the operculum of other gastropods. When the animal is retracted, the foot is folded in the midline and the aperture is closed by the sclerites of the epipodium. But, when in danger, another possibility is to pull the shell towards the substrate, and all tissues will be covered by the shell and the sclerites. The sclerites are mineralized with iron sulfide minerals containing pyrite (FeS_2) and greigite (Fe_3S_4) (Warén et al. 2003; Goffredi et al. 2004; Suzuki et al. 2006c). The presence of a conchiolin layer in the sclerites may suggest the homology between the sclerites and opercula of other gastropods (Warén et al. 2003).

An isolated sclerite is illustrated by Goffredi et al. (2004: fig. 3B). The surface of the sclerite is covered with filamentous and coccoid bacteria (Warén et al. 2003: fig. 1C, S2G; Goffredi et al. 2004: fig. 3E–F). The sclerites consist of three layers, *viz.* sulfide, mixed and conchiolin layers (Warén et al. 2003: fig. S2I, K; Suzuki et al. 2006c: fig. 2). Isotopic analyses suggest that sulfur and iron in the sclerites may be derived from hydrothermal fluids, not from bacterially precipitated substance (Suzuki et al. 2006c). The animal harbors thiotrophic γ-proteobacteria in an enormously enlarged oesophageal gland (Goffredi et al. 2004: fig. 2). Like in several gastropods suspected to have symbiotic bacteria the intestine is full of finely granular iron sulphides, particle size $<0.2\ \mu m$. There are no obviously symbiotic bacteria in the ctenidium.

Apart from the possession of sclerites, overall organization conforms to that of peltospirids: the bipectinate ctenidium with sensory buriscles, the rhipidoglossate radula, an enlarged esophageal glands, hypoathroid nervous system with cross-connected pedal cords. The esophageal gland is 10–1,000 times as large as the relative volumes of that of other gastropods. Other parts of digestive system are reduced, the volume is 1/10–1/100 of that of other gastropods (Warén et al. 2003: supporting online material). The female has spermatophore producing organ (Warén et al. 2003: fig. S2M) and sperms are conveyed with spermatophores. Development lecithotrophic, presumably with a planktonic dispersal stage (Warén et al. in Desbruyères et al. 2006: 120). Scaly-foot is an extreme example of how adaptations to the chemosynthetic environment with very special selective pressures can modify the morphology.

7.2.4 Clade Neritimorpha

The members of this clade with a shallow-sea origin have invaded a wide range of habitats ranging from the deep-sea to freshwater and terrestrial environments (Kano et al. 2002; Sasaki and Ishikawa 2002) (Fig.7.7). They are grazers and feed on microalgae and bacteria with a rhipidoglossate radula. Fertilization is internal; eggs are deposited in lenticular capsules produced by the well-developed glandular gonoduct of the female. Larval development is either planktonic or benthic. In the Neritimorpha, the presence or absence of a planktotrophic larval period can be inferred from the morphology of the larval operculum, which is very often retained in adult individuals, as well as from the more vulnerable protoconch (Kano 2006).

Family Phenacolepadidae (Fig. 7.7b–g)

This family of small limpets is clearly divided into two groups: shallow-water genera (*Phenacolepas* and *Cinnalepeta*) and deep-water, vent-associated genera

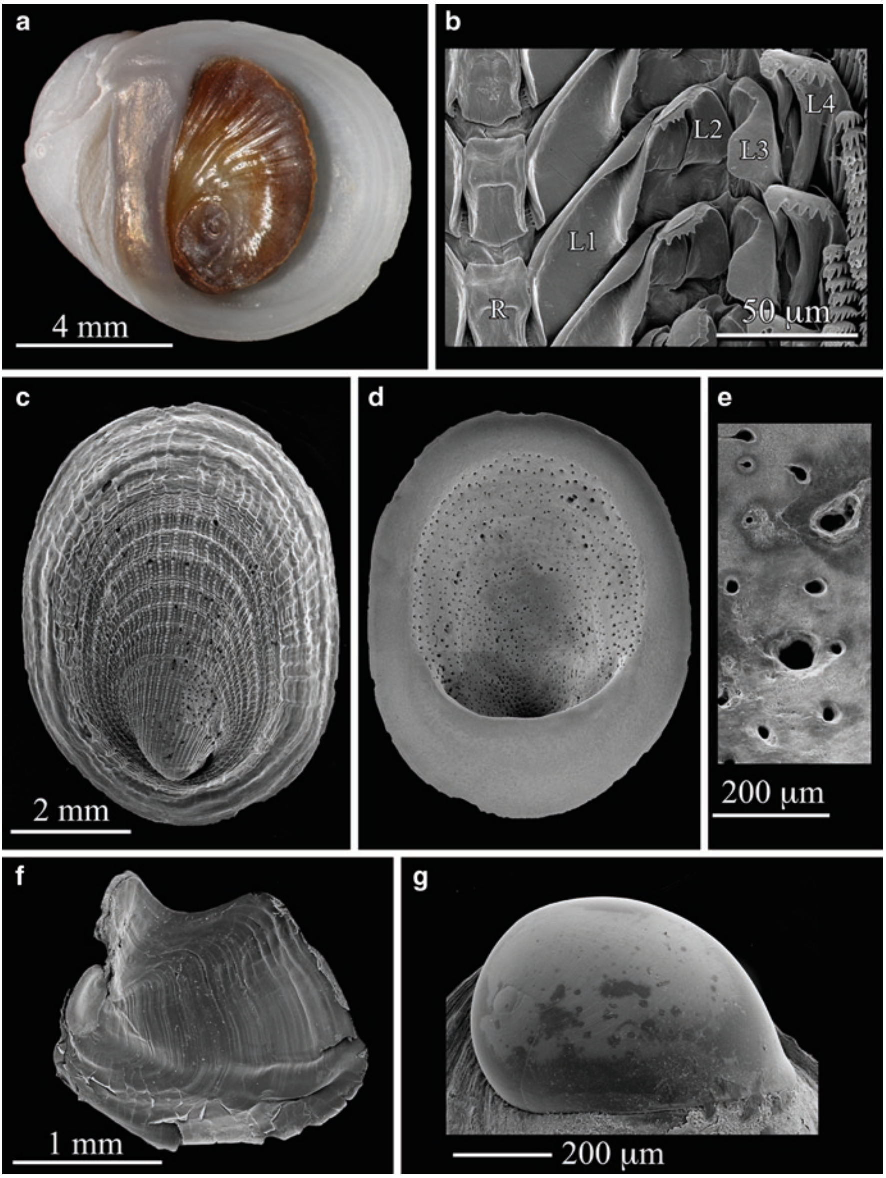

Fig. 7.7 Neritimorpha. (**a**) *Bathynerita naticoidea* Clarke 1989. SMNH21177. Gulf of Mexico, off Louisiana, 546 m, hydrocarbon seep. (**b–g**) *Shinkailepas myojinensis* Sasaki et al. 2003. (**b**) Radula. r, rachidial tooth, L1–L4, first to fourth lateral teeth. (**c**) Dorsal view of shell, (**d**) Ventral view of shell, (**e**) Magnified view of shell pores, (**f**) Operculum, (**g**) Protoconch. Myoin Knoll, Japan, 1,260–1,290 m, vent. Holotype, UMUT RM27970 (a: Photo taken by T. Sasaki at SMNH; b–g: Sasaki et al. 2003)

(*Shinkailepas* and *Olgasolaris*) (Sasaki et al. 2006b). The shallow-water species inhabit reduced environments under half-buried boulders (Kano et al. 2002; Kano and Haga 2010). Animals of the family are vividly red when alive and contain erythrocytes in blood (Fretter 1984; Sasaki 1998: fig. 85d; Sasaki et al. 2006b: fig. 10b). Globular bacteria were found on the surface of ctenidial cilia of *Olgasolaris* (Beck 1992b: pl. 6, fig. 6), but their association has not yet been examined in detail. Species of the genus *Shinkailepas* (Fig. 7.7b–g) have been described from vents in the western Pacific (*S. kaikatensis, S. myojinensis,* and *S. tufari*) and from the Mid-Atlantic Ridge (*S. briandi*). At least seven undescribed species exist at vents in the western and eastern Pacific, Indian Ocean and Mid-Atlantic Ridge. In the monotypic genus *Olgasolaris*, the type species *O. tollmanni* is distributed in the Manus Back-Arc Basin. The shell of *O. tollmanni* differs from that of *Shinkailepas* in that the apex is positioned near the center, but not at the posterior end. The interior of the shell has a very shallow septum at the posterior region (Beck 1992a: pl. 4, fig. 4). The shells of some vent-associated phenacolepadids are penetrated by numerous microtubules from the mantle, and some of the microtubules reach the outer shell surface (Sasaki et al. 2003: fig. 12). Their opercula are partly calcified (Fig. 7.7f). Reproduction is via internal fertilization. The male has a grooved penis modified from the right cephalic lappet (Beck 1992b: pl. 5, fig. 6). Egg capsules are less than 1 mm in diameter and sometimes deposited on shells (Warén and Bouchet 2001: fig. 32b). The small veliger larvae ready to hatch from the egg capsule, the multispiral protoconch (Beck 1992b: pl. 1, fig. 5; Warén and Bouchet 2001: fig. 32f), and the initial part of the operculum consisting of small embryonic and large larval regions (type A of Kano 2006: fig. 4, table 2) all suggest a planktotrophic early development for the species of *Shinkailepas* and *Olgasolaris* (Kano 2006).

Family Neritidae (Fig. 7.7a)

The genus *Bathynerita* consists of a single species, *Bathynerita naticoidea* which is distributed at hydrocarbon seep sites in the Lousiana Slope of the Gulf of Mexico. The shell is mostly occupied by the body whorl; the aperture is wide and nearly semicircular. Inside of the whorls are resorbed (Warén and Bouchet 1993: 3). However, in contrast to shallow-water neritids, the shell is pale, without denticles in the inner lip. The shell wall has three layers (Kiel 2004: 176). The operculum is calcified only inside and lacks a peg (Warén and Bouchet 1993: fig. 1C). The right cephalic lappet in *Bathynerita* is replaced by a penis in males (Warén and Bouchet 1993: fig. 2A). The radula is of the typical neritid type (Warén and Bouchet 1993: fig. 3A–C). *Bathynerita naticoidea* further differs from shallow-water neritids in sperm microstructure; its axoneme is not bent at the junction of the mid-piece and tailpiece, and the tail is not terminally expanded, as they are in most shallow-water neritids (Hodgson et al. 1998). These features suggest that *Bathynerita* is phylogenetically closer to the deep-sea phenacolepadids than to neritids (Hodgson et al. 1998). Molecular phylogenies also favor this phenacolepadid affinity of *Bathynerita*

(McArthur and Koop 1999; McArthur and Harasewych 2003; see also Kano et al. 2002). *Bathynerita naticoidea* is commonly associated with beds of *Bathymodiolus childressi* and feeds on bacteria and decomposing periostracum of *Bathymodiolus* shells (Dattagupta et al. 2007). This species can tolerate a considerable degree of salinity fluctuations by closing the operculum tightly (Van Gaest et al. 2007).

7.2.5 Clade Caenogastropoda

Caenogastropods is a large group with more than 120 families (Bouchet et al. 2005), but members in vents and seeps mostly belong to Provannidae, Elachisinidae, Turridae and Buccinidae. A few species of Rissoidae have been found on food-falls, in vents and in cold seeps but their relations to each other and to the environment are poorly known (Figs. 7.8–7.12). Scattered species of other families (e.g. Capulidae, Ceritiopsidae, Vitrinellidae and Cancellariidae) have been found in vents and seeps (see Appendix 7.3), sometimes in considerable numbers.

Family Provannnidae (Figs. 7.8–7.9, Plate 16)

The members of the family belong to five genera, *Alviniconcha*, *Ifremeria*, *Provanna, Desbruyeresia,* and *Cordesia*. A sixth genus is so far known from two whale falls only is under description (Johnson et al. in press). The systematic position of the family has been uncertain, but is currently assumed to be a member of Abyssochrysoidea along with Abyssochrysidae and extinct Hokkaidoconchidae (Kaim et al. 2008a). Colgan et al. (2007) based on several genes arrived at a position in the vicinity of Littorinoidea. Anatomically the presence of pallial tentacle in *Provanna* is shared with *Abyssochrysos* (Abyssochrysidae) (Houbrick 1979). The shell form of this family is divided into two types. Genera *Provanna* and *Desbruyeresia* have small and slender shells, whereas in *Alviniconcha* and *Ifremeria*, the shells are much larger and swollen. These two shell forms seems to be totally different in adult stage, but the protoconch of *Desbryueresia* and *Alviniconcha* (see Kaim et al. 2008a: fig. 4) suggests that they have arisen from the common larval form. The shells of *Alviniconcha* and *Ifremeria* are probably enlarged to house a hypertrophied ctenidium harboring a large quantities colony of symbiotic bacteria. The protoconch is ornamented with a uniform reticulate sculpture formed by sharp axial and spiral ribs in *Desbruyeresia* (Warén and Bouchet 1993: fig. 44D; Kaim et al. 2008a: fig. 4A; but except *D. marisindica*) and *Alviniconcha* (Warén and Bouchet 1993: fig. 44C; Kaim et al. 2008a: fig. 4B). Before settling, the top whorls of the protoconch are lost by a characteristic mode of decollation (Kaim et al. 2008a: fig. 4). In *Provanna* the sculpture consists of scattered axial ribs (e.g. Warén and Ponder 1991: fig. 1). The protoconch has never been found in *Ifremeria nautilei* whose species brood the embryos in a brood chamber in the foot (Warén in Desbruyères et al. 2006: 130; Watanabe et al. unpublished).

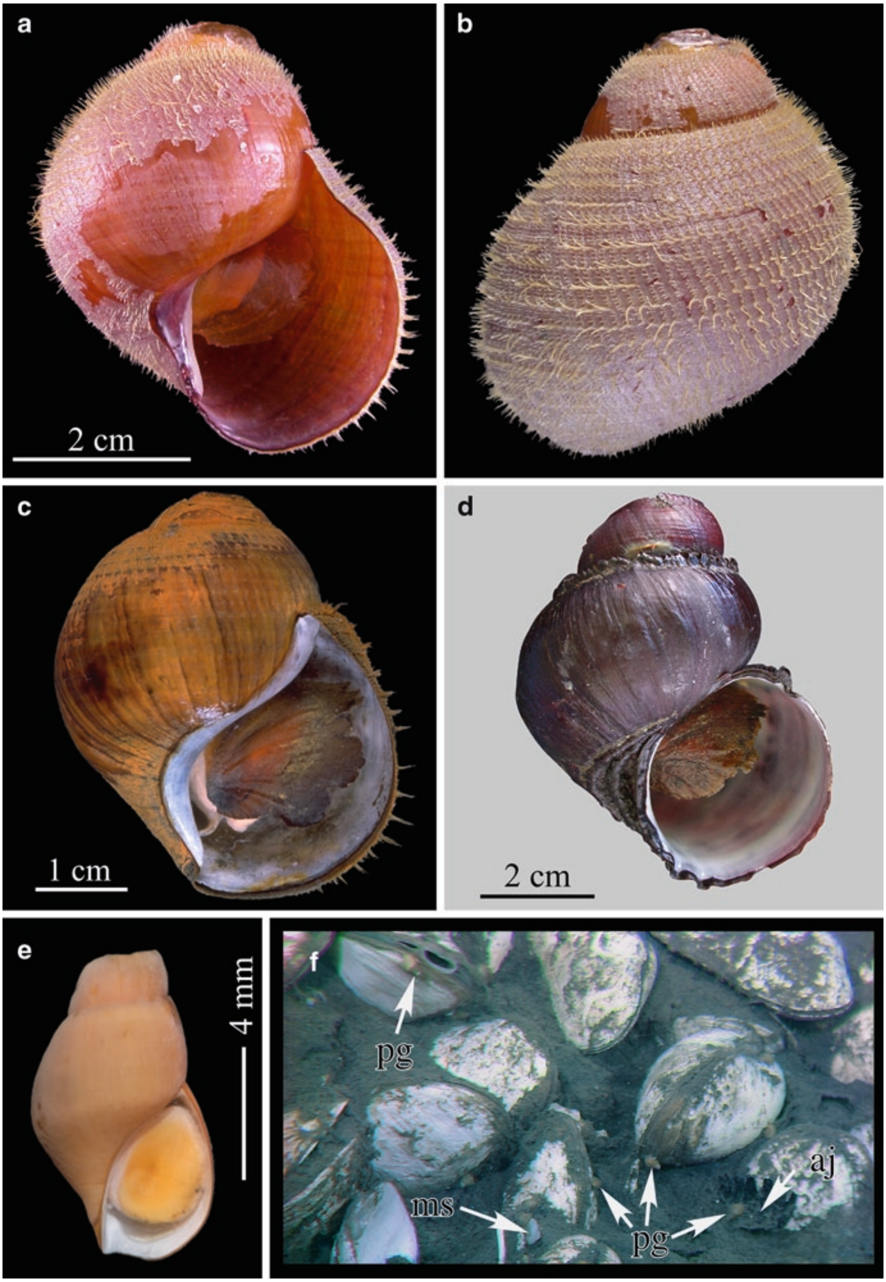

Fig. 7.8 Provannidae. (**a–b**) *Alviniconcha hessleri* Okutani and Ohta 1988. Holotype, NSMT-Mo 64489, Alice Springs site, Mariana Back-Arc Basin, 3,630–3,655 m, vent. (**c**) *Alviniconcha* aff. *hessleri* Okutani and Ohta 1988. Kairei Field, Indian Ocean, 2,422 m, vent. JAMSTEC. (**d**) *Ifremeria nautilei* Bouchet and Warén 1991. Paratype, NSMT-Mo 29992, Lau Basin, 1,750 m, vent. (**e–f**) *Provanna glabra* Okutani et al. 1992. Hatsushima seep site, Sagami Bay, Japan, seep. (**e**) Shell.

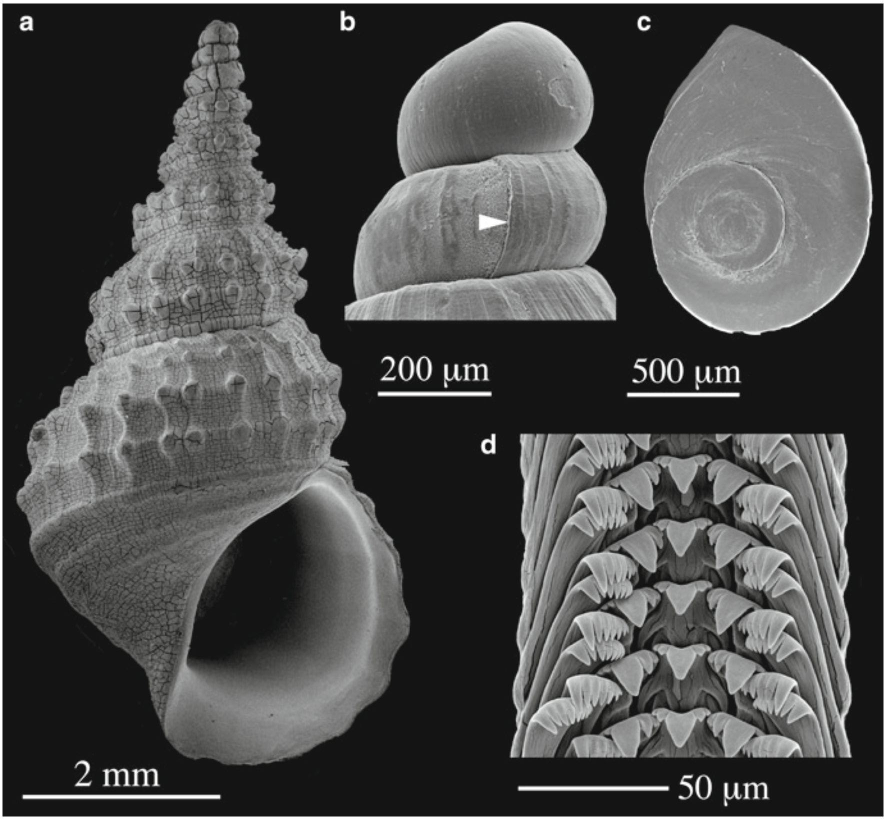

Fig. 7.9 Provannidae. (**a–d**) *Desbruyeresia marisindica* Okutani et al. 2004. Kairei Field, Indian Ocean, 2,434 m, vent. (**a**) Holotype UMUT RM28673. (**b**) Protoconch. UMUT RM28676. (**c**) Operculum. UMUT RM28674. (**d**) Radula. UMUT RM28675 (a–d: Okutani et al. 2004)

1. Genus *Alviniconcha* (Fig. 7.8a–c): *Alviniconcha* is one of most noticeable organisms of hydrothermal vents. The genus has been collected from vents of Mariana, Manus, North Fiji, Lau Back-Arc Basins and Kairei Field, but only a single species *Alviniconch hessleri* has been taxonomically described (type locality Mariana Back-arc Basin). Specimens from the southwestern Pacific and Indian Ocean are surprisingly similar in shell morphology in spite of their remotely separated habitats. Molecular phylogenetic studies have revealed several distinct genotypes (Denis et al. 1993; Kojima et al. 2001; Kojima 2004; Suzuki et al. 2005a, b, 2006a,

◄

UMUT RM30209. (**f**) Habitat at *Calyptogena* bed. Off Hatsuhima, 1,173–1,175 m, *Hyper-Dolphin* Dive 525. Abbreviations: aj, periostracum of *Acharax johnsoni*; ms, *Margarites shinkai*; pg, *Provanna glabra*. A color plate of this figure can be found in Appendix I (Plate 16). (a–b, d: Photo taken by T. Sasaki at NSMT; c: Okutani et al. 2004; f: Sasaki et al. 2007)

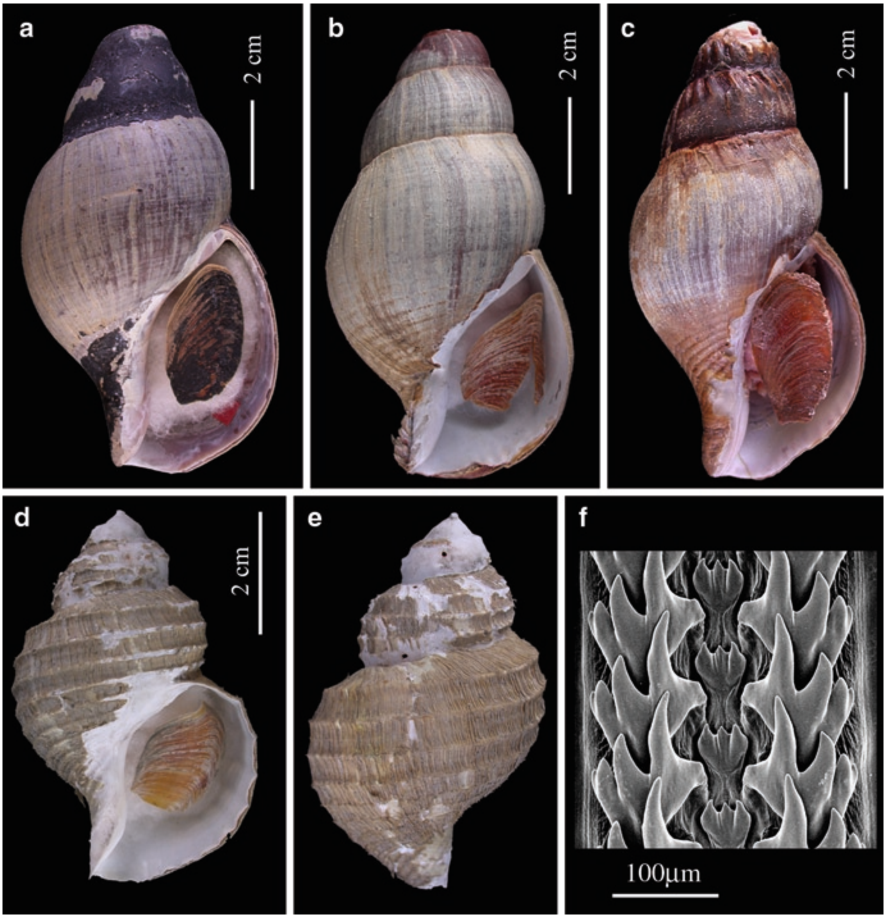

Fig. 7.10 Buccinidae. (**a**) *Eosipho desbruyeresi* Okutani and Ohta 1993. NSMT-Mo 69949. Lau Basin, 1,750 m, vent. (**b**) *Eosipho desbruyeresi nipponensis* Okutani and Fujiwara 2000. Holotype, NSMT-Mo 71689. North Knoll of Iheya Ridge, Okinawa Trough, Japan, 1,049 m, vent. (**c**) Paratype, NSMT-Mo 71691. Myojin Knoll, Japan, 1,268 m, vent. (**d–e**) *Calliloncha nankaiensis* Okutani and Iwasaki 2003. Holotype, NSMT-Mo 73525. Off Cape Muroto, Nankai Trough, Japan, 3,540 m, seep. (**f**) Radula. Paratype, NSMT-Mo 73526 (a, c: Photo taken by T. Sasaki at NSMT; b, d–e: Sasaki et al. 2005; f: Okutani and Iwasaki 2003)

Johnson and Vrijenhoek unpubl.), but so far the only general conclusion is that the Indian Ocean population is well separated and isolated from several others. The shell of *Alviniconcha* is swollen, fragile, and cracks when dried. The surface is covered with thick periostracum with spirally arranged bristles, formed by corresponding papillae on the pallial margin (Warén and Bouchet 1993: fig. 47). The bristles presumably have a protective function against fouling animals. The shell of *A. hessleri* consists of four layers of different microstructures from outer to inner sides: (1) periostracum, (2) simple prismatic, (3) complex crossed lamellar and (4) simple prismatic structures (Kiel 2004: 178).

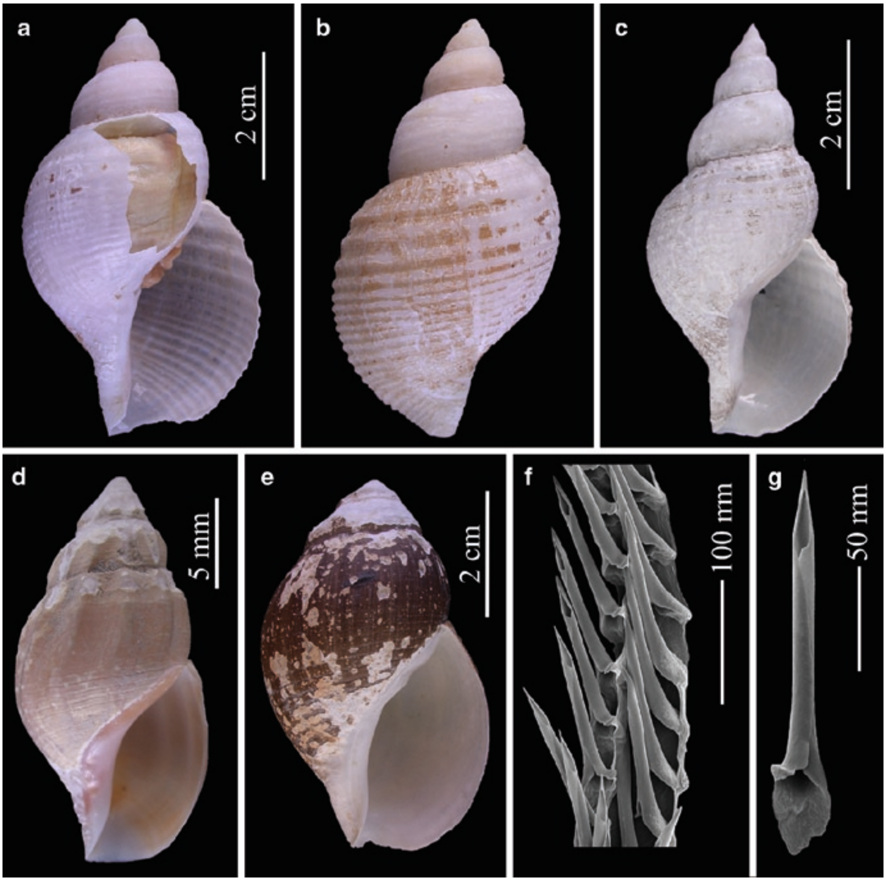

Fig. 7.11 Conidae. (**a–b**) *Phymorhynchus starmeri* Okutani and Ohta 1993. Holotype, NSMT-Mo 69950. North Fiji Basin, 2,750 m, vent. (**c**) *Phymorhynchus turris* Okutani and Iwasaki 2003. Holotype, NSMT-Mo 73527. Off Cape Muroto, Nankai Trough, Japan, 3,540 m, seep. (**d**) *Oenopota sagamiana* Okutani and Fujikura 1992. Holotype, NSMT-Mo 69645. Off Hatsushima, Sagami Bay, Japan, 1,170 m, seep. (**e–g**) *Phymorhynchus buccinoides* Okutani et al. 1993. Holotype NSMT-Mo 73527. Off Hatsushima, Sagami Bay, Ca. 1,100m, seep. (a–b: Photo taken by T. Sasaki at NSMT; c–e: Sasaki et al. 2005; f–g: Fujikura et al. 2009)

There is no pallial tentacle. A pair of neck furrows is apparent on the right side of the head: one of these often contains a mucus string with mineral particles and fragments of other organisms (Warén and Bouchet 1993: 63) and possibly used to transport filtered food material from the ctenidium to the mouth. The ctenidial lamellae are attached to the mantle on the right side, but hung into the pallial cavity towards the left side (Warén and Bouchet 1993: fig. 48). The ctenidium of *Alviniconcha* is hypertrophied to cultivate symbiotic bacteria (Stein et al. 1988; Suzuki et al. 2005a: fig. 1). In *A.* aff. *hessleri* from the Kairei Field, spherical epsilon proteobractria are contained in elongate cells around the afferent ctenidial vessel (Suzuki et al. 2005a: fig. 2). In contrast, in *A. hessleri* from

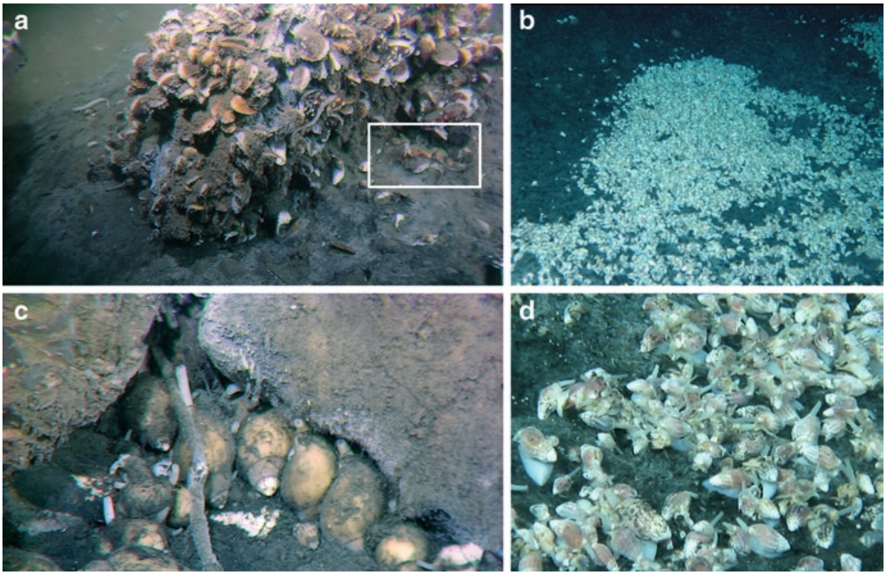

Fig. 7.12 Habitats of Conidae at the Hatsushima seep site in Sagami Bay, Japan. (**a–b**) *Phymorhynchus buccinoides* Okutani et al. 1993. *Hyper-Dolphin* Dive 524, 1,180 m. (**a**) Outcrop covered by *Bathymodiolus* spp. Rectangle is enlarged in B. (**b**) *P. buccinoides* extending siphon at base of outcrop. (**c–d**) *Oenopota sagamiana* Okutani and Fujikura 1992. *Hyper-Dolphin* Dive 525, 1,173 m. (**c**) Large colony of *O. sagamiana.* (**d**) Enlarged view of C. A color plate of this figure can be found in Appendix I (Plate 17) (a–d: Sasaki et al. 2007)

Mariana Back-Arc Basin, vermicular gamma proteobacteria are contained in round bacteriocytes on the surface of ctenidial lamellae (Suzuki et al. 2005b: fig. 1). It is interesting that different population of *Alviniconcha* have different lineages of endosymbionic bacteria. The digestive tract is reduced in volume. Species of *Provanna* have a stomach 100 times larger than *Alviniconcha* relative to whole animal volume (Warén and Bouchet 1993: 63).

2. Genus *Ifremeria* (Fig. 7.8d): *Ifremeria* is another large-sized gastropod forming massive aggregates in vents in southwestern Pacific. There is only a single species in the genus, *Ifremeria nautilei*. Contrary to *Alviniconcha*, genetic divergence is not remarkable in this species. Phylogenetic analysis using mitochondrial COI gene sequences suggests that populations from Manus, North Fiji and Lau Back-Arc Basins are the same biological species (Suzuki et al. 2006b; see also Kojima et al. 2000 for previous results). Similarly symbiotic bacteria from these populations belong to a single lineage of γ-proteobacteria (Suzuki et al. 2006b). The species is characterized by the black and shiny periostracum, the tall spire and nodular sculpture. The head-foot resembles *Alviniconcha* (Warén and Bouchet 1993: fig. 51) but numerous prominent warts cover the sides of the foot (Warén and Bouchet 1993: fig. 51–52). As in *Alviniconcha*, the ctenidium is enlarged (Windoffer and Giere 1997: figs. 1–2). Each ctenidial lamella is divided

into six distinct regions, including large area of bacteriocytes (Beck 1991: fig. 2; Windoffer and Giere 1997: figs. 3–4). The bacteriocytes are single-layered on either side and contains numerous elongate bacteria except basal areas (Windoffer and Giere 1997: fig. 9). The digestive system is reduced in size. Commensal polychaetes are known to occur in the pallial cavity (scale worms) and the umbilicus (*Amphisamytha* cf. *galapagensis*: Warén in Desbruyères et al. 2006: 130).

3. Genus *Provanna* (Fig. 7.9e–f): *Provanna* is one of most common members in vents and seeps (and more rarely on food-falls (Warén and Bouchet 2001: 178)). There are 16 described species up to 2009 (see Appendix 7.3), and there are more undescribed species (at least four in Japan). The types of habitat are vents, seeps, or food-falls depending on the species. The shell microstructure of *P. variabilis* was described by Kiel (2004: 178); the arrangement of shell layers is the same as that of *Alviniconcha hessleri*. The anatomy of *Provanna* was described by Warén and Ponder (1991). A striking feature is the presence an annulate pallial tentacle (Warén and Ponder 1991: figs. 3B–C, 4B). A similar tentacle is also possessed by *Abyssochrysos* sp. (Warén and Ponder 1991: fig. 19). The ctenidium is not hypertrophied (Warén and Ponder 1991: fig. 4A), and the digestive tract and stomach are not reduced in size (Warén and Ponder 1991: fig. 8). The male lacks a penis. The spermatozoa were described by Warén and Ponder (1991: fig. 13) and Healy (1990). *P. variabilis* is considered to be deposit feeder (Warén and Bouchet 1993; Levesque et al. 2006: table 1; Warén et al. in Desbruyères et al. 2006: 132) and grazes on bacteria and detritus. The possibility of symbiosis with autotrophic bacteria was proposed from stable carbon and nitrogen isotope composition (Bergquist et al. 2007), but may also originate from a diet of bacteria that have grown outside the body, a possibility rarely considered by microbiologists. From anatomical evidence, it is unlikely that *Provanna* have endosymbiotic bacteria, since the ctenidium of *Provanna* is not hypertrophied unlike in *Alviniconcha* and *Ifremeria*. Predation on *Provanna* is little known, but there are two records. Shell fragments of *P. variabilis* were found in the gut of the octopus *Graneledone* cf. *boreopacifica* (Voight 2000a), and a shell injury presumably caused by a crustacean was documented for a fossil (Oligocene) species (Kiel 2006).

   Adelphophagy has been reported for *P. lomana* but probably results from confusion with some other gastropods since no shell bearing veliger were observed (Warén in Kaim et al. 2008a: 430). Later observations at the seeps off Costa Rica revealed numerous egg-capsules with one, rarely up to three embryos, length 200 μm, which hatch as trochophore similar to those of *Ifremeria* (Warén unpubl.). This seems to be the second case of trochophore among the Caenogastropoda, *Ifremeria* being the other. The protoconch has been figured for several species (Table 7.2) and shell-bearing larvae can be regularly collected in sediment traps at the EPR. The lack of protoconch II and size of protoconch I suggest planktotrophic stage is absent.

4. Genus *Desbruyeresia* (Fig. 7.9): The distinction of this genus from *Provanna* was previously founded on the absence of a pallial tentacle (Warén and Bouchet 1993: 71), but later the tentacle was revealed to exist in better preserved specimens (Kaim et al. 2008a: 431). The diagnostic characters of the genus are slender

Melania-like teleoconch and the protoconch with rough cancellate sculpture (except *D. marisindica*). Other characters including the operculum and radula (Fig. 7.9) are similar to those of *Provanna*. The biology of the genus is little known. Feeding habit is grazing (Warén et al. Desbruyères et al. 2006: 129). Judging from protoconch morphology, development is probably planktotrophic in most species (e.g. *D. spinosa* and *D. cancellata*: Warén and Bouchet 1993: fig. 44D, E) but lecithotrophic in *D. marisindica* (Fig. 7.9b).

5. Genus *Cordesia*: This genus was recently described from a seep off West Africa. Its diagnostic characters are a cylindrical penis (Warén and Bouchet 2009: fig. 11B) and two right pallial tentacles (Warén and Bouchet 2009: fig. 11B–C). Its larva is inferred to have planktotrophic development from protoconch morphology (Warén and Bouchet 2009: fig. 11D–G). The larva ("Richter's larva") was collected 50–100 m below surface over the bottom of 4,570 m deep. This is obvious direct evidence for planktotrophic dispersal from deep-sea hydrocarbon seeps.

Subclade Neogastropoda (Figs. 7.10–7.12)

Neogastropods are generally predators and/or scavengers. In vents and seeps, Buccinidae and Turridae are two major groups; others are rare. Neogastropods are not known to harbor symbiotic bacteria.

Family Buccinidae (Fig. 7.10)

Vent/seep-associated buccinids include genera *Neptunea*, *Buccinum*, *Eosipho* (Fig. 7.10a–c), *Bayerius* and *Calliloncha* (Fig. 7.10d–f). *Eosipho* is a common predator-scavenger in vents and distributed from the West Pacific to the East Pacific Rise. Other groups have more limited occurrence. Species of *Neptunea* and *Buccinum* seem to favour seeps in the North Pacific. The species investigated most in detail biologically is *Buccinum thermophilum* Harasewych and Kantor 2002. The stomach contents indicate that the species is an active predator and opportunistic scavenger with a broad range of diet. Majid crabs are active predators of the species. Egg masses consist of more than 200 capsules and their morphology is similar to those of other buccinids (Martell et al. 2002). *Bayerius arnoldi* has the deepest habitat among vent/seep associated members of the family. The localities are widely spread at depths of 4,774–7,434 m along Japan Trench, Kurile-Kamchatka Trench and Aleutian Trench along with records on abyssal plain (Okutani and Fujikura 2005).

Family Conidae ("Turridae") (Figs. 7.11–7.12, Plate 17)

"Turrids" (conoidean gastropods) are common elements of predators in deep-sea environments in general. The family in a traditional sense will be split into several separate families (cf. Puillandre et al. 2008), but phylogenetic analysis of this large group is still in the beginning. The most well-known group in vents and seeps is *Phymorhynchus*. The biology of *Phymorhynchus* is relatively well examined in *P. buccinoides* which is endemic to seeps in Sagami Bay, Japan. The species inhabits exclusively large concretions covered by *Bathymodiolus* (Fig. 7.12a–b). The gut investigation could not reveal their prey, but isotopic data suggest the species utilizes *Bathymodiolus* as their food source (Fujikura et al. 2009). The egg capsules contain more than 1,000 eggs on average and are deposited on the shells of *Bathymodiolus* (Watanabe et al. 2009). The egg capsules of *Phymorhynchus* were also illustrated for an unidentified species from the Mid-Atlantic Ridge (Warén and Bouchet 2001: fig. 40b–c) and for *P. coseli* from off West Africa (Warén and Bouchet 2009: fig. 9K). *Phymorhynchus* has a well-developed funnel-shaped rhynchostome (Warén and Bouchet 2001: fig. 40d), and the true proboscis is small and everted internally near the posterior end of the rhynchostome (Warén and Bouchet 2001: 192). The radula (Fig. 7.11f–g) is small for the body size.

There are three records of *Phymorhynchus*' diet. The radula of *Neomphalus fretterae* was found in the gut of *Phymorphychus* sp. (Warén and Bouchet 1989: fig. 5), remains of *Bathymodiolus* were found in the anterior gut of *P. ovatus* (Warén and Bouchet 2001), and polychaete fragments are known from the oesophagus of *P. cingulatus* (Warén and Bouchet 2009: 2344). These are direct evidences of prey and predator (see also Voight 2000b).

Oenopota sagamiana is known exclusively from seeps. The species is associated with bacterial mats, and was found aggregated on a metachromatic area near and within the *Calyptogena* community in Sagami Bay (Okutani and Fujikura 1992: pl. 1, fig. 4). Later in 2006 a huge aggregate of extraordinarily high density were observed in a seep site in Sagami Bay (Sasaki et al. 2007; Fig. 7.12). The attractant of the colony was unidentified. One possible hypothesis is that they temporarily gather for reproduction. Seemingly there is not a large enough food source to sustain such a huge colony of predatory gastropods.

Family Cancellariidae

The family is rare in vent/seep environments, and there are only three records (see Appendix 7.3). The family is known to have a suctorial mode of feeding (O'Sullivan et al. 1987), and thus, the species from vents and seeps are assumed to parasitize other organisms (Warén and Bouchet 1993: 78).

7.2.6 Clade Heterobranchia

The diversity of heterobranchs is noticeably low compared to bathyal non-vent/seep communities (Appendix 7.3: species no. 208–218).

1. Family Pyramidellidae: The occurrence of pyramidellids is exceptional. A single species of *Odostomia* has been found at a few seeps off California and Oregon and a large species of *Eulimella* at similar biotopes from southern California to Costa Rica, among Vestimentifera and clams which are potential hosts for these parasitic species.
2. Cephalaspidea: Cephalaspids are not known from hydrothermal vents, although they are common in the surrounding deep-sea. A few specimens of *Parvamplustrum* sp. (Family Aplustridae) have been noticed in material from the seeps off Oregon.
3. Family Orbitestellidae: The genus *Lurifax* is a vent/seep-related group with species in Mediterranean and New Zealand seeps and Japanese and Mid-Atlantic vents. Nothing is known on its biology. Even its orthostrophic protoconch defies any attempt to infer the type of larval development.
4. Family Hyalogyrinidae: This family contains several species in the genera *Hyalogyra* and *Hyalogyrina*. *Hyalogyrina* may occur in large numbers on bacterial mats at sulphide-rich areas at seeps and whale falls as well as at vents (Braby et al. 2007; Warén unpublished).
5. Family Xylodisculidae: This family has several species known from food-falls, seeps and vents. Nothing is known about its biology, but their unusual radula type (Marshall 1988) may give a hint of unusual or specialized feeding biology. Both Hyalogyrinidae (*Hyalogyra* and *Hyalogyrina*) and Xylodisculidae (*Xylodiscula*) are originally known from sunken wood in the deep sea (Marshall 1988; Hasegawa 1997; Warén and Bouchet 2001).

7.3 Discussion

The following discussion of biological strategies of vent/seep gastropods concerns a wide range of topics. Interests in past publications were focused mostly on vent/seep-related life-strategies, feeding, reproduction and larval development, endemism to vents/seeps, the relation to fauna from biogenic substrates, the geographic distribution, and the correlation between type of larval development and distribution. Here the knowledge on these topics is summarized and evaluated.

7.3.1 Morphological Adaptation

Shells from deep-sea vents and seeps tend to exhibit common features (Warén and Bouchet 1993: 81) such as (1) simplification of shell shape, (2) development of periostracum especially in vents, (3) frequent damage by corrosion, and (4) crusts of mineral deposits. (1)–(3) are common features among deep-sea gastropods, and (4) is a phenomenon typical of vents/seeps or other reducing environments like on shells of species living in burrows or under rocks.

The shells of deep-sea gastropods are generally more simplified than those of their shallow-water counterparts. There are two possible factors: calcification and predation (Vermeij 1993). The shell of calcium carbonate is energetically more costly to produce and more easily corroded in deep-sea environments with colder temperatures and higher pressure. Therefore shells tend to be thin. Spines and teeth in the aperture are absent in gastropods from vents and seeps, contrary to shallow gastropods. But since the majority of vent/seep gastropods are limpets or have a very large aperture, spines and teeth should not be expected. Determinate growth forming thickened apertures (see Sasaki 2008: fig. 1) is also rare in deep-sea species. This is probably because shell-crushing or shell-peeling predation is less common in the deep sea (Vermeij 1993). Shell damage by corrosion is seen more frequently than predatory damages in the deep-sea. Especially when the periostracum is damaged by wear (or possibly bacterial activity), the corrosion starts from there and often forms a deep pit. Possibly other gastropods grazing on bacterial films on the shells contribute to the damage of the periostracum in vents and seeps. The problem with the periostracum is that it cannot be repaired, because the periostracum-secreting mantle of the animal cannot extend far away from the shell aperture. Mineral deposits are common on the shell surface at vents. The deposits are considered to be precipitated by bacterial activities (Warén and Bouchet 1989: 99, 1993: 81). They certainly contribute to the protection against corrosion and the last hope to obtain protoconchs with a preserved sculpture when very young specimens are not available is to remove crusts on the apex with bleach.

Eyes are often reduced or absent in deep-sea species. The reduction or loss of eyes has occurred independently in many gastropod lineages. Rudiments of eyes can be found as black spots in *Shinkailepas myojinensis* (Sasaki et al. 2006b), while in *S. briandi* from the MAR eyes are present only in the veliger larva (Warén and Bouchet 2001). In *Provanna*, the eyes contain the lens but lack a deeply pigmented layer of the retina (Warén and Ponder 1991). In *Bathymargarites symplector* the loss is evidently in progress since some specimens lack an eye and the pigment spots are often deformed or have split (Warén and Bouchet 1989). Other forms of specialization occur in the ctenidium and digestive tract. Among species having endosymbiotic bacteria, the ctenidium, especially the region of bacteriocytes, is hypertrophied. In filter feeding species, the ctenidial lamellae markedly develop to increase the surface area for filtering with cilia (see Declerck 1995 for general discussion) as are found in *Neomphalus* and *Lepetodrilus*. In addition, a groove is formed between the ctenidium and the mouth along the neck as in *Neomphalus, Lepetodrilus* and *Alviniconcha* (Fretter et al. 1981; Fretter 1988; Warén and Bouchet 1993). The digestive tract is reduced in relative size in the species depending largely on symbiotic bacteria (Warén and Bouchet 1993, 2001).

7.3.2 Feeding and Predation

Feeding of vent/seep gastropods is largely similar to shallow-water species or those in regular deep-sea environments. But there is one principal difference: It is not based on photosynthesis, but the community is largely sustained by chemosynthetic production by bacteria. The most common modes of feeding at vents and seeps can be categorized into four types.

Grazing: The surface layer of detritus and bacterial films is the food source for most species but not for most specimens, because the more specialized filter feeders and symbiont-dependent species usually occur in much larger numbers. Mechanical wear of radular teeth is regarded as the supportive evidence for grazing. Such wear can be recognized by the occurrence of loose radular teeth in the gut content and by SEM examination of the anterior end of the radula, where teeth are missing or broken.

Filter feeding: Neomphalus and *Lepetodrilus* employ filter feeding using ctenidial cilia in addition to grazing (Bates 2007a). *Cyathermia* and *Symmetromphalus* are also inferred to use filter feeding, based on the large size of ctenidial lamellae. This mode of feeding is accompanied by the modification of the ctenidial structure as mentioned above (Declerck 1995).

Predation and scavenging: Neogastropods are predator or scavenger in general. Houart and Sellanes (2006) reported possible borings by trophonine muricids on *Calyptogena gallardoi* and *Thyasira methanophoila* in a seep area off Chile. No naticid gastropods (specialized predators that drill holes in other molluscs) are known in vent/seep communities, but also in normal environments they seem to avoid prey with thick periostracum like mussels. When looking for stomach or gut content in predators or scavengers, it is common to find them empty. This is well known for cones (Conidae), and several *Neptunea amianta* (common in Californian seeps) were all reported to survive a year of starvation (Tamburri and Barry 1999).

Symbiotic bacteria: Alviniconcha and *Ifremeria* cultivate symbiotic bacteria intracellularly in the ctenidium (see above for references). *Lepetodrilus gordensis* and *L. fucensis* cultivate filamentous bacteria on the exterior of the gill (Johnson et al. 2006; Bates 2007a). The scaly foot gastropod cultivates bacteria in an enlarged esophageal gland. *Ctenopelta, Echinopelta* and *Hiropelta* are also to some extent probably dependent on bacteria, judging from the unusually small digestive system and that it is partly filled by extremely fine-grained iron sulphides, but low availability of specimens for investigation is hampering their study. The radula is also less important, when grazing is not a main method of feeding.

It is not always easy to specify actual food source in food web. The most direct and least complicated way for food investigations is by direct examination of the gut and stomach content, although it requires some basic knowledge on fragments of animals and sediment. The detection of bacteria in the gut also needs molecular characterization before the food is digested. Supplemented by stable isotope characterization of the tissues this gives a good picture; stable isotopes do not really indicate how the food is obtained. Predators on gastropod species have rarely been identified for species in vents. Shell repair is, however, common (*Buccinum thermophilum*: Martell et al. 2002; *Lepetodrilus fucensis*: Voight and Sigward 2007; *Lepetodrilus* spp., *Peltospira* spp. and *Cyathermia naticoides*: Warén unpublished) and predation has occasionally been more directly confirmed from the gut contents of predators (see Voight 2000b for review).

7.3.3 Reproductive Anatomy

Reproduction can be a relatively easily documented field in the studies of the ecology of deep-sea species. There is a wide variety of modes of reproduction throughout molluscs. The common questions concerning these are listed in Table 7.1. The reproductive strategy of various animals can be deduced from the anatomy of the reproductive organs.

Seasonality of reproduction: If the reproduction occurs during a limited period, the gonad development is not homogeneous throughout a year. The presence of various stages of gametes in the gonad suggests the reproduction is performed continuously. Seasonality has not been clearly documented in any gastropod in seeps and vents.

Hermaphroditism or gonochorism: Hermaphroditism is ubiquitous in heterobranchs and less common in non-heterobranch gastropods. In vents or seeps, *Protolira*, *Pyropelta* and *Adeuomphalus* are known to be simultaneously hermaphroditic. Sequential hermaphroditism (sex change) is not known in vent/seep gastropods. These features have however rarely been investigated, and vary greatly in several groups of gastropods.

Glands in pallial gonoduct: The development of glands in the gonoduct indicates internal fertilization in gastropods. The albumen gland secretes an albumen layer around eggs, and the capsule gland provides protective outer covers. In males the prostate provides mucous fluid to spermatozoa. These glands are absent in externally fertilizing species.

Table 7.1 Common questions concering reproduction and development of gastropods

Reproductive organ	Gametes in the gonad developing synchronously or continuously? Gonochoristic or hermaphroditic (simultaneous or sequential)?
	Prostate present or absent?
	Penis present or absent?
	Albumen and capsule glands present or absent?
	Receptaculum seminis present or absent?
	Receptaculum seminis connected to oviduct or isolated?
Sperm	Spermatozoa of aquasperm type or not?
	Spermatozoa dimorphic or euspermatoza only?
	Spermatophore formed or not?
	Fertilization external, internal or semi-internal (in pallial cavity)?
Egg	Eggs in ovary large and yolky or not?
	Eggs encapsulated, brooded or released freely?
	How many eggs per egg capsule?
	Embryos feeding on nurse eggs (adelphophagy) or not?
Larva	Larva with planktonic stage or entirely benthic?
	Larva hatching before or after metamorphosis?
	Larva planktotorohic or non-planktotrophic?
	How long planktonic larva can survive?
Protoconch	Protoconch symmetrical, paucispial or multispiral?
	Protoconch divided into PI and PII?
	Protoconch size within range of planktotorphic or non-prototrophic type?

Copulatory organ in male: The presence of a copulatory organ (penis) is another evidence for internal fertilization. The formation of the penis is inferred to have evolved several times in gastropods. For instance, the penis exists on the right side in most gastropods but on the left side in Neomphalidae. The position and innervation are morphological criteria to judge homology of various types of copulatory organs. Absence of a copulatory organ does not exclude internal fertilization.

Position of receptaculum seminis: The receptaculum seminis is connected to the pallial oviduct in the majority of caenogastropods and heterobranchs. However, it is located in an isolated position on the left side in Neomphalina and Seguenzoidea or isolated on the right side in *Lepetodilus*. In these groups, the spermatozoa transferred from the male are preserved in the receptaculum embedded in the pallial wall, and fertilization presumably occurs in the pallial cavity. This type of fertilization is termed "semi-internal," since the pallial cavity is not inside but not completely outside of the animal.

Sperm morphology: The shape of various parts of fertilizing sperms is known to be correlated with reproductive strategies. Most notably, the group exerting external fertilization has spermatozoa with a triangular head and long thin tail. Species with internal fertilization have a more elongate blunt head, and the difference in diameter from head to tail is less conspicuous than in externally fertilizing groups.

Sperm dimorphism: Many groups of internally fertilized caenogastropods have dimorphic sperms, eu- and paraspermatozoa, but other gastropods not. Paraspermatozoa possibly function as to convey euspermatozoa which are used for fertilization.

Spermatophore: Spermatophores occur in several internally or semi-internally fertilizing groups listed by Robertson (1989, 2007). Among the seep/vent-related gastropods, *Melanodrymia* sp. (Warén and Bouchet 2001) and the scaly foot gastropod were reported to produce spermatophores. The spermatophore from a male is deposited in the pallial cavity of a female and probably sperms are released and transferred to the receptaclum seminis from there. The number of sperm producing taxa is probably underestimated since their presence is probably very temporary after mating.

Egg size: The eggs tend to be larger in lecithotrophic species requiring a sufficient amount of yolk than in planktotrophic species. The dimensions of eggs are listed for a few vent/seep gastropods by Gustafson and Lutz (1994) and Tyler et al. (2008).

Egg capsule: Eggs are encased in an egg capsule and deposited on the substrate in internally fertilized species, but released into the seawater in externally fertilized species. The form of the egg capsules is variable, depending on taxonomic groups and sometimes also different between closely related species.

7.3.4 Larval Development

Larval ecology is basic information in the discussion of dispersal and evolution of the vent/seep fauna. Types of development can be categorized in various ways in marine invertebrates by nutritional modes, site of development, dispersal potential, and mode of morphogenesis (Levin and Bridges 1995). From an evolutionary perspective, different types of development have different selective advantages in the balance of maternal investment and larval survival (see McEdward 1995 for discussion).

Benthic or planktonic development: In species with external fertilization, the eggs are freely discharged, and larvae swim until metamorphosis. In species that deposit encapsulated eggs, larvae can be either benthic or planktonic. In benthic development, metamorphosed larvae hatch as crawling juveniles out of the egg capsules. In planktonic development, larvae can swim with the cilia and velum.

Planktotrophic or non-planktotrophic development: Some gastropods develop a plankton-feeding stage as the veliger larva (planktotrophy). During this phase the larva usually grows from a size of 0.1–0.2 mm to 0.4–2.0 mm and adds one or more whorls to the shell. This trait affects the duration of planktonic life, but little is known on the duration except in some common shallow water species. The ability of a species to shift between planktotrophy and lecithotrophy has been much discussed and occasionally reported but so far no cases can be considered well documented in deep-sea gastropods.

The type of larval development can usually be inferred from well preserved larval shells (Jablonski and Lutz 1983). The larva hatching from the egg capsule ideally has a shell of roughly one whorl with a certain sculpture; during the planktotrophic life 1–5 whorls, usually with a more prominent sculpture are added, by incremental growth at the pallial margin. These two parts are called protoconch 1 and protoconch 2, respectively. The term "non-planktotrophic" was applied originally from a paleobiological viewpoint to avoid the problem to infer the presence or absence of a planktonic dispersal phase in species with lecithotrophic development (Shuto 1974; Jablonski and Lutz 1983). This is called "Thorson's apex theory" (1950), but it is not always so easy or clearcut. To be sure about the applicability of these criteria it is necessary to have detailed knowledge of some closely related or very similar species, as pointed by Thorson (1950) but often conveniently forgotten. When there is different sculptures in the protoconchs 1 and 2, consisting of small and sharp elements, like in triphorids, cerithiids or turrids, planktotrophy can usually be safely inferred. If protoconch 2 is smooth adelphophagy cannot be excluded. For example, the world's largest gastropod *Syrinx auranus* has a protoconch of 4–5 smooth whorls, but the development is via adelphophagy. Many gastropod species at vents and seeps are presumed to be non-plankotrophic, but more interesting is the presence or absence of a planktonic dispersal phase (details of most species in Warén and Bouchet 1989, 1993, 2001). Multispiral protoconchs are limited to Neritimorpha and Caenogastropoda. Among the species in vents and seeps, almost all of the species in vents and seeps have lecithotrophic development as in Patellogastropoda, Neomphalina, and Vetigastropoda.

A special type of sculpture is formed in the protoconch of *Bathymargarites, Ventsia*, and *Bruciella* (Warén and Bouchet 1993: 82). The larval shell of these groups has two distinct sections, but this probably does not indicate planktotrophic stage as in caenogastropods. One possible hypothesis is that the section is formed when the larvae still use nutrients from eggs after metamorphosis (Warén and Bouchet 1993: 82). A similar sculptural change was also shown in the Calliostomatidae (teleoconch I: Marshall 1995: 385) and might be indicative of dietary change after metamorphosis.

7.3.5 Dispersal and Speciation

The capacity of dispersal presumably has an essential role in the evolution of vent/seep gastropods. Species with a feeding larval stage are assumed to extend their distributions to wider ranges. By contrast, the species without planktotrophic phase have little potential of long-distance dispersal, and therefore, have more restricted distributions (Table 7.2). However, this is not always the case in the deep sea. There seems to be no noticeable difference in distribution between species with a planktotrophic larva, a planktonic dispersal phase or those that crawl directly out of the egg capsule. This seems also to be the case for bivalves, where mussels (*Bathymodiolus*) with planktotrophic larvae have more geographic variation and smaller distributional areas than the clams (Vesicomyidae) with lecithotrophic development (Vrijenhoek pers. comm. 2006). Two details must be remembered here. We know nothing on how long the lecithotrophic larvae can survive. Pradillon et al. (2001) showed that some vestimentiferan larvae can hibernate and wake up when slightly warmer water is encountered. It is not only an advantage with a long larval life that may also carry the larvae far away from seeps and vents. The ideal would be to have the choice. And that may be the choice for many of the lecithotrophic ones. Most larvae will probably end up far away from any suitable environment. One possible dispersal strategy is rafting. Individuals attached to drifting object can stay afloat and drift a long distance. The only likely candidate known to us is *Buccinum* sp. They produce egg masses consisting of hundreds of egg capsules, some of which may die and the capsule fill with gas that make the whole mass buoyant. It can then drift along the bottom like a salt shaker regularly dropping young specimens (Warén and Bouchet 2001). The dispersal capabilities might be inferred from genetic distance among populations. For example in vent/seep gastropods, genetic divergence is notably different between *Alviniconcha* and *Ifremeria* (Suzuki et al. 2005a, b, 2006a, b; Kojima et al. 2001, 2004), and larval ecology of these snails may also be different. If a species is genetically homogeneous over a wide area, it probably has high dispersal capability. If a species is genetically differentiated among distant sites, its dispersal capability may be restricted. However, Johnson et al. (2008) showed that some species of *Lepetodrilus* showed virtually no variation in the COI gene from 20°N at the EPR to 38°S, while other species of the genus

Table 7.2 Assumptions on development and dispersal of gastropods. Capacity of dipersal increases to the right

Amount of yolk	Large	←→	Small
Planktotrophic stage	Absent	←→	Long
Velum	Weakly developed	←→	Well-developed
Protoconch whorls	Paucispiral	←→	Multispiral
Dispersal ability	Low	←→	High
Geographic range	Narrow	←→	Wide
Gene flow	Low	←→	High

had quite restricted distributions or considerable genetic variations, despite having a larval shell of roughly the same size and morphology.

The dispersal is considered a bottleneck for vent/seep animals (Craddock et al. 1997; Van Dover 2002; Tyler and Young 2003), because their habitats are isolated by considerable distances often hundreds of kilometers. In such a situation, the invasion and colonization of new localities may be aided by occasional or unusual habitats like when Johnson et al. (2008) found *Lepetodrilus ovalis*, normally a vents species, on whalebone, at Monterey Bay, California, 1,000 km north of its nearest known occurrence (stepping stone hypothesis). It is not clear whether long-distance dispersal of long-life planktotrophic larvae is effective for vents or seeps. If larvae cannot find suitable vents or seeps for the settlement, most larvae are consumed with high mortality. In lecithotrophic development larvae with larger yolk might be more advantageous for longer dispersal (Kelly and Metaxas 2007). In food-poor environments, nutrition from yolk is important for survival. Thus, yolk amount and egg size have a major effect on survival, dispersal and isolation of species (see discussion by Craddock et al. 1997). Reduction of hydrothermal fluid or seepage causes the decline of local production and eventually the extinction of local life. This has been well observed by repeated visits to the same sites (Fujikura personal observation, 2008; Van Dover 2000).

7.3.6 Endemism to Vents and/or Seeps

It has been widely recognized that many species in chemosynthetic communities are either vent- or seep-endemic (Tunnicliffe 1991, 1992; McArthur and Tunnicliffe 1998; Martin and Haney 2005). At family level, some groups are strict endemics. Peltospiridae and Sutilizonidae are strictly endemic to vents; Neomphalidae and Lepetodrilidae are almost endemic to vents. Provannidae and Neolepetopsidae are mainly distributed in vents but also seeps and foodfalls. In summary in 2001, at genus level, 31 out of 57 genera (54.3%) are endemic to vents; 8 genera (14%) are restricted to seeps, thus nearly 70% are endemic to these environments (Warén and Bouchet 2001: 212). Based on updated information (Tables 7.3, 7.4) and a not fully comparable data set, the number of endemic genera is 36 out of 101 (35.6%) in vents, 8 (7.9%) in seeps, and 5 (5.0%) for vents and seep. Therefore, 48.5% are endemic to vents and/or seeps. At species level, the number of endemic species is 138 out of 218 (63.3%) in vents, 52 (23.9%) in seeps, and 5 (2.3%) for vents and seep. Therefore, 89.5% are endemic to vents and/or seeps. A limited number of species occur both in vents and seeps. For examples, *Neolepetopsis gordensis*, *Margarites shinkai*, *Provanna laevis* and *P. variabilis* are known from both vents and seeps (see Appendix 7.3). As a general tendency the degree of endemism is lower in the seep fauna than at vents (Warén and Bouchet 1993: 81). It is likely that the seep fauna is more frequently invaded from ambient non-chemosynthetic environments than the vent fauna.

Table 7.3 Number of described species and type of habitat in vent/seep-assocaited gastropods at genus level

Higher taxon	Family or Superfamily	Genus	Distribution IO	WP	EP	AO	MS	Habitat of genus
Patellogastropoda	Neolepetopsidae	*Eulepetopsis*	–	–	1 sp.	–	–	Vent
		Neolepetopsis	–	–	4 spp.	–	–	Vent, seep, whale bone
		Paralepetopsis	–	2 spp.	1 sp.	2 spp.	–	Vent, seep, whale bone
	Pectinodontidae	*Bathyacmaea*	–	5 spp.	–	–	–	Vent, seep
		Serradonta	–	2 spp.	–	–	–	Seep
Vetigastropoda		*Sahlingia*	–	–	1 sp.	–	–	Seep
	Fissurellidae	*Clathrosepta*		1 sp.	1 sp.	–	–	Vent[a]
		Cornisepta	–	–	2 spp.	–	–	Vent[a]
		Puncturella	–	3 spp.	–	1 sp.	–	Vent, seep[a]
	Pseudococculinidae	*Amphiplica*	–	–	1 sp.	–	–	Vent
		Tentaoculus	–	–	–	1 sp.	–	Seep, anomuran carapaces, sunken seaweed
	Pyropeltidae	*Pyropelta*	–	3 spp.	2 sp.	2 spp.	–	Vent, seep, whale bone
	Lepetodrillidae	*Clypeosectus*	–	–	2 spp.	–	–	Vent
		Gorgoleptis	–	–	3 spp.	–	–	Vent
		Lepetodrilus	–	4 spp.	10 spp.	2 spp.	–	Vent (mostly), seep
		Pseudorimula	–	1 sp.	–	1 sp.	–	Vent
	Sutilizonidae	*Sutilizona*	–	–	2 spp.	1 sp.	–	Vent
		Temnocinclis	–	–	1 sp.	–	–	Vent
		Temnozaga	–	–	1 sp.	–	–	Vent
	Family uncertain	*Adeuomphalus*	–	2 spp.	1 sp.	–	–	Vent
		Akritogyra	–	–	1 sp.	–	–	Seep[a]
		Ventsia	–	1 sp.	–	–	–	Vent
	Seguenziidae	*Bathymargarites*	–	–	–	1 sp.	–	Vent
	Cataegidae	*Cataegis*	–	–	–	1 sp.	–	Seep
	Chilodontidae	*Bathybembix*	–	–	1 sp.	–	–	Seep[a]
		Putzeysia	–	–	–	–	1 sp.	Seep[a]

(continued)

Table 7.3 (continued)

Higher taxon	Family or Superfamily	Genus	Distribution IO	WP	EP	AO	MS	Habitat of genus
	Calliostomatidae	*Calliostoma*	–	–	1 sp.	–	–	Seep[a]
		Falsimargarita	–	–	1 sp.	–	–	Vent[a]
		Otsukaia	–	–	1 sp.	–	–	Seep[a]
	Trochidae	*Clelandella*	–	–	–	–	1 sp.	Seep[a]
	Turbinidae	*Gaza*	–	–	1 sp.	–	–	Seep[a]
		Margarites	–	2 spp.	–	1 sp.	–	Vent, seep[a]
		Bruceiella	1 sp.	1 sp.	1 sp.	–	–	Vent, seep
		Akritogyra	–	–	1 sp.	–	–	Seep[a]
		Fucaria	–	1 sp.	1 sp.	–	–	Vent, seep
		Iheyaspira	–	1 sp.	–	–	–	Vent
		Protolira	–	–	–	1 sp.	–	Vent, whale bone
		Solutigyra	–	–	1 sp.	–	–	Vent
	Collonidae	*Cantrainea*	–	2 spp.	1 sp.	1 sp.	–	Vent, seep[a]
	Solariellidae	*Zetela*	–	–	1 sp.	–	–	Seep[a]
Neomphalina	Melanodrymiidae	*Leptogyra*	–	1 sp.	–	1 sp.	–	Vent, seep, sunken wood
		Melanodrymia	–	–	3 spp.	–	–	Vent
	Family uncertain	*Helicrenion*	–	1 sp.	–	–	–	Vent
		Retiskenea	–	1 sp.	1 sp.	–	–	Seep
		Vetulonia	–	1 sp.	–	–	–	Vent[a]
	Neomphalidae	*Cyathermia*	–	–	1 sp.	–	–	Vent
		Lacunoides	–	–	2 spp.	–	–	Vent
		Neomphalus	–	–	1 sp.	–	–	Vent
		Planorbidella	–	1 sp.	1 sp.	–	–	Vent
		Symmetromphalus	–	2 spp.	–	–	–	Vent
	Peltospiridae	*Ctenopelta*	–	–	1 sp.	–	–	Vent
		Depressigyra	–	–	2 spp.	–	–	Vent
		Echinopelta	–	–	1 sp.	–	–	Vent

		Hirtopelta	–	–	2 spp.	–	–	Vent
		Lirapex	–	–	2 spp.	1 sp.	–	Vent
		Nodopelta	–	–	3 spp.	–	–	Vent
		Pachydermia	–	1 sp.	1 sp.	–	–	Vent
		Peltospira	–	–	3 spp.	1 sp.	–	Vent
		Rhynchopelta	–	–	1 sp.	–	–	Vent
Neritimorpha	Neritidae	*Bathynerita*	–	–	–	1 sp.	–	Seep
	Phenacolepadidae	*Olgasolaris*	–	1 sp.	–	–	–	Vent
		Shinkailepas	–	3 spp.	–	1 sp.	–	Vent
Caenogastropoda	Capulidae	*Hyalorisia*	–	–	–	1 sp.	–	Seep
	Cerithiopsidae	*Speculator*	–	–	1 sp.	–	–	Vent
	Elachisinidae	*Laeviphitus*	–	1 sp.	–	1 sp.	–	Vent, seep[a]
	Provannidae	*Alviniconcha*	–	1 sp.	–	–	–	Vent
		Cordesia	–	–	–	1 sp.	–	Seep
		Desbruyeresia	1 sp.	4 spp.	–	–	–	Vent
		Ifremeria	–	1 sp.	–	–	–	Vent
		Provanna	–	7 spp.	6 spp.	4 spp.	–	Vent, seep, sunken wood (rare)
	Ranellidae	*Fusitriton*	–	–	1 sp.	–	–	Seep[a]
	Rissoidae	*Alvania*	–	–	–	1 sp.	–	Vent[a]
		Benthonella	–	–	1 sp.	–	–	Seep[a]
		Pseudosetia	–	–	–	1 sp.	–	Vent[a]
	Vitrinelldiae	*Neusas*	–	–	–	1 sp.	–	Vent
	Buccinidae	*Bayerius*	–	1 sp.	2 spp.	–	–	Seep[a]
		Buccinum	–	1 sp.	1 sp.	1 sp.	–	Vent, seep[a]
		Calliloncha	–	1 sp.	–	–	–	Seep[a]
		Eosipho	–	1 sp. + 1 s. sp.	1 sp.	1 sp.	–	Vent, seep[a]

(continued)

Table 7.3 (continued)

Higher taxon	Family or Superfamily	Genus	Distribution IO	WP	EP	AO	MS	Habitat of genus
		Neptunea	–	2 spp.	2 sp.	–	–	Vent, seep[a]
		Kryptos	–	–	–	1 sp.	–	Seep[a]
	Cancellariidae	*Admete*	–	1 sp.	–	–	–	Seep[a]
		Cancellaria	–	–	1 sp.	–	–	Seep[a]
		Iphinopsis	1 sp.	–	–	–	–	Vent[a]
	Muricidae	*Trophon*	–	–	3 spp.	–	–	Seep[a]
	Conidae	*Bathybela*	–	–	–	1 sp.	–	Seep[a]
		Benthomangelia	–	–	–	–	1 sp.	Seep[a]
		Drilliola	–	–	–	–	1 sp.	Seep[a]
		Gymnobela	–	–	–	1 sp.	–	Seep[a]
		Oenopota	–	2 spp.	–	–	–	Vent, seep[a]
		Phymorhyunchus	–	5 spp.	1 sp.	5 spp.	–	Vent, seep[a]
		Taranis	–	–	–	–	1 sp.	Seep[a]
	Volutidae	*Tractolira*	–	–	1 sp.	–	–	Seep[a]
		Miomelon	–	–	–	1 sp.	–	Seep[a]
Heterobranchia	Hyalogyrinidae	*Hyalogyra*	–	1 sp.	–	–	–	Vent, sunken wood
		Hyalogyrina	–	–	3 spp.	1 sp.	–	Vent, seep, sunken wood
	Orbitestellidae	*Lurifax*	–	1 sp.	–	1 sp.	1 sp.	Vent, seep
	Pyramidellidae	*Eulimella*	–	–	1 sp.	–	–	Vent[a]
	Xylodisculidae	*Xylodiscula*	–	1 sp.	–	1 sp.	–	Vent, seep, sunken wood
	Dendronotidae	*Dendronotus*	–	–	–	1 sp.	–	Vent[a]

Data based on the species described by the end of 2009 (see Appendix 7.3). IO, Indian Ocean: Rodrigues Triple Junction; WP, Japan to New Zealand, EP, East Pacific: Aleutian to Chile; AO: Atlantic Ocean: Mid-Atlantic Ridge, Caribbean Sea and West Africa; MS, Mediterranean Sea

[a] Genera also known from 'normal' non-chemosynthetic enviroments (including possible records). sp., spp. = species, s. sp. = subspecies

Table 7.4 Habiats of described taxa at genus and species level

Habitat	Number of genera	Percentage	Number of species	Percentage
Seeps only	8	7.9%	52[a]	23.9%
Seeps and biogenic substrata	1	1.0%	3	1.4%
Seeps and regular environments	24	23.8%	18	8.2%
Vents only	36	35.6%	138[a]	63.3%
Vents and biogenic environments	2	2.0%	1	0.5%
Vents and regular environments	9	8.9%	0	0%
Vents and seeps	5	5.0%	5	2.3%
Vents, seeps and biogenic substrata	7	6.9%	1	0.5%
Vents, seeps and regular environments	9	8.9%	0	0%
Total	101	100%	218	100%

Data from Appendix 7.3

[a] Including possible records

7.3.7 Connection with Sunken Wood and Bone

Some species, genera and families are associated with vents/seeps and food falls (Smith et al. 1989; Warén and Bouchet 1989; Smith and Baco 2003), which may indicate an evolutionary link between them (Distel et al. 2000). At species level, overlapping habitats have been reported in four species (see Appendix 7.1 for references). (1) In the genus *Pyropelta,* two species, *P. musaica* and *P. corymba* have been recorded from vents and whale-fall. (2) The turbinid *Protolira thorvaldssoni* is known both from vents, seeps and whale bones. (In neither case species identity has been tested by molecular analysis). (3) *Lepetodrilus ovalis* and *L. elevatus* are common in hydrothermal vents at the EPR but have also been found and sequenced from sunken driftwood, off California (Johnson et al. 2008).

At genus or family level, connections between vent/seep and sunken wood/bone are obvious in several cases. (1) Species of Neolepetopsidae are mostly vent/seep-endemic, but two species, *Neolepetopsis nicolasensis* and *Paralepetopsis clementensis*, are known from whale skeletons off California (McLean 2008: 16, 18). (2) In Pectinodontidae, the genus *Bathyacmaea* is closely related to the wood-grazing genus *Pectinodonta* (Nakano and Ozawa 2007). Furthermore, *Serradonta* on vestimentiferan tubes has a radular morphology similar to that of *Pectinodonta*. (3) In the Melanodrymiidae, Kunze et al. (2008) and Heß et al. (2008) considered *Melanodrymia* is closely related to *Leptogyra, Xyleptogyra* and *Leptogyropsis* known from sunken wood (Marshall 1988). (4) *Pyropelta wakefieldi* was described from whale bone off California. In addition, *Pyropelta* is morphologically closely related to *Pseudococculina* which is common to sunken wood. (5) The family Provannidae is a mainly vent/seep group, but *P. macleani and P. pacifica* were collected from sunken driftwood, not from vents or seeps (Warén and Bouchet 2001: p. 179). A couple of species of *Provanna* and a new provannid genus were found on a whale skeleton off California (Braby et al. 2007; Johnson et al. in press). (6) The

Hyalogyrinidae (*Hyalogyra* and *Hyalogyrina*) and Xylodisculidae (*Xylodiscula*) also use sunken wood as habitat (Marshall 1988; Warén 1992; Haseagawa 1997).

This connection to the wood/bone-associated fauna is also evident in the fossil record. For example, *Leptogyra* from the Eocene, *Xylodiscula* from the Oligocene (Kiel and Goedert 2006, 2007), *Pyropelta*, *Retiskenea*, *Depressigyra*, *Provanna* and *Lurifax* from the Eocene to Oligocene (Kiel 2006) and *Provanna* from the Late Cretaceous (Kaim et al. 2008a) represent ancestors of modern vent/seep taxa. Before ocean-going whales radiated in the Eocene (Kiel and Little 2006), chemosysnthesis-associated gastropods utilized marine reptile bones (e.g. Kaim et al. 2008b). Abyssochrysoid Hokkaidoconchidae probably utilized a similar ecological niche as the Provannidae (Kaim et al. 2008a, b; Kiel et al. 2008).

While seep and food-fall related species seem to be recognized back to the Jurassic – Cretaceous boundary (Kiel et al. 2008), the few older records must be considered uncertain. No fossil vent faunas with identifiable gastropods are known except in Cretaceous ophiolites from Cyprus (Little and Cann 1999). This is probably due to a combination of deep sea-environment with high pressure and low temperature typical of the deep sea and low pH of the vent fluids, factors that increase the solubility of calcium carbonate. It is actually rare to find any accumulations of old shells in vents and usually the calcareous layer disappears before the periostracum.

Among the two major groups in vents, Neomphalina and Lepetodriloidea, only a few safe records, back to the Eocene, are known and only of species related to *Leptogyra* (Kiel and Goedert 2006) which now is classified in Neomphaloidea. Not a single of the larger and modified neomphalins or anything similar has been found. The same is true for the Lepetodriloidea, although they do occur also in seeps where conditions for fossilization are better. Records of *Retiskenea* from the early Cretaceous (Campbell et al. 2008) may represent the earliest known Neomphalina, but those fossils are more likely to belong to one of other skeneimorph groups.

7.3.8 Biogeography

The summary of the geographic distribution of each species (Appendix 7.3) shows that most species are endemic to a relatively narrow region in a single trench, ridge, trough, or basin. Examples of the widest distribution like *Lepetodrilus elevatus* which has been recorded the Galapagos Spreading Center, the EPR between 20°N and 17°S, to North Fiji and Lau Back-Arc Basins (Warén and Bouchet 2001) have turned out to be based on misidentifications (Johnson et al. 2008), but *L. ovalis* occurs along the EPR from 21°N to 38°S with virtually no variation in the COI gene. Although vents and seeps are widely distributed in the world oceans (see Desbruyères in Desbruyères et al. 2006: 513–517 for map), there is no wide-ranged species that occurs in two oceans, instead they follow geologic formations, like the EPR (21 – ca 25°S occasionally to 38°S), MAR (38°N to 09°S) or the seeps along the American West Coast. The EPR has been explored to 38°S (R. Vrijenhoek pers. comm.) and the MAR to 09°S (O. Giere pers. comm.). At 38°S of the EPR the fauna is largely similar to the more northern localities although often with different species; at 09°S of the MAR it is largely the same species as further north. Apparently the diversity within the vent-endemic families is the highest along the EPR, as is shown in the Neolepetopsidae (*Eulepetopsis* and *Neolepetopsis*), Lepetodriloidea (*Clypeosectus, Gorgoleptis*, *Temnocinclis* and *Temnozaga*), Neomphalidae (*Cyathermia*, *Lacunoides* and *Neomphalus*), Melanodrymidae (*Melanodrymia*) and Peltospiridae (*Ctenopelta*, *Depressigyra*, *Ecihnopelta*, *Hirtopelta*, *Nodopelta*, and *Rhynchopelta*).

The faunal link between the East Pacific and the Atlantic are suggested by a restricted occurrence of genera like *Sutilizona*, *Lirapex* and *Peltospira*, as well as a couple of species pairs, *Provanna ios – P. sculpta, P. pacifica – P. admetoides*. The northern connection of the East and West Pacific is supported by a few examples: similar species of Pyropeltidae and *Retiskenea diploura* and *Bayeryus arnoldi*, which occur in seeps along the trenches of the North Pacific. Supraspecific taxa endemic to West Pacific are represented only by *Iheyaspira*, *Serradonta*, *Symmetromphalus*, and *Ifremeria*. Similarities in the gastropod fauna of the seeps of the Central American west coast, the Gulf of Mexico and off West Africa were pointed out by Warén and Bouchet (2009). The vent fauna of the Indian Ocean is still poorly explored (Okutani et al. 2004; Johnson et al. 2008), but connections exist to the West Pacific as suggested by the presence of *Alviniconcha* and *Desbruyeresia,* and to the Atlantic by a species similar to *Lepetodrilus atlanticus*. On the other hand, two undescribed neolepetopsids, one very similar to *Eulepetopsis vitrea* and one to *Neolepetopsis densata* disturb these patterns (Warén, unpublished).

7.4 Future Topics

The fauna of especially the vents is now pretty well known and predictable, much better than the surrounding deep-sea. However, some geographical areas still remain unexplored, especially in the Indian Ocean and the Polar regions. Vent activity with vent related fauna has been reported from about 80°N at Jan Mayen in the North Atlantic but still little is known on the fauna, except that rissoid gastropods occur there (C. Schander pers. comm.). Hydrothermal activity has also been reported from the Gakkel Ridge in the Polar Basin, but only two shells of an unknown gastropod with possible vent affinity were retrieved from grabs (S. Kim pers. comm.). The area south of South America, the southern Mid-Atlantic Ridge and south of the Pacific vents are also unexplored. These areas will however be more difficult thanks to weather conditions with ice or reliably windy weather.

The faunistic knowledge is today fair, but still the gastropod fauna of some areas, like the Indian Ocean and the Manus Basin are incompletely described and explored. The seep areas are even less known, partly due to the problems with a larger and more diverse surrounding fauna which is mixed with the seep component. The evolution of the vent-seep fauna and its connection to food-falls and other temporary food sources is slowly getting documented but here the gastropod fauna of food-falls is the limiting factor. Systematic COI sequencing has usually turned out very useful to reveal cryptic species and should be routinely applied when exploring new faunas.

The feeding and symbiosis with bacteria of the gastropods is still poorly explored although there are more different types of symbioses than in any other group of animals and several probable cases remain to explore; *Ctenopelta*, *Echinopelta*, *Hirtopelta*, all species with reduced alimentary system. Also the mineralization of sulphides and in the alimentary canal of the host remains to be explored; it is usually filled with extremely finely granular sulphides or occasionally elementary sulphur. In addition to stable isotope studies of the feeding biology, also more direct examination and identification of gut content is needed to understand the ecology.

The evolution of the chemosynthetic faunas needs more exploration of fossil deposits to find better preserved material, especially from the first half of the Cretaceous. What little is known of Jurassic deposits seems to indicate a faunal shift in the upper Jurassic (Kaim 2004). The study of dispersal of vent organisms as well as other marine fauna needs more real data, not only assumptions, but studies of the transport of larvae with bottom currents, where do the planktotrophic species live and feed, and intensive study of settlement in new vents.

Acknowledgements We deeply thank Dr. Steffen Kiel (Christian-Albrechts-University Kiel) for his editorial work. We are also grateful to those who kindly reviewed this manuscript and supported our research on vent/seep molluscs since the 1980s. Many samples illustrated here were provided though kind help by crew and staff of IFREMER and JAMSTEC. Photographs of type specimens were taken at NSMT with help by Dr. Hiroshi Saito. Specimens, ecological and molecular information were given by Prof. Kazutaka Amano (Joetsu University of Education), Dr. Erik E. Cordes (Temple University), Dr. Daniel Desbruyères (IFREMER), Dr. Cindy Lee van Dover (Duke University), Dr. Yoshihiro Fujiwara (JAMSTEC), Dr. Shannon Johnson (Monterey Bay Aquarium Research Institute: MBARI), Dr. Andrzej Kaim (Polish Academy of Sciences), Dr. Steffen Kiel (Christian-Albrechts-University Kiel), Prof. Shigeru Kojima (Atmosphere and Ocean Research Institute, University of Tokyo: AORI), Dr. Lisa Levin (Scripps Institute of Oceanography), Dr. Tomoyuki Nakano (NSMT), and Dr. Heiko Sahling (Bremen University), Dr. Michel Segonzac (IFREMER), Dr. Verena Tunnicliffe (University of Victoria), Dr. Robert Vrijenhoek (MBARI) and Dr. Hiromi Watanabe (JAMSTEC). Dr. Robert G. Jenkins (AORI), Dr. Takami Nobuhara (Shizuoka University), and Dr. Ryuichi Majima (Yokohama National University) shared fruitful discussion on fossil vent/seep fauna with us. Part of this work was supported by a Grant-in-Aid from Japan Society of the Proton of Science (no. 18340165).

Appendix 7.1: References to Internal Anatomy of Vent/Seep-Associated Gastropods

Higher taxon	Family	Species	References
Patellogastropoda	Neolepetopsidae	*Eulepetopsis vitrea*	Fretter 1990: 531–544
		Neolepetopsis denstata	Fretter 1990: 545–546
		Neolepetopsis gordensis	Fretter 1990: 546–547
		Neolepetopsis occulta	Fretter 1990: 545
		Paralepetopsis floridensis	Fretter 1990: 547–548
		Paralepetopsis rosemariae	Beck 1996: 89–90
	Pectinodontidae	*Bathyacmaea jonassoni*	Beck 1996: 90–92
		Bathyacmaea secunda	Sasaki et al. 2006a: 295–303
Vetigastropoda	Pyropeltidae	*Pyropelta bohlei*	Beck 1996: 93
		Pyropelta corymba	McLean and Haszprunar 1987: 200–202
		Pyropelta musaica	McLean and Haszprunar 1987: 198–200
		Pyropelta ryukyuensis	Sasaki et al. 2008: 309–310
	Lepetodrilidae	*Clypeosectus curvus*	Haszprunar 1989a: 5–10
		Clypeosectus delectus	Haszprunar 1989a: 5–10
		Gorgoleptis emarginatus	Fretter 1988: 58–64
		Gorgoleptis patulus	Fretter 1988: 65–67
		Gorgoleptis spiralis	Fretter 1988: 64–65
		Lepetodrilus guaymasensis	Fretter 1988: 54–56
		Lepetodrilus cristatus	Fretter 1988: 53–54
		Lepetodrilus elevatus	Fretter 1988: 35–50
		Lepetodrilus fucensis	Fretter 1988: 56–58
		Lepetodrilus gordensis	Johnson et al. 2006: 155–156
		Lepetodrilus nux	Sasaki 1998: 94–100
		Lepetodrilus ovalis	Fretter 1988: 50–53
		Lepetodrilus pustulosus	Fretter 1988: 35–49
		Lepetodrilus schrolli	Beck 1993: 171–173
		Pseudorimula marianae	Haszprunar 1992: 5–10
	Sutilizonidae	*Sutilizona theca*	Haszprunar 1992: 3–5
		Temnocinclis euripes	Haszprunar 1992: 3
		Temnozaga parilis	Haszprunar 1992: 3
	family uncertain, Segenzioidea	*Ventsia tricarinata*	Kunze et al. 2008: 124
Neomphalina	Melanodrymiidae	*Melanodrymia aurantiaca*	Israelsson 1998: 105–108; Haszprunar 1989: 176–180
	Neomphalidae	*Neomphalus fretterae*	Fretter et al. 1981: 338–353
		Pachydermia laevis	Israelsson 1998: 95–105
		Symmetromphalus hageni	Beck 1992: 246–254
	Peltospiridae	*Echinopelta fistulosa*	Fretter 1989: 149–150
		Hirtopelta hirta	Fretter 1989: 150–152
		Hirtopelta tufari	Beck 2002: 252

(continued)

Appendix 7.1 (continued)

Higher taxon	Family	Species	References
		Nodopelta heminoda	Fretter 1989: 146–147
		Nodopelta subnoda	Fretter 1989: 148–149
		Peltospira delicata	Fretter 1989: 141–145
		Peltospira operculata	Fretter 1989: 141–145
		Rhynchopelta concentrica	Fretter 1989: 125–141
		scaly foot gastropod	Warén et al. 2003: supporting on-line material
Neritimorpha	Neritidae	*Bathynerita naticoidea*	Warén and Bouchet 1993: 3–6
	Phenacolepadidae	*Olgasolaris tollmanni*	Beck 1992: 266–269
		Shinakilepas tufari	Beck 1992: 262–265
		Shinkailepas myojinensis	Sasaki et al. 2006a: 2–14
Caenogastropoda	Provannidae	*Alviniconcha hessleri*	Warén and Bouchet 1993: 56–64
		Ifremeria nautilei	Beck 1991: 282–284 as *Olgaconcha tufari*; Warén and Bouchet 1993: 64–71
		Provanna sculpta, P. laevis, P. adametoides, P. variabilis and *P. lomana*	Warén and Ponder 1991: 28–48
	Buccinidae	*Buccinum thermophilum*	Harasewych and Kantor 2002: 40–43
	Conidae	*Phymorhynchus moskalevi*	Sysoev and Kantor 1995: 22–25

Appendix 7.2: References to Protoconch Morphology of Vent/Seep-Associated Gastropods

Higher taxon	Family	Species	References
Patellogastropoda	Neolepetopsidae	*Eulepetopsis vitrea*	McLean 1990a: pl. VII, fig. h
		Neolepetopsis densata	Gustafson and Lutz 1994: figs. 4.11–4.12; Warén and Bouchet 2001: fig. 15a–c
		Paralepetopsis floridensis	McLean 1990a: pl. X, fig. g
		Paralepetopsis sasakii	Warén and Bouchet 2009: fig. 3C, E, F
Vetigastropoda	Family uncertain, Vetigastropoda	*Sahlingia xandaros*	Warén and Bouchet 2001: fig. 15d
	Pseudococculinidae	*Amphiplica gordensis*	McLean 1991: figs. 29, 30
		Tentaoculus granulatus	Warén and Bouchet 2009: fig. 5D

(continued)

Appendix 7.2 (continued)

Higher taxon	Family	Species	References
	Lepetodrilidae	*Clypeosectus delectus*	McLean 1989a: fig. 9C, F; Mullineaux et al. 1996: fig. 2J–K
		Gorgoleptis emarginatus	Mullineaux et al. 1996: fig. 2H
		Gorgoleptis sp.	Mullineaux et al. 1996: fig. 2G
		Lepetodrilus atlanticus	Warén and Bouchet 2001: fig. 15i
		Lepetodrilus elevatus	Mullineaux et al. 1996: fig. 1E
		Lepetodrilus elevatus galriftensis	Mullineaux et al. 1996: fig. 1D
		Lepetodrilus fucensis	Johnson 2006: fig. 5A–B
		Lepetodrilus nux	Sasaki et al. 2003: fig. 11D
		Lepetodrilus ovalis	Mullineaux et al. 1996: fig. 1F
		Lepetodrilus schrolli	Beck 1993: pl. 5, fig. 1
		Lepetodrilus sp.	Mullineaux et al. 1996: fig. 1A–C
		Pseudorimula marianae	McLean 1989a: fig. 13B
		Pseudorimula midatlantica	Warén and Bouchet 2001: fig. 15h
	Sutilizonidae	*Sutilizona pterodon*	Warén and Bouchet 2001: fig. 15g
		Sutilizona theca	McLean 1989a: fig. 4F
		Sutilizona tunnicliffae	Warén and Bouchet 2001: fig. 15f
	Scissurellidae	*Sinezona* sp.	Warén and Bouchet 1989: fig. 4
	Family uncertain, Seguenzioidea	*Adeuomphalus collinsi*	Kano et al. 2009: fig. 4D, E
		Adeuomphalus elegans	Kano et al. 2009: fig. 3F, I
		Adeuomphalus trochanter	Warén and Bouchet 2001: fig. 15l; Kano et al. 2009: fig. 2F
		Ventsia tricarinata	Warén and Bouchet 1993: fig. 18I
	Seguenziidae	*Bathymargarites symplector*	Warén and Bouchet 1993: fig. 1A–C
	Turbinidae	*Bruceiella athlia*	Warén and Bouchet 2001: fig. 15e
		Bruceiella globulus	Warén and Bouchet 1993: fig. 18E–F
		Protolira valvatoides	Warén and Bouchet 1993: fig. 18D, G

(continued)

Appendix 7.2 (continued)

Higher taxon	Family	Species	References
Neomphalina	Family uncertain	*Helicrenion reticulatum*	Warén and Bouchet 1993: fig. 32C
		Vetulonia phalcata	Warén and Bouchet 1993: fig. 18C
	Melanodrymiidae	*Leptogyra costellata*	Warén and Bouchet 2009: fig. 8A
		Leptogyra inflata	Warén and Bouchet 1993: fig. 32A
		Melanodrymia aurantiaca	Warén and Bouchet 1989: fig. 82; Mullineaux et al. 1996: fig. 4A, C
		Melanodrymia galeronae	Warén and Bouchet 2001: fig. 15k
	Neomphalidae	*Lacunoides vitreus*	Warén and Bouchet 2001: fig. 29f
		Neomphalus fretterae	McLean 1981: fig. 10A; Warén and Bouchet 1989: fig. 79; Mullineaux et al. 1996: fig. 2D–E
		Planorbidella planispira	Warén and Bouchet 1989: fig. 84
		Retiskenea diploura	Warén and Bouchet 2001: fig. 15j; Okutani and Fujikura 2002: fig. 2B
		Solutigyra reticulata	Warén and Bouchet 1989: figs. 89–90
		Symmetromphalus hageni	Beck 1992: pl. 3, fig. 4
		Symmetromphalus regularis	McLean 1990b: fig. 14
	Peltospiridae	? Peltospiridae sp. A	Warén and Bouchet 1993: fig. 32F
		Ctenopelta porifera	Warén and Bouchet 1993: fig. 26F
		Depressigyra globulus	Warén and Bouchet 1989: fig. 83; Warén and Bouchet 2001: fig. 15o
		Echinopelta fistulosa	Gustafson and Lutz 1994: figs. 4.9
		Lirapex costellata	Warén and Bouchet 2001: fig. 15m
		Lirapex granularis	Warén and Bouchet 1989: fig. 88; Mullineaux et al. 1996: fig. 3G–H
		Lirapex humata	Warén and Bouchet 1989: fig. 87
		Nodopelta subnoda	McLean 1989b: fig. 29

(continued)

Appendix 7.2 (continued)

Higher taxon	Family	Species	References
		Pachydermia laevis	Warén and Bouchet 1989: figs. 85–86
		Pachydermia sculpta	Warén and Bouchet 1993: fig. 32E
		Peltospira operculata	Mullineaux et al. 1996: fig. 3E
		Peltospira operculata?	Mullineaux et al. 1996: fig. 3D
		Peltospira smaragdina	Warén and Bouchet 2001: fig. 15n
		Rhynchopelta concentrica	McLean 1989b: figs. 37–38; Mullineaux et al. 1996: fig. 3A–B
Neritimorpha	Neritidae	*Bathynerita naticoidea*	Warén and Bouchet 2001: fig. 30d–e
	Phenacolepadidae	*Olgasolaris tollmanni*	Beck 1992: pl. 5, figs. 1–2
		Shinkailepas briandi	Warén and Bouchet 2001: fig. 32f
		Shinkailepas myojinensis	Sasaki et al. 2003: fig. 13C
		Shinkailepas tufari	Beck 1992: pl. 1, fig. 5
Caenogastropoda	Elachisinidae	*Laeviphitus desbruyeresi*	Warén and Bouchet 2001: fig. 37b
		Laeviphitus japonicus	Okutani et al. 1993: figs. 39–40
	Provannidae	*Alviniconcha hessleri*	Warén and Bouchet 1993: fig. 44C
		Cordesia provannoides	Warén and Bouchet 2009: fig. 11D, G
		Desbruyeresia cancellata	Warén and Bouchet 1993: fig. 44E
		Desbruyeresia marisindica	Okutani et al. 2004: fig. 4B
		Desbruyeresia spinosa	Warén and Bouchet 1993: fig. 44D
		Provanna reticulata	Warén and Bouchet 2009: fig. 10J
		Provanna segonzaci	Warén and Bouchet 1993: fig. 57A–B
		Provanna spp.	Warén and Ponder 1991: fig. B, D, F
		Provanna variabilis	Gustafson and Lutz 1994: figs. 4.14–4.15
	Rissoidae	*Alvania stenolopha*	Bouchet and Warén 1993: fig. 1447
		Alvania cf. *stenolopha*	Warén and Bouchet 2001: fig. 37a
		Pseudosetia azorica	Bouchet and Warén 1993: figs. 1603–4

(continued)

Appendix 7.2 (continued)

Higher taxon	Family	Species	References
	Conidae	*Phymorhunchus* sp.	Gustafson and Lutz 1994: figs. 4.17
		Phymorhynchus alberti	Bouchet and Warén 1980: fig. 239
		Phymorhynchus ovatus	Warén and Bouchet 2001: fig. 42a
Heterobranchia	Hyalogyrinidae	*Hyalogyra vitrinelloides*	Warén and Bouchet 1993: fig. 42C
		Hyalogyrina globularis	Warén and Bouchet 2001: fig. 37f
		Hyalogyrina rissoella	Warén and Bouchet 2009: fig. 12K
		Hyalogyrina umbellifera	Warén and Bouchet 2001: fig. 37e, g
	Orbitestellidae	*Lurifax japonica*	Sasaki and Okutani 2005: fig. 1C
		Lurifax vitreus	Warén and Bouchet 2001: fig. 37c–d
	Xylodisculidae	*Xylodiscula major*	Warén and Bouchet 1993: fig. 42A–B

Appendix 7.3: A List of Gastropods Described from Recent Vents and/or Seeps Up to the End of 2009

Families, genera and species are arranged alphabetically within clades. Unavailable names that appeared in the past literature are excluded. Type localities are given for the species distributed in more than a single vent/seep area. Abbreviations: EPR, East Pacific Rise; JdF, Juan de Fuca Ridge; MAR, Mid-Atlantic Ridge; WP, West Pacific. *Undescribed or unidentified species. [ ] Probably not vent-seep species.

Clade Patellogastropoda
Family Neolepetopsidae

1. *Eulepetopsis vitrea* McLean 1990. McLean 1990b: 503, pls. VIIa–i, VIIIa–j, IXa–f; Warén and Bouchet 2001: 123, figs. 2b, g, 14c, appendix 2; Kiel 2004: 170, figs. 3–5; Warén et al. in Desbruyères et al. 2006: 83. EPR: 21°N–17°S (type locality: 21°N), Galapagos Spreading Center, 2,447–2,635 m, vent.
2. *Neolepetopsis densata* McLean 1990. McLean 1990b: 496, pls. IIIa–g, IVa–d; Gustafson and Lutz 1994: figs. 4.10–4.12; Warén and Bouchet 2001: 123, figs. 2a, 3a, 15a–c, appendix 2; Warén et al. in Desbruyères et al. 2006: 84. EPR: 13–12°N (type locality: 12°N), Galapagos Spreading Center, 2,630–2,735 m vent.
3. *Neolepetopsis gordensis* McLean 1990. McLean 1990b: 492, pls. Ia–h, IIa–g; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 84. EPR: Gorda Ridge, 41°N (type locality); South of Gulf of California, 20°N; possibly also off Peru, 5°S; 3,200–3,271 m, vent/seep.

***Neolepetopsis* cf. *gordensis* McLean 1990. Warén and Bouchet 2001: 120, figs. 2d, 3f–g; Kiel 2004: 170, figs. 1–2. Gorda Ridge, south of Gulf of California, off Peru, 5°S, 3,200–3,795 m.

4. *Neolepetopsis occulta* McLean 1990. McLean 1990b: 501, pl. VIa–g; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 84 EPR: 21°N, 1,990 m, vent.
5. *Neolepetopsis verruca* McLean 1990. McLean 1990b: 499, pl. Va–g; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 84. EPR: 21°N, 2,593 m, vent.
6. *Paralepetopsis ferrugivora* Warén and Bouchet 2001. Kiel 2004: 170, figs. 6–7; Warén and Bouchet 2001: 123, figs. 2e–f, 3b–e, 4a–b, e, 14a–b, appendix 2; Warén et al. in Desbruyères et al. 2006: 85. MAR: Lucky Strike, 37°N, ca. 1,700 m, vent.
7. *Paralepetopsis floridensis* McLean 1990 McLean 1990b: 510, pls. Xa–h, XIa–f; Warén and Bouchet 2001: appendix 2. Florida Escarpment, 3,270 m, seep.
8. *Paralepetopsis lepichoni* Warén and Bouchet 2001. Warén and Bouchet 2001: 125, figs. 2c, 5a–f, appendix 2; Okutani and Iwasaki 2003: 2, fig. 2B; Sasaki et al. 2005: 107. WP: Nankai Trough: south off Shizuoka Prefecture (type locality), south-southeast off Cape Muroto, Japan, 2,140–3,571 m, seep.
9. *Paralepetopsis rosemariae* Beck 1996. Beck 1996: text-fig. 2, pl. 1, figs. 1–7; Warén and Bouchet 2001: appendix 2 WP: Edison Seamount, 1,483 m, vent.
10. *Paralepetopsis sasakii* Warén and Bouchet 2009. Warén and Bouchet 2009: 2331, figs. 2A–E, 3A–I. Regab site, West Africa, 750–3,150 m, seep.

Family Pectinodontidae ("Acmaeidae")

11. *Bathyacmaea jonassoni* Beck 1996. Beck 1996: text-fig. 3, pl. 2, figs. 1–7; Warén and Bouchet 2001: appendix 2. WP: Edison Seamount, 1,483 m, vent.
12. *Bathyacmaea nipponica* Okutani et al. 1992. Okutani et al. 1992: 140, figs. 7–11; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 109. WP: Off Hatsushima, Sagami Bay, 1,110–1,200 m, seep
13. *Bathyacmaea secunda* Okutani et al. 1993. Okutani et al. 1993: 130, figs. 13–19; Okutani and Fujiwara 2000: 124, figs. 2–3; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2003, figs. 2, 3A; Fuchigami and Sasaki 2005: 156, fig. 10H; Sasaki et al. 2005: 109, fig. 12D. Okinawa Trough: Minami Ensei Knoll (type locality), Iheya Ridge, North Knoll of Iheya Ridge, Izena Hole, 700–1,049 m, vent.
14. *Bathyacmaea subnipponica* Sasaki et al. 2003. Sasaki et al. 2003: 193, fig. 6; Sasaki et al. 2005: 111, fig. 12E. WP: Nankai Trough: Ryuyo Canyon, 1,100 m, seep
15. *Bathyacmaea tertia* Sasaki et al. 2003. Sasaki et al. 2003: 190, figs. 3B, 4, 5; Sasaki et al. 2005: 111, fig. 12F. WP: Okinawa Trough: North Knoll of Iheya Ridge, 996–1,000 m, vent

***Bathyacmaea* sp. 1. Okutani and Iwasaki 2003: 2; Sasaki et al. 2005: 111. WP: Off Cape Muroto, Nankai Trough, Japan, 3,571 m, seep.

***Bathyacmaea* sp. 2. Sasaki et al. 2003: 195; Sasaki et al. 2005: 111. WP: Sumisu Caldera, Japan, 676 m, vent.

16. *Serradonta kanesunosensis* Sasaki et al. 2003. Sasaki et al. 2003: 195, fig. 8; Sasaki et al. 2005: 108, fig. 12A. WP: Kanesunose Bank, Nankai Trough, 284–322 m, seep.
17. *Serradonta vestimentifericola* Okutani et al. 1992. Okutani et al. 1992: 139, figs. 2–6; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 109, fig. 12B–C. WP: Off Hatsushima, Sagami Bay, 1,110–1,200 m, seep.

Family Lepetidae

**Bathylepeta* sp. [mistake for *Iothia*] Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom?

Clade Vetigastropoda
Family uncertain

18. *Sahlingia xandaros* Warén and Bouchet 2001. Warén and Bouchet 2001: 129, figs. 7d–f, 8a–b, 9a–d, 15d, 16h, appendix 2; Kiel 2004: 171: fig. 10. EP: Aleutian Trench, 4,800–4,900 m, seep.

Superfamily Fissurelloidea
Family Fissurellidae

[19.] *Clathrosepta becki* McLean and Geiger 1998. McLean and Geiger 1998: 14, fig. 7; Warén and Bouchet 2001: appendix 2. WP: Manus Basin, Vienna Woods, 2,494 m, vent.
[20.] *Clathrosepta depressa* McLean and Geiger 1998. McLean and Geiger 1998: 13, fig. 6; Warén and Bouchet 2001: appendix 2. EPR: 13°N, 1,160 m, vent.
[21.] *Cornisepta levinae* McLean and Geiger 1998. McLean and Geiger 1998: 22, fig. 13; Warén and Bouchet 2001: appendix 2. EPR: 13°N, 1,775 m, vent.
[22.] *Cornisepta verenae* McLean and Geiger 1998. McLean and Geiger 1998: 23, fig. 14; Warén and Bouchet 2001: appendix 2. EP: JdF, Axial Seamount, 1,530 m, vent.

23. *Puncturella parvinobilis* Okutani et al. 1993. Okutani et al. 1993: 128, figs. 8–12; Okutani and Fujiwara 2000: 123, fig. 4; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2003: 197, fig. 10; Sasaki et al. 2005: 111, fig. 13A. WP: Okinawa Trough: Minami Ensei Knoll (type locality), North Knoll of Iheya Ridge, Izena Hole, 690–1,340 m, vent.
24. *Puncturella rimaizenaensis* Okutani et al. 1993. Okutani et al. 1993: 126, figs. 2–7; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 112, fig. 13B. WP: Okinawa Trough: Izena Hole, 1,340 m, vent.
25. *Puncturella similis* Warén and Bouchet 2009. Warén and Bouchet 2009: 2335, figs. 2H–I, 6H–J. Guiness Site, West Africa, 750 m, seep.
26. *Puncturella solis* Beck 1996. Beck 1996: pl. 3, figs. 1–9; Warén and Bouchet 2001: appendix 2. WP: Edison Seamount, 1,492 m, vent.

**Puncturella* sp. 1. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom?

**Puncturella* sp. 2. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

Superfamily Lepetelloidea
Family Lepetellidae

**Lepetella* sp. Olu-Le Roy et al. 2004: table 2. Anaximander area, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep, on vestimentiferan tube.

Family Pseudococculinidae

27. *Amphiplica gordensis* McLean 1991. McLean 1991: 44, fig. 25–32; Warén and Bouchet 2001: appendix 2. Gorda Ridge, 3,305 m, vent.
28. *Tentaoculus granulatus* Warén and Bouchet 2009. Warén and Bouchet 2009: 2333, figs. 5A–H. Off Angola, West Africa, 1,307 m, seep.

**Tentaoculus?* sp. Warén and Bouchet 2001: appendix 2. New Zealand, seep.

Family Pyropeltidae

29. *Pyropelta bohlei* Beck 1996. Beck 1996: text-fig. 4, pl. 4, figs. 1–7; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 93 WP: Edison Seamount, 1,483 m, vent.
30. *Pyropelta corymba* McLean and Haszprunar 1987. McLean and Haszprunar 1987: 200, figs. 9–11; McLean 1992b: 409, figs. 17–24; Warén and Bouchet 2001: 125, figs. 4c–d, 6c–f, 7a–b, appendix 2; Warén et al. in Desbruyères et al. 2006: 93. Guaymas Basin, seep (type locality) and Oregon Margin (Warén et al. in Desbruyères et al. 2006); off California, whale-fall (McLean 1992b), 2,022–524 m.
31. *Pyropelta musaica* McLean and Haszprunar 1987. McLean and Haszprunar 1987: 198, figs. 1–8, 9A; McLean 1992b: 406, figs. 9–16; Warén and Bouchet 1993: 2; Warén and Bouchet 2001: appendix 2; Kiel 2004: 171, figs. 8–9; Warén et al. in Desbruyères et al. 2006: 93. JdF: Axial Seamount, 1,546–1,575 m, vent (type locality) and Jalisco Block, seep (Warén and Bouchet 2001) and off California, 1,240 m, whal-fall (McLean 1992b).

**Pyropelta* cf. *musica* McLean and Haszprunar 1987. Warén and Bouchet 2001: 125, figs. 6a–b, 7c. JdF, Axial Seamount, off California 33–36°N, possibly also Jalisco Block Seeps, 20°N, 940–1,575 m, possibly also 3,000–3,775 m, vent, whale skeletons.

32. *Pyropelta oluae* Warén and Bouchet 2009. Warén and Bouchet 2009: 2332, figs. 4G–J. Regab site, West Africa, 3,150 m, seep.
33. *Pyropelta ryukyuensis* Sasaki et al. 2008. Sasaki et al. 2008: 309, figs. 2–9. WP: Okinawa Trough: Hatoma Knoll (type locality) and Daiyon Yonaguni Knoll, 1,451–1,523 m, vent.
34. *Pyropelta sibuetae* Warén and Bouchet 2009. Warén and Bouchet 2009: 2332, figs. 4A–F, 13B–D. Guiness Site, West Africa, 750 m, seep.
35. *Pyropelta yamato* Sasaki et al. 2003. Sasaki et al. 2003: 197, fig. 9; Sasaki et al. 2005: 112, fig. 12G; Warén et al. in Desbruyères et al. 2006: 93. WP: Sumisu Caldera, 676 m, vent.

Superfamily Lepetodriloidea
Family Lepetodrilidae

36. *Clypeosectus curvus* McLean 1989. McLean 1989b: 21, figs. 10A–H, 11F; Haszprunar 1989a: 5, figs. 3, 4B–C, E, 5–6; McLean 1989b: 21, figs. 10A–H, 11F; Warén and Bouchet 2001: 155, appendix 2; Warén et al. in Desbruyères et al. 2006: 86. JdF: Axial Seamount (type locality), Endeavour Segment; Explorer Ridge; 1,575–2,212 m, vent.
37. *Clypeosectus delectus* McLean 1989. McLean 1989b: 18, figs. 7A–H, 8A–H, 9A–F, 11A–E; Haszprunar 1989a: 5, fig. 4A, D; Mullineaux et al. 1996: fig. 2J–L; Warén et al. in Desbruyères et al. 2006: 86. EPR: Galapagos Spreading Center (type locality), 21°N–17°S, ca. 2,400–2,600 m, vent.
38. *Gorgoleptis emarginatus* McLean 1988. McLean 1988a: 22, figs. 21–24, 84–92; Fretter 1988: 58, figs. 16–17; Mullineaux et al. 1996: fig. 2H–I; Warén and Bouchet 2001: 154, fig. 17b, appendix 2; Warén et al. in Desbruyères et al. 2006: 87. EPR: 21–9°N (type locality: 21°N), ca. 2,600 m, vent.
39. *Gorgoleptis patulus* McLean 1988. McLean 1988a: 24, figs. 98–102; Fretter 1988: 65, figs. 18b–c; Warén and Bouchet 2001: 154, fig. 17a, appendix 2; Warén et al. in Desbruyères et al. 2006: 87. EPR: Galapagos Spreading Center (type locality), 13°N, ca. 2,480–2,600 m, vent.
40. *Gorgoleptis spiralis* McLean 1988. McLean 1988a: 23, figs. 93–97; Fretter 1988: 64, fig. 18b–c; Warén and Bouchet 2001: 155, fig. 17a, appendix 2; Warén et al. in Desbruyères et al. 2006: 87. EPR: 13°N, ca. 2,630 m, vent.
41. *Lepetodrilus atlanticus* Warén and Bouchet 2001. Warén and Bouchet 2001: 143, figs. 14d, f, 15i, 19a–f, 20a–d, 21a, b, appendix 2; Warén et al. in Desbruyères et al. 2006: 88. MAR: 38–23°N (type locality: Menez Gwen), 850–3,500 m, vent.
42. *Lepetodrilus corrugatus* McLean 1993. McLean 1993: 29, fig. 11–16; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 88. JdF, 2,420 m, vent. Only known from the holotype.
43. *Lepetodrilus cristatus* McLean 1988. McLean 1988a: 15, figs. 13–14, 57–61; Fretter 1988: 53, figs. 11–12; Warén and Bouchet 2001: 151, fig. 22a, appendix 2; Warén et al. in Desbruyères et al. 2006: 88. EPR: 21–13°N (type locality: 21°N), Galapagos Spreading Center, ca. 2,500–2,600 m, vent.
44. *Lepetodrilus elevatus* McLean 1988. McLean 1988a: 18, figs. 17–20, 75–83; McLean 1993: 32, figs. 17–25; Fretter 1988: 49, figs. 7–8; Beck 1993: 175, figs. 5–6, 36–44; Mullineaux et al. 1996: fig. 1E, H; Warén and Bouchet 2001: 151, fig. 22c, appendix 2; Warén et al. in Desbruyères et al. 2006: 88. EPR: 21°N–17°S (type locality: 21°N), Galapagos Spreading Center, WP: North Fiji Basin, Lau Basin, Mariana Basin, ca. 2,400–2,700 m, vent. *Remarks:* Johnson et al. (2008) showed that records from localities other than EPR are misidentifications; at the EPR and Galapagos spreading Centre there are probably 4–6 sympatric and cryptic species.
45. *Lepetodrilus fucensis* McLean 1988. McLean 1988a: 18, figs. 17–20, 75–83; Fretter 1988: 56, fig. 15; McLean 1993: 32; Warén and Bouchet 2001: 154, appendix 2; Warén et al. in Desbruyères et al. 2006: 88; Johnson et al. 2006:

figs. 3E–H, 4B–C, 5A–B, 5D–F. JdF (type locality: Endeavor Segment), ca. 1,500–2,200 m, vent. *Remarks:* Records from the Gorda Ridge are based on *L. gordensis* (Johnson et al. 2006).

46. *Lepetodrilus galriftensis* McLean 1988. McLean 1988a: 13, figs. 7–8, 45–50 [as *L. elevatus galriftensis*]; Mullineaux et al. 1996: fig. 1D, G [as *L. e. galriftensis*]; Warén et al. in Desbruyères et al. 2006: 88. EPR 9°N, Galapagos Spreading Center, 2,451 m, vent.
47. *Lepetodrilus gordensis* Johnson et al. 2006. Johnson et al. 2006: 151, figs. 3A–D, I–J, A, D–I, 5C, G–L. Gorda Ridge, 2,696–2,716 m, vent.
48. *Lepetodrilus guaymasensis* McLean 1988. McLean 1988a: 16, figs. 15–16, 66–74; Fretter 1988: 54, figs. 13–14; McLean 1993: 32; Warén and Bouchet 2001: 153, appendix 2; Warén et al. in Desbruyères et al. 2006: 88. Guaymas Basin, 2,000–2,019 m, seep.
49. *Lepetodrilus japonicus* Okutani et al. 1993. Okutani et al. 1993: 134, figs. 30–33; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 113, fig. 14A; Warén et al. in Desbruyères et al. 2006: 88. WP: Okinawa Trough: Minami Ensei Knoll, 700–710 m, vent.
50. *Lepetodrilus nux* (Okutani et al. 1993). Okutani et al. 1993: 132 [as *Rynchopelta*?]; Sasaki 1998: 94, figs. 62–65; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2003: 199, fig. 11; Sasaki et al. 2005: 114, fig. 14B; Warén et al. in Desbruyères et al. 2006: 88. WP: Okinawa Trough: Izena Hole (type locality) and Iheya Ridge, 990–1,390 m, vent.
51. *Lepetodrilus ovalis* McLean 1988. McLean 1988a: 14, figs. 9–12, 51–56; Fretter 1988: 50, figs. 8–10; Mullineaux et al. 1996: fig. 1F, I; Warén and Bouchet 2001: 153, fig. 22b, appendix 2; Warén et al. in Desbruyères et al. 2006: 88. EPR: 21°N–17°S (type locality: 21°N), Galapagos Spreading Center, ca. 2,500–2,600 m, vent.
52. *Lepetodrilus pustulosus* McLean 1988. McLean 1988a: 8, figs. 1–4, 25–35; Fretter 1988: 35, figs. 1–6; Warén and Bouchet 2001: 153, fig. 22d–e, appendix 2; Kiel 2004: 173, figs. 15–16; Warén et al. in Desbruyères et al. 2006: 88. EPR: Galapagos Spreading Center (type locality), 21°N–17°S, ca. 2,600 m, vent.
53. *Lepetodrilus schrolli* Beck 1993. Beck 1993: 171, figs. 2–3, pls. 1–5; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 88. WP: Manus Back-Arc Basin, 1,450–2,505 m, vent.
54. *Lepetodrilus shannonae* Warén and Bouchet 2009. Warén and Bouchet 2009: 2335, figs. 2F–G, 6A–F, 7A–F. Regab site (type locality) and Diapir site, West Africa, 2,300–3,150 m, seep.
55. *Lepetodrilus tevnianus* McLean 1993. McLean 1993: 28, figs. 1–10; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 88. EPR: 11°N, 2,536 m, vent.

**Lepetodrilus* sp. Warén and Bouchet 2001: appendix 2. WP: Manus, vent.

**Lepetodrilus* spp. 20 species were barcoded by Johnson et al. (2008) for an ongoing revision of the group. At least 6 species were not available for sequencing. This indicates the group to be even more species rich than generally assumed.

56. *Pseudorimula marianae* McLean 1989. McLean 1989b: 24, figs. 12A–H, 13A–D; Haszprunar 1989a: 5, figs. 7–9; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 91. WP: Mariana Back-Arc Basin, 3,640–3,660 m, vent.
57. *Pseudorimula midatlantica* McLean 1992. McLean 1992a: 116, figs. 1–7; Warén and Bouchet 2001: 155, figs. 15h, 18c, 23a–h, appendix 2; Kiel 2004: 173; Warén et al. in Desbruyères et al. 2006: 91 MAR: 38–15°N, ca. 1,500–3,500 m, vent.

Family Sutilizonidae (Ongoing work indicates these species to belong to the Lepetodrilidae.)

58. *Sutilizona pterodon* Warén and Bouchet 2001. Warén and Bouchet 2001: 141, figs. 15g, 17c, e, g–h, 18a, f, appendix 2; Warén et al. in Desbruyères et al. 2006: 98. MAR: Snake Pit, 3,470–3,520 m, vent.
59. *Sutilizona theca* McLean 1989. McLean 1989b: 15, figs. 3A–C, 4D–F, 5E–F; Haszprunar 1989a: 3, fig. 2; Kiel 2004: 173, fig. 14; Warén and Bouchet 2001: 141, fig. 17f, I, appendix 2; Warén et al. in Desbruyères et al. 2006: 98. EPR: 12–13°N, ca. 2,500–2,700 m, vent.
60. *Sutilizona tunnicliffae* Warén and Bouchet 2001. Warén and Bouchet 2001: 143, figs. 15f, 17d, 18b, d, g, appendix 2; Warén et al. in Desbruyères et al. 2006: 98. JdF: Endeavour Segment, 2,202 m, vent.
61. *Temnocinclis euripes* McLean 1989. McLean 1989b: 7, figs. 1A–H, 4A, 5A–B; Haszprunar 1989a: 3, fig. 1; Warén and Bouchet 2001: 143, appendix 2; Warén et al. in Desbruyères et al. 2006: 99. JdF, ca. 44–50°N (type locality: Axial Seamount), ca. 1,500–2,300 m, vent.
62. *Temnozaga parilis* McLean 1989. McLean 1989b: 9, figs. 2A–H, 4B–C, 5C–D; Haszprunar 1989a: 3; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 100 (figured). EPR: 21–13°N (type locality: 21°N), ca. 2,600 m, vent.

Superfamily Scissurelloidea
Family Scissurellidae

**Sinezona* sp. Warén and Bouchet 1989: 68, figs. 3–4. EP: off Mexico, 25.50N, 109,06W, 2,633 m, vent.

**Anatoma* sp.: Warén and Bouchet 1993: 7 [as Scissurellidae] WP: Lau Basin, Hine Hina, vent.

Superfamily Seguenzioidea
Family uncertain

63. *Adeuomphalus collinsi* Kano et al. 2009. Kano et al. 2009: 408, figs. 4C–H, 6. Manus Basin, off Papua New Guinea, ca. 1,440 m, vent.
64. *Adeuomphalus elegans* Kano et al. 2009. Kano et al. 2009: 404, fig. 3. Lau Basin, South Pacific, 1,737 m, vent.

65. *Adeuomphalus trochanter* Warén and Bouchet 2001. Warén and Bouchet 2001: 132, figs. 8f, 15l, 16d, appendix 2. Kano et al. 2009: 404, fig. 2D–F. EP: Jdf: CoAxial Segment, 2,060 m, vent.

Moelleriopsis sp. Warén and Bouchet 1989: 86, fig. 91 [family uncertain, Seguenzioidea(?)]; Warén and Bouchet 2001: appendix 2. EPR: 13°N, 2,635 m, vent.

66. *Akritogyra conspicua* (Monterosato 1880). Olu-Le Roy et al. 2004: table 2. Olimpi and Anaximander areas, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep and regular deep-sea bottom?

67. *Ventsia tricarinata* Warén and Bouchet 1993. Warén and Bouchet 1993: 31, figs. 18I, 23C–F, 24B–F, 25A–C; Warén and Bouchet 2001: appendix 2. WP: Lau Basin, 1,750–1,900 m, vent.

**Ventsia* sp. aff. *tricarinata* Warén and Bouchet 1993. Warén and Bouchet 2001: appendix 2. WP: Marianas, vent.

Family Cataegidae

68. *Cataegis meroglypta McLean and Quinn 1987. McLean and Quinn 1987: 115,* figs. 3–4, 7–8; Warén and Bouchet 1993: 19, figs. 14A–G, 15A–B; Warén and Bouchet 2001: 133, appendix 2. Louisiana Slope to Barbados Prism, 421–1,135 m (type locality: off Louisiana, 845–858 m), seep.

Family Chilodontidae

[69.] *Bathybembix macdonaldi* (Dall 1891). Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

**Calliotropis* sp. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

70. *Putzeysia wiseri* (Calcara 1841). Olu-Le Roy et al. 2004: table 2. Olimpi and Anaximander areas, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep and regular deep-sea bottom.

Family Seguenziidae

[71.] *Bathymargarites symplector* Warén and Bouchet 1989. Warén and Bouchet 1989: 91, figs. 92–95, 100–101, 104–107, 110; Warén and Bouchet 1993: 11, figs. 10A–E, 11A–B; Warén and Bouchet 2001: 132, appendix 2; Kiel 2004: 173, figs. 17–18; Warén et al. in Desbruyères et al. 2006: 101, figured [as Chilodontidae]. MAR: 13–21°N (type locality: 21°N), ca. 2,500–2,600 m, vent.

Superfamily Trochoidea
Family Calliostomatidae

72. *Calliostoma chilena* Rehder 1971. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom [not seep dependent?].

[73.] *Falsimargarita nauduri* Warén and Bouchet 2001. Warén and Bouchet 2001: 133, figs. 8e, 10a–d, 11a–b, 14e, 16c, appendix 2. EPR: 17°S, 2,578 m, vent deep-sea bottom [not seep dependent?].

[74.] *Otsukaia crustulum* Vilvens and Sellanes 2006. Vilvens and Sellanes 2006: 16, figs. 1–5; Sellanes et al. 2008: table 2 [as *Calliostoma*]. Off Central Chile, Concepción Methane Seep Area, 728–870 m, seep and regular deep-sea bottom [not seep dependent].

Family Solariellidae

75. *Zetela alphonsi* Vilvens 2002. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom [presumably not seep dependent].

Family Trochidae

76. *Clelandella myriamae* Gofas 2005. Olu-Le Roy et al. 2004: table 2 [as *Clelandella* sp.]. Gofas 2005: 141, figs. 11, 12E–F, 13H. Anaximander (type locality) and Olimpi seamounts, Eastern Mediterranean Sea, 1,700–2,030 m, seep and regular deep-sea bottom?

Family Turbinidae

77. *Gaza fisheri* Dall 1889. Warén and Bouchet 1993: 13; Warén and Bouchet 2001: appendix 2. Louisiana Slope and Caribbean Sea, 600–1,061 m, seep.
78. *Margarites huloti* Vilvens and Sellanes 2006. Vilvens and Sellanes 2006: 16, figs. 1–5; Sellanes et al. 2008: table 2. Off Central Chile, 843–728 m, seep.
79. *Margarites ryukyuensis* Okutani et al. 2000. Okutani et al. 2000: 273, fig. 6; Sasaki et al. 2005: 114, fig. 15A. WP: Okinawa Trough: North Knoll of Iheya Ridge, 968–1,053 m, vent.
80. *Margarites shinkai* Okutani, Tsuchida and Fujikura 1992. Okutani et al. 1992: 142, figs. 12–16; Okutani et al. 1993: 132, figs. 20–21; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 115, fig. 15B. WP: Sagami Bay (type locality) and Okinawa Trough, 1,110–1,340 m, seep/vent.

**Margarites* sp. Warén and Bouchet 2001: appendix 2. WP: Manus, vent.

Subfamily Skeneinae, Family Turbinidae

81. *Bruceiella athlia* Warén and Bouchet 2001. Warén and Bouchet 2001: 139, figs. 8d, 11d–f, 13a–d, 15e, 16j, appendix 2; Kiel 2004: 173, fig. 13. Aleutian Trench, ca. 4,800 m, seep.
82. *Bruceiella globulus* Warén and Bouchet 1993. Warén and Bouchet 1993: 27, figs. 17C–F, 18E–F, 21A–C, 22A–D; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 94. WP: North Fiji (type locality) and Lau Back-Arc Basins, 1,750–2,443 m, vent.
83. *Bruciella wareni* Okutani et al. 2004. Okutani et al. 2004: 2, fig. 2A–F. IO: Kairei Field, Rodriguez Triple Junction, 2,422–2,443 m, vent.
84. *Fucaria mystax* Warén and Bouchet 2001. Warén and Bouchet 2001: 136, figs. 8c, 11c, 12a–d, 16e, appendix 2 [as Trochidae]; Warén et al. in Desbruyères et al. 2006: 95. WP: Edison Seamount, 1,483 m, vent.

**Fucaria* sp. Warén and Bouchet 2001: appendix 2 [as Trochidae]. Florida Escarpment, seep.

85. *Fucaria striata* Warén and Bouchet 1993. Warén and Bouchet 1993: 16, figs. 9E–H, 12A–C, 13A–C, 38C [as Trochidae]; Warén and Bouchet 2001: 136, appendix 2 [as Trochidae]; Warén et al. in Desbruyères et al. 2006: 95. JdF, 2,425 m, vent.
86. *Iheyaspira lequios* Okutani et al. 2000. Okutani et al. 2000: 268, figs. 2–5; Sasaki et al. 2005: 115, fig. 15C. WP: Okinawa Trough: North Knoll of Iheya Ridge, 968–1,053 m, vent.
87. *Protolira thorvaldssoni* Warén 1996. Warén 1996: 201, figs. 3E–F, 4A–D [as *thorvaldsoni*]; Warén and Bouchet 2001: 138, appendix 2; Warén et al. in Desbruyères et al. 2006: 97. MAR: Snake Pit to Iceland (type locality: off southwestern Iceland), ca. 850–3,700 m, vents and whale bone.
88. *Protolira valvatoides* Warén and Bouchet 1993. Warén and Bouchet 1993: 22, figs. 17A–B, 18D, G, 19A–C, 20A–F; Warén and Bouchet 2001: 138, appendix 2; Kiel 2004: 173, figs. 11–12; Warén et al. in Desbruyères et al. 2006: 97. MAR: 23°N, 3,478 m (Warén and Bouchet 1993: type locality) and Menez Gwen to Lucky Strike, 850–1,800 m (Warén and Bouchet 2001), vent.

Family Collonidae

89. *Cantrainea jamsteci* (Okutani and Fujikura 1990). Okutani and Fujikura 1990: 85, figs. 2–6 [as *Thermocollonia*]; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 115, fig. 15D. WP: Okinawa Trough: Minami-Ensei Knoll, 700–720 m, vent.
90. *Cantrainea macleani* Warén and Bouchet 1993. Warén and Bouchet 1993: 8, figs. 4A–C, 5B, F–G, 6A; Warén and Bouchet 2001: 132, appendix 2. Louisiana Slope, ca. 500–1,000 m, seep.
91. *Cantrainea nuda* Okutani 2001. Okutani 2001: 122, fig. 4. WP: Okinawa Trough, 730 m, vent.
92. *Cantrainea panamense* (Dall 1908). Sellanes et al. 2008: table 2 [as *Homalopoma*]. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

Clade Neompahlina
Family uncertain

93. *Helicrenion reticulatum* Warén and Bouchet 1993. Warén and Bouchet 1993: 45, figs. 32C–D, 33A, C, 36A–C [as Peltospiridae]; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 102 (figured). WP: Lau Back-Arc Basin, 1,900 m, vent.
94. *Retiskenea diploura* Warén and Bouchet 2001. Kiel 2004: 174, fig. 19; Warén and Bouchet 2001: 158, figs. 15j, 16g, 18e, 24c, appendix 2; Okutani and Fujikura 2002: 212, fig. 2A–I; Sasaki et al. 2005: 114. Aleutian Trench (type locality) and Japan Trench, ca. 4,800–6,290 m, seep.

**Retiskenea* sp. Warén and Bouchet 2001: 158, fig. 25a–e, appendix 2. Oregon Margin, seep.

95. *Vetulonia phalcata* Warén and Bouchet 1993. Warén and Bouchet 1993: 11, figs. 7A–B, 8E–F, 11C, 18C; Warén and Bouchet 2001: appendix 2; Warén

et al. in Desbruyères et al. 2006: 103 (figured). WP: North Fiji Back-Arc Basin, 2,000 m, vent.

Family Melanodrymiidae

96. *Leptogyra costellata* Warén and Bouchet 2009. Warén and Bouchet 2009: 2337, figs. 6H, 8A–D. Regab site, West Africa, 3,150 m, seep.
97. *Leptogyra inflata* Warén and Bouchet 1993. Warén and Bouchet 1993: 47, figs. 29E–F, 32A–B, 37A–C, 38A–B, D [as Peltospiridae]; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 96. WP: Lau Basin, 1,750 m, vent.
98. *Melanodrymia aurantiaca* Hickman 1984. Hickman 1984: 20, figs. 1–2; Israelsson 1998: 105; Haszprunar 1989b: 175, figs. 1–11; Warén and Bouchet 1989: 75, figs. 26–27, 32–33, 35–36, 75, 82 [as Peltospiridae]; Warén and Bouchet 1993: 41 [as Peltospiridae]; Mullineaux et al. 1996: fig. 4A, C–D; Warén and Bouchet 2001: 159, appendix 2 [Neomphalidae]; Kiel 2004: 174, fig. 20; Warén et al. in Desbruyères et al. 2006: 106 (figured). EPR: 21°N–17°S (type locality: 29°50′N), ca. 2,500–2,600 m, vent.
99. *Melanodrymia brightae* Warén and Bouchet 1993. Warén and Bouchet 1993: 43, figs. 34A–C, 35A–B; Warén and Bouchet 2001: 159, appendix 2; Warén et al. in Desbruyères et al. 2006: 106. JdF: Endeavour Segment, 2,200 m, vent.
100. *Melanodrymia galeronae* Warén and Bouchet 2001. Warén and Bouchet 2001: 161, 15k, 16f, 21c, 14a–b, d, appendix 2; Warén et al. in Desbruyères et al. 2006: 106 (figured). EPR: 13°N, ca. 2,600 m, vent.

*_Melanodrymia_ sp. Warén and Bouchet 2001: appendix 2. Galapagos Rift, vent.

*_Melanodrymia_ sp. "rust covered". Warén and Bouchet 2001: 159, figs. 21d, 24e–f, appendix 2; Warén et al. in Desbruyères et al. 2006: 106. EPR: 13°N, vent.

Family Neomphalidae

101. *Cyathermia naticoides* Warén and Bouchet 1989. Warén and Bouchet 1989: 70, figs. 6–10, 15, 16, 18, 21–23, 71, 80; Warén and Bouchet 1993: 33 [as Cyathermidae]; Kiel 2004: 175, fig. 21; Mullineaux et al. 1996: fig. 2A–C; Warén and Bouchet 2001: 158, appendix 2; Warén et al. in Desbruyères et al. 2006: 104 (figured). EPR: 21–9°N (type locality: 13°N), ca. 2,600 m, vent.
102. *Lacunoides exquisitus* Warén and Bouchet 1989. Warén and Bouchet 1989: 72, figs. 13–14, 17, 20, 72, 81; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 105 (figured). EPR: Galapagos Spreading Center, 2,447–2,518 m, vent.
103. *Lacunoides vitreus* Warén and Bouchet 2001. Warén and Bouchet 2001: 162, fig. 29a–e, appendix 2; Warén et al. in Desbruyères et al. 2006: 105 (figured). JdF: Axial Seamount, 1,543 m, vent.

104. *Neomphalus fretterae* McLean 1981. McLean 1981: 294, figs. 1–10; Warén and Bouchet 1989: 69, figs. 5, 11, 12, 19, 79; Warén and Bouchet 1993: 33; Mullineaux et al. 1996: fig. 2D–F; Warén and Bouchet 2001: 162, appendix 2; Warén et al. in Desbruyères et al. 2006: 107 (figured). EPR: 21–9°N, Galapagos Spreading Center, ca. 2,400–2,600 m, vent.
105. *Planorbidella depressa* Warén and Bouchet 1993. Warén and Bouchet 1993: 38, figs. 30B–D, 31C–D, F; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 109. WP: Lau Basin, Hine Hina, vent.
106. *Planorbidella planispira* (Warén and Bouchet 1989). Warén and Bouchet 1989: 81, figs. 48–50, 53–54, 74, 84 [as *Depressigyra*]; Warén and Bouchet 1993: 37, fig. 29D [as Peltospiridae]; Warén and Bouchet 2001: 162, appendix 2; Kiel 2004: 175; Warén et al. in Desbruyères et al. 2006: 109 (figured). EPR: 21°N–17°S (type locality: 21°N), ca. 2,500–2,600 m, vent.
107. *Solutigyra reticulata* Warén and Bouchet 1989. Warén and Bouchet 1989: 82, figs. 44, 57–58, 59–62, 77, 89–90 [as Peltospiridae]; Warén and Bouchet 1993: 32 [as Skeneidae]; Warén and Bouchet 2001: appendix 2. EPR: 21–13°N (type locality: 21°N), ca. 2,000–2,600 m, vent.
108. *Symmetromphalus hageni* Beck 1992. Beck 1992a: 246, figs. 2–6, pls. 1–6; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 110. WP: Manus Basin, 2,488–2,500 m, vent.
109. *Symmetromphalus regularis* McLean 1990. McLean 1990a: 79, figs. 1–17; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 110 (figured). WP: Mariana Back-Arc Basin, 3,640 m, vent.

**Symmetromphalus* sp. Warén and Bouchet 2001: appendix 2. WP: North Fiji and Lau Basins, vent.

Family Peltospiridae

110. *Ctenopelta porifera* Warén and Bouchet 1993. Warén and Bouchet 1993: 34, figs. 26D–G, 27A–F, 28A–D; Warén and Bouchet 2001: 170, appendix 2; Kiel 2004: 175, figs. 24–25; Warén et al. in Desbruyères et al. 2006: 111 (figured). EPR: 13°N, ca 2,600 m vent
111. *Depressigyra globulus* Warén and Bouchet 1989. Warén and Bouchet 1989: 80, figs. 30–31, 45–47, 51–52, 73, 83; Warén and Bouchet 1993: 35; Warén and Bouchet 2001: 173, fig. 15o, appendix 2; Warén et al. in Desbruyères et al. 2006: 112 (figured). JdF, 1,500–2,400 m, vent.
112. *Echinopelta fistulosa* McLean 1989. McLean 1989a: 60, figs. 41–48; Gustafson and Lutz 1994: figs. 4.7–4.9; Warén and Bouchet 2001: 170, fig. 28b, appendix 2; Warén et al. in Desbruyères et al. 2006: 113 (figured). EPR: 21–13°N (type locality: 21°N), ca. 2,600 m vent
113. *Hirtopelta hirta* McLean 1989. McLean 1989a: 62, figs. 49–55; Warén and Bouchet 1993: 35, fig. 26A–C; Warén and Bouchet 2001: 169, appendix 2; Warén et al. in Desbruyères et al. 2006: 114 (figured). EPR: 21–13°N (type locality: 13°N), ca. 2,500–2,600 m vent

114. *Hirtopelta tufari* Beck 2002. Beck 2002: 252, figs. 1–15; Desbruyères et al. 2006: 114. EPR: 21°S, 2,802 m, vent.
115. *Lirapex costellata* Warén and Bouchet 2001. Warén and Bouchet 2001: 170, figs. 15m, 16i, 30a–c, 31a–c, appendix 2; Kiel 2004: 176; Warén et al. in Desbruyères et al. 2006: 115 (figured). MAR: Lucky Strike (type locality), ca. 1,600–1,700 m, and Snake Pit, vent.
116. *Lirapex granularis* Warén and Bouchet 1989. Warén and Bouchet 1989: 85, figs. 68–70, 88; Mullineaux et al. 1996: fig. 3G–I; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 115. EPR: 21–9°N (type locality: 21°N), ca. 2,600 m, vent.
117. *Lirapex humata* Warén and Bouchet 1989. Warén and Bouchet 1989: 84, figs. 43, 55–56, 63–65, 78, 87, appendix 2; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 115. EPR: 21°N, 2,616 m, vent.

**Lirapex* sp. Warén and Bouchet 2001: 171, appendix 2. MAR: 23°N, vent.

118. *Nodopelta heminoda* McLean 1989. McLean 1989a: 53, figs. 17–23; Warén and Bouchet 2001: 169, figs. 27g, j. 28e, appendix 2; Warén et al. in Desbruyères et al. 2006: 116 (figured). EPR: 21–13°N (type locality: 21°N), ca. 2,600 m, vent.
119. *Nodopelta rigneae* Warén and Bouchet 2001. Warén and Bouchet 2001: 169, figs. 21e–f, 27a–b, f, i, 28a, d, appendix 2; Warén et al. in Desbruyères et al. 2006: 116 (figured). EPR: 13°N, 2,630 m, vent.
120. *Nodopelta subnoda* McLean 1989. McLean 1989a: 56, figs. 24–31; Warén and Bouchet 2001: 169, figs. 27e, h, 28c, appendix 2; Warén et al. in Desbruyères et al. 2006: 116 (figured). EPR: 13°N–17°S (type locality: 13°N), ca. 2,500–2,600 m, vent
121. *Pachydermia laevis* Warén and Bouchet 1989. Warén and Bouchet 1989: 76, figs. 28–29, 34, 37–40, 41, 42, 76, 85–86 [as Peltospiridae]; Warén and Bouchet 1993: 40 [as Peltospiridae]; Israelsson 1998: 95, figs. 1–7; Kiel 2004: 175, fig. 22; Warén and Bouchet 2001: 161, appendix 2; Warén et al. in Desbruyères et al. 2006: 108 (figured). EPR: 21°N–17°S (type locality: 13°N), ca. 2,500–2,600 m, vent.
122. *Pachydermia sculpta* Warén and Bouchet 1993. Warén and Bouchet 1993: 41, figs. 29A–C, 30E–F, 31A–B, E, 32E, 35C; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 108. WP: North Fiji Basin (type locality) and Lau Basin, 1,750–2,000 m, vent.

**Pachydermia* sp. aff. *sculpta* Warén and Bouchet 1993. Warén and Bouchet 2001: appendix 2. WP: Mariana Back-Arc Basin, vent.

123. *Peltospira delicata* McLean 1989. McLean 1989a: 53, figs. 9–16; Warén and Bouchet 2001: 168, fig. 29f, appendix 2; Warén et al. in Desbruyères et al. 2006: 118 (figured). EPR: 13–9°N, ca. 2,500–2,600 m, vent.
124. *Peltospira lamellifera* Warén and Bouchet 1989. Warén and Bouchet 1989: 74, fig. 24; Warén and Bouchet 2001: 168, figs. 16k, 46b, 48c–d, appendix 2; Warén et al. in Desbruyères et al. 2006: 118. EPR: 13°N, ca. 2,600 m, vent.

125. *Peltospira operculata* McLean 1989. McLean 1989a: 51, figs. 1–8; Mullineaux et al. 1996: fig. 3E–F; Warén and Bouchet 2001: 168, appendix 2; Warén et al. in Desbruyères et al. 2006: 118 (figured). EPR: 21–9°N, 17°S, ca. 2,500–2,600 m, vent.
126. *Peltospira smaragdina* Warén and Bouchet 2001. Warén and Bouchet 2001: 165, figs. 15n, 26a–d, 27c–d, 31e–f, appendix 2; Kiel 2004: 175, fig. 23; Warén et al. in Desbruyères et al. 2006: 118 (figured) MAR: 38–15°N (type locality: Lucky Strike at 37°N), 850–3,500 m, vent
127. *Rhynchopelta concentrica* McLean 1989. McLean 1989a: 58, figs. 32–40; Mullineaux et al. 1996: fig. 3A–C; Warén et al. in Desbruyères et al. 2006: 119 (figured). EPR: 21°N–17°S, ca. 2,500–2,600 m, vent.

*“Scaly foot gastropod”. Warén et al. 2003: fig. 1; Goffredi et al. 2004: fig. 1; Warén et al. in Desbruyères et al. 2006: 120 (figured); Suzuki et al. 2006c: fig. 1. IO: Kairei Field, Rodriguez Triple Junction, ca. 2,420 m, vent.

*Peltospiridae sp. A. Warén and Bouchet 1993: 41, figs. 30A, 32F, 33B. WP: Lau Basin, Hine Hina, vent.

Clade Neritimorpha
Family Neritidae

128. *Bathynerita naticoidea* Clarke 1989. Clarke 1989: 125, figs. 3–4, text figs.; Warén and Bouchet 1993: 3, figs. 1–2, 3A–C; Warén and Bouchet 2001: 177, fig. 30d–f, appendix 2; Kiel 2004: 176, figs. 26–27. Louisiana Slope (type locality) and Barbados Prism, 550–1,135 m, seep.

Family Phenacolepadidae

**Olgasolaris* sp. Warén et al. in Desbruyères et al. 2006: 121. WP: North Fiji and Lau Back-Arc Basins, vent.

129. *Olgasolaris tollmanni* Beck 1992. Beck 1992b: 266, figs. 2–5, pls. 4–6; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 121 (figured). WP: Manus Back-Arc Basin, 2,489–2,505 m, vent.
130. *Shinkailepas briandi* Warén and Bouchet 2001. Warén and Bouchet 2001: 174, figs. 16a–b, 31d, 32a–h, 33a–e, appendix 2; Kiel 2004: 177, fig. 28–29; Warén et al. in Desbruyères et al. 2006: 122 (figured). MAR: Menez Gwen (type locality), Lucky Strike, and Logatchev (15°N), 850–3,500 m, vent.
131. *Shinkailepas kaikatensis* Okutani et al. 1989. Okutani et al. 1989: 225, figs. 2–8, 10–15; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 116, fig. 16A; Warén et al. in Desbruyères et al. 2006: 122. WP: Kaikata Seamout, off Ogasawara Islands, Japan, 470 m, vent.
132. *Shinkailepas myojinensis* Sasaki et al. 2003. Sasaki et al. 2003: 201, figs. 12–13; Sasaki et al. 2005: 117, fig. 16B; 2006: figs. 1–16; Warén et al. in Desbruyères et al. 2006: 122. WP: Myojin Knoll, Japan, 1,260–1,340 m, vent.
133. *Shinkailepas tufari* Beck 1992. Beck 1992b: 262, fig. 5C, pls. 1–3; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 122. WP: Manus Back-Arc Basin, 2,450–2,505 m, vent.

Shinkailepas sp. Warén et al. in Desbruyères et al. 2006: 122. WP: North Fiji Basin, vent.
Shinkailepas sp. Sasaki et al. 2003: 203, fig. 14; Sasaki et al. 2005: 117. WP: Okinawa Trough: North Knoll of Iheya Ridge, 976 m, vent.
Shinkailepas sp. Warén and Bouchet 2001: appendix 2. WP: Manus, vent.

Clade Caenogastropoda
Family Capulidae

[134.] *Hyalorisia galea* (Dall 1889). Warén and Bouchet 1993: 76; Warén and Bouchet 2001: appendix 2. Louisiana Slope to Barbados, 329–768 m (Warén and Bouchet 1993), seep. Probably not a really seep favoured species.

Family Cerithiopsidae

[135.] *Speculator cariosus* Warén and Bouchet 2001. Warén and Bouchet 2001: 180, figs. 34c–d, 36c, 49g, appendix 2; Warén et al. in Desbruyères et al. 2006: 126 (figured). JdF: Explorer Ridge, 1,762 m, vent. Probably not a really seep favoured species.

Family Elachisinidae

136. *Laeviphitus desbruyeresi* Warén and Bouchet 2001. Warén and Bouchet 2001: 182, figs. 34e–f, 36a, 37b, 49e, appendix 2; Warén et al. in Desbruyères et al. 2006: 127 (figured). MAR: Menz Gwen to Rainbow (type locality: Lucky Strike), 850–2,300 m, vent.

137. *Laeviphitus japonicus* Okutani et al. 1993. Okutani et al. 1993: 135, figs. 37–43; Sasaki et al. 2005: 119; Warén and Bouchet 2001: appendix 2. WP: Kaikata Seamount, Japan, 440 m, vent

Laeviphitus sp. Warén and Bouchet 2001: appendix 2. New Zealand, seep.
Laeviphitus sp. (veligers only). Warén and Bouchet 2001: appendix 2. EPR: 13–10°N, vent.

Family Provannidae

138. *Alviniconcha hessleri* Okutani and Ohta 1988. Okutani and Ohta 1988: 2, figs. 1–9; Kiel 2004: 178, fig. 33; Warén and Bouchet 1993: 56, figs. 44A–C, 45A–C, 46, 47, 48A–E, 49, 50C–D; Warén and Bouchet 2001: appendix 2; Warén in Desbruyères et al. 2006: 128 (figured). WP: Mariana (type locality: 3,600–3,680 m), North Fiji and Lau Back-Arc Basins, 1,750–3,680 m, vent. *Remarks*: These records possibly include several different biological species (see review herein).

Alviniconcha aff. hessleri Okutani and Ohta 1988. Okutani et al. 2004: 6, figs. 5A–B, 6; Suzuki et al. 2005a: 5442, fig. 1. Kairei Field, Rodriguez Triple Junction, 2,420–2,454 m, vent.

139. *Cordesia provannoides* Warén and Bouchet 2009. Warén and Bouchet 2009: 2341, figs. 9E, 11A–F. Regab site, West Africa, 3,150 m (type locality) and Florida Escarpment, seep.

140. *Desbruyeresia cancellata* Warén and Bouchet 1993. Warén and Bouchet 1993: 71, figs. 44E, 54D, F–H, 55B; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 129 (figured). WP: Lau Basin (type locality) and North Fiji Basin, 1,750–2,000 m, vent.
141. *Desbruyeresia marianaensis* (Okutani 1990). Okutani 1990: 22, figs. 3–4, 7–8, 10 [as *Provanna*]; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 129 [not (Okutani and Fujikura 1990)]. WP: Mariana Back-Arc Basin, 3,670–3,680 m, vent.
142. *Desbruyeresia marisindica* Okutani et al. 2004. Okutani et al. 2004: 4, figs. 3A–C, 4A–B; Warén et al. in Desbruyères et al. 2006: 129. Kairei Field, Rodriguez Triple Junction, 2,422–2,454 m, vent.
143. *Desbruyeresia melanoides* Warén and Bouchet 1993. Warén and Bouchet 1993: 71, figs. 54C, 55A, 56D, 57C; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 129 (figured). WP: Lau Basin (type locality) and Manus Basin, 1,900 m, vent.
144. *Desbruyeresia spinosa* Warén and Bouchet 1993. Warén and Bouchet 1993: 72, figs. 44D, 54A, 56C–D; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 129 (figured). WP: North Fiji Back-Arc Basin, 1,900–2,765 m, vent.

**Desbruyeresia* aff. *spinosa* Warén and Bouchet 1993. Warén and Bouchet 2001: appendix 2. WP: Mariana Back-Arc Basin, vent.

**Desbruyeresia* sp. aff. *spinosa* Warén and Bouchet 1993. Warén et al. in Desbruyères et al. 2006: 129. WP: Mariana Back-Arc Basin, vent.

145. *Ifremeria nautilei* Bouchet and Warén 1991. Bouchet and Warén 1991: 498, figs. 1A–C, 2A–E; Beck 1991: 282, fig. 2, pls. 1–4 (as *Olgaconcha tufari*); Warén and Bouchet 1993: 64, figs. 25D, 45D–F, 50A–B, 51A–B, 52, 53A–B, 55C–D; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 130 (figured). Lau Basin, 1,750 m (type locality), North Fiji Basin, 2,000 m and Manus Back-Arc Basin, 2,500 m, vent.
146. *Provanna abyssalis* Okutani and Fujikura 2002. Okutani and Fujikura 2002: 214, fig. 3A–C; Sasaki et al. 2005: 118. WP: Japan Trench, 5,379 m, seep.
147. *Provanna admetoides* Warén and Ponder 1991. Warén and Ponder 1991: 53, figs. 4B, figs. 20A–B, 22D, 23A; Warén and Bouchet 2001: appendix 2. Florida Escarpment, 624–631 m, seep.
148. *Provanna buccinoides* Warén and Bouchet 1993. Warén and Bouchet 1993: 74, figs. 54B, E, 56A–B; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 132 (figured). WP: Lau Basin (type locality) and North Fiji Basin, 1,900–2,765 m, vent.
149. *Provanna chevalieri* Warén and Bouchet 2009. Warén and Bouchet 2009: 2340, figs. 9A, B, 10E–H. Regab site, West Africa, 3,150 m, seep.
150. *Provanna glabra* Okutani et al. 1992. Okutani et al. 1992: 143, figs. 17–21; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 118; Warén et al. in Desbruyères et al. 2006: 132. WP: Sagami Bay: off Hatsushima, 1,110–1,200 m, seep.

151. *Provanna goniata* Warén and Bouchet 1986. Warén and Bouchet 1986: 163, figs. 5, 6, 19, 25; Warén and Ponder 1991: 51; Warén and Bouchet 2001: 178, appendix 2. Guaymans Basin, 2,000–2,020 m, seep.
152. *Provanna ios* Warén and Bouchet 1986. Warén and Bouchet 1986: 162, figs. 8–9, 20, 22; Warén and Ponder 1991: 51; Warén and Bouchet 2001: 178, appendix 2; Warén et al. in Desbruyères et al. 2006: 132 (figured). EPR: 21°N–17°S (type locality: 12°49′N), Galapagos Spreading Center, 2,450–2,620 m, vent.
153. *Provanna laevis* Warén and Ponder 1991. Warén and Ponder 1991: 53, figs. 3C–D, 4A, 20H–I, 21C–D, 23D; Warén and Bouchet 2001: 178, fig. 6c, appendix 2; Warén et al. in Desbruyères et al. 2006: 132 (figured). Gulf of California, Guaymas Basin (type locality), ca. 2,000 m, to Oregon Margin, 500–600 m, JdF, ca. 1,500 m (Warén and Bouchet 2001), vent/seep.
154. *Provanna lomana* (Dall 1918). Warén and Bouchet 1986: 161, figs. 1–2, 18, 23; Warén and Ponder 1991: 53, fig. 12; Warén and Bouchet 2001: 178, appendix 2. Oregon Margin, ca. 450–1,200 m, seep.
155. *Provanna macleani* Warén and Bouchet 1989. Warén and Bouchet 1989: 94, figs. 111–114; Warén and Bouchet 2001: 179, appendix 2. Oregon Margin, 2,713–2,750 m, seep and sunken drift wood.
156. *Provanna muricata* Warén and Bouchet 1986. Warén and Bouchet 1986: 163, figs. 3, 12, 21; Warén and Ponder 1991: 51; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 132. EPR: 21°N, 2,615 m and Galapagos Spreading Center, 2,451–2,457 m (Warén and Ponder 1991), and also North Fiji and Lau Back-Arc Basins (Warén et al. in Desbruyères et al. 2006), vent. Type locality: Galapagos Rift, 2,450 m. Remarks: Records from Fiji and Lau are wrong.
157. *Provanna nassariaeformis* Okutani 1990. Okutani 1990: 20, figs. 1–2, 5–6, 9; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 132. Mariana Back-Arc Basin, 3,670–3,680 m, vent (type locality: Okutani 1990) and also Manus Back-Arc Basins, vent (Warén et al. in Desbruyères et al. 2006).
158. *Provanna reticulata* Warén and Bouchet 2009. Warén and Bouchet 2009: 2339, figs. 9C–D, 10I–L. Regab, Guiness and MPS 1-Congo sites, West Africa, 750–3,150 m, seep.
159. *Provanna sculpta* Warén and Ponder 1991. Warén and Ponder 1991: 53, figs. 2, 3A–B, 8, 14, 18, 20C, E, 21A–B, 23B; Warén and Bouchet 2001: 179, appendix 2. Louisiana Slope, ca. 550 m, seep.
160. *Provanna segonzaci* Warén and Ponder 1991. Warén and Ponder 1991: 51, figs. 20D, G, 22A–C, 23C; Warén and Bouchet 1993: 75, fig. 57A–B; Warén et al. in Desbruyères et al. 2006: 132; Warén and Bouchet 2001: appendix 2. WP: Lau Back-Arc Basin, 1,750–1,900 m, vent.
161. *Provanna shinkaiae* Okutani and Fujikura 2002. Okutani and Fujikura 2002: 216, fig. 4A–C; Sasaki et al. 2005: 118. WP: Japan Trench, 5,343 m, seep.
162. *Provanna variabilis* Warén and Bouchet 1986. Warén and Bouchet 1986: 163, figs. 13–15, 26–28; Warén and Ponder 1991: 53, figs. 5–7, 9–11, 13, 15–17; Warén and Bouchet 1993: 76; Gustafson and Lutz 1994: figs. 4.13–4.15;

Warén and Bouchet 2001: 179, appendix 2; Kiel 2004: 178, figs. 30–32; Warén et al. in Desbruyères et al. 2006: 132 (figured). JdF: Endeavour Segment (type locality), Gorda Ridge, Oregon Margin, 675–2,200 m, vent, seep.

Provanna sp. Okutani et al. 1993: 135, fig. 5 [as *P. glabra*]; Okutani and Fujiwara 2000: 124, figs. 34–36 [as *P. glabra*]; Sasaki et al. 2005: 118. WP: Okinawa Trough, 710–1,049 m, vent.

Provanna sp. Warén and Ponder 1991: 51. Galapagos Spreading Center, 2,494 m and EPR: 21°N, 2,617 m, vent.

Provanna sp. 1. Warén and Bouchet 1986, 2001: 179, appendix 2. WP: Edison Seamount, Manus, vent.

Provanna sp. 2. Warén and Bouchet 1986, 2001: 179, appendix 2. Aleutian Trench, seep.

Provanna sp. 3. Warén and Bouchet 1986, 2001: 179, appendix 2. Jalisco Block, vent.

Provanna spp. Warén and Bouchet 2001: appendix 2. New Zealand, seep.

Family Naticidae

[*] *Natica* sp. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

Family Ranellidae

[163.] *Fusitriton magellanicus* (Röding 1798). Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

Family Rissoidae

164. *Alvania stenolopha* Bouchet and Warén 1993. Bouchet and Warén 1993: 653, figs. 1147, 1482–4; Warén and Bouchet 2001: appendix 2. Following records as *Alvania* cf. *stenolopha*. Warén and Bouchet 2001: 186, figs. 34a–b, 36b, 37a; Warén and Bouchet in Desbruyères et al. 2006: 133 (figured). MAR: Lucky Strike, Menez Gwen and surroundings (type locality: off Azores), 650–1,850 m, vent.

165. *Pseudosetia azorica* Bouchet and Warén 1993. Bouchet and Warén 1993: 690, figs. 1603–4, 1615–7; Warén and Bouchet 2001: 186. Off Azores (type locality), ca. 350–850 m; MAR: Menez Gwen, vent.

[166.] *Benthonella tenella* (Jeffreys 1869). Olu-Le Roy et al. 2004: table 2. Anaximander area, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep and regular deep-sea bottom.

Family Vitrinellidae

[167.] *Neusas marshalli* (Sykes 1925). Warén and Bouchet 2001: 186, figs. 35a–c, 36d–f, 49f, appendix 2; Warén et al. in Desbruyères et al. 2006: 134 (figured). MAR: Menez Gwen (38°N), 850–2,000 m.

Clade Neogastropoda

Remarks: It seems likely that many or most of the larger caenogastropods recorded from seeps and vents are generalist scavengers or predators that are attracted by the concentration of organic material.

Family Buccinidae

168. *Bayerius arnoldi* (Lus 1981). Lus 1981: 140, figs. 1–4 [as *Tactia*]; Warén and Bouchet 2001: 189, figs. 38b–e, 39b, 49c, appendix 2; Okutani and Fujikura 2002: 217, fig. 5A–B; Okutani and Fujikura 2005: 121, fig. 1; Sasaki et al. 2005: 120. Aleutian Trench, Kuril Trench, Japan Trench (type locality: north-eastern Pacific, 37°56′N, 146°24′E), 4,800–7,434 m, seep and regular deep-sea bottom.
169. *Bayerius peruvianus* Warén and Bouchet 2001. Warén and Bouchet 2001: 187, figs. 38h, 39c, 49d, appendix 2. Off Peru, 5,996–5,385 m, seep.

**Bayerius* sp. Warén and Bouchet 2001: 189, appendix 2. Jalisco Block Seeps, seep

170. *Buccinum soyomaruae* Okutani 1977. Okutani et al. 1992: 145, figs. 22–23; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 119. WP: Sagami Bay: off Hatsushima, Japan, 1,110–1,500 m, seep and normal muddy sea bottom.
171. *Buccinum thermophilum* Harasewych and Kantor 2002. Warén and Bouchet 1993: 77 as *Buccinum* sp.; Warén and Bouchet 2001: 190 as *Buccinum* sp.; Harasewych and Kantor 2002: 40, figs. 1–3, 5–17; Martell et al. 2002: fig. 3. JdF: Endeavour Segment, 2,192–2,225 m, vent. *Remarks: Buccinum* sp. (*viridum* Dall 1890?) in Warén and Bouchet (2001: appendix 2) also indicates this species. *Buccinum viridum* (Dall 1890) is common on methane bottoms and whale carcasses off California and Oregon (Warén, unpubl.).
172. *Calliloncha nankaiensis* Okutani and Iwasaki 2003. Okutani and Iwasaki 2003: 3, figs. 3A–C, 4A–B; Sasaki et al. 2005: 120, fig. 17A. WP: Nanaki Trough: off Cape Muroto, Japan, 3,540–3,571 m, seep.

**Costaria?* sp. Warén and Bouchet 1993: 77, fig. 58A–B; Sasaki et al. 2005: 120. WP: Nankai Trough: Tenryu Canyon, Japan, 3,800–4,020 m, seep.

173. *Eosipho auzendei* Warén and Bouchet 2001. Warén and Bouchet 2001: 191, figs. 38j–k, 39a, 49a, appendix 2; Bouchet in Desbruyères et al. 2006: 124. EPR: 17–23°S (type locality: 17°S), Pacific-Antarctic Ridge: 31–38°S, vent.
174. *Eosipho canetae* (Clench and Aguayo 1944). Warén and Bouchet 1993: 76, fig. 59D (as "*Buccinum*"); 2001: 191, figs. 38i, 39d, 49b, appendix 2. Louisiana Slope, 420–850 m, seep.
175. *Eosipho desbruyeresi* Okutani and Ohta 1993. Okutani and Ohta 1993: 217, figs. 1–5; Warén and Bouchet 2001: 191, appendix 2; Bouchet in Desbruyères et al. 2006: 124 (figured). WP: Lau Basins (type locality) and North Fiji, 1,750–2,000 m (Okutani and Ohta 1993), also Mariana Basin (Bouchet in Desbruyères et al. 2006), vent.

176. *Eosipho desbruyeresi nipponensis* Okutani and Fujiwara 2000. Okutani and Fujiwara 2000: 125, figs. 6–10; Sasaki et al. 2005: 121, fig. 17B; Bouchet in Desbruyères et al. 2006: 124. WP: Okinawa Trough (Norht Knoll of Iheya Ridge: type locality), Myojin Knoll and Sumisu Caldera, Japan, 676–1,362 m, vent.
177. *Neptunea acutispiralis* Okutani 1968. Okutani et al. 1993: 137, figs. 51–54; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 119. WP: Sagami Bay, 1,100–1,380 m, seep and normal muddy sea bottom.
178. *Neptunea insularis* (Dall 1895). Warén and Bouchet 2001: appendix 2. WP: Okinawa Trough, vent.
179. *Neptunea pribiloffensis* (Dall 1919). Warén and Bouchet 1993: 78. Off northern California, seep.
180. *Neptunea amianta* (Dall 1890). Warén and Bouchet 2001: 224, Oregon Margin, seep.

Neptunea sp. cf. *insularis* (Dall 1895). Okutani et al. 1993: 138, fig. 55 [as *N. incularis* var.]; Sasaki et al. 2005: 119. WP: Okinawa Trough, 690–710 m, vent.

[181.] *Kryptos explorator* Fraussen and Sellanes 2007. Fraussen and Sellanes 2007: 102, figs. 5–6, 16–25; Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 708–850 m, seep and regular deep-sea bottom.

Family Cancellariidae

182. *Admete tenuissima* Okutani and Fujikura 2002. Okutani and Fujikura 2002: 218, fig. 6A–B; Sasaki et al. 2005: 123. Japan Trench, 5,343–5,379 m, seep.
183. *Cancellaria rosewateri* Petit 1983. Warén and Bouchet 1993: 78; Warén and Bouchet 2001: appendix 2. Louisiana Slope, off Mississippi and off Alabama, 360–580 m, seep.
184. *Iphinopsis boucheti* Okutani et al. 2004. Okutani et al. 2004: 9, fig. 5C–D. Kairei Field, Rodriguez Triple Junction, 2,422–2,442 m, vent.

Family Muricidae

Coronium cf. *wilhelmense*. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

[185.] *Trophon condei* Houart 2003: Houart 2003: 102, figs. 1–2, 23, 31; Houart and Sellanes 2006: 55, figs. 1–4, 33; Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 728–1,350 m, seep and regular deep-sea bottom.
[186.] *Trophon ceciliae* Houart 2003: Houart 2003: 104, text fig. A, figs. 3–5, 24, 31; Houart and Sellanes 2006: 56, figs. 5–10; Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 728–1,350 m, seep and regular deep-sea bottom.
[187.] *Pagodula concepcionensis* Houart and Sellanes 2006: Houart and Sellanes 2006: 59, figs. 15–19, 34–35; Sellanes et al. 2008: 2008: table 2. Concepción Methane Seep Area, Chile, 726–930 m, seep and regular deep-sea bottom.

**Pagodula cf. concepcionensis* Houart and Sellanes 2006: Houart and Sellanes 2006: 61, figs. 20–21. Off Chile, Concepción seep area, 930 m, possibly seep-associated.
**Trophon* sp. 1. Warén and Bouchet 2001: appendix 2. Barbados Prism, seep.
**Trophon* sp. 2. Warén and Bouchet 2001: appendix 2. Barbados Prism, seep.

Family Conidae ("Turridae")

[*] *Aforia* cf. *goniodes* (Watson 1881). Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom. Certainly not seep related.

188. *Bathybela papyracea* Warén and Bouchet 2001. Warén and Bouchet 2001: 200, fig. 42f, appendix 2. Jalisco Block, 3,662 m, seep.

**Bathybela* spp. Warén and Bouchet 1993: 79. Off Barbados, 4,935 m; WP: Nankai Trough, Tenryu Canyon, 3,835 m, seep.

[189.] *Benthomangelia macra* (Watson 1881). Olu-Le Roy et al. 2004: table 2. Anaximander area, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep and regular deep-sea bottom.

**Benthomangelia* sp. Okutani and Iwasaki 2003: 7, fig. 2C; Sasaki et al. 2005: 12. WP: Nankai Trough: off Cape Muroto, Japan, 3,581 m, seep.

[190.] *Drilliola loprestiana* (Calcara 1841). Olu-Le Roy et al. 2004: table 2. Anaximander area, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep and regular deep-sea bottom (very comman on normal bottom).
191. *Gymnobela extensa* (Dall 1881). Warén and Bouchet 1993: 78, fig. 59A–C; Warén and Bouchet 2001: 199, appendix 2. Yucatan Channel to off Louisiana, 512–1,463 m, seep.

**Gymnobela* sp. A. Warén and Bouchet 2001: 199, fig. 42d, appendix 2. EPR: 13°N, vent.
**Gymnobela?* sp. B. Warén and Bouchet 2001: 199, fig. 42c, appendix 2. MAR: 23°N, vent.

192. *Oenopota ogasawarana* Okutani et al. 1993. Okutani et al. 1993: 138, figs. 47–50; Warén and Bouchet 2001: appendix 2; Sasaki et al. 2005: 121, fig. 17C. WP: Kaikata Seamount, off Ogasawara Islands, Japan, 440–450 m, vent.
193. *Oenopota sagamiana* Okutani and Fujikura 1992. Okutani and Fujikura 1992: 2, figs. 2–3, pl. 1; Warén and Bouchet 2001: appendix 2 [as *Gymnobela*]; Sasaki et al. 2005: 121, fig. 17D. WP: Sagami Bay: off Hatsushima, 1,170 m, seep.

**Oenopota* sp. Okutani and Fujiwara 2000: 126; Sasaki et al. 2005: 121. WP: Okinawa Trough: North Knoll of Iheya Ridge, 1,049 m, vent.
[*] *Phymorhynchus* aff. *alberti* (Dautzenberg and Fischer 1906). Warén and Bouchet 2001: 199, fig. 42e, appendix 2. Northeastern Atlantic, 16–47°N, 1,850–4,800 m, seep.

194. *Phymorhynchus buccinoides* Okutani et al. 1992. Okutani et al. 1993: 140, figs. 44–46; Warén and Bouchet 2001: 199, fig. 42e, appendix 2. WP: Sagami Bay: off Hatsushima, Japan, 1,160 m, seep.
195. *Phymorhynchus carinatus* Warén and Bouchet 2001. Warén and Bouchet 2001: 195, figs. 42g–h, 43g–I, appendix 2; Desbruyères et al. 2006: 138 (figured). MAR: 23–15°N (type locality: Logatchev site at 14°45′N, 3,040 m), vent.
196. *Phymorhunchus cingulatus* Warén and Bouchet 2009. Warén and Bouchet 2009: 2344, figs. 9F, 10A. Regab site, West Africa, 3,150 m, seep.
197. *Phymorhunchus coseli* Warén and Bouchet 2009. Warén and Bouchet 2009: 2344, figs. 9G–K, 10B–D, 12L. Regab site, West Africa, 3,150 m, seep.
198. *Phymorhynchus hyfifluxi* Beck 1996. Beck 1996: text-fig. 1d, pl. 1, figs. 1–8; Warén and Bouchet 2001: appendix 2; Okutani in Desbruyères et al. 2006: 138. WP: North Fiji Basin, 2,003 m, vent.
199. *Phymorhynchus major* Warén and Bouchet 2001. Warén and Bouchet 2001: 197, figs. 41h, 43a, appendix 2; Okutani in Desbruyères et al. 2006: 138. EPR: 13–9°N (type locality: 9°50′N), ca. 2,500–2,600 m, vent.
200. *Phymorhynchus moskalevi* Sysoev and Kantor 1995. Sysoev and Kantor 1995: 22, figs. 1H–I, 4, 5D–F; Warén and Bouchet 2001: 195, figs. 41a–d, 43e–f, appendix 2; Okutani in Desbruyères et al. 2006: 138 (figured). MAR: 26–23°N, 3,400–3,700 m, vent.
201. *Phymorhynchus ovatus* Warén and Bouchet 2001. Warén and Bouchet 2001: 194, figs. 41e–g, 42a–b, 43b–d, appendix 2; Okutani in Desbruyères et al. 2006: 138 (figured). MAR: 37–15°N (type locality: Logatchev site at 14°45′N), 1,600–3,500 m, vent.
202. *Phymorhynchus starmeri* Okutani and Ohta 1993. Okutani and Ohta 1993: 220, figs. 6–7; Warén and Bouchet 2001: appendix 2; Okutani in Desbruyères et al. 2006: 138. WP: North Fiji Basin, 2,750 m (type locality), and Manus Back-Arc Basin, vent.
203. *Phymorhynchus turris* Okutani and Iwasaki 2003. Okutani and Iwasaki 2003: 6, fig. 3D; Sasaki et al. 2005: 123, fig. 17F. WP: Nankai Trough: off Cape Muroto, Japan, 3,540–3,581 m, seep.
204. *Phymorhynchus wareni* Sysoev and Kantor 1995. Sysoev and Kantor 1995: 19, figs. 1A–D, G, 2, 3, 5A–C; Warén and Bouchet 2001: appendix 2; Okutani in Desbruyères et al. 2006: 138. WP: Edison Seamount, 1,483 m, vent.

**Phymorhynchus* sp. Warén and Bouchet 1989: 95, figs. 115–116. [= *P. major* Warén and Bouchet 2001]

**Phymorhynchus* sp. 1 Warén and Bouchet 1993: 79, fig. 59E. MAR: Snake Pit, 3,478 m, vent.

**Phymorhynchus* sp. 2 Warén and Bouchet 1993: 79. [= *P. carinatus* Warén and Bouchet 2001]

**Phymorhynchus* sp. 3 Warén and Bouchet 1993: 79. JdF: Endeavour Ridge, vent.

[205.] *Taranis moerchi* (Malm 1861). Olu-Le Roy et al. 2004: table 2. Olimpi and Anaximander areas, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep and regular deep-sea bottom (mainly non-seep areas)

*Turrid sp. Warén and Bouchet 1993: 79. EPR: 13°N, vent.
[*] Turridae, gen. sp. 1. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.
[*] Turridae, gen. sp. 2. Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

Family Volutidae

[206.] *Tractolira sparta* Dall 1896. Poppe and Goto 1992: 121, pl. 39, figs. 7–8 (holotype); Warén and Bouchet 2001: 192, fig. 38a, appendix 2. Off Peru, 3,100–5,300 m, off Acapulco, Mexico to Gulf of Panama, 3,043–4,062 m, seep.
[207.] *Miomelon philippiana* (Dall 1890). Sellanes et al. 2008: table 2. Concepción Methane Seep Area, Chile, 740–870 m, seep and regular deep-sea bottom.

Clade Heterobranchia
Family Hyalogyrinidae

208. *Hyalogyra vitrinelloides* Warén and Bouchet 1993. Warén and Bouchet 1993: 52, figs. 39A–C, 40A, D, F, 41A, 42C; Warén and Bouchet 2001: appendix 2. WP: Lau Basin, 1,900 m, vent
209. *Hyalogyrina globularis* Warén and Bouchet 2001. Warén and Bouchet 2001: 202, figs. 37f, 44a, 46a, 47e–f, appendix 2; Warén et al. in Desbruyères et al. 2006: 135 (figured). JdF, Endeavour Segment, 2,200–2,250 m, vent.
210. *Hyalogyrina grasslei* Warén and Bouchet 1993. Warén and Bouchet 1993: 49, figs. 39D–G, 40B–C, E, 41B–D, 42E; Warén and Bouchet 2001: appendix 2; Warén et al. in Desbruyères et al. 2006: 135. Guaymas Basin, ca. 2,000 m, seep
211. *Hyalogyrina rissoella* Warén and Bouchet 2009. Warén and Bouchet 2009: 2345, figs. 8E, 12A–K. Regab site (type locality) and Guiness site, West Africa, 600–3,150 m, seep.
212. *Hyalogyrina umbellifera* Warén and Bouchet 2001. Warén and Bouchet 2001: 200, figs. 37e, g, 44h–j, 45a–d, 47d, 48a–b, 49i, appendix 2; Kiel 2004: 179, figs. 35–36. Aleutian Trench, 4,800 m, seep.

**Hyalogyrina?* sp.: Warén and Bouchet 2001: appendix 2. New Zealand, vent.

Family Orbitestellidae

213. *Lurifax japonica* Sasaki and Okutani 2005: Sasaki and Okutani 2005: 121, fig. 1A–D. WP: Sumisu Caldera, Japan, 676 m, vent.
214. *Lurifax vitreus* Warén and Bouchet 2001: Warén and Bouchet 2001: 207, figs. 37c–d, 44e–g, 46c–d, 47a–b, appendix 2; Warén et al. in Desbruyères et al. 2006: 136 (figured). Mid-Atlantic Ridge: Menez Gwen (type locality)

and Lucky Strike, 38–36°N, ca. 850–1,800 m, vent. Olu-Le Roy et al. 2004: table 2. Anaximander area, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep. *Remarks:* Smriglio and Mariottini (2002) reported a single empty shell from Western Mediterranean Sea.

**Lurifax* sp.: Warén and Bouchet 2001: appendix 2. New Zealand, seep.

Family Pyramidellidae

215. *Eulimella lomana* (Dall 1908). Warén and Bouchet 1993: 55, fig. 59F–G. Southern California and Gulf of California, 1,168–2,008 m, seep.

**Eulimella* sp. Okutani and Fujiwara 2000: 126, fig. 11; Sasaki et al. 2005: 124. WP: Okinawa Trough, North Knoll of Iheya Ridge, 1,049 m, vent.
[*] *Odostomia* sp. Olu-Le Roy et al. 2004: table 2. Anaximander area, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep. No evidence for seep relations.

Family Xylodisculidae

216. *Xylodiscula analoga* Warén and Bouchet 2001. Warén and Bouchet 2001: 208, figs. 44b–d, 47c, 49h, appendix 2; Kiel 2004: 178, fig. 34; Warén et al. in Desbruyères et al. 2006: 137 (figured). MAR: Lucky Strike (type locality) and Menez Gwen, 37–36°N, 850–1,728 m, vent.
217. *Xylodiscula major* Warén and Bouchet 1993. Warén and Bouchet 1993: 53, figs. 42A–B, 43A–E; Warén and Bouchet 2001: appendix 2. WP: North Fiji Basin, 2,000 m, vent.

**Xylodiscula* sp. Warén and Bouchet 2001: appendix 2. New Zealand, seep.
**Xylodiscula* sp. Olu-Le Roy et al. 2004: table 2. Anaximander area, Eastern Mediterranean Sea, ca. 1,700–2,000 m, seep and regular deep-sea bottom?

Family Dendronotidae

218. *Dendronotus comteti* Valdés and Bouchet 1998. Valdés and Bouchet 1998: 320, figs. 1–3; Warén and Bouchet 2001: appendix 2; Bouchet and Segonzac in Desbruyères et al. 2006: 140 (figured). MAR: Lucky Strike, 37°N, 1,685 m, vent.

References

Aktipis SW, Giribet G, Lindberg DR et al (2008) Gastropoda: An overview and analysis. In: Ponder WF, Lindberg DR (eds) Phylogeny and evolution of the mollusca. University of California Press, Berkeley, CA

Bates AE (2007a) Feeding strategy, morphological specialisation and presence of bacterial episymbionts in lepetodrilid gastropods from hydrothermal vents. Mar Ecol Prog Ser 347:87–99

Bates AE (2007b) Persistence, morphology, and nutritional state of a gastropod hosted bacterial symbiosis in different levels of hydrothermal vent flux. Mar Biol 152:557–568

Batten RL (1984) Shell structure of the Galapagos rift limpet *Neomphalus fretterae* McLean, 1981, with notes on muscle scars and insertions. Am Mus Novitates 2276:1–13

Beck LA (1991) *Olgaconcha tufari* n. gen. et n. sp. – an new mesogastropod (Gastropoda: Prosobranchia) from hydrothermal vents in the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea). Ann Naturhist Mus Wien B92:277–286

Beck LA (1992a) *Symmetromphalus hageni* sp. n., a new neomphalid gastropod (Prosobranchia: Neomphalidae) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea). Ann Naturhist Mus Wien B93:243–257

Beck LA (1992b) Two new neritacean limpets (Gastropoda: Prosobranchia: Neritacea: Phenacolepadidae) from active hydrothermal vents at Hydrothermal Field 1 “Wienerwald” in the Manus Back Arc Basin (Bismarck Sea, Papua New Guinea). Ann Naturhist Mus Wien B93:259–275

Beck LA (1993) Morphological and anatomical studies on a new lepetodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Ginea). Ann Naturhist Mus Wien B94(95):167–179

Beck LA (1996) Morphology and anatomy of new species of neolepetopsid, acmaeid, fissurellid and pyropeltid limpets from Edison Seamount off Lihir Islands (West Pacific). Arch Mollusk 125:87–103

Beck LA (2002) *Hirtopelta tufari* sp. n., a new gastropod species from hot vents at the East Pacific Rise (21degree S) harbouring endocytosymbiotic bacteria in its gill: (Gastropoda: Rhipidoglossa: Peltospiridae). Arch Mollusk 130:249–257

Bergquist DC, Eckner JT, Urcuyo IA et al (2007) Using stable isotopes and quantitative community characteristics to determine a local hydrothermal vent food web. Mar Ecol Prog Ser 330:49–65

Bouchet P, Warén A (1991) *Ifremeria nautilei*, a new gastropod from hydrothermal vents, probably associated with symbiotic bacteria. C R Acad Sci III 312:495–501

Bouchet P, Warén A (1993) Revision of the Northeast Atlantic bathyal and abyssal Mesogastropoda. Boll Malac Suppl 3:580–840

Bouchet P, Fryda J, Hausdorf B et al (2005) Working classification of the Gastropoda. In: Bouchet P, Rocroi JP (eds) Classification and nomenclator of gastropod families. Malacologia 47:240–283

Braby CE, Rouse GW, Johnson SB et al (2007) Temporal variation among *Osedax* boneworms and related megafauna on whale-falls in Monterey Bay, California. Deep Sea Res Pt I 54:1773–1791

Campbell KA, Peterson DE, Alfaro AC (2008) Two new species of *Retiskenea*? (Gastropoda: Neomphalidae) from lower Cretaceous hydrocarbon-seep carbonates of northern California. J Paleontol 82:140–153

Clarke AH (1989) New mollusks from under-sea oil seep sites off Louisiana. Malac Data Net 2:122–134

Colgan DJ, Ponder WF, Beacham E, Macaranas JM (2007) Molecular phylogenetics of Caenogastropoda (Gastropoda: Mollusca). Mol. Phyloget Evol 42:717–737

Craddock C, Lutz RA, Vrijenhoek RC (1997) Patterns of dispersal and larval development of archaeogastropod limpets at hydrothermal vents in the eastern Pacific. J Exp Mar Biol Ecol 210:37–51

Cruz R, Farina M (2005) Mineralization of major lateral teeth in the radula of a deep-sea hydrothermal vent limpet (Gastropoda: Neolepetopsidae). Mar Biol 147:163–168

Dattagupta S, Martin J, Liao SM et al (2007) Deep-sea hydrocarbon seep gastropod *Bathynerita naticoidea* responds to cues from the habitat-providing mussel *Bathymodiolus childressi*. Mar Ecol 28:193–198

Declerck C (1995) The evolution of suspension feeding in gastropods. Biol Rev 70:549–569

Denis F, Jollivet D, Moraga D (1993) Genetic separation of two allopatric populations of hydrothermal snails *Alviniconcha* spp. (Gastropoda) from two South Western Pacific Back-arc Basins. Biochem Syst Ecol 21:431–440

Desbruyères D, Segonzac M, Bright M (eds) (2006) Handbook of deep-sea hydrothermal vent fauna. Denisia 18:1–544

Distel DL, Baco AR, Chuang E et al (2000) Do mussels take wooden steps to deep-sea vents? Nature 403:725–726

Fraussen K, Sellanes J (2007) Three new buccinid species (Gastropoda: Neogastropoda) from Chilean deep-water, including one from a methane seep. Veliger 50(2):97–106

Fretter V (1988) New archaeogastropod limpets from hydrothermal vents, superfamily Lepetodrilacea. II. Anatomy. Philos T Roy Soc B319:33–82

Fretter V (1989) The anatomy of some new archaeogastropod limpets (Superfamily Peltospiracea) from hydrothermal vents. J Zool 218:123–169

Fretter V (1990) The anatomy of some new archaeogastropod limpets (Order Patellogastropoda, Suborder Lepetopsina) from hydrothermal vents. J Zool 222:529–555

Fretter V, Graham A, McLean JH (1981) The anatomy of the Galapagos Rift limpet, *Neomphalus fretterae*. Malacologia 21:337–361

Fuchigami T, Sasaki T (2005) The shell structure of the Recent Patellogastropoda (Mollusca: Gastropoda). Paleontol Res 9:143–168

Fujikura K, Sasaki T, Yamanaka T et al (2009) Turrid whelk, *Phymorhynchus buccinoides* feeds on *Bathymodiolus* mussels at a seep site in Sagami Bay, Japan. Plankton Benthos Res 4:23–30

Geiger DL, Thacker CE (2006) Molecular phylogeny of basal gastropods (Vetigastropoda) show stochastic colonization of chemosynthetic habitats at least from the mid Triassic. Cah Biol Mar 47:343–346

Geiger DL, Nützel A, Sasaki T (2008) Vetigastropoda. In: Lindberg DR, Ponder WF (eds) Phylogeny and evolution of the Mollusca. University of California Press, Berkeley, CA

Gofas S (2005) Geographical differentiation in *Clelandella* (Gastropoda: Trochidae) in the Northeastern Atlantic. J Moll Stud 71:133–144

Goffredi SK, Warén A, Orphan VJ et al (2004) Novel forms of structural integration between microbes and a hydrothermal vent gastropod from the Indian Ocean. Appl Environ Microb 70:3082–3090

Gustafson RG, Lutz RA (1994) Molluscan life history traits at deep-sea hydrothermal vents and cold methane/sulfide seeps. In: Young CM, Eckelbarger KJ (eds) Reproduction, larval biology, and recruitment of the deep-sea benthos. Columbia University Press, New York

Harasewych MG, Kantor YI (2002) *Buccinum thermophilum* (Gastropoda: Neogastropoda: Buccinidae), a new species from the Endeavour vent field of the Juan de Fuca Ridge. J Moll Stud 68:39–44

Harasewych MG, McArthur AG (2000) A molecular phylogeny of the Patellogastropoda (Mollusca: Gastropoda). Mar Biol 137:183–194

Hasegawa K (1997) Sunken wood-associated gastropods collected from Suruga Bay, Pacific side of the central Honshu, Japan, with descriptions of 12 new species. Nat Sci Mus Monogr 12:59–123

Haszprunar G (1989a) New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 2. Anatomy and relationships. Contrib Sci Nat Hist Mus Los Angeles Co 408:1–17

Haszprunar G (1989b) The anatomy of *Melanodrymia aurantiaca* Hickman, a coiled archaeogastropod from the East Pacific hydrothermal vents (Mollusca, Gastropoda). Acta Zool 70:175–186

Healy JM (1990) Taxonomic affinities of the deep-sea genus *Provanna* (Caenogastropoda): new evidence from sperm ultrastructure. J Moll Stud 56:119–122

Heß M, Beck F, Gensler H et al (2008) Microanatomy, shell structure and molecular phylogeny of *Leptogyra*, *Xyleptogyra* and *Leptogyropsis* (Gastropoda: Neomphalida: Melanodrymiidae) from sunken wood. J Moll Stud 74:381–401

Hickman CS (1984) A new archaeogastropod (Rhipidoglossa, Trochacea) from hydrothermal vents on the East Pacific Rise. Zool Scr 13:19–25

Hickman CS, McLean JH (1990) Systematic revision and suprageneric classification of trochacean gastropods. Nat Hist Mus Los Angeles County Sci Ser 35:1–169

Hodgson AN, Healy JM, Tunnicliffe V (1997) Spermatogenesis and sperm structure of the hydrothermal vent prosobranch gastropod *Lepetodrilus fucensis* (Lepetodrilidae, Mollusca). Invertebr Reprod Dev 31:87–97

Hodgson AN, Eckelbarger KJ, Young CM (1998) Sperm morphology and spermiogenesis in the methane-seep mollusc *Bathynerita naticoidea* (Gastropoda: Neritacea) from the Louisiana slope. Invertebr Biol 117:199–207

Hodgson AN, Eckelbarger KJ, Young CM (2009) Sperm ultrasptructure and spermatogenesis in the hydrothermal vent gastropod *Rhynchopelta concentrica* (Peltospiridae). J Moll Stud 75:159–165

Houart R (2003) Description of three new species of *Trophon* s. 1. Montfort, 1810 (Gastropoda: Muricidae) from Chile. Novapex 4:101–110

Houart R, Sellanes J (2006) New data on recently described Chilean trophonines (Gastropoda: Muricidae), description of a new species and notes of their occurrence at cold seep site. Zootaxa 1222:53–68

Houbrick RS (1979) Classification and systematic relationships of the Abyssochrysidae, a relict family of bathyal snails (Prosobranchia: Gastropoda. Smithsonian Contrib Zool 290:1–21

Hunt S (1992) Structure and composition of the shell of the archaeogastropod limpet *Lepetodrillus elevatus elevatus* (McLean, 1988). Malacologia 34:129–141

Israelsson O (1998) The anatomy of *Pachydermia laevis* (Archaeogastropoda: 'Peltospiridae'). J Moll Stud 64:93–109

Jablonski D, Lutz RA (1983) Larval ecology of marine benthic invertebrates: paleobiological implications. Biol Rev 58:21–89

Jenkins RG, Kaim A, Hikida Y (2007a) Antiquity of the substrate choice among acmaeid limpets from Late Cretaceous chemosynthesis-based communities. Acta Palaeontol Pol 52:369–373

Jenkins RG, Kaim A, Hikida Y et al (2007b) Methane-flux-dependent lateral faunal changes in a Late Cretaceous chemosymbiotic assemblage from the Nakagawa area of Hokkaido, Japan. Geobiology 5:127–139

Johnson SB, Young CR, Jones WJ et al (2006) Migration, isolation, and speciation of hydrothermal vent limpets (Gastropoda; Lepetodrilidae) across the Blanco Transform Fault. Biol Bull 210:140–157

Johnson SB, Warén A, Lee RW, Kaim A, Davis A, Kano Y, Strong EE, Vrijenhoek RC. in press. Living fossils: *Rubyspira*, a new genus of bone-eating snails from the deep-sea. *Biol. Bull.*

Johnson SB, Warén A, Vrijenhoek RC (2008) DNA barcoding of *Lepetodrilus* limpets reveals cryptic species. J Shellfish Res 27:43–51

Kaim A (2004) The evolution of conch ontogeny in Mesozoic open sea gastropods. Palaeontol Pol 62:6–183

Kaim A, Jenkins RG, Warén A (2008a) Provannid and provannid-like gastropods from the Late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda: Abyssochrysoidea). Zool J Linn Soc 154:421–436

Kaim A, Kobayashi Y, Echizenya H et al (2008b) Chemosynthesis-based associations on Cretaceous plesiosaurid carcasses. Acta Palaeontol Pol 53:97–104

Kano Y (2006) Usefulness of the opercular nucleus for inferring early development in neritimorph gastropods. J Morphol 267:1120–1136

Kano Y (2008) Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. Zool Scr 37:1–21

Kano Y, Haga T (2010) Marine ecosystems: Sulfide rich environments. In: Bouchet P, Le Guyader H, Pascal O (eds) The natural history of Santo. Patrimoines Naturels. 69 Muséum National d'Histoire Naturelle, Paris

Kano Y, Chiba S, Kase T (2002) Major adaptive radiation in neritopsine gastropods estimated from 28S rRNA sequences and fossil records. P Roy Soc Lond B269:2457–2465

Kano Y, Chikyu E, Warén A (2009) Morphological, ecological and molecular characterization of the enigmatic planispiral snail genus *Adeuomphalus* (Vetigastropoda: Seguenzioidea). J Moll Stud 75:397–418

Kelly NE, Metaxas A (2007) Influence of habitat on the reproductive biology of the deep-sea hydrothermal vent limpet *Lepetodrilus fucensis* (Vetigastropoda: Mollusca) from the Northeast Pacific. Mar Biol 151:649–662

Kelly NE, Metaxas A (2008) Population structure of two deep-sea hydrothermal vent gastropods from the Juan de Fuca Ridge, NE Pacific. Mar Biol 153:457–471

Kiel S (2004) Shell structures of selected gastropods from hydrothermal vents and seeps. Malacologia 46:169–183

Kiel S (2006) New records and species of molluscs from Tertiary cold-seep carbonates in Washington State, USA. J Paleontol 80:121–137

Kiel S, Goedert JL (2006) A wood-fall association from late Eocene deep-water sediments of Washington State, USA. Palaios 21:548–556

Kiel S, Goedert JL (2007) New mollusks associated with biogenic substrates in Cenozoic deep-water sediments of Washington State. Acta Palaeontol Pol 52:41–52

Kiel S, Little CTS (2006) Cold-seep mollusks are older than the general marine mollusk fauna. Science 313:1429–1431

Kiel S, Campbell KA, Elder WP et al (2008) Jurassic and Cretaceous gastropods from hydrocarbon seeps in forearc basin and accretionary prism settings, California. Acta Palaeontol Pol 53:679–703

Kojima S, Segawa R, Fujiwara Y et al (2000) Genetic differentiation of populations of a hydrothermal vent-endemic gastropod, *Ifremeria nautilei*, between the North Fiji Basin and the Manus Basin revealed by nucleotide sequences of mitochondrial DNA. Zool Sci 17:1167–1174

Kojima S, Segawa R, Fijiwara Y et al (2001) Phylogeny of hydrothermal-vent-endemic gastropods *Alviniconcha* spp. from the western Pacific revealed by mitochondrial DNA sequences. Biol Bull 200:298–304

Kojima S, Fujikura K, Okutani T et al (2004) Phylogenetic relationship of *Alviniconcha* gastropods from the Indian Ocean to those from the Pacific Ocean (Mollusca: Provannidae) revealed by nucleotide sequences of mitochondrial DNA. Venus 63:65–68

Kunze T, Heß M, Brückner M et al (2008) Skeneimorph gastropods in Neomphalina and Vetigastropoda – A preliminary report. Zoosymposia 1:119–131

Levesque C, Juniper SK, Limen H (2006) Spatial organization of food webs along habitat gradients at deep-sea hydrothermal vents on Axial Volcano, Northeast Pacific. Deep Sea Res Pt I 53:726–739

Levin LA, Bridges TS (1995) Pattern and diversity in reproduction and development. In: McEdward L (ed) Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL

Limén H, Levesque C, Juniper SK (2007) POM in macro-/meiofaunal food webs associated with three flow regimes at deep-sea hydrothermal vents on Axial Volcano, Juan de Fuca Ridge. Mar Biol 153:129–139

Lindberg DR (2008) Patellogastropoda, Neritimorpha, and Cocculinoidea. The low-diversity gastropod clades. In: Ponder WF, Lindberg DR (eds) Phylogeny and Evolution of the Mollusca. University of California Press, Berkeley, CA

Lindberg DR, Hedegaard C (1996) A deep water patellogastropod from Oligocene water-logged wood of Washington State, USA (Acmaeoidea: *Pectinodonta*). J Moll Stud 62:299–314

Little CRS, Cann JR (1999) Late Cretaceous hydrothermal vent communities from the Troodos ophiolite, Cyprus. Geology 27:1027–1030

Lus VJ (1981) New species of *Tacita* (Prosobranchia, Buccinidae) with wide distribution in the north-western part of the Pacific Ocean. Trudy Instit Okeanol P P Shirshov 115:140–154 (in Russian)

McArthur AG, Tunnicliffe V (1998) Relics and antiquity revisited in the modern vent fauna. In: Mills RA, Harrison K (eds), Modern Ocean floor processes and the geological record. Geol Soc Lond Spec Pub 148:271–291

Marshall BA (1986) Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. New Zeal J Zool 12:505–546

Marshall BA (1988) Skeneidae, Vitrinellidae, and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depth off New Zealand and New South Wales. J Nat Hist 22:949–1004

Marshall BA (1995) Callistomatidae (Gastropoda: Trochoidea) from New Caledonia, the Loyalty Islands, and the northern Lord Howe Rise. Mem Mus Nat Hist Natur 167:381–458

Martell KA, Tunnicliffe V, MacDonald IR (2002) Biological features of a buccinid whelk (Gastropoda, Neogastropoda) at the Endeavour ventfields of Juan de Fuca Ridge, Northeast Pacific. J Moll Stud 68:45–53

Martin JW, Haney TA (2005) Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2005. Zool J Linn Soc 145:445–552

Matabos M, Thiébaut 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. *Mar Biol* 153:545–563

McArthur AG, Harasewych MG (2003) Molecular systematics of the major lineages of the Gastropoda. In Lydeard EC, Lindberg DR, (eds) Molecular Systematics and Phylogeography of Mollusks. Smithsonian Institution Press, Washington, DC

McArthur AG, Koop BF (1999) Partial 28S rDNA sequences and the antiquity of the hydrothermal vent endemic gastropods. Mol Phyloget Evol 13:255–274

McEdward L (ed) (1995) Ecology of Marine invertebrate larvae. CRC Press, Boca Raton, FL

McLean JH (1981) The Galapagos Rift limpet *Neomphalus*: relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. Malacologia 21:291–336

McLean JH (1988a) New archaeogastropod limpets from hydrothermal vents, superfamily Lepetodrilacea. Part I: Systematic descriptions. Philos T Roy Soc Lond B319:1–32

McLean JH (1988b) Three new limpets of the family Pseudococculinidae from abyssal depths (Mollusca, Archaeogastropoda). Zool Scr 17:155–160

McLean JH (1989a) New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea. Zool Scr 18:49–66

McLean JH (1989b) New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 1. Systematic descriptions and comparisons based on shell and radular characters. Contrib Sci Nat Hist Mus Los Angeles County 407:1–29

McLean JH (1990a) A new genus and species of neomphalid limpet from the Mariana vents with a review of current understanding of relationships among Neomphalacea and Peltospiracea. Nautilus 104:77–86

McLean JH (1990b) Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. J Zool 222:485–528

McLean JH (1991) Four new pseudococculinid limpets collected by the deep-submersible Alvin in the Eastern Pacific. Veliger 34:38–47

McLean JH (1992a) A new species of *Pseudorimula* (Fissurellacea: Clypeosectidae) from hydrothermal vents of the Mid-Atlantic Ridge. Nautilus 106:115–118

McLean JH (1992b) Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. J Moll Stud 58:401–414

McLean JH (1993) New species and records of *Lepetodrilus* (Vetigastropoda: Lepetodrilidae) from hydrothermal vents. Veliger 36:27–35

McLean JH (2008) Three new species of the family Neolepetopsidae (Patellogastropoda) from hydrothermal vents and whale falls in the northeastern Pacific. J Shellfish Res 27:15–20

McLean JH, Geiger DL (1998) New genera and species having the *Fissurisepta* shell form, with a generic level phylogenetic analysis (Gastropoda: Fissurellidae). Contrib Sci Nat Hist Mus Los Angeles County 475:1–32

McLean JH, Harasewych MG (1995) Review of western Atlantic species of cocculinid and pseudococculinid limpets, with descriptions of new species (Gastropoda: Cocculiniformia). Contrib Sci Nat Hist Mus Los Angeles County 453:1–33

McLean JH, Haszprunar G (1987) Pyropeltidae, a new family of cocculiniform limpets from hydrothermal vents. Veliger 30:196–205

McLean JH, Quinn JF Jr (1987) *Cataegis*, a new genus of three new species from the continental slope (Trochidae: Cataeginae new subfamily). Nautilus 101:111–116

Mills SW, Beaulieu SE and Mullineaux LS (2007). Photographic identification guide to larvae at hydrothermal vents in the eastern Pacific. Published at: http://www.whoi.edu/science/B/vent-larvel-id

Mullineaux LS, Kim SL, Pooley A, Lutz RA (1996) Identification of archaeogastropod larvae from a hydrothermal vent community. Mar Biol 124:551–560

Nakano T, Ozawa T (2007) Worldwide phylogeography of limpets of the older Patellogastropoda: Molecular, morphological and palaeontological evidence. J Moll Stud 73:79–99

O'Sullivan JB, McConnaughey RR, Huber ME (1987) A blood sucking snail – the cooper nutmeg, *Cancellaria cooperi* Gabb, parasitizes the California electric ray, *Torpedo californica* Ayres. Biol Bull 172:362–366

Okutani T (1990) Two new species of *Provanna* (Gastropoda: Cerithiacea) from "snail pit" in the hydrothermal vent site at the Mariana Back-arc Basin. Venus 49:19–24

Okutani T (2001) Six new bathyal and shelf trochoidean species in Japan. Venus 60(3):121–127

Okutani T, Fujikura K (1990) A new turbinid gastropod collected from the warm seep site in the Minami-Ensei Knoll west of the Amami-Oshima Island, Japan. Venus 49:83–92

Okutani T, Fujikura K (1992) A new turrid gastropod associated with metachromatic seabed near the *Calyptogena* community in Sagami Bay. Venus 51:1–7

Okutani T, Fujikura K (2002) Abyssal gastropods and bivalves collected by Shinkai 6500 on slope of the Japan Trench. Venus 60:211–224

Okutani T, Fujikura K (2005) Distribution of a deep-sea whelk *Bayerius arnoldi* (Gastropoda: Buccinidae). Chiribotan 35:121–124 (in Japanse)

Okutani T, Fujiwara Y (2000) Gastropod fauna of a thermal vent site on the North Knoll of Iheya Ridge, Okinawa Trough. Venus 59:123–128

Okutani T, Iwasaki N (2003) Noteworthy abyssal mollusks (excluding vesicomyid bivalves) collected from the Nankai Trough off Shikoku by the ROV Kaiko of the Japan Marine Science and Technology Center. Venus 62:1–10

Okutani T, Ohta S (1988) A new gastropod mollusk associated with hydrothermal vents in the Mariana Back-arc Basin, Western Pacific. Venus 47:1–10

Okutani T, Ohta S (1993) New buccinid and turrid gastropods from North Fiji and Lau Basins. Venus 52:217–221

Okutani T, Saito H, Hashimoto J (1989) A new neritacean limpet from a hydrothermal vent site near Ogasawara Islands, Japan. Venus 48:223–230

Okutani T, Tsuchida E, Fujikura K (1992) Five bathyal gastropods living within or near the *Calyptogena* community of the Hatsushima Islet, Sagami Bay. Venus 51:137–148

Okutani T, Fujikura K, Sasaki T (1993) New taxa and new distribution records of deepsea gastropods collected from or near the chemosynthetic communities in the Japanese waters. Bull Nat Sci Mus Ser A (Zool) 19:123–143

Okutani T, Sasaki T, Tsuchida S (2000) Two additional new species to gastropod fauna of chemosynthetic site on North Knoll of Iheya Ridge, Okinawa Trough. Venus 59:267–275

Okutani T, Hashimoto J, Sasaki T (2004) New gastropod taxa from hydrothermal vent (Kairei Field) in the central Indian Ocean. Venus 63:1–11

Olu-Le Roy K, Sibuet M, Fiala-Médioni A et al (2004) Cold seep communities in the deep eastern Mediterranean Sea: composition, symbiosis and spatial distribution on mud volcanoes. Deep Sea Res Pt I 51:1915–1936

Plouviez S, Shank TM, Faure B et al (2009) Comparative phylogeography among hydrothermal vent species along the East Pacific Rise reveals vicariant processes and population expansion in the South. Mol Ecol 18:3903–3917

Ponder WF, Lindberg DR (1997) Towards a phylogeny of gastropod mollusks: a preliminary analysis using morphological characters. Zool J Linn Soc 19:83–265

Pradillon F, Shillito B, Young CM et al (2001) Developmental arrest in vent worm embryos. Nature 413:698–699

Puillandre N, Samadi S, Boisselier MC et al (2008) Starting to unravel the toxoglossan knot: Molecular phylogeny of the "turrids" (Neogastropoda: Conoidea). Mol Phylogenet Evol 47:1122–1134

Robertson R (1989) Spermatophores of aquatic non-stylommatophoran gastropods: a review with new data on *Heliacus* (Architectonicidae). Malacologia 30:341–364

Robertson R (2007) Taxonomic occurrences of gastropod spermatozeugmata and non-stylommatophoran spermatophores updated. Am Malacol Bull 23:11–16

Salvini-Plawen Lv, Steiner G (1996) Synapomorphies and plesiomorphies in higher classification of Mollusca. In: Taylor JD (ed) Origin and evolutionary radiation of the Mollusca. Oxford University Press, Oxford

Sasaki T (1998) Comparative anatomy and phylogeny of the Recent Archaeogastropoda (Mollusca: Gastropoda). Univ Mus Univ Tokyo Bull 38:1–223

Sasaki T (2008) Micromolluscs in Japan: taxonomic composition, habitats, and future topics, In: Geiger DL, Ruthensteiner B (eds) Micromolluscs: methodological challenges – exciting results. Zoosymposia 1:147–232

Sasaki T, Ishikawa H (2002) The first occurrence of a neritopsine gastropod from phreatic community. J Moll Stud 68:286–288

Sasaki T, Okutani T (2005) A new species of *Lurifax* (Gastropoda: Heterobranchia: Orbitestellidae) from Sumisu Caldera, southern Japan. Venus 63:121–124

Sasaki T, Okutani T, Fujikura K (2003) New taxa and new records of patelliform gastropods associated with chemoautosynthesis-based communities in Japanese waters (Mollusca: Gastropoda). Veliger 46:189–210

Sasaki T, Okutani T, Fujikura K (2005) Molluscs from hydrothermal vents and cold seeps in Japan: A review of taxa recorded in twenty recent years (1984–2004). Venus 64:87–133

Sasaki T, Okutani T, Fujikura K (2006a) Anatomy of *Bathyacmaea secunda* Okutani, Fujikura and Sasaki, 1993 (Patellogastropoda: Acmaeidae). J Moll Stud 72:295–309

Sasaki T, Okutani T, Fujikura K (2006b) Anatomy of *Shinkailepas myojinensis* Sasaki, Okutani and Fujikura, 2003 (Gastropoda: Neritopsina). Malacologia 48:1–26

Sasaki T, Fujikura K, Okutani T (2007) Molluscs collected in the cruise NT06-04 of R/V *Natsushima* from methane-seeps off Hatsushima Island. Sagami Bay. Chiribotan 37:197–207 (in Japanese)

Sasaki T, Okutani T, Fujikura K (2008) A new species of *Pyropelta* (Lepetelloidea: Pyropeltidae) from hydrothermal vents off Yaeyama Islands, Okinawa, Japan. J Moll Stud 74:309–316

Sellanes J, Quiroga E, Neira C (2008) Megafauna community structure and trophic relationships at the recently discovered Concepción Methane Seep Area, Chile, 36°S. ICES J Mar Sci 65:1102–1111

Shuto T (1974) Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. Lethaia 7:239–256

Smith CR, Baco AR (2003) Ecology of whale falls at the deep-sea floor. Oceanogr Mar Biol Ann Rev 41:311–354

Smith CR, Kukert H, Wheatcroft RA et al (1989) Vent fauna on whale remains. Nature 34:127–128

Smriglio C, Mariottini P (2002) *Lurifax vitreus* Warén and Bouchet, 2001 (Gastropoda, Orbitestellidae), first report from Western Mediterranean Sea. Boll Malacol 38:45–47

Stein JL, Cary SC, Hessler RR et al (1988) Chemoautotrophic symbiosis in a hydrothermal vent gastropod. Biol Bull 174:373–378

Suzuki Y, Sasaki T, Suzuki M et al (2005a) Novel chemoautotrophic endosymbiosis between a member of the e-Proteobacteria and the hydrothermal-vent gastropod *Alviniconcha* aff. *hessleri* (Gastropoda: Provannidae) from the Indian Ocean. Appl Environ Microb 71:5440–5450

Suzuki Y, Sasaki T, Suzuki M et al (2005b) Molecular phylogenetic and isotopic evidence of two lineages of chemoautotrophic endosymbionts distinct at the subdivision level harbored in one host-animal type: the genus *Alviniconcha* (Gastropoda: Provannidae*)*. FEMS Microb Lett 249:105–112

Suzuki Y, Kojima S, Sasaki T et al (2006a) Host-symbiont relationships in hydrothermal vent gastropods of the genus *Alviniconcha* from the Southwest Pacific. Appl Environ Microb 72:1388–1393

Suzuki Y, Kojima S, Watanabe H et al (2006b) Single host and symbiont lineages of hydrothermalvent gastropods *Ifremeria nautilei* (Provannidae): biogeography and evolution. Mar Ecol Prog Ser 325:167–175

Suzuki Y, Kopp RE, Kogure T et al (2006c) Sclerite formation in the hydrothermal-vent "scaly-foot" gastropod – possible control of iron sulfide biomineralization by the animal. Earth Planet Sci Lett 242:39–50

Sysoev AV, Kantor YI (1995) Two new species of *Phymorhynchus* (Gastropoda, Conoidea, Conidae) from the hydrothermal vents. Ruthenica 5:17–26

Tamburri MN, Barry JP (1999) Adaptations for scavenging by three diverse bathyal species, *Eptatretus stouti*, *Neptuea amianta* and *Orchomene obtusus*. Deep Sea Res Pt I 46:2079–2093

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45

Tunnicliffe V (1991) The biology of hydrothermal vents ecology and evolution. Oceanogr Mar Biol Ann Rev 29:319–407

Tunnicliffe V (1992) The nature and origin of the modern hydrothermal vent fauna. Palaios 7:338–350

Tyler PA, Young CM (2003) Dispersal at hydrothermal vents: a summary of recent progress. Hydrobiologia 503:9–19

Tyler PA, Pendlebury S, Mills SW et al (2008) Reproduction of gastropods from vents on the East Pacific Rise and the Mid-Atlantic Ridge. J Shellfish Res 27:107–118

Valdés À, Bouchet P (1998) Naked in toxic fluids: A nudibranch mollusc from hydrothermal vents. Deep sea Res Pt II 45:319–327

Van Dover CL (2000) The ecology of deep-sea hydrothermal vents. Princeton University Press, Princeton, NJ

Van Gaest AL, Young CM, Young JJ et al (2007) Physiological and behavioral responses of *Bathynerita naticoidea* (Gastropoda: Neritidae) and *Methanoaricia dendrobranchiata* (Polychaeta: Orbiniidae) to hypersaline conditions at a brine pool cold seep. Mar Ecol 28:199–207

Vermeij GJ (1993) A natural history of shells. Princeton University Press, Princeton, NJ

Vilvens C, Sellanes J (2006) Descriptions of *Otukaia crustulum* new species (Gastropoda: Trochoidea: Calliostomatidae) and *Margarites huloti* new species (Gastropoda: Trochoidea: Trochidae) from a methane seep area off Chile. Nautilus 120:15–20

Voight JR (2000a) A deep-sea octopus (*Graneledone* cf. *boreopacifica*) as a shell-crushing hydrothermal vent predator. J Zool 252:335–341

Voight JR (2000b) A review of predators and predation at deep-sea hydrothermal vents. Cah Biol Mar 41:155–166

Voight JR, Sigwart JD (2007) Scarred limpets at hydrothermal vents: evidence of predation by deep-sea whelks. Mar Biol 152:129–133

Warén A (1992) New and litte known "skeneimorph" gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. Boll Malacol 27:149–248

Warén A (1996) New and little known Mollusca from Iceland and Scandinavia, Part 3. Sarsia 81:197–245

Warén A, Bouchet P (1986) Four new species of *Provanna* Dall (Prosobranchia, Cerithiacea) from East Pacific hydrothermal sites. Zool Scr 15:157–164

Warén A, Bouchet P (1989) New gastropods from east Pacific hydrothermal vents. Zool Scr 18:67–102

Warén A, Bouchet P (1993) New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. Zool Scr 22:1–90

Warén A, Bouchet P (2001) Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. Veliger 44:116–231

Warén A, Bouchet P (2009) New gastropods from deep-sea hydrocarbon seeps off West Africa. Deep Sea Res Pt II 57:2326–2349

Warén A, Ponder WF (1991) New species, anatomy and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam. n. (Caenogastropoda). Zool Scr 20:27–56

Warén A, Bengtson S, Goffredi SK et al (2003) A hot-vent gastropod with iron sulfide dermal sclerites. Science 302:1007

Watanabe H, Fujikura K, Kinoshita G et al (2009) Egg capsule of *Phymorhynchus buccinoides* (Gastropoda: Turridae) in a deep-sea methane seep site in Sagami Bay, Japan. Venus 67:181–188

Williams ST, Ozawa T (2006) Molecular phylogeny suggests polyphyly of both the turban shells (family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). Mol Phylogenet Evol 39:33–51

Williams ST, Karube S, Ozawa T (2008) Molecular systematics of Vetigastropoda: Trochidae, turbinidae and trochoidea redefined. Zool Scr 37:483–506

Windoffer R, Giere O (1997) Symbiosis of the hydrothermal vent gastropod *Ifremeria nautilei* (Provannidae) with endobacteria – structural analyses and ecological considerations. Biol Bull 193:381–392