

Chapter 11

A Review of Gastropods at Ancient Hydrocarbon Seeps



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11.1 Introduction

Gastropods are one of the major animal classes inhabiting hydrothermal vents, hydrocarbon seeps, and organic falls. Although only a few seep/vent gastropods host bacterial symbionts, many taxa on specific and generic (or even higher) levels are seep/vent obligates or seep/vent favored taxa (i.e., occurring in much larger densities in chemosynthesis-based environments). Sasaki et al. (2010) presented an exhaustive review of Recent gastropods occurring in chemosynthesis-based communities. This seminal work along with the *Handbook on Deep-sea Hydrothermal Fauna* (Desbruyères et al. 2006) is used here as a source of basic information on living seep and vent gastropods. A brief summary of the fossil record of gastropods in chemosynthesis-based environments has been presented by Kiel (2010), but the knowledge on fossil seep/vent gastropods has expanded significantly since that publication rendering a new more comprehensive review necessary (Table 11.1). The gastropods from shallow-water seep sites from the Western Interior Seaway (Kiel et al. 2012; Landman et al. 2012; Meehan and Landman 2016) are intentionally left aside and not discussed here as none of the reported taxa so far is seep obligate or even seep favored but rather taxa typical of ambient environments (see also Landman et al. this volume). Some reports of seep faunas provide only very rough identifications pending more comprehensive taxonomic work; good examples of that are gastropods from Miocene seeps in New Zealand mentioned in Campbell et al. (2008a). Since there are no illustrations of these gastropods (except for Saether et al. 2010), it is difficult to treat them with any confidence, especially because taxonomic concepts of ancient seep gastropods have changed dramatically over the last decade.

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The systematics in this chapter are basically those from the nomenclator of Bouchet et al. (2017) with additions from newer literature, and the *World Register of Marine Taxa* (<http://www.marinespecies.org/>) kept up to date by their editors. Two new families (Desbruyeresidae and Rubyspiridae) and one subfamily (Alviniconchinae) of abyssochrysoidea are diagnosed as it is known already since over a decade that they cluster separately from the family Provannidae (where they are traditionally included) in all molecular studies (Johnson et al. 2010; Chen et al. 2016, 2019b; Linse et al. 2019; Souza et al. 2020). For general information on the biology of Recent gastropods, the reader is referred to the milestone works of Beesley et al. (1998) and Ponder et al. (2020). The organization of the sections follows the relative importance of particular groups in ancient hydrocarbon seeps rather than systematics.

11.2 Abyssochrysoidea

The superfamily Abyssochrysoidea Tomlin, 1927, is a group of deep-water gastropods, and all but species of the eponymous genus *Abyssochrysos* Tomlin, 1927, are intimately associated with chemosynthesizing communities. According to morphological features (Warén and Ponder 1991) and molecular data (Colgan et al. 2007), the abyssochrysoidea are caenogastropods most closely related to Littorinidae. The group possesses also a long and robust fossil record (Fig. 11.1), perhaps the richest among gastropods obligate to chemosynthesis-based environments. All molecular phylogenies produced so far (Johnson et al. 2010; Chen et al. 2016, 2019a, b; Linse et al. 2019; Souza et al. 2020) recover five main clades. The clades are as follows: Abyssochrysoidea (contains non-chemosynthetic *Abyssochrysos* and species of *Cordesia* in Souza et al. 2020), Provannidae (contains all species of *Provanna*), a clade named Alviniconchinae here (contains species of *Alviniconcha* and monospecific *Ifremeria*; Souza et al. (2020) recovered *Ifremeria* as a separate clade sister to Alviniconchinae and all other abyssochrysoidea but Provannidae), a clade named Desbruyeresidae here (contains all species of *Desbruyeresia*), and a clade named Rubyspiridae here (contains all species of *Rubyspira*). The divergence time of *Provanna* and *Desbruyeresia* ranges down to at least Cenomanian (approx. 97 Mya) (Kaim et al. 2008a, 2021) rendering their separate familial status feasible. All analyses recover Provannidae as the most basal living group of abyssochrysoidea. The extinct family Hokkaidoconchidae (Kaim et al. 2008a), most likely a stem group of Abyssochrysoidea, is rooted in Triassic zygopleuroidea (early Ptenoglossa). Abyssochrysoidea display a number of different shell morphologies ranging from very elongated ptenoglossan-like shells in *Abyssochrysos* and *Hokkaidoconcha*, tiny cerithioid shells of *Desbruyeresia* and *Provanna*, and robust, expanded shells of *Paskentana*, *Alviniconcha*, and *Ifremeria*. This variety of shell morphologies resulted in difficulties in identification of the group in the fossil record. Fortunately, if planktotrophic, all taxa display characteristic high-spired reticulate protoconchs, typically decollated in *Desbruyeresia*, *Cordesia*, and *Provanna* (if planktotrophic). Several species of *Provanna* and *Abyssochrysos*, in particular modern ones, possess

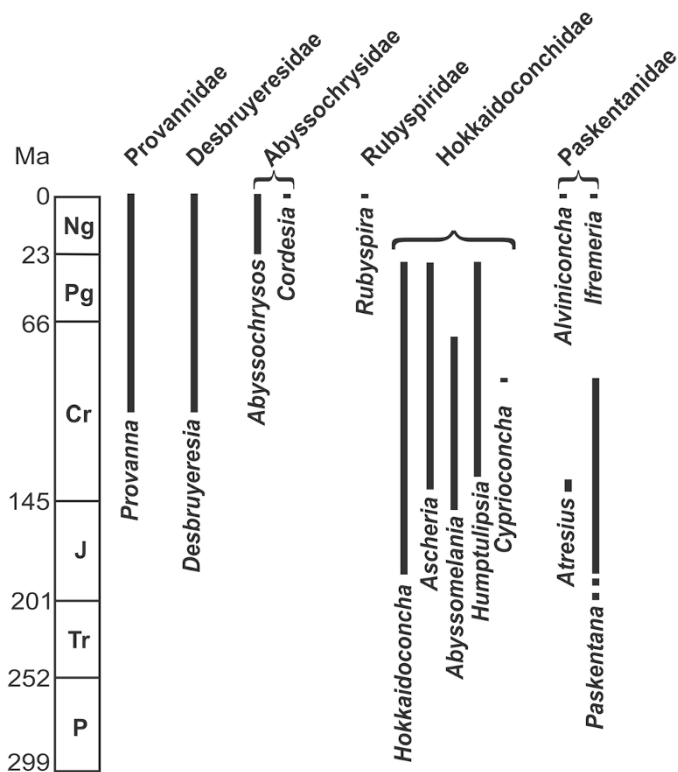


Fig. 11.1 Geological ranges of abyssochrysid gastropods

lecithotrophic larval shells. The family Paskentanidae (Kaim et al. 2014), which is based on the extinct genus *Paskentana*, is proposed herein to be a parent taxon of Recent Alviniconchinae.

11.2.1 Hokkaidoconchidae

Hokkaidoconchidae (Kaim et al. 2008a) are known only from the fossil record and range from the Early Jurassic seep deposits of Argentina (Kaim et al. 2015, 2016) to the early Miocene seeps of Barbados (“zygopleurid sp. A” of Gill et al. (2005), reinterpreted as Hokkaidoconchidae by Kaim et al. 2008a). Both earliest and latest occurrences await formal descriptions (see also Gill and Little this volume). Currently, the family consists of *Abyssomelania* Kaim et al., 2014; *Ascheria* Kaim et al., 2014; *Cyprioconcha* Kaim et al., 2021; *Hokkaidoconcha* Kaim et al., 2008a; and *Humptulipsia* Kiel, 2008. The acme of hokkaidoconchid occurrences (both in diversity and number of individuals) is in the Cretaceous. Although hokkaidoconchids are yet to be found in the Triassic, the presence of *Paskentana*-like shells in the Upper Triassic seep deposits in Turkey (Kiel et al. 2017) suggests that both

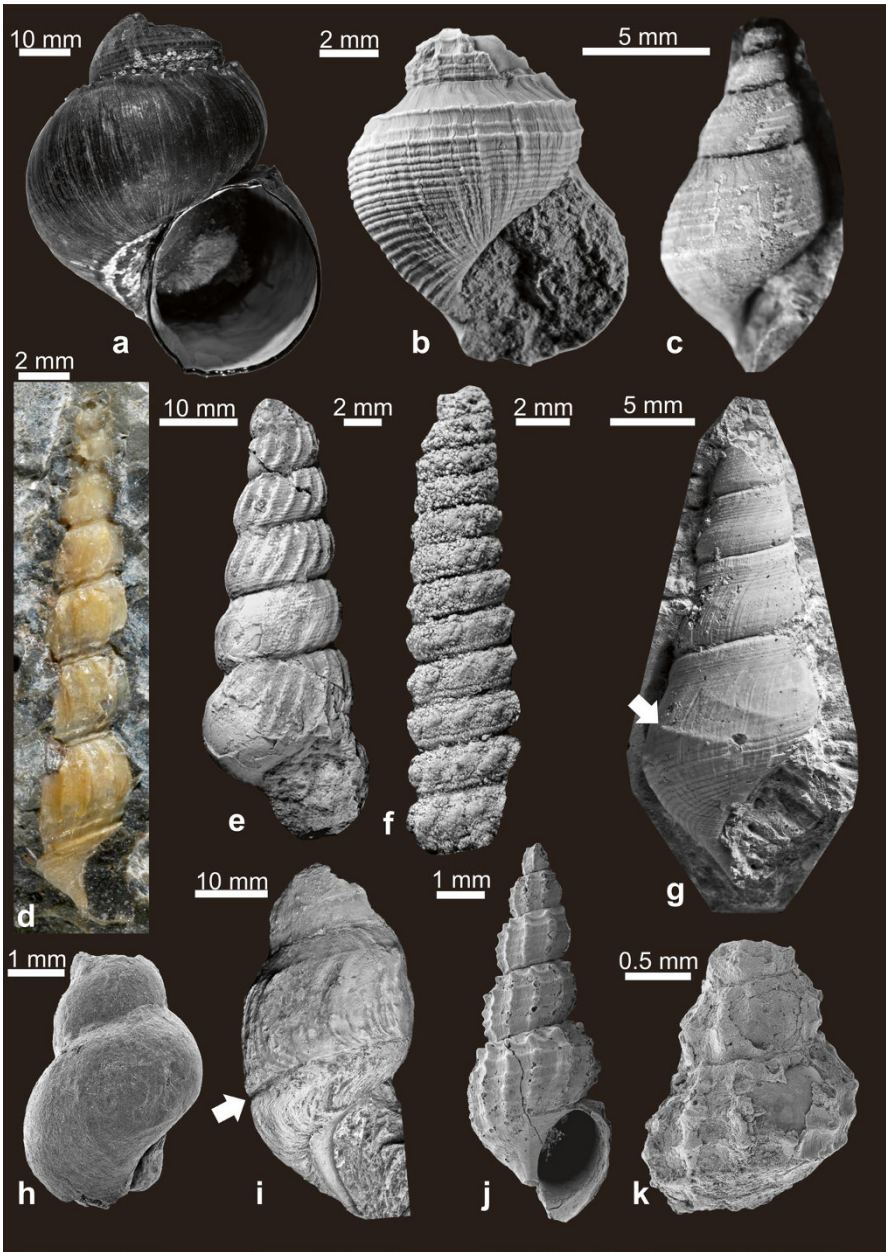


Fig. 11.2 Abyssochrysoide gastropods. (a) Recent shell of *Ifremeria nautili* Bouchet and Warén, 1991, from the Manus Basin (see Kaim et al. 2012). (b) *Paskentana humerosa* (Stanton, 1895) from Valanginian (Early Cretaceous) seep carbonates at Bear Creek, California, USA (see Kaim et al. 2014). (c) *Atresius liratus* Gabb, 1869, from Valanginian (Early Cretaceous) seep carbonates at Rocky Creek, California, USA (see Johnson et al. 2010). (d) *Hokkaidoconcha hikidai*

lineages had already diverged at that time. The gross ptenoglossan morphology of hokkaidoconchids suggests that they most likely diverged from *Zygopleura*-like ptenoglossans after the Permian–Triassic extinction events, perhaps in the Early or Middle Triassic.

Species of *Hokkaidoconcha* are characterized by a very tall and multispiral teleoconch (Fig. 11.2d) reminiscent of some coeval ptenoglossans (e.g., *Confusiscalia* or *Gibboscalia*) and abyssochrysoid multispiral (non-decollate) protoconch (Kaim et al. 2008a). The oldest formally described species of *Hokkaidoconcha* is *H. novacula* from the Oxfordian seep of Beauvoisin, Southeastern France (Kiel et al. 2010), and the youngest is *H. hikidai* from the Campanian Yasukawa seep site in Hokkaido, Japan (Kaim et al. 2008a). Another two species described from the Oligocene asphalt mine in Cuba by Cooke (1919) such as *Hemisinus bituminifer* Cooke, 1919, and *Hemisinus costatus* Cooke, 1919, may also belong to *Hokkaidoconcha*, but their revision is pending. The Toarcian (Early Jurassic) hokkaidoconchid from La Elina seep in Argentina mentioned by Kaim et al. (2015, 2016) is most likely also a species of *Hokkaidoconcha*, and the early Miocene “zygopleurid sp. A” of Gill et al. (2005) from a seep in Barbados most likely belongs here. All known species of *Hokkaidoconcha* were found at ancient seep sites with the sole exception of *H. morisseaui* described from hydrothermal vent deposits in Cyprus (Kaim et al. 2021). *Hokkaidoconcha* displays cosmopolitan distribution and is known from the Americas, Asia, Australasia, Europe, and, with some doubt, Antarctica.

Humptulipsia is a genus of middle-sized abyssochrysoids (Fig. 11.2i) included in the Hokkaidoconchidae by Kaim et al. (2014) due to the hokkaidoconchid-like ornamentation of the juvenile shell in its type species, *H. raii* (see Fig. 1.9 in Kiel 2008 and Fig. 7H in Kaim et al. 2014). All species of *Humptulipsia* are characterized by a slit located in the abapical portion of the whorl. There are just three species of *Humptulipsia* described so far. The oldest species is *H. macsotayi* Kiel et al., 2010, from the Hauterivian (Early Cretaceous) seep deposits in Rottier, Southeastern France (Kiel et al. 2010); another is *H. nobuharai* known from the Sada Limestone in Shikoku, Japan (Kaim et al. 2014); while the youngest is the type species *H. raii* from the Eocene of Washington State (Goedert and Kaler 1996; Kiel 2008; Kaim et al. 2014). All occurrences are at ancient hydrocarbon seeps.



Fig. 11.2 (continued) Kaim et al., 2009, from a Campanian (Late Cretaceous) Yasukawa seep site in Hokkaido, Japan (see Kaim et al. 2009). (e) *Ascheria gigantea* (Kiel et al., 2008) from Early Cretaceous seep carbonates at East Berryessa, California, USA (see Kaim et al. 2014). (f) *Cypriocconcha robertsoni* Kaim et al., 2021, from Cenomanian–Turonian (Late Cretaceous) hydrothermal vent sulfide deposits at Kambia, Cyprus (see Kaim et al. 2021). (g) *Abyssomelania cramptoni* Kaim et al., 2014, from Campanian (Late Cretaceous) seep carbonates at Waipiro III, New Zealand (see Kaim et al. 2014), the arrow indicates an abyssomelanid riblet. (h) *Provanna?* sp. from Miocene seep carbonates at Tanohama, Tsushima Island, Japan (see Hryniewicz et al. 2021). (i) *Humptulipsia raii* (Goedert and Kaler, 1996) from seep carbonates in Western Washington State (see Kaim et al. 2014), the arrow indicates a humptulipsid slit. (j) *Desbruyeresia kanajirisawensis* Kaim et al., 2008a, from Cenomanian (Late Cretaceous) seep carbonates at Kanajirisawa, Hokkaido, Japan (see Kaim et al. 2008a). (k) *Provanna nakagawensis* Kaim et al., 2009, from a Campanian (Late Cretaceous) Yasukawa seep site in Hokkaido, Japan (see Kaim et al. 2009)

Ascheria is a genus of hokkaidoconchids having tall and relatively high shells (Fig. 11.2e) with characteristic subsutural constriction. *Ascheria* is known from Lower Cretaceous seeps of California and the Czech Republic (Kaim et al. 2013, 2014) and ranges temporally to Oligocene seeps in Peru (Kiel et al. 2020b). All species of *Ascheria* are known from ancient hydrocarbon seeps except for *Ascheria canni* Kaim et al., 2021, described from hydrothermal vent deposits in Cyprus.

Abyssomelania unites big abyssochrysoids (Fig. 11.2g) bearing characteristically widely spaced prosocline riblets (named abyssomelanid riblets by Kaim et al. 2014) on their shells. The type species *A. cramptoni* Kaim et al., 2014, has been described from the Campanian (Upper Cretaceous) seep carbonates at Waipiro Bay, New Zealand. Another species, *Abyssomelania campbellae* Kaim et al., 2014, is known from the Albian (Early Cretaceous) seep carbonates of Cold Fork of Cottonwood Creek in California (Kaim et al. 2014). The oldest occurrence is that of *Abyssomelania* sp. in the Tithonian (Late Jurassic) seep carbonates at Sassenfjorden, Svalbard (Kaim et al. 2017).

Monospecific genus *Cypriiconcha* (type species, *Cypriiconcha robertsoni*) has been recently described by Kaim et al. (2021) from the Turonian (Late Cretaceous) hydrothermal vent deposits in Cyprus. *Cypriiconcha* differs from the other genera in Hokkaidoconchidae in lacking axial ornamentation on the early whorls, in having exceptionally narrow whorls (Fig. 11.2f) with a nearly flat-topped profile, and its continuous bend toward the sutures.

11.2.2 *Abyssochrysidae*

Abyssochrysidae Tomlin, 1927, consists of non-chemosynthetic *Abyssochrysos* and *Cordesia* Warén and Bouchet, 2009, dwelling on organic falls and at hydrocarbon seeps (Souza et al. 2020). Modern species of *Abyssochrysos* constitute a small and very uniform group of six species (see Houbrick 1979; Bouchet 1991; Killeen and Oliver 2000), which are known from Brazil, West and South Africa, Oman, and Indonesia. All described species display a smooth, lecithotrophic larval shell, while one undescribed species from deep water off New Caledonia reported by Kaim et al. (2008a) has an unusual lecithotrophic protoconch of two whorls, similar to that of *Provanna*. None of the Recent species of *Abyssochrysos* is reported to be a member of a chemoautotrophic-based community so far. Apparently, they are regular deep-water taxa, and it remains disputable whether it is a primary condition or secondary adaptation. The fossil record of *Abyssochrysos* is very poor. The Miocene counterpart of *Abyssochrysos melvilli* (Schepman, 1909) was reported from Fiji (Ladd 1977; Houbrick 1979) from non-seep deep-sea deposits. It has been suggested by Kaim et al. (2008a) that the Middle Jurassic *Acanthostrophia acanthica* Conti and Fischer, 1984, from Italy could be an abyssochrysoid, but the detailed study of Kaim and Conti (2010) has shown that it is a member of Protorculidae, according to an earlier suggestion by Nützel (1998). All other species of *Abyssochrysos* reported previously from ancient seep deposits have been reinterpreted as hokkaidoconchids (see Table 11.1 in Kaim et al. 2008a).

Table 11.1 A list of gastropods from ancient seep and vent localities (and some more important organic falls)

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
Abyssochrysoidea	Hokkaidoconchidae	<i>?Hokkaidoconcha</i> sp.	Gill et al., 2005	Miocene	Belleplaine, Barbados	Seep	As zygopleurid
		<i>Hokkaidoconcha bituminiifer</i>	Cooke, 1919	Eocene	Bejuical, Cuba	Seep	As <i>Hemisinus</i>
		<i>Hokkaidoconcha costata</i>	Cooke, 1919	Eocene	Bejuical, Cuba	Seep	As <i>Hemisinus</i>
		<i>Hokkaidoconcha hikidai</i>	Kaim et al., 2008a	Campanian	Yasukawa, Japan	Seep	
		<i>Hokkaidoconcha morenoensis</i>	Kiel et al., 2008	Santonian	Moreno Gulch, CA, USA	Seep	
		<i>Hokkaidoconcha morisseaui</i>	Kaim et al., 2021	Turonian	Troodos, Cyprus	Vent	
		<i>Hokkaidoconcha</i> sp. 2	Kiel et al., 2013	Cenomanian	Port Awanui, New Zealand	Seep	
		<i>Hokkaidoconcha tanabei</i>	Kaim et al., 2008a, b	Cenomanian	Kanajirisawa, Japan	Seep	Type species
		<i>Hokkaidoconcha</i> sp.	Agirrezabala et al., 2013	Albian	Ispaster, Spain	Seep	
		<i>Hokkaidoconcha</i> sp. 1	Kiel et al., 2013	Albian	Port Awanui, New Zealand	Seep	
		<i>Hokkaidoconcha</i> sp.	Kaim et al., 2013	Barremian	Baška, Czechia	Seep	
		<i>Hokkaidoconcha biltrata</i>	Kiel et al., 2008	Hauterivian	Wilbur Springs, CA, USA	Seep	
		<i>Hokkaidoconcha</i> sp.	Kaim et al., 2017	Berriassian	Sassenfjorden, Svalbard	Seep	

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Table 11.1 (continued)

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
		<i>Hokkaidoconcha occidentalis</i>	Kiel et al., 2008	Tithonian	Paskenta, CA, USA	Seep	Also NW Beryessa and Wilbur Springs
		<i>Hokkaidoconcha tehmaensis</i>	Kiel et al., 2008	Tithonian	Paskenta, CA, USA	Seep	
		<i>Hokkaidoconcha</i> sp.	Kiel et al., 2008	Tithonian	NW Beryessa, CA, USA	Seep	Might be <i>Atresius</i> or <i>Paskentana</i>
		<i>Hokkaidoconcha hignalli</i>	Kaim and Kelly, 2009	Tithonian	Alexander Island, Antarctica	Seep	Might be <i>Boreomica</i>
		? <i>Hokkaidoconcha</i> sp.	Kaim et al., 2017	Tithonian	Sassenfjorden, Svalbard	Seep	
		<i>Hokkaidoconcha novacula</i>	Kiel et al., 2010	Oxfordian	Beauvoisin, France	Seep	
		<i>Humtulpisia raii</i>	Goedert and Kaler, 1996	Eocene	Humtulpis, WA, USA	Seep	Type species
		<i>Humtulpisia nobuharai</i>	Kaim et al., 2014	Campanian–Maastirhtian	Sada Limestone, Japan	Seep	
		<i>Humtulpisia macsotayi</i>	Kiel et al., 2008	Hauterivian	Rottier, France	Seep	
		<i>Ascheria elenensis</i>	Olsson, 1931, Kiel et al., 2020b	Eocene	Ecuador	Seep	Described by Olsson (1931) as <i>Anconia</i>
		<i>Ascheria salina</i>	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep	
		<i>Ascheria</i> sp.	Kaim et al., 2014	Eocene	Joes River, Barbados	Seep	
		<i>Ascheria canni</i>	Kaim et al., 2021	Turonian	Troodos, Cyprus	Vent	

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
		<i>Ascheria gigantea</i>	Kiel et al., 2008	Early Cretaceous	East Berryessa, CA, USA	Seep	Type species
		<i>Ascheria euscosmeta</i>	Kaim et al., 2013	Early Cretaceous	Hradiště and Koňákov, Czechia	Seep	
		<i>Abyssomelania cramptoni</i>	Kaim et al., 2014	Campanian	Waipiro Bay, New Zealand	Seep	Type species
		<i>Abyssomelania campbellae</i>	Kaim et al., 2014	Albian	Cold Fork of Cottonwood Creek, CA, USA	Seep	
		<i>Abyssomelania</i> sp.	Kaim et al., 2017	Tithonian	Sassenfjorden, Svalbard	Seep	
		<i>Cypriocoencha robertsoni</i>	Kaim et al., 2021	Cenomanian–Turonian	Troodos, Cyprus	Vent	Type species
	Pakentamidae	<i>Paskentana dixoni</i>	Kaim et al., 2021	Turonian	Troodos, Cyprus	Vent	
		<i>Paskentana xenophontosi</i>	Kaim et al., 2021	Turonian	Troodos, Cyprus	Vent	
		<i>Paskentana wilburensis</i>	Stanton, 1895; Kiel et al., 2008	Hauterivian	Wilbur Springs, CA, USA	Seep	
		<i>Paskentana hamiltonensis</i>	Kaim et al., 2014	Valanginian	Bear Creek, CA, USA	Seep	
		<i>Paskentana humerosa</i>	Stanton, 1895; Kiel et al., 2008	Valanginian	Bear Creek, CA, USA	Seep	
		<i>Paskentana anistrattenkorum</i>	Kiel et al., 2010	Berriassian	Planerskoje, Crimea	Seep	

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Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
	Provannidae	<i>Provanna azurini</i>	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep	
		<i>Provanna marshalli</i>	Saether et al., 2010	Miocene	Rocky Knob, New Zealand	Seep	
		<i>Provanna</i> sp.	Gill et al., 2005; Kiel and Hansen, 2015	Miocene	Trinidad/Venezuela	Seep	
		<i>Provanna hirokoeae</i>	Amano and Little, 2014	Miocene	Kita–Kuroiwa, Japan	Seep	
		<i>Provanna alexi</i>	Amano and Little, 2014	Miocene	Shosanbetsu, Japan	Whale fall	
		<i>Provanna fortis</i>	Hybertsen and Kiel, 2018	Eocene	Washington State, USA	Seep	
		<i>Provanna antiqua</i>	Squires, 1995	Oligocene	Washington State, USA	Seep	Also wood, also in Peru
		<i>Provanna urahoroensis</i>	Amano and Jenkins, 2013	Oligocene	Kami-Atsunai, Japan	Seep	
		<i>Provanna pelada</i>	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep	
		<i>Provanna tappuensis</i>	Kaim et al., 2008a	Cenomanian	Kanajirisawa, Japan	Seep	
		<i>Provanna?</i> sp.	Kaim et al., 2008b; Saether et al., 2010	Coniacian	Shirochiunzawa, Japan	Plesiosaurid carcasses	<i>Desbruyeresia?</i>
		<i>Provanna nakagawensis</i>	Kaim et al., 2009	Campanian	Omagari, Japan	Seep	

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Table 11.1 (continued)

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
Neomphalida	Neomphalidae	<i>Retiskenea?</i> sp.	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep	
		<i>Retiskenea?</i> sp.	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep	
		<i>Retiskenea statura</i>	Goedert and Benham, 1999	Eocene–Oligocene	Washington State, USA	Seep	
		<i>Retiskenea?</i> sp.	Kiel et al., 2012	Albian–Cenomanian	Awanui, New Zealand	Seep	
		<i>Retiskenea tuberculata</i>	Campbell et al., 2008b	Hauterivian	Wilbur Springs, CA, USA	Seep	
		<i>Retiskenea kieli</i>	Campbell et al., 2008b	Albian	Cold Fork of Cottonwood Creek, CA, USA	Seep	
		<i>Planorbidella?</i> sp.	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep	
		<i>Leptogyra squiresi</i>	Kiel and Goedert, 2007	Eocene	Washington State, USA	Seep	
		<i>Depressigyra</i> sp.	Hybertsen and Kiel, 2018	Eocene	Washington State, USA	Seep	Peltopspird identity uncertain
			Melanodrymiidae	<i>Lithomphalus enderlini</i>	Kiel and Campbell, 2005	Valanginian	Rocky Creek, CA, USA
	uncertain	<i>Elmira cornuarietis</i>	Cooke, 1919 ; Kiel and Hansen, 2015	Eocene	Elmira, Cuba	Seep	Type species, spelled <i>E. cornuarietis</i> by Kiel and Hansen, 2015
		<i>Elmira shimantoensis</i>	Nobuhara et al., 2016	Campanian–Maastrichtian	Sada Limestone, Japan	Seep	

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments	
Cocculinida	Cocculimidae	<i>Coccolpiza</i> sp.	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep		
		Gastropod limpet 1	Hybertsen and Kiel, 2018	Eocene	Washington State, USA	Seep		
Lepetelida	Pyropeltidae	<i>Pyropelta seca</i>	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep		
		<i>Pyropelta</i> sp.	Kiel, 2006	Oligocene	Washington State, USA	Seep		
	Fissurellidae	Gastropod limpet 2	Hybertsen and Kiel, 2018	Eocene	Washington State, USA	Seep	Or pseudococculinid	
		Fissurellid? limpet	Goedert and Squires, 1990	Eocene	Washington State, USA	Seep		
		Fissurellid	Gill et al., 2005	Eocene–Miocene	Windy Hill, Barbados	Seep		
Patellida	Sutilizonidae	<i>Fissurella bipunctata</i>	Kiel et al., 2010	Albian	Cold Fork of Cottonwood Creek, CA, USA	Seep		
		<i>Puncturella mcleani</i>	Kiel et al., 2010	Valanginian	Bear Creek, CA, USA	Seep		
		<i>Triassurella goederti</i>	Kiel et al., 2010	Valanginian	Bear Creek, CA, USA	Seep		
		Limpet gastropod sp. 1	Saether et al., 2012	Miocene	Hawke's Bay, New Zealand	Seep	Originally as <i>Serradonta</i>	
		<i>Bathyacmaea kimberleyae</i>	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep	Probably <i>Bathyacmaea</i>	
	Pectinodontidae	<i>Bathyacmaea omagariensis</i>	Kaim et al., 2009	Campanian	Omagari and Yasukawa, Japan	Seep	Two morphotypes	
		<i>Bathyacmaea</i> sp.	Kiel et al. 2013	Campanian	Waipiro Bay, New Zealand	Seep	Originally as <i>Serradonta</i>	
		? <i>Pectinodonta borealis</i>	Kaim et al., 2017	Berriassian	Sassenfjorden, Svalbard	Seep		

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Table 11.1 (continued)

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
Seguenziida	Chilodontaidae	<i>Chilodonta? reticulata</i>	Kaim et al., 2014	Valanginian	Bear Creek, CA, USA	Seep	
		<i>Cataegis ramosi</i>	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep	
	<i>Cataegis godineauensis</i>	Kiel and Hansen, 2015	Miocene	Freeman's Bay and Jordan Hill, Trinidad	Seep		
	<i>Cataegis godineauensis</i>	Kiel and Hansen, 2015	Oligocene	Sta. Clara, Colombia	Seep		
	<i>Cataegis nakagawensis</i>	Kaim et al., 2009	Campanian	Omagari, Japan	Seep		
	<i>Cataegis? sp.</i>	Kaim et al., 2014	Valanginian	Bear Creek, CA, USA	Seep		
	<i>Bathybembix aeola</i>	Nobuhara and Tanaka, 1993	Pliocene	Kakegawa, Japan	Seep		
	<i>Bathybembix sp.</i>	Kiel and Goedert, 2006	Eocene	Washington State, USA	Wood		
	<i>Ambercyclus morganensis</i>	Kiel et al., 2008; Kaim et al., 2017	Valanginian	Rocky Creek, CA, USA	Seep		
	<i>Ambercyclus dilleri</i>	Kiel et al., 2008; Kaim et al., 2017	Tithonian	Paskenta, CA, USA	Seep		
	<i>Ambercyclus cf. dilleri</i>	Kiel et al., 2008; Kaim et al., 2017	Tithonian–Valanginian	NW Berryessa, CA, USA	Seep		
	<i>Eucycloidea bitnerae</i>	Kaim et al., 2017	Tithonian	Sassenfjorden, Svalbard	Seep		
	<i>Eucyclid sp.</i>	Hryniewicz et al., 2015	Oxfordian–Kimmeridgian	Novaya Zemlya, Russia	Seep		
Seguenziidae	<i>Vetulonia philippinensis</i>	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep		Familial status of <i>Vetulonia</i> uncertain

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
Trochida	Collomiidae	<i>Cantrainea</i> sp.	Kiel and Hansen, 2015	Miocene	Freeman's Bay and Jordan Hill, Trinidad	Seep	
		<i>Cantrainea</i> sp.	Kiel et al., 2020a , b	Oligocene	Talara Basin, Peru	Seep	
		<i>Hikidea yasukawensis</i>	Kaिम et al., 2009	Campanian	Yasukawa, Japan	Seep	
		<i>Hikidea omagariensis</i>	Kaिम et al., 2009	Campanian	Omagari, Japan	Seep	
		<i>Hikidea osoensis</i>	Kaिम et al., 2014	Valanginian	Bear Creek, CA, USA	Seep	Type species
		<i>Hikidea svalbardensis</i>	Kaिम et al., 2017	Berriastian	Sassenfjorden, Svalbard	Seep	
		<i>Hikidea</i> -like	Kiel et al., 2017	Late Triassic	Terziler, Turkey	Seep	
		<i>Homalopoma</i> ? sp. B	Goedert and Squires, 1990 ; Kiel 2006	Eocene–Oligocene	Washington State, USA	Seep	
		<i>Homalopoma</i> ? sp.	Amano et al., 2018	Miocene	Hawke's Bay, New Zealand	Seep	Not illustrated
		<i>Homalopoma domeniconii</i>	Moroni, 1966	Miocene	Calcare a Lucine, Italy	Seep	
		<i>Homalopoma abeshinaensis</i>	Kaिम et al., 2009	Campanian	Omagari, Japan	Seep	
	<i>Phaneralopoda onoensis</i>	Kaिम et al., 2014	Barremian	Eagle Creek, CA, USA	Seep		
Trochidae		<i>Margarita naticoides</i>	Cooke, 1919	Eocene	Elmira, Cuba	Seep	<i>Hikidea</i> ?
		Trochoid incertae sedis	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep	
		<i>Margarites hayashii</i>	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep	

(continued)

Table 11.1 (continued)

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
		<i>Margarites</i> sp.	Tanaka, 1959	Miocene	Akanuda, Japan	Seep	<i>Hikiidea?</i>
		<i>Margarites (Pupillaria) columbiana</i>	Squires and Goedert, 1991; Kiel 2006	Eocene–Oligocene	Washington State, USA	Seep	
		<i>Margarites sasakii</i>	Kaim et al., 2009	Campanian	Omagari, Japan	Seep	
		<i>Francisciconcha maslennikovi</i>	Little et al., 2004	Platensbachian	Figueroa, CA, USA	Vent	Trochid identity uncertain
	Solariellidae	Solariellimid incertae sedis	Kiel, 2006	Oligocene	Washington State, USA	Seep	
		<i>Solariella</i> sp.	Kiel et al., 2020a	Pleistocene	Leyte, Philippines	Seep	
	Skeneidae	<i>Dilwynella</i> sp.	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep	
		<i>Lopheliella?</i> sp.	Kiel et al., 2020a	Pliocene	Leyte, Philippines	Seep	
	Uncertain	“ <i>Pseudoliotia?</i> sp.”	Miyajima et al., 2018	Pliocene	Matsunoyama, Japan	Seep	
	Phenacolepadidae	<i>Thalassonerita megastoma</i>	Moroni, 1966	Miocene	Calcare a Lucine, Italy	Seep	Type species
		<i>Thalassonerita eocenica</i>	Squires and Goedert, 1996	Eocene	Washington State, USA	Seep	
	Neritimorpha indet.	Neritimorpha indet.	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep	
	Neritidae	Neritid gastropod	Kiel et al., 2010	Berriassian	Planerskoje, Crimea	Seep	
		Neritid	Kiel et al., 2010	Oxfordian	Beauvoisin, France	Seep	

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments	
Neogastropoda	Buccinidae	<i>Eosipho?</i> sp.	Miyajima et al., 2018	Pliocene	Matsumoyama, Japan	Seep		
		<i>Eosipho hoernesii</i>	Moroni, 1966	Miocene	Calcare a Lucine, Italy	Seep	Described as <i>Neptunea hoernesii</i>	
		<i>Mitrella</i> sp.	Amano et al., 2018	Miocene	Hawke's Bay, New Zealand	Seep		
		<i>Ancistrolepis koyamai</i>	Kiel and Amano, 2010	Miocene	Morai, Japan	Seep	Not illustrated	
		<i>Ancistrolepis koyamai</i>	Tanaka, 1959; Amano and Oleinik, 2016	Miocene	Akanuda, Japan	Seep		
		<i>Ancistrolepis teglandae</i>	Kiel and Amano, 2010	Oligocene	Chilkat, AK, USA	Seep		
		<i>Ancistrolepis modestoideus</i>	Amano and Oleinik, 2016	Eocene	Poronai, Japan	Seep		
		<i>Ancistrolepis</i> sp.	Amano and Oleinik, 2016	Eocene	Kiritachi, Japan	Seep		
		<i>Bathyancistrolepis mikasaensis</i>	Amano and Oleinik, 2016	Eocene	Poronai, Japan	Seep		
		<i>Trominina japonica</i>	Amano and Jenkins, 2013	Oligocene	Kami-Atsunai, Japan	Seep		
		<i>Tritia ruggierii</i>	Moroni, 1966	Miocene	Calcare a Lucine, Italy	Seep	Described as <i>Hinia ruggierii</i>	
		Conoidea	<i>Benthomangelia?</i> sp.	Kiel, 2006	Oligocene	Washington State, USA	Seep	
			<i>Xanthodaphne campbellae</i>	Kiel, 2006	Oligocene	Washington State, USA	Seep	
	<i>Turrinosyrinx hickmanae</i>		Kiel, 2006	Oligocene	Washington State, USA	Seep		

(continued)

Table 11.1 (continued)

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
	Muricoidea	<i>Abyssotrophi</i> ? sp.	Amano et al., 2013	Eocene–Oligocene	Tanami, Japan	Seep	
	uncertain	Turrid, Buccinid, Mitrid	Campbell et al., 2008a	Miocene	East Coast Basin, New Zealand	Seep	Not illustrated
		“ <i>Neadmete</i> sp.”	Miyajima et al., 2018	Pliocene	Matsunoyama, Japan	Seep	<i>Ancistrolepis</i> ?
		“ <i>Riuguhirillia</i> sp.”	Miyajima et al., 2018	Pliocene	Matsunoyama, Japan	Seep	
		“ <i>Propebela</i> sp. A”	Miyajima et al., 2018	Pliocene	Matsunoyama, Japan	Seep	
		“ <i>Propebela</i> sp. B”	Miyajima et al., 2018	Pliocene	Matsunoyama, Japan	Seep	
		Tall neogastropod	Kiel and Hansen, 2015	Oligocene	Mata Cana, Colombia	Seep	
		Neogastropod	Kiel and Hansen, 2015	Oligocene	Sta. Clara, Colombia	Seep	
		Neogastropoda indet.	Kaim et al., 2009	Campanian	Yasukawa, Japan	Seep	
	Pseudotritonidae	Maturifusid sp.	Hryniewicz et al., 2015	Berriasian–Valanginian	Novaya Zemlya, Russia	Seep	
	Purpurinidae	<i>Bathypurpurinopsis stantoni</i>	Kiel et al., 2008	Albian	Cold Fork of Cottonwood Creek, CA, USA	Seep	Purpurinid identity uncertain
		<i>Cretadmete</i> sp.	Kaim et al., 2017	Tithonian	Sassenfjorden, Svalbard	Seep	

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments	
Heterobranchia	Cephalaspidea	" <i>Acteon</i> " sp.	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep		
		<i>Acteon</i> sp.	Kiel, 2006	Eocene to Oligocene	Washington State, USA	Seep		
		? <i>Sulcoactaeon</i> sp.	Kaim et al., 2009	Campanian	Yasukawa, Japan	Seep		
		<i>Acteon exculptus</i>	Hryniewicz et al., 2015	Berriasian–Valanginian	Novaya Zemlya, Russia	Seep	As Bullimid sp.	
		<i>Acteon frearsianus</i>	Hryniewicz et al., 2015	Berriasian–Valanginian	Novaya Zemlya, Russia	Seep	As Bullimid sp.	
		<i>Cylichna</i> cf. <i>kozukensis</i>	Tanaka, 1959	Miocene	Akanuda, Japan	Seep		
		<i>Cylichna</i> sp.	Kiel et al., 2020b	Oligocene	Talara Basin, Peru	Seep		
		<i>Cylichna</i> sp.	Kiel, 2006	Oligocene	Washington State, USA	Seep		
		<i>Ellipsoscapha</i> sp.	Hryniewicz et al., 2019	Paleocene	Basilika Formation, Svalbard	Seep		
		<i>Diaphana</i> sp.	Kaim et al., 2014	Valanginian	West Berryessa, CA, USA	Seep		
		Opisthobranch	Kiel et al., 2017	Late Triassic	Terziler, Turkey	Seep		
		<i>Lurifax goederi</i>	Kiel, 2006	Eocene-Oligocene	Washington State, USA	Seep		
		Hyalogyrinidae	<i>Hyalogyrina knorringsfjellensis</i>	Kaim et al., 2017	Berriasian	Sassenfjorden, Svalbard	Seep	
			<i>Hyalogyrina?</i> sp.	Kiel, 2006	Oligocene	Washington State, USA	Seep	
	<i>Hyalogyrina</i> sp.	Hybertsen and Kiel, 2018	Eocene	Washington State, USA	Seep			
Xylodisculidae	<i>Xylodiscula okatanii</i>	Kiel and Goedert, 2007	Oligocene-Miocene	Washington State, USA	Wood			

(continued)

Table 11.1 (continued)

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
Rissooidea	Rissooidea	<i>Boreomica hammeri</i>	Kaim et al., 2017	Berriassian	Sassenfjorden, Svalbard	Seep	
		<i>Boreomica pusilla</i>	Hryniewicz et al., 2015	Berriassian–Early Valanginian	Novaya Zemlya, Russia	Seep	
		<i>Boreomica undulata</i>	Hryniewicz et al., 2015	Tithonian	Novaya Zemlya, Russia	Seep	
		<i>Hokkaidoconcha? hignalli</i>	Kaim and Kelly, 2009	Tithonian	Alexander Island, Antarctica	Seep	Familial status uncertain
		<i>Aporrhais cf. gracilis</i>	Hryniewicz et al., 2019	Paleocene	Basilika Formation, Svalbard	Seep	
Stromboidea	Aporrhaidae	Aporrhaidae indet.	Schwartz et al., 2003	Paleocene	Panoche Hills, CA, USA	Seep	Originally as provannids
		Aporrhaid gastropod from Awanui	Kiel et al., 2013	Cenomanian	Awanui, New Zealand	Seep	
		<i>Pseudanchura biangulata</i>	Kaim et al., 2014	Barremian	Eagle Creek, CA, USA	Seep	
		<i>Xenophora borsoni</i>	Moroni, 1966	Miocene	Calcare a Lucine, Italy	Seep	

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
Naticoidea	Naticidae	<i>Euspira pallida</i>	Miyajima et al., 2018	Pliocene	Matsumoyama, Japan	Seep	
		<i>Euspira pallida</i>	Amano, 2003	Miocene	Morai, Japan	Seep	
		Naticidae gen. et sp. indet.	Amano et al., 2018	Miocene	Hawke's Bay, New Zealand	Seep	
		<i>Tectonatica janthosomoides</i>	Tanaka, 1959	Miocene	Akanuda, Japan	Seep	
		<i>Cryptonatica</i> sp.	Amano et al., 2013	Eocene–Oligocene	Tanami, Japan	Seep	
Campaniloidea	Ampullinidae	<i>Euspira meisenis</i>	Amano et al., 2013	Oligocene	Kami-Atsunai, Japan	Seep	
		<i>Sassenfjordia sassenfjordensis</i>	Kaim et al., 2017	Berriassian	Sassenfjorden, Svalbard	Seep	Naticid identity uncertain; type species
		<i>Globularia isfjordensis</i>	Hryniewicz et al., 2019	Paleocene	Basilika Formation, Svalbard	Seep	
		Ampullinid gastropod	Kiel and Peckmann, 2008	Berriassian	Planerskoje, Crimea	Seep	
		Cerithiopsid incertae sedis	Kiel, 2006	Oligocene	Washington State, USA	Seep	
Triphoroidea	Cerithiopsidae	<i>Niso littlei</i>	Kiel, 2006	Oligocene	Washington State, USA	Seep	
		Eulimid sp. 1	Kiel, 2006	Oligocene	Washington State, USA	Seep	
		Eulimid sp. 2	Kiel, 2006	Oligocene	Washington State, USA	Seep	
Vanikoroidea	Eulimidae	<i>Cypraea semen</i>	Cooke, 1919; Kiel and Peckmann, 2007	Eocene	Elmira, Cuba	Seep	

(continued)

Table 11.1 (continued)

Higher taxon	Family	Species name	References	Type horizon	Locality/region	Substrate	Comments
Cerithioidea	Turritellidae	<i>Orectospira wadana</i>	Amano and Jenkins, 2013	Oligocene	Kami-Atsunai, Japan	Seep	
		<i>Orectospira wadana</i>	Amano et al., 2013	Eocene– Oligocene	Tanami, Japan	Seep	
Pyramidelloidea	Amathinidae	<i>Carinorbis clathrata</i>	Moroni, 1966	Miocene	Calcare a Lucine, Italy	Seep	Described as <i>Phasianema taurocrassum</i>
Tonnoidea	Cassidae	<i>Galeodea delibrata</i>	Moroni, 1966	Miocene	Calcare a Lucine, Italy	Seep	

Paleozoic taxa and species from the Western Interior Seaway shallow-water seeps are not included

Additionally, it has been recently suggested by Souza et al. (2020) that *Cordesia* Warén and Bouchet, 2009, with two described species, one dwelling on organic falls (*C. atlantica*) and one at hydrocarbon seeps (*C. provannoides*), in the Atlantic Ocean might be another genus belonging to the Abysochrysidae according to their molecular data. The shells of *Cordesia* are relatively small (the holotype of *C. atlantica* is 7.05 mm high and 4.90 mm wide) and quite broad with weak spiral and axial sculpture and a large aperture with a distinct, short siphonal canal (Warén and Bouchet 2009; Souza et al. 2020).

11.2.3 *Paskentanidae*

The family Paskentanidae Kaim et al., 2014, which comprises the genera *Paskentana* Kiel et al., 2008, and *Atresius* Gabb, 1869, are moderately sized gastropods with a littoriniform to high-spined teleoconch and a subsutural ramp on the early whorls. According to Kiel et al. (2008), *Paskentana* possesses a protoconch resembling that of provannids. Both *Paskentana* and monospecific *Atresius* have similar early ontogenetic shells that inclined Kaim et al. (2014) to unite them into a single family.

The species of *Paskentana* are characterized by a littoriniform shell of moderate size (Fig. 11.2b) with very thin shell wall, similar in several aspects to Recent *Alviniconcha*. In some localities, *Paskentana* occurs in great numbers (e.g., the Valanginian seep site at Bear Creek, California). The oldest *Paskentana*-like gastropod is reported by Kiel et al. (2017) from the Carnian (Late Triassic) seep deposit of Turkey. An undescribed species of *Paskentana* is also known from the Toarcian (Early Jurassic) site in Argentina (Kaim et al. 2015, 2016). The oldest formally described species is *P. umbilicata* from the Oxfordian (Late Jurassic) seep site at Beauvoisin, southeastern France (Kiel et al. 2010). The youngest known *Paskentana* from a seep site is from the Hauterivian in California (Kiel et al. 2008), but two younger species are known from Turonian hydrothermal vent deposits in Cyprus (Kaim et al. 2021). One may hypothesize that *Paskentana* moved from hydrocarbon seeps to hydrothermal vents in the mid-Cretaceous.

Although Kaim et al. (2014) placed *Atresius liratus* Gabb, 1869, in Paskentanidae (Fig. 11.2c) due to the similarity of its early whorls to the corresponding whorls in *Paskentana*, its taxonomic position remains somewhat controversial (see Kiel et al. 2008 for a review). The extraordinarily similar shell morphology of this species to the Recent bone eating abyssochrysoid *Rubyspira osteovora* Johnson et al., 2010, led to a suggestion that they may be related (Johnson et al. 2010). Even the juvenile shells are somewhat similar but less so than that of the coeval *Paskentana humerosa* (compare Fig. 8D, I and 8E, J in Kaim et al. 2014). Clarifying the relation between *Atresius* and *Rubyspira* requires further research and collection effort.

11.2.4 *Alviniconchinae* New Subfamily

Type genus: *Alviniconcha* Okutani and Ohta, 1988

Genera included: Type genus and *Ifremeria* Bouchet and Warén, 1991

Diagnosis: Shell large and globose and shell wall thin with thick periostracum.

Aperture with a shallow anterior sinus or notch.

Remarks: Alviniconchinae differ markedly from all other abyssochrysoids in having globose shells (Fig. 11.2a) expanded for sheltering hypertrophied symbiont-bearing gills. In the majority of molecular phylogenies, they are recovered as a separate clade that diverged not later than in the Cretaceous (e.g., Johnson et al. 2010). In the most recent molecular study, *Ifremeria* is placed as a sister taxon to all other abyssochrysoids but Provannidae. The only similar group is Paskentanidae, also having globose to littorinimorph shells with thin shells and with shallow anterior sinus. They are slightly smaller and less globose as one might have expected for a more ancient stage in the evolution of Alviniconchinae. It is worth noting that Alviniconchinae inhabit exclusively hydrothermal vents while Paskentanidae first appeared at hydrocarbon seeps and then moved to hydrothermal vents in the middle Cretaceous (compare Kaim et al. 2021). One may therefore suggest that Alviniconchinae is a crown group of Paskentanidae. It is suggested herein that Paskentanidae consists of two subfamilies: Mesozoic Paskentaninae (*Paskentana* and *Atresius*) and Cenozoic Alviniconchinae (*Alviniconcha* and *Ifremeria*). The link between both groups is missing so far due to the lack of a fossil record of Cenozoic hydrothermal vent deposits with preserved mollusk fauna.

11.2.5 *Desbruyeresidae* New Family

Type genus: *Desbruyeresia* Warén and Bouchet, 1993

Genera included: Type genus only.

Diagnosis: Shell small and slender with high spire (Fig. 11.2j) and small rounded aperture. Suture usually moderately to deeply incised. Sculpture composed of axial ribs and spiral cords with intersections occasionally equipped with knobs or spines. Protoconchs multispiral with finely cancellate ornamentation indicating planktotrophic development. Central teeth of radula divided into large central cusp and several lateral cusps.

Remarks: Desbruyeresidae are similar in many respects to Provannidae sensu stricto (i.e., genus *Provanna*), differing mainly in central radular teeth, multispiral larval shells indicative of planktotrophic development, and usually more slender and higher-spined shells. They also are invariably recovered in different positions in molecular trees (Johnson et al. 2010; Chen et al. 2016, 2019a, b; Souza et al. 2020). Today, species of *Desbruyeresia* occur at the West Pacific vent sites and serpentinization-related seeps, and there is a single species on record from Indian Ocean vents (Sasaki et al. 2010; Chen et al. 2016). *Desbruyeresia* is rela-

tively rare in the fossil record. In addition to the newly described three species from the Turonian (Late Cretaceous) hydrothermal vents in Cyprus, the genus is known from Cenomanian seep deposits in Japan (Kaim et al. 2008a) and Eocene seeps in Washington State, USA (Hybertsen and Kiel 2018). Possible species of *Desbruyeresia* have been reported from Pliocene seeps in Leyte Island, Philippines (Kiel et al. 2020a). Another species of *Desbruyeresia* has been reported (as Provannidae gen. et spp. indet.) from the Coniacian plesiosaur fall in Hokkaido, Japan, by Kaim et al. (2008b). The divergence time between Desbruyeresidae and Provannidae is therefore estimated to be at least mid-Cretaceous. It is worth noting that all Cretaceous occurrences of *Desbruyeresia* and *Provanna* are known from Western Pacific and Tethys while there are none in the numerous Early Cretaceous seep sites of California, though other abyssochrysoids are fairly common there. This may suggest that both groups originated in the Western Pacific; this is, however, hard to confirm since the oldest in this region is of Albian age (e.g., Shimazu and Jenkins 2019).

11.2.6 *Provannidae*

As understood herein, Provannidae are composed exclusively of species of the nominative genus *Provanna* Dall, 1918, as they are recovered separately in all available molecular phylogenies (Johnson et al. 2010; Chen et al. 2016, 2019a, b; Souza et al. 2020). The genus *Provanna* is very rich in species (Fig. 11.2h, k) and distributed worldwide in all types of chemosynthesis-based communities. The fossil record is also relatively rich starting with the Cenomanian (Upper Cretaceous) seep site of Kanajirisawa, Hokkaido, Japan (Kaim et al. 2008a), and being particularly common in Cenozoic seeps (e.g., Squires 1995; Gill et al. 2005; Saether et al. 2010; Amano and Jenkins 2013; Amano and Little 2014; Kiel and Hansen 2015; Hybertsen and Kiel 2018; Kiel et al. 2020a, b; Hryniewicz et al. 2021).

Another genus that has been included in Provannidae by Bouchet et al. (2005) is *Pseudonina* Sacco, 1896, with a single Miocene–Pliocene species of *Pseudonina bellardii* (Michelotti, 1847) reported from sunken wood in Italy (Bertolaso and Palazzi 1994). The protoconch of this species is, however, more similar to protoconchs of epitoniids as already observed by Bertolaso and Palazzi (1994).

11.2.7 *Rubyspiridae* New Family

Type genus: *Rubyspira* Johnson et al., 2010

Genera included: Type genus only.

Diagnosis: Adult shell tall, whorls sculptured spirally covered by a periostracum forming small bristles, no siphonal canal, protoconch multispiral, and two pallial tentacles present.

Remarks: All species of Rubyspiridae predominantly thrive on whale carcasses (Johnson et al. 2010; Hasegawa et al. 2019; Souza et al. 2020) with some additional occurrences on sunken wood (Souza et al. 2020). Molecular phylogenies invariably recover Rubyspiridae as a sister clade of Abysochrysidae. The only fossil abysochrysoid reminiscent of *Rubyspira* is *Atresius liratus* Gabb, 1869, and according to Kaim et al. (2014), *Atresius* belongs to Paskentanidae. The relation between *Atresius* (and Paskentanidae) and *Rubyspira* requires further research and collection effort.

11.3 Neomphalida

Neomphalida McLean, 1990, is a clade of order rank, which together with Cocculinida comprise the subclass Neomphaliones in the class Gastropoda (Bouchet et al. 2017). Anatomical characters suggest inclusion of neomphalids in Vetigastropoda (Aktipis et al. 2008), but molecular studies recover them as basal to Vetigastropoda (Geiger and Thacker 2006). The exact position of Neomphalina on the gastropod tree of life is still controversial. Neomphalids were originally considered to be endemic to hydrothermal vents, but now, they are known also from hydrocarbon seeps and organic falls (Kano 2008; Warén and Bouchet 2009; Sasaki et al. 2010), although they are much less common there than at the vents. The living neomphalids are divided into three families (Melanodrymiidae, Neomphalidae, and Peltospiridae), which display a very wide range of shell morphologies from limpets (e.g., *Neomphalus*, *Echinopelta*) through small and simple skeneiforms (e.g., *Retiskenea*, *Depressigyra*) to trochoid-like forms (e.g., *Melanodrymia*). Therefore, the fossil record of neomphaline gastropods is a difficult matter since there are only a few characters that could be used to recognize them from shells alone. Seemingly, the best character is the protoconch morphology, which in neomphalids occurs in two types: either with a fine net sculpture, especially on the initial part (Melanodrymiidae and Neomphalidae), or a strongly bent type with prominent spiral ridges in the Peltospiridae (Sasaki et al. 2010). Auxiliary characters helpful in recognition of neomphalids in the fossil record are the presence of shell pores in some taxa, for example, in *Leptogyra squiresi* from the Eocene sunken wood of Washington State (Kiel and Goedert 2006, 2007), and crossed-lamellar shell structure in trochiform neomphalids (Kiel and Campbell 2005) in contrast to similar trochoids and turbinids, which usually have a nacreous shell layer.

Nearly all Mesozoic reports of neomphalids concern *Retiskenea*- or *Retiskenea*-like gastropods. The genus *Retiskenea* (Fig. 11.3b), with type species *R. diploura* Warén and Bouchet, 2001, from the Aleutian Trench is the only neomphaline restricted to hydrocarbon seeps today. No wonder then that it is also the most common neomphaline in the fossil record. Possibly, the oldest occurrence to date is the *Retiskenea*-like gastropod reported by Kaim et al. (2015, 2016) from the Toarcian (Early Jurassic) La Elina seep in Argentina. The oldest formally described species is *Retiskenea? kieli* Campbell et al., 2008b, from the Tithonian (Late Jurassic) seep

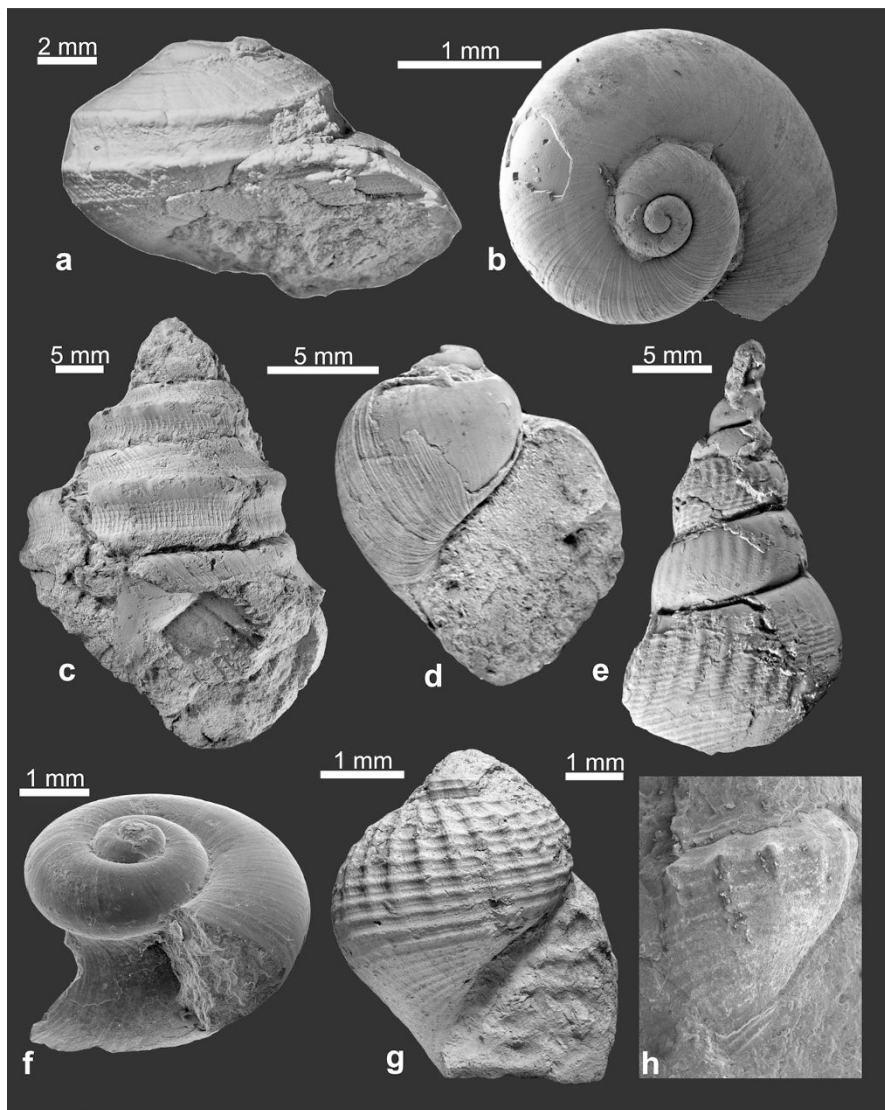


Fig. 11.3 Neomphalid and other gastropods. (a) Neomphalid *Lithomphalus enderlini* Kiel and Campbell, 2005, from Valanginian (Early Cretaceous) seep carbonates at Bear Creek, California, USA (see Kaim et al. 2014). (b) Neomphalid *Retiskenea? tuberculata* Campbell et al., 2008a, b, from Valanginian (Early Cretaceous) seep carbonates at Bear Creek, California, USA (see Kaim et al. 2014). (c) Eucyclid *Eucycloidea bitnerae* Kaim et al. 2017, from Tithonian (Late Jurassic) seep carbonates in Sassenfjorden, Svalbard (see Kaim et al. 2017). (d) Ampullinid *Globularia isfjordensis* (Vonderbank, 1970) from Paleocene seep carbonates in Hollendarbukta, Svalbard (see Hryniewicz et al. 2019). (e) Aporrhaid *Aporrhais* cf. *gracilis* Koenen, 1885, from Paleocene seep carbonates in Hollendarbukta, Svalbard (see Hryniewicz et al. 2019). (f) Hyalogyrinid *Hyalogyrina knorringfjelletensis* sp. nov. from the Berriasian (Early Cretaceous) seep carbonates at Sassenfjorden, Svalbard (see Kaim et al. 2017). (g) Purpurinid *Cretadmete* sp. from Tithonian (Late Jurassic) seep carbonates at Sassenfjorden, Svalbard (see Kaim et al. 2017). (h) Neogastropoda indet. From the Campanian (Late Cretaceous) Yasukawa seep site in Hokkaido, Japan (see Kaim et al. 2009)

site at Paskenta, California (Kaim et al. 2014). Other species of *Retiskenea* are known from the Cretaceous of California (Campbell et al. 2008a, b; Kaim et al. 2014) and New Zealand (Kiel et al. 2013) as well as from the Cenozoic seeps of Washington State (Goedert and Benham 1999; Kiel 2006), the Philippines (Kiel et al. 2020a), and Peru (Kiel et al. 2020b).

More problematic is alleged Cretaceous melanodrymiid *Lithomphalus enderlini* Kiel and Campbell, 2005 (Fig. 11.3a). Kiel and Campbell (2005) considered it possible that *L. enderlini* represented a Cretaceous neomphaline gastropod based on its shell shape and its crossed-lamellar shell structure. The general gross morphology is reminiscent of several vetigastropods and in particular cataegins (e.g., Kaim et al. 2014), which, however, possess nacreous rather than crossed-lamellar shell structure. Nevertheless, the neomphaline and melanodrymiid identity of *L. enderlini* proposed by Kiel and Campbell (2005) requires further research and collecting effort. *Lithomphalus enderlini* has been found in two Valanginian (Lower Cretaceous) seep sites of Rocky Creek and Bear Creek in California (Kiel and Campbell 2005; Kaim et al. 2014).

Two additional neomphaline gastropods are known from the Eocene sunken wood and seeps of Washington State. The neomphalid *Leptogyra squiresi* is known from sunken wood (Kiel and Goedert 2006, 2007) while the peltospirid *Depressigyra* sp. is known from hydrocarbon seeps (Kiel 2006; Hybertsen and Kiel 2018). Another possible neomphalid gastropod genus is *Elmira* Cooke, 1919, with two described species *E. cornuarietis* Cooke, 1919, from Eocene seeps in Cuba, and *E. shimantoensis* Kiel and Nobuhara in Nobuhara et al., 2016, from a Maastrichtian (Late Cretaceous) seep in Shikoku, Japan (Kiel and Hansen 2015; Nobuhara et al. 2016). Nobuhara et al. (2016) suggest that *Elmira* might be related to peltospirids based on general shell morphology and microstructure. *Elmira shimantoensis* occurs in mass aggregations in a way similar to Recent neomphalids but also alviniconchins. The shells of alviniconchins and paskentanids, in general, however, are very thin in contrast to *Elmira*, which is rather thick shelled. The exact taxonomic position of *Elmira* requires further work.

Surprising is the absence of any neomphaline gastropods in the Turonian (Upper Cretaceous) hydrothermal vent deposits in Cyprus, the richest and most diverse ancient vent site (Kaim et al. 2021). The only potential ancient vent neomphaline gastropod is *Francisciconcha maslennikovi* Little et al., 2004, a trochomorph gastropod from an Early Jurassic hydrothermal vent community in the Franciscan complex, San Rafael Mountains, California. Neither the shell structure nor protoconch of *F. maslennikovi* is known (Little et al. 2004). In general, it remains largely unknown when the radiation of neomphaline gastropods in vent communities took place since the fossil data are so scarce. The only certain point is that the neomphalids appeared in chemosynthesis-based communities (seeps) already in early Mesozoic times and are represented most of all by *Retiskenea*-like species.

11.4 Limpets

Limpet gastropods do not constitute a monophyletic group, and limpet-shaped taxa have evolved repeatedly in nearly all major gastropod clades. Since they have few diagnostic shell characters and in many cases their identity in fossil material is poorly constrained (see, for example, Kiel et al. 2020a), they are treated jointly here. Gastropod limpets are very common at Recent vents and seeps while they are less so in their ancient counterparts.

11.4.1 *Cocculinida*

Cocculinida Haszprunar, 1987, is a small group of deep-water limpet-shaped gastropods living on organic substrates (e.g., Haszprunar 1998). Currently, they are treated as a clade of order rank, sister to Neomphalida, with which they form the subclass Neomphaliones (Bouchet et al. 2017). The family Pyropeltidae McLean and Haszprunar, 1987, is known to occur at hydrothermal vents (McLean and Haszprunar 1987; Warén and Bouchet 2001; Sasaki et al. 2003) and is currently placed in Lepetellida and order Vetigastropoda (Bouchet et al. 2017) in contrast to previous classifications (e.g., Desbruyères et al. 2006; Kiel 2010).

Possible fossil cocculinides are known from Mesozoic (Kiel et al. 2009; Kaim 2011), Eocene (Kiel and Goedert 2006), Miocene, and Pliocene (Marshall 1986) wood falls, and *Coccapigya* sp. is reported from an Oligocene seep in Peru (Kiel et al. 2020b). Another limpet reported by Hybertsen and Kiel (2018) from the Eocene of Washington State as “gastropod limpet 1” might be a cocculinide while “gastropod limpet 2” might be a lepetellide (pseudococculinid or pyropeltid) (Hybertsen and Kiel 2018).

11.4.2 *Lepetellida*

Superfamily Lepetelloidea Dall, 1882, is a small group of deep-water limpets which are currently placed in Lepetellida, Vetigastropoda (Bouchet et al. 2017). One of its families, Pyropeltidae McLean and Haszprunar, 1987, is known to occur abundantly at hydrothermal vents (McLean and Haszprunar 1987; Warén and Bouchet 2001; Sasaki et al. 2003) but occurs also at seeps and organic falls (McLean 1992; Sasaki et al. 2010). Fossil pyropeltids are known from ancient seeps in the Eocene of Washington State (Kiel 2006; Hybertsen and Kiel 2018) and Oligocene of Peru (Kiel et al. 2020b).

Another superfamily of Lepetellida, the keyhole and slit limpets of Fissurelloidea Fleming, 1822, are also known to occur at vents and seeps though they are not particularly common in such environments (Sasaki et al. 2010). Nevertheless, they

occur also in ancient seeps including two species from Early Cretaceous seeps in California (Kiel et al. 2010). *Fissurella bipunctata* Stanton, 1895, is known from the Albian Cold Fork of Cottonwood Creek site, while *Puncturella mcleani* Kiel et al., 2010, is known from the Valanginian Bear Creek site. Additional fissurellids are known from Eocene seeps in Washington State (Goedert and Squires 1990) and from Eocene–Miocene seep deposits on Barbados (Gill et al. 2005).

One more group of lepetellides known from chemosynthesis-based communities are Sutilizonidae McLean, 1989, characterized by a long and wide slit (McLean 1989). Fossil sultizonid *Triassurella goederti* Kiel et al., 2010, have been identified at the Valanginian seep site of Bear Creek in California (Kiel et al. 2010).

11.4.3 *Patellida*

Patellida Ihering, 1876, is the only order of the subclass Patellogastropoda Lindberg, 1986, and it consists of three superfamilies: Eoacmaeoidea Nakano and Ozawa, 2007; Patelloidea Rafinesque, 1815; and Lottioidea Gray, 1840 (Bouchet et al. 2017). Patellogastropods are arguably the most primitive group of living gastropods (e.g., Lindberg 1998), inhabiting a wide variety of marine environments. Members of two lottiid families (Neolepetopsidae McLean, 1990, and Pectinodontidae Pilsbry, 1891) occur in chemosynthesis-based communities. Neolepetopsids are unknown from the fossil record while pectinodontids are relatively common, particularly in Late Cretaceous seeps in Japan. The seep pectinodontids in Japan were previously classified into two distinct genera: *Bathyacmaea* Okutani et al., 1992, and *Serradonta* Okutani et al., 1992. The same genera were identified at modern (Okutani et al. 1992; Sasaki et al. 2003) and ancient seep sites (Hikida et al. 2003; Jenkins et al. 2007a, b; Kaim et al. 2009; Saether et al. 2012). Subsequently, it turned out that both genera should be merged into one (with the name *Bathyacmaea* having priority) and the differences in morphology and radula are of ecophenotypic nature (Chen et al. 2019a; Sato et al., 2020). *Bathyacmaea* with a low and wide shell (Fig. 11.4a, b) predominantly attaches to bivalve shells while laterally compressed *Serradonta* (Fig. 11.4c, d) thrives on worm tubes and at localities where worm tubes occur in large quantities, for example, the Campanian Omagari site in Hokkaido, Japan (Hikida et al. 2003; Jenkins et al. 2007a, b; Kaim et al. 2009). Additionally, some species of genus *Pectinodonta* live on Recent and ancient sunken wood ranging back to the Oligocene of Washington State (Lindberg and Hedegaard 1996) and Miocene of New Zealand (Marshall 1985). Another possible species of the genus has been described by Kaim et al. (2017) as *Pectinodonta borealis* from the Berriasian (Early Cretaceous) seep in Svalbard.

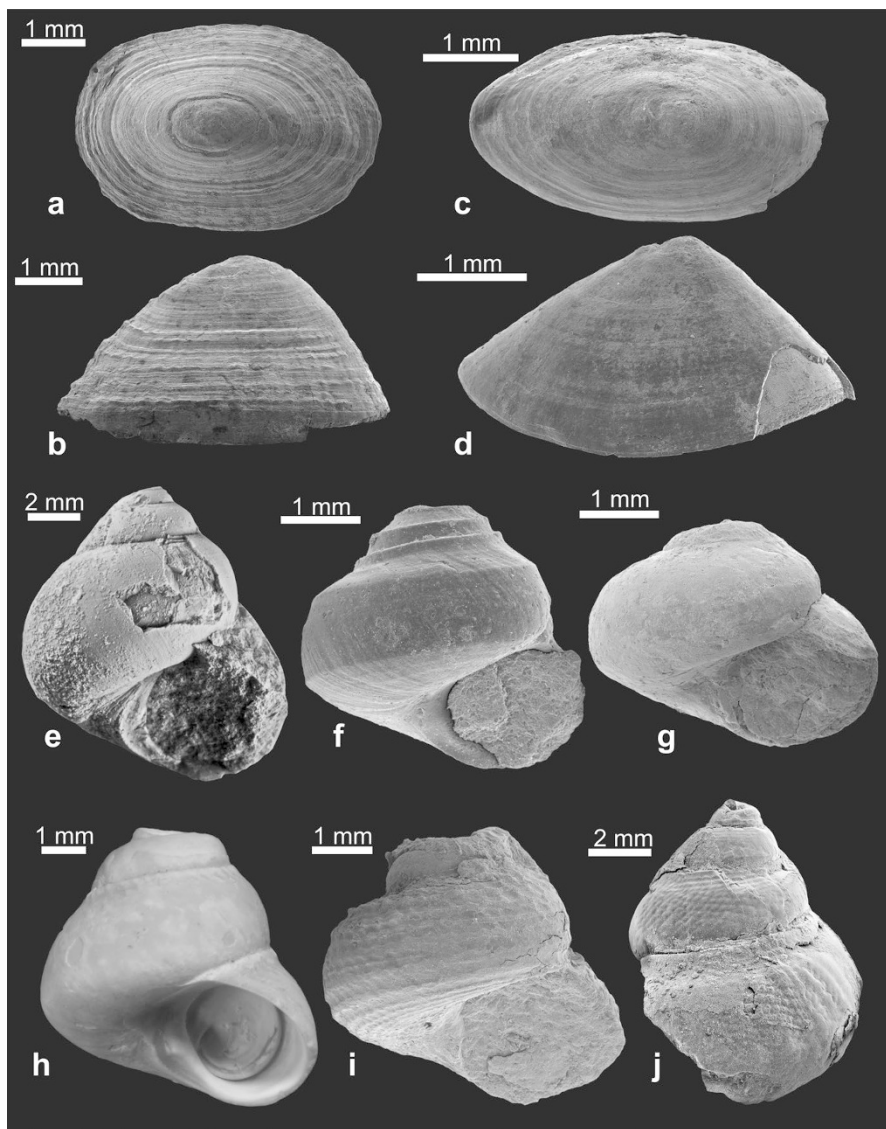


Fig. 11.4 Patellid and trochomorph gastropods. The flattened (a, b) and compressed (c, d) morphotypes of the pectinodontid patellid *Bathyaemaea omagariensis* (Kaim et al., 2009) from the Campanian (Late Cretaceous) Omagari seep site in Hokkaido, Japan (see Kaim et al. 2009). (e) Colloniid *Hikidea osoensis* Kaim et al., 2014, from Valanginian (Early Cretaceous) seep carbonates at Bear Creek, California, USA. (f) Colloniid *Hikidea yasukawensis* (Kaim et al., 2009) from the Campanian (Late Cretaceous) Yasukawa seep site in Hokkaido, Japan (see Kaim et al. 2009). (g) Colloniid *Hikidea omagariensis* (Kaim et al., 2009) from the Campanian (Late Cretaceous) Omagari seep site in Hokkaido, Japan (see Kaim et al. 2009). (h) Recent shell of *Cantrainea nuda* Okutani, 2001, from “depression B” of the Minami-Ensei Knoll, Okinawa Trough, Japan (see Kaim et al. 2009), note the similarity to the species of *Hikidea*. (i) Colloniid *Homalopoma abeshinaiensis* Kaim et al., 2009, from the Campanian (Upper Cretaceous) Omagari seep site in Hokkaido, Japan (see Kaim et al. 2009). (j) Colloniid *Phanerolepida onoensis* Kaim et al., 2014, from the Barremian (Early Cretaceous) seep site at Eagle Creek, California, USA (see Kaim et al. 2014)

11.5 Trochomorph Vetigastropods

Trochomorphs (or trochoideans) are the most diverse group among vetigastropods and are known worldwide from the tropics to the polar regions and from the shallowest intertidal zone to bathyal depths (Hickman and McLean 1990; Hickman 1996). Hickman and McLean (1990) suggested that they have an extensive fossil record ranging back to the Middle Triassic, though gastropods similar to trochoideans are reported from as early as the Ordovician (Hynda 1986; Dzik 1994). However, trochoideans as they were understood in the twentieth century are a polyphyletic group with at least two major groups of similar morphology known since the Mesozoic: Seguenziida and Trochida. Representatives of both orders occur at chemosynthesis-based communities at least since the early Mesozoic times. The oldest trochomorphs are known already from Paleozoic seeps and vents (see Little 2002 and Georgieva et al. 2021 for a review), but their preservation precludes any meaningful identification. The oldest Mesozoic trochoideans, though lacking identifications, are illustrated by Kiel et al. (2017) from Carnian–Norian (Late Triassic) seeps in Turkey (i.e., “gastropod with three keels,” “gastropod with one strong keel,” “*Hikidea*-like gastropod”). Of special interest is trochomorph *Francisciconcha maslennikovi* Little et al., 2004, from the Pliensbachian (Early Jurassic) hydrothermal vent deposit at Figueroa, California (Little et al. 2004), but its attribution to trochoideans remains disputable due to diagenetic distortion of pyrite-replaced shell; *F. maslennikovi* could be even a neomphalid.

11.5.1 *Seguenziida*

The molecular analyses of Kano (2008) and Kano et al. (2009) showed that the clade of deep-sea gastropods forming the order Seguenziida Verrill, 1884, is a monophyletic clade in Vetigastropoda consisting not only of the family Seguenziidae but also the trochoid-like families traditionally included in Trochida: Calliotropidae (=Eucyclidae), Chilodontidae, and Cataegidae. Species of all the abovementioned groups occur at chemosynthesis-based communities, though Chilodontidae is only known from the fossil record. Apart from that, there are four genera of Seguenziida, which were encountered at seeps or vents but not yet assigned to families (Sasaki et al. 2010). Those are *Adeuomphalus* Seguenza, 1876; *Moelleriopsis* Bush, 1897; *Akritogyra* Warén, 1992; and *Ventsia* Warén and Bouchet, 1993. Of these four, only *Adeuomphalus* occurs in the fossil record, but only as a regular deep-water dweller (Kaim 2004). One genus and species of Seguenziidae Verrill, 1884, is known exclusively from vents. *Bathymargarites symplector* Warén and Bouchet, 1989, is relatively common from the vents at the East Pacific Rise. No taxa of Seguenziidae have been found so far in the fossil record of seeps and vents though *Vetulonia philippinensis* (a genus of uncertain position among Seguenziida) from Pliocene seeps in Leyte Island, Philippines, has been classified in this family by Kiel et al. (2020a).

Cataegidae McLean and Quinn, 1987, are present both in Recent and fossil seeps. *Cataegis meroglypta* McLean and Quinn, 1987, is known from Recent seeps in the Caribbean (Sasaki et al. 2010). The fossil record of possible seep cataegids ranges back to the Valanginian (Early Cretaceous). Kaim et al. (2014) described *Cataegis?* sp. from Bear Creek seep site in California. Another species, *Cataegis nakagawensis*, has been described from a Campanian (Late Cretaceous) seep at Omagari, Hokkaido, Japan, by Kaim et al. (2009). *Cataegis godineauensis* (Van Winkle, 1919) occurs in Oligocene–Miocene seeps in the Caribbean (Colombia and Trinidad; Kiel and Hansen 2015), and *Cataegis ramosa* has been described from Pliocene seeps in Leyte Island, Philippines (Kiel et al. 2020a).

Two Recent species occasionally found at seeps, *Bathybembix macdonaldi* (Dall, 1890) and *Putzeysia wiseri* (Calcara, 1842), were previously attributed to the family Chilodontidae Wenz, 1938, but currently, they are included in Eucyclidae (MolluscaBase eds. 2021a, b). Both are rather uncommon at seeps and vents, and both also occur on the regular deep-sea bottom (Sasaki et al. 2010). A possible seep chilodontid has been described by Kaim et al. (2014) as *Chilodonta? reticulata* from the Valanginian (Early Cretaceous) Bear Creek seep site in California. In contrast, the extinct species of Eucyclidae Koken, 1896, are relatively common in Mesozoic seep sites. The oldest occurrence is the “Eucyclid sp.” from Oxfordian–Kimmeridgian seeps in Novaya Zemlya, Arctic Russia (Hryniewicz et al. 2015). *Ambercyclus dilleri* (Stanton, 1895) from Paskenta, California, is of Tithonian age (Kiel et al. 2008), and *Eucycloidea bitnerae* Kaim et al., 2017, from Sassenfjorden, Svalbard (Fig. 11.3c), ranges from Tithonian to Berriasian (Kaim et al. 2017). Another species of *Ambercyclus*, *A. morganensis* (Stanton, 1895), is known from a Valanginian seep site at Rocky Creek in California (Kiel et al. 2008, see also Kaim et al. 2017). Additionally, *Bathybembix* sp. has been reported by Kiel and Goedert (2006) from an Eocene sunken wood community in Washington State.

11.5.2 Trochida

The order Trochida Cox and Knight, 1960, is represented by several families in Recent chemosynthesis-based communities, including Calliostomatidae, Trochidae, Turbinidae, Colloniidae, Margaritidae, and Solariellidae (Sasaki et al. 2010). However, only Colloniidae have abundant representation in ancient seeps while Margaritidae and Solariellidae have only single reports. It might be related to relative difficulty in interpretation of trochomorph shells when they are poorly preserved, and for that reason, many specimens are treated in the open nomenclature.

11.5.2.1 Colloniidae Cossmann in Cossmann and Peyrot, 1917

Colloniid trochomorphs are represented in the fossil record by species of *Cantrainea*, *Hikidea*, *Phanerolepida*, and *Homalopoma*. Particularly common are the Campanian *Hikidea yasukawensis* (Kaim et al., 2009) and *Hikidea omagariensis* (Kaim et al.,

2009) in the Campanian (Late Cretaceous) seeps of Yasukawa and Omagari in Hokkaido, Japan (Fig. 11.4f, g; Kaim et al. 2009). Besides that, *Hikidea svalbardensis* occurs in a Berriasian seep in Sassenfjorden, Svalbard (Kaim et al. 2017), and the type species of *Hikidea osoensis* has been described from a Valanginian seep at Bear Creek, California (Fig. 11.4e; Kaim et al. 2014). Other possible species are a *Hikidea*-like gastropod from a Triassic seep in Turkey (Kiel et al. 2017) and “*Margarita naticoides* Cooke, 1919,” from an Oligocene seep in Cuba (Cooke 1919). The closest Recent relative of *Hikidea* is seemingly *Cantrainea nuda* Okutani, 2001, the species that possesses totally smooth shells apart from a finely pleated subsutural cord (Fig. 11.4h; see also Kaim et al. 2009: Fig. 7G). This species is known from a single specimen, its diagnosis is based solely on shell characters, and it actually may belong to the genus *Hikidea*. The single occurrence of *C. nuda* is known from a vent in Okinawa Trough (Okutani 2001) while other species of *Cantrainea* occur both at seeps and vents and also on regular deep-sea bottoms (Sasaki et al. 2010). Occurrences of *Cantrainea* at ancient seeps include *Cantrainea* sp. at the Miocene seep in Trinidad (Kiel and Hansen 2015) and another *Cantrainea* sp. at the Oligocene seep in Peru (Kiel et al. 2020b). Another species of *Hikidea* has been reported (as vetigastropod gen. et sp. indet.) by Kaim et al. (2008b) from the Coniacian plesiosaur fall in Hokkaido, Japan. A species of *Homalopoma*, *H. abeshinaiensis* (Fig. 11.4i), has been described from the Campanian Omagari seep in Hokkaido, Japan (Kaim et al. 2009). Two additional species have been reported in open nomenclature from Oligocene seeps in Washington State (Goedert and Squires 1990; Kiel 2006). Another species *Homalopoma domeniconii* has been described by Moroni (1966) from Miocene seep in Italy. It seems that *Cantrainea*, *Hikidea*, and *Homalopoma* are closely related, but a molecular study, including *C. nuda*, is required to clarify the nature of this relation.

Phanerolepida Dall, 1907, is a colloniid genus based on the Recent deep-water species *Turbo transenna* Watson, 1879, from Japan (Okutani and Iwahori 1992) with a bathymetric range that overlaps with the bathymetric range of hydrocarbon seep sites occurring in the same area. Some additional fossil species are described from upper Eocene deep-water sediments on the Pacific coast of North America and from the Miocene of Kamchatka and Miocene/Pliocene deposits of Japan (see Hickman 1972; Amano 2005). The only seep occurrence so far is *Phanerolepida onoensis* (Fig. 11.4j) from the Barremian Eagle Creek seep deposit in California (Kaim et al. 2014), which is also the oldest occurrence of this genus.

Margaritidae Thiele, 1924, are represented by three species (*Margarites ryukyuensis*, *M. huloti*, and *M. shinkai*) in seeps and vents off Japan (Sasaki et al. 2010). Three fossil species of *Margarites* are known to date. *Margarites sasakii* has been described from a Campanian Omagari seep in Hokkaido, Japan (Kaim et al. 2009); *M. columbianus* Squires and Goedert, 1991, has been reported from Eocene–Oligocene seeps in Washington State (Goedert and Squires 1990; Squires and Goedert 1991; Kiel 2006); and *Margarites hayashii* has been reported from Pliocene seeps in Leyte Island, Philippines (Kiel et al. 2020a). The occurrences of Solariellidae Powell, 1951, at fossil seeps are reported by Kiel (2006) from an Oligocene seep in Washington State and by Kiel et al. (2020a) from Pleistocene seeps in Leyte Island, Philippines.

11.6 Neritimorpha

Neritimorpha Koken, 1896, is a distinct clade of gastropods of uncertain relationship to other gastropods. Most recent molecular studies (Cunha and Giribet 2019) suggest that it forms a sister clade to a clade comprising Caenogastropoda and Heterobranchia. Neritimorphs are typically shallow-water, but there are also a few taxa adapted to deep water including seeps and vents (Sasaki et al. 2010). The family Phenacolepadidae Pilsbry, 1895, is clearly divided into two distinct sub-families: shallow-water Phenacolepadinae Pilsbry, 1895, and deep-water Shinkailepadinae Okutani et al., 1989. Species of the genus *Shinkailepas* are known from vents worldwide (Sasaki et al. 2010), while the monotypic genus *Olgasolaris* Beck, 1992, with the type species *O. tollmanni* from the Manus back-arc basin has been recently synonymized with *Shinkailepas* (Fukumori et al. 2019). Another monotypic genus *Bathynnerita* Clarke, 1989, with the type species *Bathynnerita naticoidea*, which is distributed at hydrocarbon seep sites in the Louisiana Slope of the Gulf of Mexico and the Caribbean (Warén and Bouchet 2001), has been recently synonymized with *Thalassonerita* Moroni, 1966, and relocated from Neritidae to Shinkailepadinae (Fukumori et al. 2019). The type species of *Thalassonerita*, *T. megastoma* Moroni, 1966, has been described from a Miocene seep in Italy (Moroni 1966). Another species, *Thalassonerita eocenica* Squires and Goedert, 1996, has been described from middle Eocene seep deposits in Washington State, USA (Squires and Goedert 1996; Hybertsen and Kiel 2018). Another neritid from an Oligocene cold-seep deposit of the Lomitos cherts, Peru, has been mentioned by Olsson (1931) but never illustrated (Kiel et al. 2020b). The only available specimen from that locality is badly preserved and left by Kiel et al. (2020a, b) in open nomenclature as Neritimorpha indet.

Two poorly preserved neritids have been also found in the Oxfordian (Late Jurassic) seep carbonates at Beauvoisin, France (Kiel et al. 2010), and an Early Cretaceous seep in the Crimea (Kiel and Peckmann 2008), but they are most likely not related to *Thalassonerita* (Kiel, 2010), being more conchologically similar to other Mesozoic neritoids (Fukumori et al. 2019). Molecular age estimates suggest that shinkailepadids diverged from neritids in the Late Cretaceous (Kano et al. 2002).

11.7 Neogastropoda

The order Neogastropoda Wenz, 1938, is one of the most extremely diversified and abundant groups of benthic predators and scavengers. Nearly all are marine forms and they constitute about one-third of all living gastropod species. No wonder then that they also adapted to vent and seep environments. The most common in such environments are Buccinidae and Turridae while the other groups are rare (Sasaki et al. 2010). Almost all modern families of neogastropods emerged in the Cretaceous

and starting with the Late Cretaceous neogastropods are common fossils in marine sediments, while older findings are rare and all need a critical review. Based on shell morphology, it seems that the first true neogastropods appeared in the Early Cretaceous (Kollmann 1982; Taylor and Morris 1988; Kaim 2004) with the oldest known record from the Valanginian (early Early Cretaceous) of Poland (Kaim 2004). The earliest known occurrence of a true neogastropod at ancient seeps is “Neogastropoda indet.” (Fig. 11.3h) reported by Kaim et al. (2009) from the Campanian (Late Cretaceous) seep at Yasukawa, Hokkaido, Japan. Some neogastropods are also recorded from Miocene and Pliocene seeps in Japan, but their preservation is rather poor and their taxonomy is not fully resolved (see, for example, Tanaka 1959; Miyajima et al. 2018).

Two extinct groups of Mesozoic caenogastropods are repetitively discussed as possible stem and/or sister groups of Neogastropoda, Purpurinidae and Pseudotrionidae (= Maturifusidae), with a fossil record reaching back to the Triassic. Both groups are reported from ancient seeps.

11.7.1 *Purpurinidae and Pseudotrionidae*

The family Purpurinidae Zittel, 1895, was proposed to be a sister (Taylor et al. 1980) or ancestral group of neogastropods (Kaim 2004) and may represent ancestors of Tonnoidea (Bandel 1993). The purpurinid *Cretadmete* sp. (Fig. 11.3g) has been reported by Kaim et al. (2017) from the Tithonian (Late Jurassic) seep in Sassenfjorden, Svalbard. According to Kiel et al. (2008), another possible purpurinid is *Bathypurpurinopsis stantoni* Kiel et al., 2008, from the Albian (Early Cretaceous) seep of Cold Fork of Cottonwood Creek in California.

The Pseudotrionidae Golikov and Starobogatov, 1987 (= Maturifusidae Gründel, 2001), is commonly regarded as a stem group of the Neogastropoda (e.g., Taylor et al. 1980; Szabó 1983; Riedel 2000; Kaim 2004). A possible pseudotrionid has been reported as “Maturifusid sp.” by Hryniewicz et al. (2015) from a Berriasian–Early Valanginian seep in Novaya Zemlya, Arctic Russia.

11.7.2 *Buccinoidea*

Buccinidae Rafinesque, 1815, are relatively common and diversified at Recent seeps and vents and include the genera *Neptunea*, *Buccinum*, *Eosipho*, *Bayerius*, and *Calliloncha* (Sasaki et al. 2010). Buccinids have also been encountered in Cenozoic seeps. *Colus sekiuensis* Kiel and Goedert, 2007, has been found both at an Oligocene seep in Peru (Kiel et al. 2020b) and organic falls in Washington State (Kiel and Goedert 2007). Additionally, *Colus?* sp. has been reported by Hybertsen and Kiel (2018) from an Eocene seep in Washington State. Another species, *Colus* cf. *fujimotoi* Hirayama, 1955, is known from Eocene and Oligocene seeps in Hokkaido, Japan

(Amano and Kiel 2011). Furthermore, *Trominina japonica* (Takeda, 1953) has been identified in the Oligocene seep carbonate at Kami-Atsunai in Hokkaido (Amano et al. 2013). *Eosipho hoernesii* and nassarid *Tritia ruggierii* have been reported by Moroni (1966) from Miocene seep in Italy.

Another bunch of buccinid species encountered at seeps represent the family Parancistrolepidinae Habe, 1972. Amano and Oleinik (2016) reported *Ancistrolepis modestoideus* (Takeda, 1953) and *Bathyancistrolepis mikasaensis* Amano and Oleinik, 2016, from an Eocene seep at Mikasa in Hokkaido, *Ancistrolepis* sp. from an Eocene Kiritachi seep in Hokkaido, and *Ancistrolepis koyamai* (Kuroda, 1931) from a Miocene Akanuda seep in Nagano Prefecture, Central Honshu. The latter species is also known from non-seep deposits (Amano et al., 1996). *Clinopegma* aff. *borealis* Tiba, 1969, is known from a Miocene seep at Morai in Hokkaido (Amano, 2003). Another occurrence might be *Ancistrolepis teglandae* (Weaver, 1942) where this species is associated with Oligocene vesicomysids but seep carbonates were not found (Kiel and Amano 2010). One other possible buccinid is also *Levifusus? angelicus* Cooke, 1919, from an Eocene seep of Cuba (Kiel and Peckmann 2007). Questionable buccinid *Urahorosphaera kanekoi* were described from the sunken wood community of the Paleocene Katsuhira Formation (Amano and Oleinik 2014).

11.7.3 *Conoidea*

Species of Conoidea Fleming, 1822, are generally common predators in deep-sea environments, and they are also abundant at Recent seeps and vents (Sasaki et al. 2010). Species of three different conoidean families (Mangeliidae, Raphitomidae, and Turridae) are known from Oligocene seeps in Washington State (Kiel 2006), namely, *Benthomangelia?* sp.; *Xanthodaphne campbellae* Kiel, 2006; and *Turrinosyrinx hickmanae* Kiel, 2006; respectively.

11.7.4 *Muricoidea*

Muricoidea Rafinesque, 1815, are rather uncommon at Recent seeps, basically restricted to three species of *Trophon* Montfort, 1810, which also occur on the regular deep-sea bottom (Sasaki et al. 2010). Two species of Muricoidea are known from Cenozoic seeps in Japan: *Abyssotrophon?* sp. is reported from a late Eocene to early Oligocene seep at Tanami, Southern Honshu (Amano et al. 2013), and *Trophonopsis* sp. is recorded from a Miocene Akanuda seep in Nagano Prefecture, Central Honshu (Miyajima et al. 2017).

11.8 Heterobranchia

Heterobranchia Burmeister, 1837, is a clade of subclass rank comprising highly diversified taxa in marine, freshwater, and continental environments. In contrast, the diversity of heterobranchs is relatively low in Recent vent and seep communities (Sasaki et al. 2010). Five major groups of heterobranchs are reported so far from Recent seeps and vents, Pyramidellidae, Cephalaspidea, Orbitestellidae, Hyalogyrinidae, and Xylodisculidae (Sasaki et al. 2010), with the latter being more characteristic to wood falls. All but Pyramidellidae are known from ancient chemosynthesis-based communities.

11.8.1 *Cephalaspidea*

Cephalaspids are unknown from Recent hydrothermal vents and rare at seeps. Also in the fossil record, they are uncommon and may constitute fortuitous occurrences. Most common in ancient seeps are acteonoids. *Acteon exsculptus* Tullberg, 1881, and *Acteon frearsianus* Tullberg, 1881, are known from a Berriasian–Early Valanginian seep in Novaya Zemlya (Tullberg 1881; Hryniewicz et al. 2015), both species awaiting revision (Hryniewicz et al. 2015). Moreover, *?Sulcoactaeon* sp. (Fig. 11.5b) has been reported from a Campanian Yasukawa seep in Hokkaido, Japan (Kaim et al. 2009), and two species of *Acteon* in open nomenclature have been reported from Eocene to Oligocene seeps in Washington State (Kiel 2006) and an Oligocene seep in Peru (Kiel et al. 2020a, b). Besides acteonoids, the diaphanid *Diaphana* sp. has been recorded by Kaim et al. (2014) from the Valanginian seeps of West Berryessa, California, scaphandrid *Ellipsocephala* sp. (Fig. 11.5c) from Paleocene seeps in Svalbard (Hryniewicz et al. 2019), and two species of *Cylichna* in open nomenclature from Oligocene seeps in Washington State and Peru by Kiel (2006) and Kiel et al. (2020a, b), respectively. *Eocylichna multistriata* (Takeda, 1953) has been reported from the Oligocene Kami-Atsunai seep in Hokkaido (Amano and Jenkins 2013). An unidentified cephalaspid has also been reported by Kiel et al. (2017) from a Late Triassic seep in Turkey.

11.8.2 *Orbitestellidae*

The orbitestellid genus *Lurifax* unites vent and seep taxa in the Mediterranean, New Zealand, Japan, and the Mid-Atlantic Ridge (Sasaki et al. 2010). A single fossil species, *Lurifax goederti* Kiel, 2006, is known from the Eocene to Oligocene seeps in Washington State (Kiel 2006).

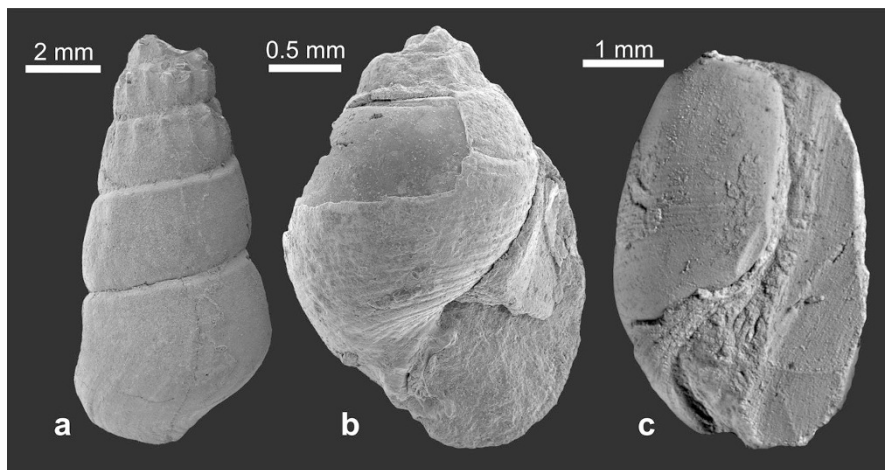


Fig. 11.5 Rissoid? (or hokkaidoconchid) and heterobranch gastropods. (a) Rissoid (or hokkaidoconchid) *Hokkaidoconcha? hignalli* Kaim and Kelly, 2009, from Tithonian (Late Jurassic) Gateway Pass seep carbonates in Alexander Island, Antarctica (see Kaim and Kelly 2009). (b) Cephalaspid ?*Sulcoactaeon* sp. from the Campanian (Late Cretaceous) Yasukawa seep site in Hokkaido, Japan (see Kaim et al. 2009). (c) Scaphandrid *Ellipsoscapa* sp. from the Paleocene seep carbonates in Hollendarbukta, Svalbard (see Hryniewicz et al. 2019)

11.8.3 *Hyalogyrinidae*

Hyalogyrinids occur abundantly on bacterial mats in sulfide-rich areas at seeps and whale falls as well as at vents (Braby et al. 2007; Sasaki et al. 2010). Their simple small shells are difficult to tell apart from other similar forms of skeneids, trochids, and neomphalids, in particular in fossil material when shells are poorly preserved (see, e.g., “skeneiform gastropod” in Kaim et al. 2009: p. 483, which highlights this problem). Therefore, only two species of *Hyalogyrina* have been identified so far: *Hyalogyrina knorringfjelletensis* Kaim et al., 2017 (Fig. 11.3f), from the Berriasian seep in Sassenfjorden, Svalbard (Kaim et al. 2017), and *Hyalogyrina* sp. from the Eocene to Oligocene seeps in Washington State (Kiel 2006; Hybertsen and Kiel 2018).

11.8.4 *Xylodisculidae*

Though some xylodisculids have been found at seeps and vents, they are most common at wood falls (Sasaki et al. 2010). A single fossil species, *Xylodiscula okutanii* Kiel and Goedert, 2007, is known from an Oligocene–Miocene wood fall in Washington State (Kiel and Goedert 2007).

11.9 Other Groups

Several other groups of gastropods have some representatives in Recent and ancient seeps, but they most commonly constitute fortuitous occurrences or possess only a few taxa typical of chemosynthesis-based communities. Such singular occurrences can be highlighted by the presence of *Cypraea semen* Cooke, 1919, at an Eocene seep in Cuba (Kiel and Peckmann 2007), “Cerithiopsid incertae sedis” of Kiel (2006) at an Oligocene seep in Washington State, and the turritellid *Orectospira wadana* (Yokoyama, 1890) at a late Eocene–early Oligocene seep at Tanami, Southern Honshu, Japan (Amano et al. 2013), and at an early Oligocene seep at Kami-Atsunai, Hokkaido, Japan (Amano and Jenkins 2013). Amathinid *Carinorbis clathrata* (described as *Phasianema taurocrassum*) and cassid *Galeodea delibrata* have been reported by Moroni (1966) from Miocene seep in Italy. Occurrences of other groups are listed below.

11.9.1 Rissoidae

Rissoids are not typical gastropods of chemosynthesis-based communities. Although some rissoids (*Alvania*, *Benthonella*, *Pseudosetia*, and *Rissoa*) do occur at seeps and vents, especially in the North Atlantic (e.g., Gebruk et al. 2003; Sasaki et al. 2010; Schander et al. 2010; Génio et al. 2013), it seems that it is a relatively recent colonization event rather than ancient adaptation (Kaim et al. 2017). One possible genus with ancient history in seeps is the extinct *Boreomica* Guzhov, 2017, which was established for taxa thus far classified as *Hudlestoniella* Cossmann, 1909. Guzhov (2017) argued that these taxa differ from the type species of *Hudlestoniella*, warranting description of a new genus. Kaim et al. (2004) and, subsequently, Guzhov (2017) classified *Hudlestoniella* (and thus *Boreomica*) in the Rissoidae based on protoconch morphology.

Boreomica undulata (Tullberg 1881) and *Boreomica pusilla* (Tullberg 1881) are known from Tithonian and Berriasian–Early Valanginian seeps in Novaya Zemlya, respectively (Hryniewicz et al. 2015), while *Boreomica hammeri* (Kaim et al., 2017) is known from a Berriasian seep in Sassenfjorden, Svalbard (Kaim et al. 2017). Another species of *Boreomica* might be *Hokkaidoconcha hignalli* Kaim and Kelly, 2009 (Fig. 11.5a), known from a mass occurrence in the Tithonian (Late Jurassic) Gateway Pass seep from Alexander Island in Antarctica (Kaim and Kelly 2009), since it is similar to *Boreomica hammeri* from Svalbard (Kaim et al. 2017). The protoconch of *H. hignalli* is unknown; therefore, its hokkaidoconchid or rissoid identity cannot be confirmed (Kaim et al. 2017).

11.9.2 *Aporrhaidae*

Aporrhaidae are gastropods that live on muddy and sandy bottoms, sometimes in very large populations, but in Recent seas they are restricted to two genera only (*Aporrhais* and *Arrhoges*). In the past, this group was much more diversified, especially in the Jurassic and Cretaceous (see, for example, Kaim 2004), and depleted in diversity in Cenozoic times. Seep occurrences of aporrhaidae should be considered fortuitous and include *Pseudanchura biangulata* (Anderson, 1938) from a Barremian seep at Eagle Creek, California (Kaim et al. 2014); *Aporrhais* cf. *gracilis* Koenen, 1885 (Fig. 11.3e), from a Paleocene seep in Svalbard (Hryniewicz et al. 2019); *Aporrhaidae* indet. (originally as a provannid) from a Paleocene seep in Panoche Hills, California (Schwartz et al. 2003); and “aporrhaid gastropod” from a Cenomanian seep at Awanui, New Zealand (Kiel et al. 2013). Xenophorid *Xenophora borsoni* has been reported by Moroni (1966) from Miocene seep in Italy.

11.9.3 *Ampullinidae and Naticidae*

The Ampullinidae vs. Naticidae conundrum is another highlight of a problem in identification of morphologically simple shells in the fossil record. Naticids are predatory littorinimorphs while ampullinids are campaniloid grazers with similarly smooth and globular shells (for more information, see, for example, Kase and Ishikawa 2003). Representatives of both groups have been identified in ancient seeps. “Ampullinid gastropod” has been reported by Kiel and Peckman (2008) from a Berriasian seep in the Crimea (Kiel and Peckmann 2008), while *Globularia isfjordensis* (Vonderbank, 1970) is common from a Paleocene seep in Svalbard (Fig. 11.3d; Hryniewicz et al. 2019).

Naticids at ancient seeps are represented by *Cryptonatica* sp. from a late Eocene to early Oligocene Tanami seep in Southern Honshu, Japan (Amano et al. 2013), and from a Miocene Morai seep in Hokkaido, Japan (Amano 2003); *Euspira meisensis* (Makiyama, 1926) from an Oligocene seep at Kami-Atsunai, Hokkaido, Japan (Amano and Jenkins 2013); *E. pallida* (Broderip and Sowerby, 1829) from a Miocene Morai seep, Hokkaido, Japan (Amano 2003), and Pliocene Matsunoyama seep, Central Japan (Miyajima et al. 2018); *Euspira?* sp. from an Eocene Poronai seep, Hokkaido, Japan (Amano and Jenkins 2007); and possibly *Sassenfjordia sassenfjordensis* Kaim et al., 2017, from a Berriasian seep in Sassenfjorden, Svalbard (Kaim et al. 2017). Occurrences of naticid-like shells are commonly associated with predatory drill holes, which may suggest that they are indeed naticids. Such drill holes have been noted previously in fossil cold-seep mollusks by Amano (2003), Amano and Jenkins (2007), Amano and Kiel (2007), Kiel et al. (2008, 2016), and Hryniewicz et al. (2019).

11.9.4 *Eulimidae*

Eulimids are parasitic snails common in Recent oceans but not yet reported from seeps and vents (Sasaki et al. 2010). Three species of eulimids (*Niso littlei* Kiel, 2006, Eulimid sp. 1, and Eulimid sp. 2) were reported by Kiel (2006) from Oligocene seeps in Washington State.

11.10 Conclusions and Future Directions

Gastropods are one of the most important groups of organisms adapted to thrive in chemosynthesis-based communities. Trochomorph gastropods are known already from Paleozoic seeps and vents (Peckmann et al. 2001; Little 2002) though their taxonomy remains poorly explored due to poor preservation.

The Carnian–Norian (Late Triassic) seep fauna from Turkey (Kiel et al. 2017) display a high diversity of gastropods including possible abyssochrysoid *Paskentana*, possible trochoidean *Hikidea*, and an unidentified cephalaspid (Fig. 11.6). The Jurassic and Cretaceous were times of abyssochrysoid dominance in seep and vent gastropod communities. *Abyssomelania*, *Hokkaidoconcha*, and *Paskentana* are known already in the Jurassic. *Ascheria*, *Atresius*, and *Humptulipsia* appear in the Early Cretaceous, while *Cypriocconcha*, *Desbruyeresia*, and *Provanna* are reported from the Late Cretaceous (the latter two are most likely present already in the latest Early Cretaceous). In several ancient seeps, abyssochrysoids occur in mass accumulations (e.g., *Paskentana* in the Valanginian Bear Creek seep and *Desbruyeresia* in the Cenomanian Kanajirisawa seep). Also from the Jurassic is the oldest report of neomphalid gastropods in seeps, though their diversity is much restricted in comparison to present diversity. Most common are species of *Retiskeneia*, which also today occur in seeps. Noteworthy is the absence of neomphalids in Late Cretaceous vents in Cyprus, while abyssochrysoids are common and well diversified there. This may suggest that the neomphalid radiation in vents came much later. The time of this radiation is unknown due to the absence of fossiliferous vent deposits from Cenozoic times. Limpet-shaped gastropods occur occasionally at seeps already in the Jurassic but are really common only in Campanian (Late Cretaceous) seeps in Japan where a compressed morphotype of *Bathyacmaea* thriving on worm tubes is very abundant. Similarly, colloniid vetigastropods appear in large quantities only in Late Cretaceous seeps although they were present already in the Early Cretaceous. Eucyclid seguenziids are extremely common in Jurassic seas (e.g., Ferrari et al. 2014) and they apparently migrated to Jurassic seeps while cataegids appeared in the Cretaceous and still occur at seeps today. Stem and/or sister groups of neogastropods (Purpurinidae and Pseudotritonidae) first appeared at seeps in the Jurassic, while true neogastropods are nearly absent in Mesozoic seeps, apart from a single poorly preserved specimen in a Campanian (Late Cretaceous) seep in Japan. Otherwise, neogastropods appear in larger numbers in Oligocene seeps. Cephalaspids

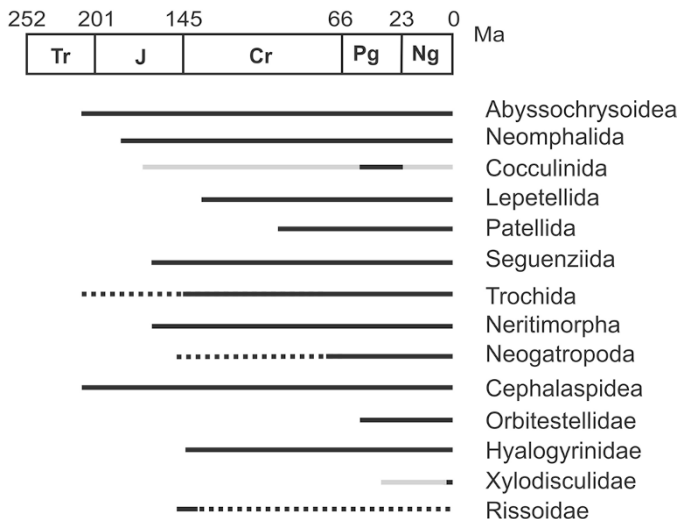


Fig. 11.6 Geological ranges of major gastropod clades at seep/vents (black lines) and organic falls (gray lines). Paleozoic occurrences (as taxonomically uncertain) not included

are recorded at seeps from the Triassic but never occur in larger numbers, being apparently only opportunistic in these environments.

Nearly nothing is known about gastropods from Paleozoic seeps, and still too little is known about gastropods from the Triassic and Early Jurassic seeps. A Toarcian seep fauna from Argentina (currently under study) may partially fill this gap. Another poorly known period in the evolution of chemosynthesis-based communities is the latest Cretaceous–Paleocene interval. This paucity of information causes a major problem in evaluating the influence of the Cretaceous–Paleogene extinction event on the evolution of seep and vent faunas. Another major problem in interpreting the evolution of chemosynthesis-based communities is the paucity of ancient vent communities in general and Cenozoic ones in particular.

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