Chapter 8
The Fossil Record of Vent and Seep Mollusks

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Contents

8.1   Introduction

Mollusks have by far the most extensive and best-investigated fossil record of all organism groups inhabiting hydrothermal vents and hydrocarbon seeps. More than 250 bivalve, gastropod, and polyplacophoran species have been reported from ancient vents and seeps, nearly 200 of them from the Cenozoic alone. Members of at least five bivalve families live in symbiosis with sulfur- or methane-oxidizing bacteria, and among the gastropods at least three groups took this path of adaptation. Mollusks are common at vent communities of Mesozoic and Paleozoic age, but appear to be less common in seep communities of this age. It is generally believed that brachiopods were the dominant taxon at Mesozoic and Paleozoic seeps; however, an increasing number of Paleozoic and Mesozoic seep sites with mollusks have been discovered in recent years.

Mollusks have often been used to formulate hypotheses on the evolutionary history of the vent and seep fauna, because they dominate many modern sites and

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because of their high degree of adaptation. Their rich fossil record has been used to test such hypotheses and to outline a paleobiologic view of their evolutionary history. A wealth of taxonomic work on mollusks especially from seeps during the past 5 years significantly enhanced the quality of the paleontologic data. However, many faunas remain to be described and revised. This chapter provides an outline and a critical evaluation of the current knowledge of the fossil history of the major mollusk groups at ancient vents and seeps. It also presents certain aspects of the evolution of the vent and seep fauna from a paleontologic point of view, and indicates gaps and not-well-understood aspect of the fossil record of these faunas.

8.2 Bivalvia

Bathymodiolins. The two bivalve groups that dominate vents and seeps today, the Vesicomyidae (Fig. 8.1) and Bathymodiolinae (Figs. 8.2a, b), are geologically speaking young groups. They first appear in the fossil record in the middle Eocene. Compared to the vesicomyids which dominated fossil seeps since the late Eocene, the bathymodiolins apprently made a slow start. They are common at a few late Eocene and Oligocene seep deposits in Washington State, USA, where they are also found on fossil whale- and wood-falls (Goedert and Squires 1990; Squires and Goedert 1991; Kiel 2006; Kiel and Goedert 2006a). But otherwise only few bathymodiolins have been found at some Oligocene to Pliocene seep sites in the Caribbean, Italy, and Japan (Taviani 1994; Gill et al. 2005; Majima et al. 2005). This sparse Neogene record is surprising considering the ubiquity of bathymodiolins at modern vents and seeps. It is
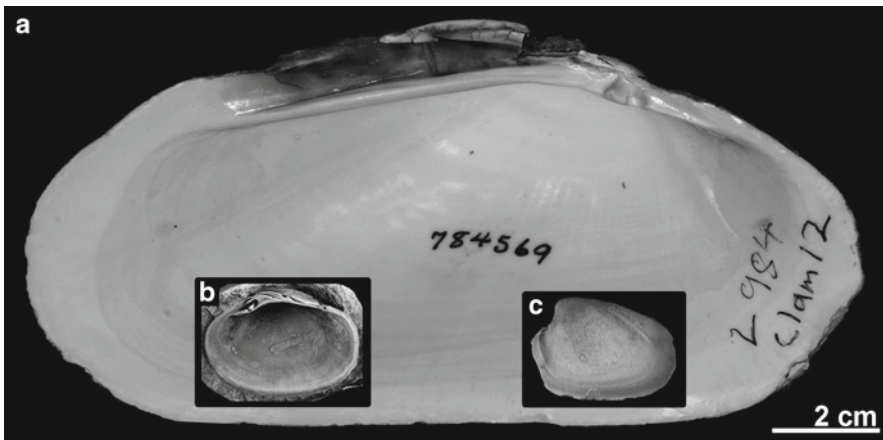

Fig. 8.1 Vesicomyid bivalves, (**a**) Recent *Calyptogena magnifica* from a hydrothermal vent on the Galapagos Rift; (**b**) The oldest *Calyptogena*, a new species from Early Oligocene dark shales the Katalla district in southern Alaska; (**c**) The oldest vesicomyid: *Archivesica* cf. *tschudi* from a middle Eocene seep deposit in western Washington State, USA (Images from Kiel and Amano [2010; b] and Amano and Kiel [2007; c])
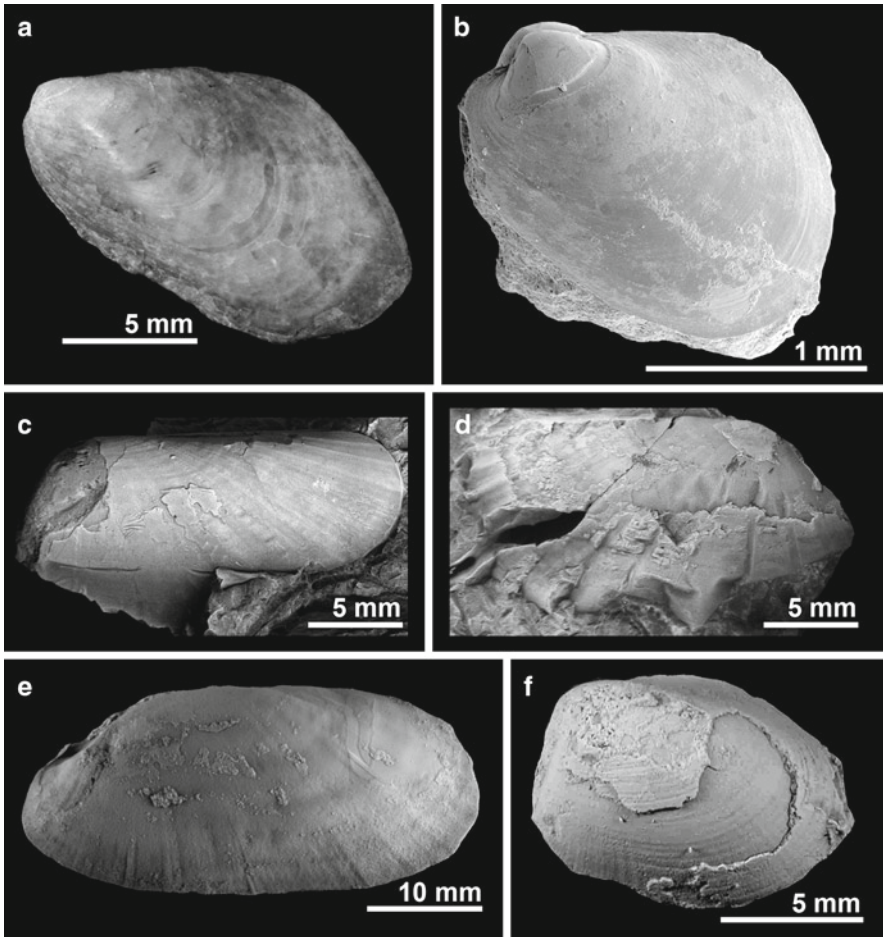
Fig. 8.2 Bathymodiolins, solemyids and *Nucinella*. (**a**), (**b**) The oldest fossil bathymodiolin, *Bathymodiolus willapaensis*, from Eocene seep deposits in Washington State, USA; adult shell (**a**) and juvenile shell (**b**). (**c**), (**d**) Solemyids from an Early Miocene seep deposit in Washington State, showing the outer organic layer (periostracum) that overlaps the calcareous shell. (**e**) Internal mold of the Early Cretaceous *Acharax mikasaensis* from Hokkaido, Japan, showing characteristic features of the anterior muscle attachment scar. (**f**) Late Cretaceous *Nucinella gigantea* from Hokkaido, Japan, with internal radial striations (lower *left*) (Images from Kiel [2006; b], Kiel [2010; d] and Kiel et al. [2008a; e, f])

also at odds with the suggestion of Miyazaki et al. (2008) that bathymodiolins spread worldwide during the early/middle Miocene climate optimum. There is molecular and morphologic evidence that several lineages of large bathymodiolins exist and that these lineages adapted independently to seeps and vents, possibly at different geologic times (Jones et al. 2006; Cosel and Janssen 2008; Chapter 6, this volume). The geologically oldest bathymodiolins, *Bathymodiolus willapaensis* Squires and Goedert 1991 and *Idas*? *olympicus* Kiel and Goedert 2007 have been identified based on the shape of

their early juvenile shells and their shell microstructure (Kiel 2006; Kiel and Goedert 2007; Génio and Kiel 2010), but to clarify to which of the modern lineages they belong, if at all, needs further investigation. Muscle and mantle attachment scars in fossil bathymodiolins might provide further insight to their identity and to the evolutionary history of bathymodiolins. The only pre-Cenozoic record of a putative seep-related mytilid, *Modiola major* from late Jurassic to early Cretaceous seep deposits in California, is in fact a member of the extinct bivalve clade Modiomorphida (Stewart 1930; Kiel and Peckmann 2008).

Vesicomyids. The recorded history of the vesicomyids is very different from that of the bathymodiolins, and can probably be called the most successful adaptation to vents and seeps by any mollusk group. After their first appearance in seep deposits of the middle Eocene Humptulips Formation in Washington State, vesicomyids are found, often in large numbers, in virtually every seep deposit world-wide from the Late Eocene onward. The family is not restricted to vents and seeps, there is a series of records from turbidite deposits, organic-rich shales, and whale-falls (Goedert and Squires 1993; Amano et al. 2001; Amano and Kanno 2005; Amano and Little 2005; Kiel and Amano 2010). Generic distinctions within the family have long been neglected, but systematic improvements have recently begun (Cosel and Salas 2001; Krylova and Sahling 2006; Amano and Kiel 2007; Kiel 2007) and are likely to reveal more about the evolutionary and biogeographic history of this family. Previous reports of vesicomyids from the Cretaceous period could not be confirmed. These had been described from Japanese seep deposits. Recent re-investigations of these sites and their fossils showed that an Albian species does in fact belong to the solemyids (Kiel et al. 2008a), a Cenomanian record belongs to a new large and veneriform lucinid genus (Amano et al. 2008), and a large Campanian specimen previously coined '*Calyptogena*' most likely belongs to the extinct bivalve clade Modiomorphida (Amano and Kiel 2007; Kiel and Peckmann 2008).

Further bivalve families that are frequently encountered at modern vents and seeps are the solemyids, tyasirids, and lucinids. The species of these families live buried within the sediment and are thus less obvious than the surface-dwelling vesicomyids and bathymodiolins. In the fossil record, however, where seep carbonates can easily be broken up to recover fossils, these families are quite common.

Solemyids. The Solemyidae are among the most basal families among the Bivalvia with a fossil record dating back to the Ordovician. They are well-represented – although never abundant – at seeps from the later Mesozoic onwards, and there are also a couple of Paleozoic records. Modern and Mesozoic-Cenozoic solemyids are usually differentiated into two genera depending on the position of the ligament: in *Solemya* the ligament is internal, in *Acharax* it is external. Of the two genera, *Acharax* appears to be more common at seeps, perhaps because it is adapted to greater water depth (Chapter 5, this volume). Modern solemyids with their elongate shells and characteristic radial ribs (Figs. 8.2c–e) first appear at seeps in the late Jurassic of California (Campbell and Bottjer 1993; Campbell 2006).

At modern seep sites, solemyids are usually found in the periphery of the seep where sulfide flux and concentrations are low (Sahling et al. 2002). The same pattern of

distribution was reported from a Late Cretaceous (Campanian) seep site on Hokkaido, Japan (Jenkins et al. 2007b) and from an Early Cretaceous seep site in eastern Greenland (Kelly et al. 2000) where solemyids occur in patches at the periphery of the seep carbonates. Also at some of the Paleogene seep sites in Washington State, USA, peripheral clusters of solemyids were found, whereas at other sites, solemyids were rare and scattered through the deposit (own observation). In contrast, at an early Cretaceous seep site on Hokkaido (the Albian Ponbetsu site) solemyids, along with thyasirids and lucinids are common throughout the deposit (Kiel et al. 2008a). This site, however, consists of two silty carbonate blocks with few authigenic cements which most likely resulted from low seepage rates and diffuse seepage (Peckmann et al. 2009) which could explain the relative abundance of solemyids.

An Early Carboniferous record from a seep in the Harz Mountains in Germany has been questioned because the specimens found so far are poorly preserved internal molds lacking the characteristic radial ribs and muscle attachment scars (Peckmann et al. 2001; Goedert et al. 2003). From a middle Devonian seep deposit in Morocco known as Hollard Mound, a potential sole-myid was reported as *Dystactella*? (Peckmann et al. 1999; Aitken et al. 2002). The description and figure of this species does indeed resemble that of other well-known Paleozoic members of this genus (Pojeta 1988). Solemyids might thus have been exploiting sulfides at seeps for nearly 400 million years.

Nucinella. Phylogenetically related to solemyids is *Nucinella* (family Manzanellidae), a genus of generally very small deep-sea species that rarely exceed a few millimeters in length. Recently, comparatively large specimens of *Nucinella*, reaching nearly 2 cm in length, have been reported from Late Cretaceous seep deposits on Hokkaido, Japan (Fig. 8.2f; Amano et al. 2007a; Kiel et al. 2008a) and a similar shell has been found in a late Triassic seep site in Oregon (Peckmann et al. 2010). Their large size, internal radiating striae similar to those in the chemosymbiotic lucinids and thyasirids, and the lack of a gut in the large extant *Nucinalla maxima* lead Amano et al. (2007a) to suggest the possibility of chemosymbiosis in such large *Nucinella* species (see also Chapter 5, this volume).

Thyasirids. Living members of the Thyasiridae are apparently able to host both sulfur- and methane-oxidizing symbionts, although small species may have no symbionts at all (Kamenev et al. 2001; Dufour 2005; Chapter 5, this volume). In fossil seeps thyasirids usually occur in small clusters or scattered throughout the deposit. Despite their basal position among the heterodont bivalves, thyasirids have a relatively short fossil record (Taylor et al. 2007). The oldest species with typical thyasirid characters is from the Early Cretaceous (Hauterivian) of Europe, the oldest record from a seep deposit is of Albian age (Kiel et al. 2008a) and it has been reported from a late Cretaceous wood-fall (Kiel et al. 2009). These early records can be attributed to the genus *Thyasira*. From the Maastrichtian onward the large genus *Conchocele* is more commonly found (cf., Kiel et al. 2008a). There is a tendency among paleontologists to lump large Cenozoic thya-sirids from the North Pacific rim into a single species: *Conchocele bisecta* (Fig. 8.3b). However, Kiel and Peckmann (2007) and Kiel and Goedert (2007) indicated that thya-sirid specimens from Eocene to Oligocene seeps and organic substrates in this region show distinctive shell features and do in fact belong to more than one species.
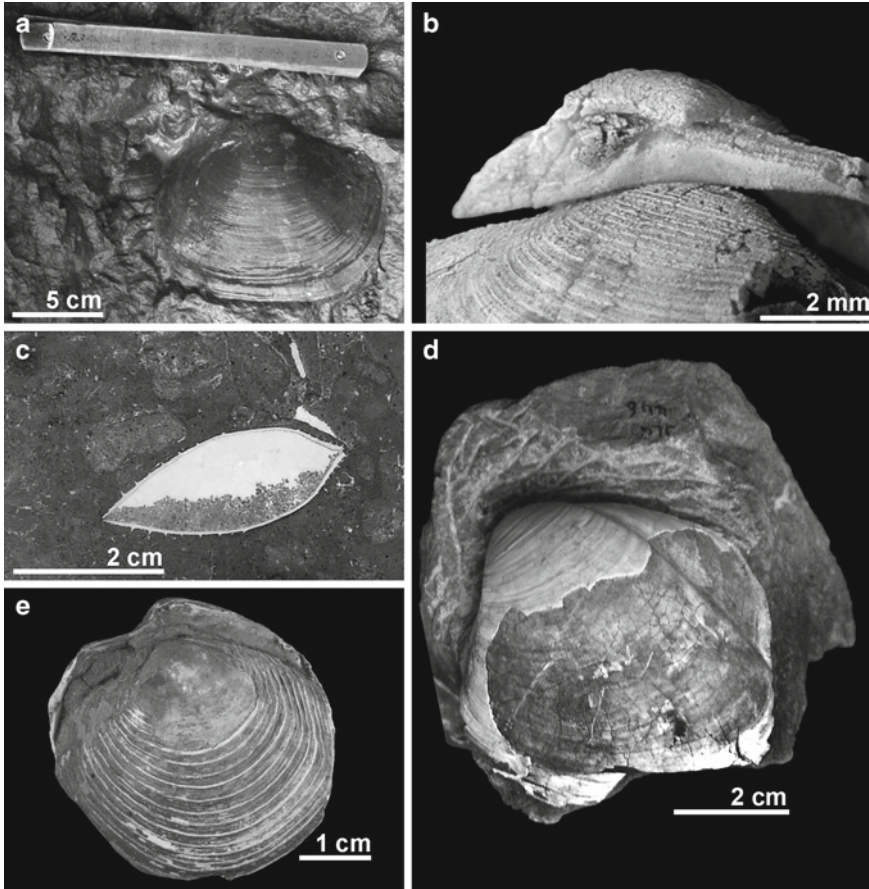
Fig. 8.3 Lucinids and thyasirids. (**a**) The lucinid *Nipponothracia ponbetsensis* from an Albian (Early Cretaceous) seep site on Hokkaido, Japan. (**b**) Close-up on the edentulous hinge of the lucinid *Nipponothracia yezoensis* from a Cenomanian (Late Cretaceous) seep site on Hokkaido, Japan. (**c**) Cross-section of an articulated specimen of *Lucinoma* spp. in an Early Miocene seep limestone in Washington State, USA. (**d**) *Lucinoma acutilineata*, a common species in Oligocene seep deposits in Washington. (**e**) The thyasirid *Conchocele bisecta* from the Early Miocene Astoria Formation in Washington (Images from Kiel et al. [2008a; b], and with courtesy of Jörn Peckmann [c])

Lucinids. Lucinids live in symbiosis with sulfur-oxidizing bacteria. They do not, however, rely entirely on their endosymbionts for nutrition but are also capable of suspension-feeding (see also Chapter 5, this volume). In contrast to the thyasirids the fossil history of lucinids can be traced back into the Silurian and it is assumed that the chemosymbiotic lifestyle is as old as the family (Taylor and Glover 2006). It is thus surprising that lucinids are found at ancient seeps only from the Late Jurassic onward (Gaillard et al. 1985, 1992). They are usually found as articulated shells, often in large clusters or shell beds, but also as scattered individuals. At

modern vents and seeps they appear to be rare, but this might be a sampling artifact because most attention has been given to the larger epifaunal animals with less sampling effort devoted to the deeper-burrowing infauna (Hashimoto et al. 1995; Salas and Woodside 2002; Glover et al. 2004).

In Late Jurassic to Eocene seeps lucinids are taxonomically diverse and many species appear to be restricted to individual seep sites or regions. *Nymphalucina occidentalis* is one such example: it occurs exclusively in the Western Interior Seaway of the United States, a shallow seaway that connected the Gulf of Mexico and the Arctic Ocean during the Late Cretaceous. Here *Nymphalucina* is especially abundant in methane seep deposits known as Tepee Buttes (Speden 1970; Kauffman et al. 1996). In the Eocene of the Pacific coast of North America, *Cryptolucina* occurs in methane seep deposits in Washington State and *Epilucina* in oil seeps in southern California (Saul et al. 1996; Squires and Gring 1996; Kiel and Peckmann 2007). Older seep deposits in this region also include some lucinids, but these are generally rare and poorly preserved and have so far escaped a modern systematic evaluation (cf., Campbell 2006). Several as-yet poorly identified lucinids are known from European Jurassic and Cretaceous seep deposits (Lemoine et al. 1982; Gaillard et al. 1992; Kiel and Peckmann 2008) as well as from Cretaceous seeps in Japan (Hikida et al. 2003; Kiel et al. 2008a).

In contrast, members of the edentulous, large and elongate-oval lucinid genus *Nipponothracia* (Figs. 8.3a, b) are geographically widespread, with occurrences in Japan, the western United States, and Greenland. In the western Pacific (Japan, Indonesia and the Philippines) *Nipponothracia* apparently survived until Pliocene time (Kase et al. 2007). Despite being taxonomically diverse, lucinids at Late Jurassic to Eocene seeps consistently lack ornamentation. This is in contrast to the sharply ribbed *Lucinoma* (Figs. 8.3c, d), which is the most common lucinid at seeps from the Oligocene onwards. *Lucinoma* is known from numerous Neogene seep deposits in Japan (Majima et al. 2005), from Oligocene seeps in the Caribbean and Peru (Kiel and Peckmann 2007), from Miocene seep deposits in New Zealand (Campbell 2006), from several Oligocene and Neogene sites in Washington (Campbell 1992; Goedert and Campbell 1995; Peckmann et al. 2002), and from the Miocene 'Calcare a *Lucina*' in Italy (Moroni 1966). Lucinids other than *Lucinoma* in post-Eocene seep deposits have hesitantly been assigned to *Myrtea*, like specimens from the Oligocene of Peru and Cuba (Cooke 1919; Olsson 1931; Kiel and Peckmann 2007), although their systematic affiliations are still unclear. Likewise, the affinities of *Lucina hoernea* which dominates many seep carbonates in the Italian Miocene 'Calcare a *Lucina*' have yet to be evaluated.

Modiomorphids. As the name suggests, members of this clade resemble modiolins (family Mytilidae) in general shell shape and certain seep-related modiomorphids have indeed been mistaken for members of the mytilids in the past. The Modiomorphida are an extinct clade of bivalves that is commonly associated with the Anomalodesmata. Modiomorphids had sporadically been reported from ancient vents and seeps over the past 10 years. Records include *Sibaya ivanovi* from a middle Devonian hydrothermal vent deposit in the Ural Mountains (Little et al. 1999b). The identification was based on external shell morphology only and remains

to be confirmed. Recent research interest focuses on the Late Jurassic to Cretaceous genus *Caspiconcha*, first described from seep deposits in eastern Greenland (Kelly et al. 2000). Modiomorphids are extinct and thus the reconstruction of the mode of life of vent- and seep-inhabiting species – especially the question whether they harbored chemotrophic symbionts – is not as straight-forward as in the groups discussed so far. The current knowledge on the live habits of vent and seep modiomorphids is here outlined using the relatively well-studied *Caspiconcha*.

Species of *Caspiconcha* are usually quite large, reaching 20–30 cm in length. They are found exclusively at ancient seeps where they are associated with a variety of other seep-related taxa, including tube worms, the brachiopod *Peregrinella*, various gastropods, and solemyid and lucinid bivalves (Kelly et al. 2000; Hikida et al. 2003; Kiel et al. 2008b; Kiel and Peckmann 2008; Jenkins et al. 2009). At the seep sites on Greenland and on the Crimean peninsula, *Caspiconcha* occurs in clusters and was found positioned at an angle of about 30° relative to the bedding plane, with the posterior side pointing upwards, which suggests a semi-infaunal mode of life (Kelly et al. 2000; Kiel and Peckmann 2008). *Caspiconcha* species from different parts of the world apparently share another feature: the interior of their shells show traces of burrowing organisms, especially in their posterior part.

Non-chemosymbiotic groups. A few other, non-chemosymbiotic bivalves frequently occur at vents and seeps. Most commonly found are nuculids and nuculanids (Protobranchia). *Nuculana grasslei* occurs in large numbers in a Recent, sediment-hosted vent in the Guaymas Basin. The detailed description of its anatomy, however, showed no evidence for any particular adaptation to this environment. Rather than being chemosymbiotic, *Nuculana grasslei* is a suspension- and deposit-feeder like nuculanids in general (Allen 1993). Nearly identical specimens have been recorded from seeps as old as Eocene along with other nuculanid bivalves (Kiel 2006). The ribbed nuculid *Acila* and its subgenus *Truncacila* are frequently collected at Cretaceous to Neogene seeps in Japan and a few other sites of the Pacific rim (Majima et al. 2005; Kiel et al. 2008a). Surprisingly, *Acila* has not been reported from any of the many well-studied modern seeps in this region.

Also commonly encountered are certain pectinoids. Two species of small, filter-feeding propeamussiids, *Bathypecten vulcani* and *Sinepecten segonzaci*, have been found at Recent hydrothermal vents (Schein-Fatton 1985; Schein 2006). The supposedly basal anatomy of *Bathypecten vulcani* has recently been questioned (Dijkstra and Gofas 2004) and these authors also indicated that *Bathypecten* is a synonym of the deep-water genus *Catillopecten*. A member of *Catillopecten* is known from an Oligocene seep deposits in Washington State, USA (Kiel 2006). Deep- and cold-water pectinids frequently found in Late Jurassic-Early Cretaceous seep deposits are *Buchia* and *Aucellina*. These two closely related genera occur in mudstones of this age throughout the northern Hemisphere and have been reported from geographically distant seeps in California (Campbell and Bottjer 1993; Campbell 2006) and the southern Ukraine (Kiel and Peckmann 2008).

Inoceramids. The inoceramids are a group of pteriomorph bivalves that originated in the Permian and became extinct at the end of the Mesozoic. Inoceramids lived in a

wide range of habitats, including oxygen-poor basins, where they are often quite common and large. Due to this unusual mode of occurrence, Kauffman (1988) considered them as chemosymbiotic, a view that was supported by a comparison of stable oxygen and carbon isotopes of inoceramid shells and those of planktic and benthic foraminifera (MacLeod and Hoppe 1992). Grossman (1993) challenged MacLeod and Hoppe's (1992) interpretation of their stable isotope data and considered inoceramids as non-chemosymbiotic. The question has not yet been resolved. However, I find the idea of chemosymbiosis in inoceramids based on their occurrence in organic-rich, oxygen-poor sediments not convincing. Suspended food would have been abundant for filter-feeding inoceramids in this environment, and due to the absence of any other taxa they were save from predation and competitors. This could easily explain their large and often extremely thin shells, as well as their abundance.

8.3 Gastropoda

The high degree of endemism encountered at vents and seeps has long fascinated researchers, and indeed, many classes of animals include genera and families living exclusively in these environments. But only among the gastropods is an entire order apparently endemic to chemosynthetic ecosystems: the Neomphalina (McLean 1981; Warén and Bouchet 2001; Heß et al. 2008; Chapter 7, this volume). Most of the living neomphalids are found at hydrothermal vents, a single genus has so far been reported from seeps. In addition, a fair number of taxa living on sunken driftwood (wood falls) have recently been identified as neomphalids (Kiel and Goedert 2006b; Heß et al. 2008). Whereas neomphalids are not known from ancient vent deposits, the seep-inhabiting genus *Retiskenea* has a fossil record going back to the Early Cretaceous (Figs. 8.4a–c; Kiel 2006; Campbell et al. 2008b). A potential neomphalid was described as *Lithomphalus enderlini* from Early Cretaceous seeps in California (Kiel and Campbell 2005), although its affiliation with the Neomphalina needs confirmation.

Provannids. The Provannidae is a caenogastropod family that lives exclusively in chemosynthetic habitats, including vents, seeps, whale- and wood-falls. Most provannids are relatively small and graze on biofilms, but the two large genera *Alviniconcha* and *Ifremeria* harbor sulfur-oxidizing symbionts (Warén and Bouchet 2001; see also Chapter 7, this volume). Fossil provannids (Fig. 8.5a) are known from a similar range of habitats, including records from Late Cretaceous and Eocene wood-falls, Miocene whale-falls, Late Cretaceous plesiosaur-falls, and Late Cretaceous and Paleogene cold seeps (Squires 1995; Amano and Little 2005; Gill et al. 2005; Kiel and Goedert 2006b; Amano et al. 2007b; Kaim et al. 2008a, b; Kiel et al. 2009). Provannids may even occur at a fossil vent deposit: Little et al. (1999a) described several high-spired gastropods from volcanogenic massive sulfide deposits of the Late Cretaceous Troodos Ophiolite on Cyprus, which were subsequently interpreted as potential provannids (Little 2002; Kaim et al. 2008a).

Relatives of provannids. There is an assortment of globular to high-spired gastropods known from Late Jurassic to Oligocene seep deposits that might be related to
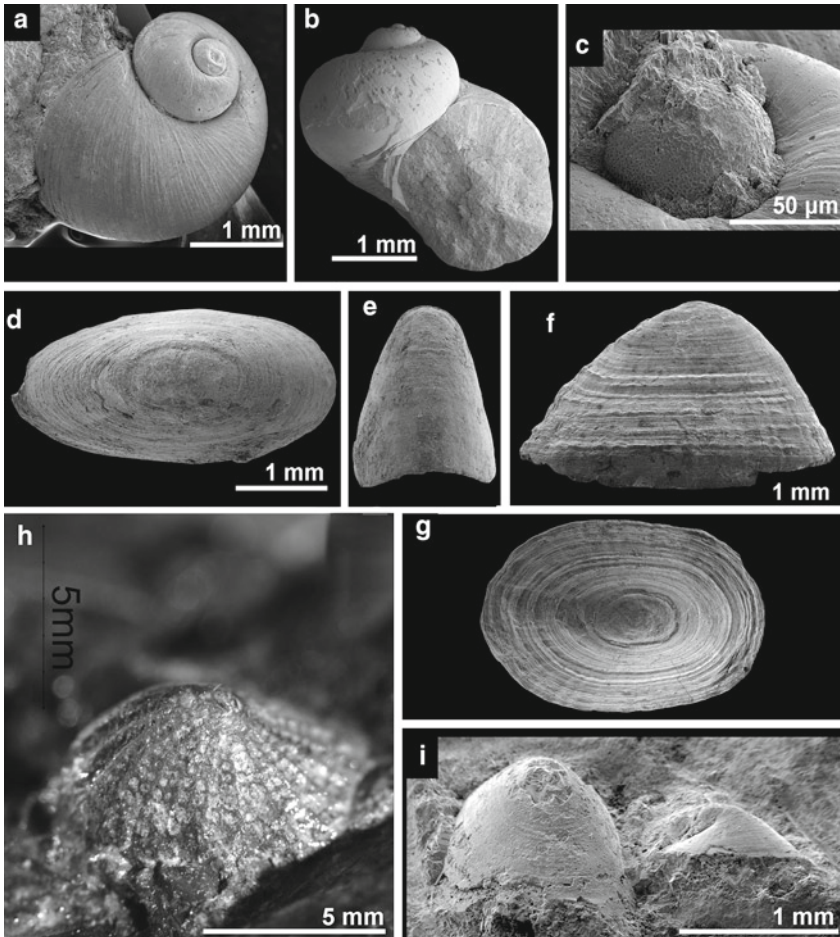
Fig. 8.4 Neomphalid and limpet gastropods. (**a–c**) The neomphalid *Retiskenea statura* from an Oligocene seep deposit in Washington, note fine tuberculate sculpture on the protoconch on Fig. c. (**d, e**) Patellogastropod *Serradonta* cf. *vestimentifericola* from a Late Cretaceous seep deposit on Hokkaido. (**f, g**) Patellogastropod *Bathyacmaea* cf. *subnipponica* from a Late Cretaceous seep deposit on Hokkaido. (**h**) Vetigastropod *Fissurella bipunctata* from an Early Cretaceous seep deposit in California. (**i**) Two specimens of the vetigastropod *Pyropelta* sp. from a Mid-Eocene seep deposit in Washington (Images from Kiel [2006; a, c. i] and Jenkins et al. [2007a; d–g])

the modern provannids. The more slender examples had previously been identified as abyssochrysids, zygopleurids, or cerithioids. Based on Late Cretaceous material from Japan, in which the taxonomically important larval shells were preserved, Kaim et al. (2008a) introduced the family Hokkaidoconchidae for these high-spired taxa (Figs. 8.5d, e). This family can now be traced back into late Jurassic time (Kaim and Kelly 2009; Kiel et al. 2010). A large and high-spired and due to its two apertural notches somewhat unusual genus that may either belong to the hokkaido-conchids or the abyssochrysids is *Humptulipsia*. Originally described from Eocene
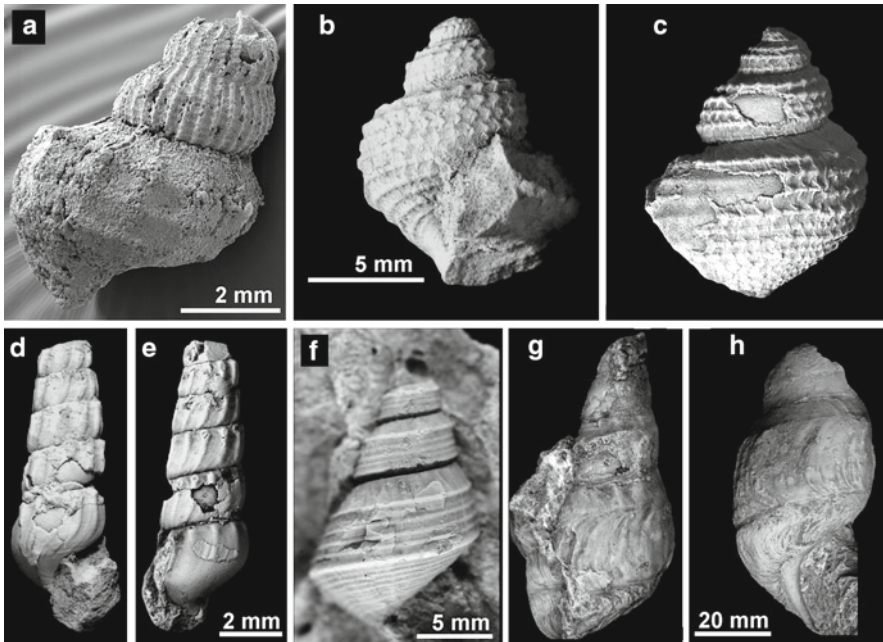
Fig. 8.5 Provannids and related gastropods. (**a**) Silicified early ontogenetic shell of the Late Cretaceous *Provanna tappuensis* from a seep deposit on Hokkaido, Japan, note the fine cancellate pattern on the larval shell. (**b, c**) *Paskentana paskentaensis* from a Late Jurassic seep deposit in California. (**d, e**) *Hokkaidoconcha tahemaensis* from the same seep deposit. (**f**) Early Cretaceous *Atresius liratus* from California. (**g, h**) *Humptulipsia raui*, a possible abyssochrysid from middle Eocene seep limestones in Washington State (Images from Kiel [2008b] and Kiel et al. [2008b])

seep sites in the Humptulips River area in western Washington (Kiel 2008b), another species was recently identified at an early Cretaceous seep site in southern France (Kiel et al. 2010). At these sites, *Humptulipsia* is abundant and is associated with large lucinid bivalves. The more globular provannid-like species belong to the genera *Atresius* (Fig. 8.5f) and *Paskentana* (Figs. 8.5b, c), and larval shell data indicate a relationship to provannids or zygopleuroids also for these two genera. Just as provannids today, hokkaidoconchids as well as *Atresius* and *Paskentana* are often found in large numbers in ancient seep deposits (Kaim et al. 2008a; Kiel et al. 2008b; Kaim and Kelly 2009).

Limpets. Gastropod limpets are well-represented at Recent and fossil vents and seeps. Limpets are not a monophyletic group but have evolved repeatedly in many different gastropod clades. They have few diagnostic shell characters and those they have often require exceptional preservation to be recognized in the fossil record. However, there are promising exceptions.

The extant Japanese patellogastropod *Serradonta vestimentifericola* lives at seeps attached to vestimentiferan tubes (Okutani et al. 1992). Jenkins et al. (2007a) showed that a similar, if not identical, species had the same habitat preference

already in the Late Cretaceous, about 80 million years ago (Figs. 8.4d, e). Based on this observation, Jenkins et al. (2007a) argued that the geographic limitation of extant *Serradonta* to Japanese waters is a result of this habitat preference: it could disperse only through vent and seep sites that had already been inhabited by vestimentiferan tube worms. In contrast, members of the patellogastropod genus *Bathyacmaea* (Figs. 8.4f, g) have a wider geographic range, and their ability to inhabit a wide range of substrates appears to be as old as the adaptation of *Serradonta* to worm tubes (Jenkins et al. 2007a). Pyropeltids are cocculiniform limpets known to inhabit a broad range of chemosynthetic habitats (McLean and Haszprunar 1987; Warén and Bouchet 2001; Sasaki et al. 2003) and they have been reported from ancient seeps as old as Eocene (Fig. 9.4i; Kiel 2006).

Limpets with a rather poor fossil record at vents and seeps are slit- and keyhole-limpets. Several groups of slit- and keyhole-limpets are endemic to modern vents and seeps (McLean 1988, 1989, 1992). But the few examples that have been found at fossil seeps are poorly identified and their relations to the endemic modern groups are unclear. Stanton (1895) described *Fissurella bipunctata* from Early Cretaceous limestone nodules in California (Fig. 8.4h), which have subsequently been identified as ancient seep deposits (Campbell and Bottjer 1993; Birgel et al. 2006). The same rocks yield two new fissurellids and sutilizonids (Kiel et al. 2010). Further fissurellids were reported by Goedert and Squires (1990) from Eocene seeps in Washington and by Gill et al. (2005) from poorly dated (Eocene to Miocene) seep deposits on Barbados. But these specimens are likely to be limpets with the apical tip corroded away rather than true keyhole limpets (J.L. Goedert, pers. comm. and own observations).

Neritids. Neritids are a distinctive gastropod group typically found on hard substrate in the intertidal zone, but a few taxa adapted to cold seeps. These are *Bathynerita* in the Gulf of Mexico and the Caribbean (Warén and Bouchet 2001) and the limpets of the family Shinkailepadidae (Okutani 1989; Sasaki et al. 2003). The latter lack a fossil record, but shells resembling *Bathynerita* have been found at Miocene and Oligocene seeps and are usually referred to as *Thalassonerita*; an Eocene record has been questioned (Squires and Goedert 1996; Warén and Bouchet 2001). Neritids found at Late Jurassic and Early Cretaceous seeps (Kiel and Peckmann 2008; Kiel et al. 2010) appear to be unrelated to modern *Bathynerita*. This scenario is consistent with molecular age estimates for shinkailepadids which indicate an early Cenozoic origin of this group (Kano et al. 2002).

8.4   Mono- and Polyplacophorans

A single monoplacophoran species, *Rokopella segonzaci*, is known from a vent site on the Mid-Atlantic ridge. This species is less than a millimeter long, its radula does not indicate a particular adaptation to the vent environment, and it is not clear whether it is a regular member of the vent fauna (Warén and Bouchet 2001). Large conical shells (height >5 cm) from a Silurian vent site in the Ural Mountains attracted attention when they were described as ancient monoplacophorans

(Little et al. 1999b). However, the specimens lack the serial muscle attachment scars that are diagnostic for monoplacophorans. They could thus just as well be limpet-shaped gastropods or bellerophontids, as suggested earlier (Kuznetsov et al. 1993; Zaikov et al. 1995).

Polyplacophorans (commonly known as chitons) have so far only been reported from four modern vent and seeps sites in Japan, California, the Caribbean, and the Gulf of Mexico (Saito and Okutani 1990; Barry et al. 1996; Olu et al. 1996; Chapter 10, this volume). This wide geographic distribution together with several fossil specimens of *Leptochiton* from Eocene to Oligocene seep deposits in Washington State (Goedert and Campbell 1995; Peckmann et al. 2002) make it likely that chitons occur at more vent and seep sites than currently appreciated. However, the known species show no particular adaptation to the vent and seep habitat and may be deep-sea generalists (Saito and Okutani 1990).

8.5   Ancient Mollusks in Evolutionary Biology

The highly specialized and endemic fauna at vents and seeps has often been regarded as a relict fauna. Apart from the high degree of endemism, the idea was based on comparison to related, or supposedly related, fossil taxa. One such example is the iconic gastropod limpet *Neomphalus fretterae*, which McLean (1981) considered as a living relative of the Paleozoic euomphalids (the name *Neomphalus* was coined to indicate this affinity). Although the link to these Paleozoic gastropods is unlikely considering their different early ontogenetic shells (cf., Bandel and Frýda 1998), Jim McLean certainly gets credit for recognizing the neomphalids as a clade that must have split from all other gastropod groups very early in the evolutionary history of gastropods (cf., Heß et al. 2008). Whether this implies that already the earliest neomphalids inhabited vents and seeps, as assumed by Geiger and Thacker (2005) remains to be tested; their recorded history in these environments goes only back to the Early Cretaceous (Campbell et al. 2008b).

Warén and Bouchet (2001) used the fossil record of the respective sister or higher taxa of vent and seep gastropods to test the relict fauna hypothesis. Their results indicate that new taxa have continuously adapted to vents and seeps through earth history. Kiel and Little (2006) reached a similar conclusion when they compared the geologic ranges of the extant mollusk genera at seeps with those of the marine mollusk fauna in general. This study yielded another result that is promising from a paleontologists' perspective. Despite the intuitive assumption that deep-sea fossils are rare, the major taxa at modern vents and seeps in fact do have a fossil record, and those taxa without a fossil record are very rare also in the modern oceans. Furthermore, there appears to be very little bias in the fossil record of seep mollusks towards large-sized taxa (Kiel and Little 2006).

Evidence for a geologically young vent and seep fauna comes from molecular biologists who use molecular clocks to infer a Cenozoic origin of most major clades inhabiting vents and seeps today (Baco et al. 1999; Shank et al. 1999; Distel et al. 2000;

Kano et al. 2002). In case of the two major bivalve groups, vesicomyids and bathymodiolins, Little et al. (1999b) and Little and Vrijenhoek (2003) noted that these young ages appear to be contradicted by the longer geologic record of these families at seeps. However, none of these older records could be confirmed by a critical evaluation. In fact, both molecular age estimates and fossil data indicate an Eocene origin of the two groups in question (Kiel 2006; Amano and Kiel 2007; Amano et al. 2008; Kiel et al. 2008a; Kiel and Peckmann 2008).

Since there is a growing body of evidence that the vent and seep fauna is not the relict fauna it was regarded as initially, another hypothesis on its origin attracted a lot of attention. When vent-type taxa were found on decaying whale carcasses in the deep sea (Smith et al. 1989) it was suggested that whale carcasses could act as dispersal stepping stones for the vent fauna that enabled it to radiate much further than before the origin of whales. This hypothesis was supported by molecular age estimates of the bivalve family Vesicomyidae that dated the origin of this family at about 40 million years ago, coinciding roughly with the origin of whales (Baco et al. 1999; Smith 2007). One implication of this hypothesis is that vesicomyids inhabited whale falls from the Eocene onward, but this appears not to be the case. A survey of fossil whale-fall communities from the North Pacific rim showed that vesicomyids colonized whale falls only from the middle Miocene onward. The Eocene and Oligocene whale falls lacked vesicomyids, despite the fact that vesicomyids were abundant in cold-seep deposits of the same sediments (Kiel and Goedert 2006a). The reason for this appears to lie in the bone physiology of the whales. Whale bones today consist of up to 65% of lipids and the anaerobic decay of these lipids sets free the sulfides that fuel the chemosynthetic fauna at whale falls (Smith and Baco 2003). Thus Kiel and Goedert (2006a) suggested that either an increase in the size of whales or an increase in the relative lipid content of their bones should have caused the observed changes in whale fall communities from the Oligocene to the Miocene. Since these suggestions were published, two further Miocene whale falls with abundant vesicomyids were found, one on Hokkaido (Amano et al. 2007b) and one in California (Pyenson and Haasl 2007). In both cases the whales had an estimated length of about 4 m, which is considerably smaller than the up to 6 m long Oligocene whales that lacked vesicomyids. It was thus concluded that a relative increase in the lipid content of the bones was the more likely cause for the change from sulfide-poor Oligocene whale falls to sulfide-rich Miocene ones (Pyenson and Haasl 2007; Kiel 2008a).

Yet another hypothesis that triggered a lot of research is the 'wooden steps to deep-sea vents'-hypothesis (Distel et al. 2000). It claims that bathymodiolin mussels first adapted to habitats with low sulfide levels like wood- and whale-falls in the deep-sea and colonized sulfide-rich environments like seeps and vents from there. It is based on molecular evidence showing that the wood- and bone-inhabiting bathymodiolins *Idas* and *Adipicola* are basal to the larger taxa at vents and seeps (Distel et al. 2000; Jones et al. 2006; Samadi et al. 2007; see also Chapter 6, this volume). These habitats and their respective mussel inhabitants are preserved in the fossil record. Thus comparing the first occurrences of mussels at the respective

habitats could be a way to test this hypothesis. Presently the first occurrences are in the opposite sequence as predicted by the hypothesis: in the mid-Eocene at seeps, in the late Eocene at wood. However, these occurrences are stratigraphically very close to each other. It seems possible that the time between the adaptation to wood and bone on the one hand, and from there to seeps and vents on the other hand, was so short that it cannot be resolved in the fossil record.

8.6 Fossil Mollusks and Seep Biogeography

The first modern groups of seep mollusks started to appear in the mid-Cretaceous, and from the Late Eocene onwards most of the principle modern endemic seep taxa had reached a world-wide distribution (Majima et al. 2005; Campbell 2006; Kiel 2006; Kiel and Little 2006; Amano and Kiel 2007; Jenkins et al. 2007a; Kaim et al. 2008a). It has recently become apparent that a globally distributed, seep-restricted fauna existed also in older geologic time. Late Jurassic to Early Cretaceous seeps were inhabited by a distinct set of taxa, including the modiomorphid *Caspiconcha*, the gastropods *Paskentana* and *Hokkaidoconcha*, and, though only shortly, the brachiopod *Peregrinella*. Perhaps the most interesting aspect of this fauna is that even on the family level it shows no close phylogenetic relation to the modern vent and seep fauna (Campbell and Bottjer 1995; Kaim et al. 2008a; Kiel et al. 2008a, b, 2010; Kiel and Peckmann 2008; Kaim and Kelly 2009).

The modern Mediterranean seep fauna, especially its mollusks, is surprisingly distinct from that of the western Atlantic. Whereas the latter includes *Bathymodiolus*, large vesicomyids, provannids, lepetodrilids, and other gastropods typical for seep faunas around the world (Olu-Le Roy et al. 2007; Warén and Bouchet 2009), the Mediterranean seep fauna is dominated by the small bathymodiolin mussel *Idas*, a vesicomyid genus (*Isorropodon*) that is unusual for seeps, and by local lucinid bivalves and trochid gastropods (Olu et al. 2004). This is an interesting contrast to the late Miocene seep fauna of the Mediterranean Sea, which includes large vesicomyids, bathymodiolins, buccinids, and neritids, and in general resembles that of the Gulf of Mexico today (Taviani 1994). This difference probably lies in the geologic history of the Mediterranean Sea. The entire deep-water fauna of the Mediterranean, including its seep fauna, had been wiped out by the Messinian salinity crisis about 6 million years ago. In the subsequent re-colonization local and shallow-water species had an advantage because the relatively shallow Strait of Gibraltar seems to be an effective barrier for deep Atlantic seep taxa: *Bathymodiolus* has apparently not managed to re-colonize the Mediterranean Sea until the present day, despite its occurrence on mud volcanoes in the Gulf of Cadiz, just outside the Strait of Gibraltar (Génio et al. 2008). Instead, its place has been taken by the small bathymodiolin *Idas*. *Idas* species can live also in comparably shallow water of a few hundred meter depth and thus the Strait of Gibraltar poses no barrier for them (Dell 1987; Warén and Carrozza 1990; Jones et al. 2006).

An area with perhaps a similar history of local extinction and unsuccessful repopulation is the Japan Sea. The vesicomyid genus *Calyptogena* lived here since the middle Miocene (Kanno et al. 1989; Amano et al. 2001; Amano and Kanno 2005) and disappeared during the Pleistocene glaciations, when this isolated basin became anoxic (Tada 1994; Amano 2001). Apparently, *Calyptogena* has not yet repopulated the Japan Sea, possibly because the seaways linking the Japan Sea with the Pacific Ocean and the Okhotsk Sea are too shallow (see also Chapter 12, this volume).

8.7 Conclusions and Outlook

Mollusks have a long and relatively well-researched history at ancient vents and seeps. In contrast to the early 'relict fauna' hypothesis, the fossil record of mollusks shows that new taxa have more-or-less continuously adapted to vents and seeps through Earth history. The first modern seep mollusks started to appear in the mid-Cretaceous (Fig. 8.6), and seep faunas from the Late Eocene onwards have a largely modern appearance. This Late Eocene age seems to support the idea that the rise of whales played a role in the radiation of the seep faunas, but the fossil record contradicts this hypothesis because it shows that the major groups of seep mollusks did not colonize whale-falls before the Miocene. The existence of a globally distributed fauna of seep
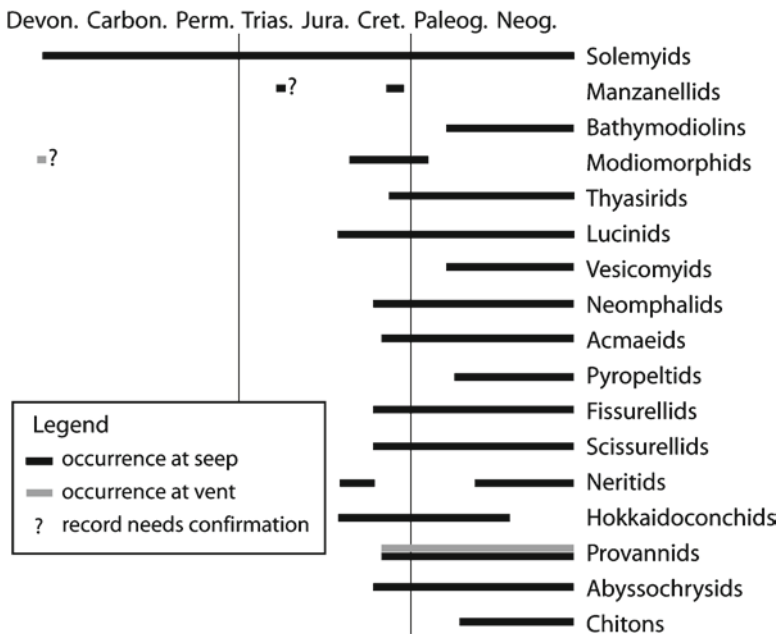

Fig. 8.6 Geologic ranges of selected mollusks at vents and seeps

obligates is not unique to the modern ocean. Also Late Jurassic to Early Cretaceous seeps world-wide were inhabited by a distinct set of taxa. Interestingly, these taxa show no close phylogenetic relation to the modern vent and seep fauna.

All extant chemosymbiotic bivalve families adapted to vents and seeps at or shortly after their first appearance in the geologic record. The only exception seems to be the Lucinidae. This family took up a chemosymbiotic lifestyle as early as Silurian (cf., Taylor and Glover 2006) but is known from ancient seep deposits only from the Late Jurassic onward. This is most likely a sampling artifact and it might be worthwhile to re-investigate lucinid occurrence of pre-Jurassic age. There are indications that some species of the manzanellids (incl. *Nucinella* spp.) might be chemosymbiotic (cf., Amano et al. 2007a) and indeed, manzanellids start to appear in Mesozoic seep deposits. Members of this group might turn up more frequently at ancient seeps when more Mesozoic seep site become known. A group that is also likely to have played a more important role at Paleozoic and Mesozoic seep than currently appreciated is the modiomorphids. The modiomorphid genus *Caspiconcha* is now known from late Mesozoic seeps world-wide and there are potential modiomorphids at seeps and vents as old as the Devonian. Surely, more is to be found.

There is a great interest in the biogeographic patterns seen in the modern vent and seep fauna, and many of these patterns are likely to have an historic basis (e.g. Tunnicliffe and Fowler 1996; Bachraty et al. 2009). Recent observations and hypotheses on the biogeography of vent and seep mollusks include multiple trans-Pacific migrations of vesicomyid clams (Kojima et al. 2004), amphi-Atlantic species complexes among bathymodiolins (Olu et al. 2007), dispersal of the vesicomyid *Calyptogena* along continental margins (Krylova and Sahling 2006), and an accumulation of biodiversity on southwest Pacific seamounts (Krylova and Janssen 2006; Cosel and Janssen 2008). The fossil record can provide further evidence for the origin and history of such pattern, although Cenozoic seep fossils are certainly not equally distributed around the globe. The tectonically active Pacific Rim is already the region with the best-investigated Cenozoic record of seep faunas. Within this region, the most promising areas with known deep-water deposits that may yield further seep faunas are Alaska (cf. Kiel and Amano 2009), the West Coast of South America from which Oligocene seep fossil have been described (cf. Olsson 1931; Kiel and Peckmann 2007), and the Philippines that recently revealed early Pliocene seep deposits (Majima et al. 2007). Work on Miocene seep faunas from New Zealand that include bathymodiolins, vesicomyids, lucinids, and other typical seep mollusks is in progress (Campbell 2006; Campbell et al. 2008a).

Much more problematic in this respect is the Atlantic Ocean. It is bordered by passive continental margins only and there is little in respect to tectonic processes that would uplift deep-water sediments here. Consequently, evidence for the Cenozoic evolution of the Atlantic seep fauna needs to be inferred from seep deposits in the adjacent Mediterranean basin to the East and from the Caribbean and Gulf of Mexico to the West. Likewise, the Indian Ocean is largely bordered by passive continental margins. Only the Indo-Malayan archipelago on its eastern side is tectonically active, and has been so throughout the Cenozoic. It has thus the potential

to yield fossil seep faunas. The late Miocene asphalt deposits of Buton which produced small vesicomyids and lucinids (Beets 1942, 1953) have sometimes been considered as an ancient seep deposit but this suggestion needs confirmation.

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