

Chapter 10

Bivalvia in Ancient Hydrocarbon Seeps



Kazutaka Amano, Steffen Kiel, Krzysztof Hryniewicz, and Robert G. Jenkins

10.1 Introduction

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Bivalves are one of the major animal classes inhabiting hydrothermal vents, hydrocarbon seeps, and whale-fall and wood-fall sites, because several bivalve clades developed symbiotic associations with chemotrophic bacteria that provide them with the bulk of their nutrition. Bivalves house the symbionts in their enlarged gills, either intra- or extracellularly. The symbionts are thiotrophic or methanotrophic gammaproteobacteria and are obtained either by environmental acquisition (also called horizontal transmission), or they are passed on from the parent to the offspring (called vertical transmission) (e.g., Duperron 2010; Taylor and Glover 2010) (Table 10.1).

In extant bivalves, chemosymbiosis has been documented in nine families or subfamilies. These are widely dispersed among the bivalve tree of life, showing that chemosymbiosis was repeatedly and independently acquired by several bivalve groups through Earth history (Figs. 10.1 and 10.2). The degree to which their

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Table 10.1 Chemosymbiotic type and symbiotic acquisition methods in six extant bivalve families. References are in the text

Family	Symbiont type	Symbiont acquisition
Solemyidae	Thiotrophic	Mostly maternal
Nucinelidae	Potentially chemoautotrophic	?
Mytilidae	Thiotrophic, methanotrophic	Environmental
Lucinidae	Thiotrophic	Environmental
Thyasiridae	Thiotrophic	Environmental
Vesicomidae	Thiotrophic	Mostly maternal

members depend on chemosymbiosis for nutrition varies considerably. Some have reduced their gut and rely largely or exclusively on their symbionts (Solemyidae, Nucinelidae, Bathymodiolinae, Pliocardiinae among Vesicomidae), while others retain a functional gut and can derive a significant part of their nutrition from other sources (Lucinidae, Thyasiridae). Whereas all investigated lucinids have symbionts, most smaller species of Thyasiridae and Vesicomidae do not harbor symbionts at all (Taylor and Glover 2010; Krylova and Sahling 2010). Among the Montacutidae, Basterotiidae, and Teredinidae, chemosymbiosis is rare and only documented in a single species of each family: *Syssitomya pourtalesiana* among the Montacutidae, *Atopomya dolobrata* among the Basterotiidae, and *Kuphus polythalamia* among the Teredinidae (Oliver et al. 2012; Oliver 2013; Distel et al. 2017, respectively).

Bivalves have a remarkable fossil history at seeps, with about 150 named species and many more reported in open nomenclature. In addition to the main groups of modern chemosymbiotic bivalves, all of which occur at fossil seeps, a few others have been abundant at seeps in the older geologic past, suggesting even further instances of the acquisition of chemosymbiosis in Earth history. These groups include the families Kalenteridae and Modiomorphidae among the Archiheterodonta (Hryniewicz et al. 2017b; Jenkins et al. 2018b) and a genus of the Anomalodesmata not assigned to any family (Kiel et al. 2017; Kiel 2018). Furthermore, chemosymbiosis was inferred for the large Permian bivalve *Shikamaia* of the family Alatoconchidae, which, however, does not occur in an ancient seep environment (Asato and Kase 2019). Some authors suggested or stressed that large Cretaceous inoceramids might have depended on the chemosymbiosis, based on their size, their mode of occurrence, and stable carbon isotope data (MacLeod and Hoppe 1992; Kauffman et al. 2007; Walliser et al. 2018, 2019). However, the isotope data are inconclusive (Grossman 1993), and the structure of well-preserved, phosphatized gills of *Inoceramus sutherlandi* and *Platyceramus* sp. is very different from that

rences of chemosymbiosis, ? chemosymbiosis suggested but questionable, (*)extinct family with assumed chemosymbiotic members. Chemosymbiosis is inferred for the Triassic anomalodesmatan species *Aksumya krystyni*, but it has not been assigned to any anomalodesmatan family; hence, a + sign is placed at the base of the anomalodesmatans. Note that among Mytilidae only members of the subfamily Bathymodiolinae are chemosymbiotic, not the entire family. Kalenteridae are here placed basal to all other archiheterodonts except Modiomorphidae solely. Tree compiled from Bieler et al. (2014), Combosch et al. (2017), and Sato et al. (2020)

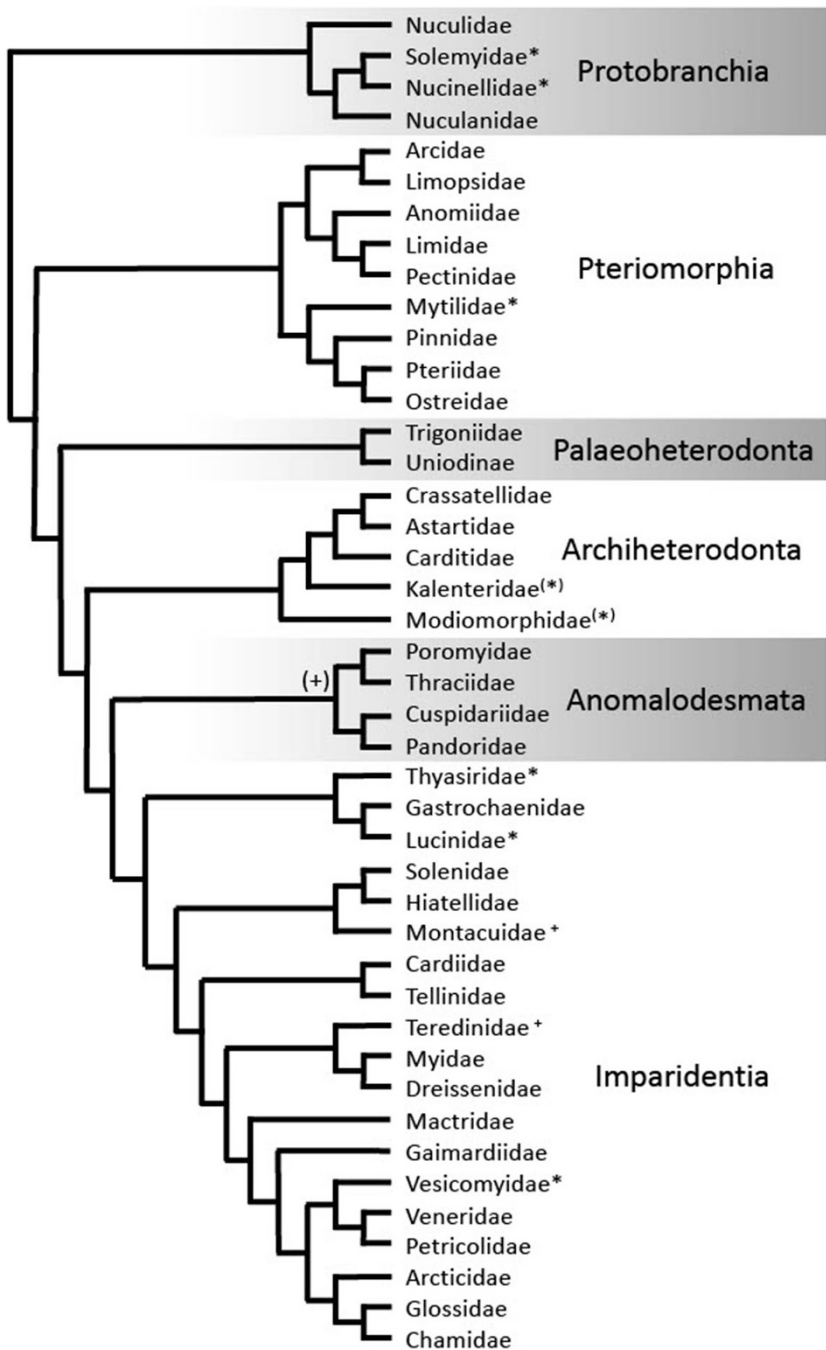


Fig. 10.1 Simplified phylogenetic tree of the Bivalvia showing the distribution of chemosymbiotic clades. *Families with chemosymbiosis as dominant feeding mode, + families with rare occur-

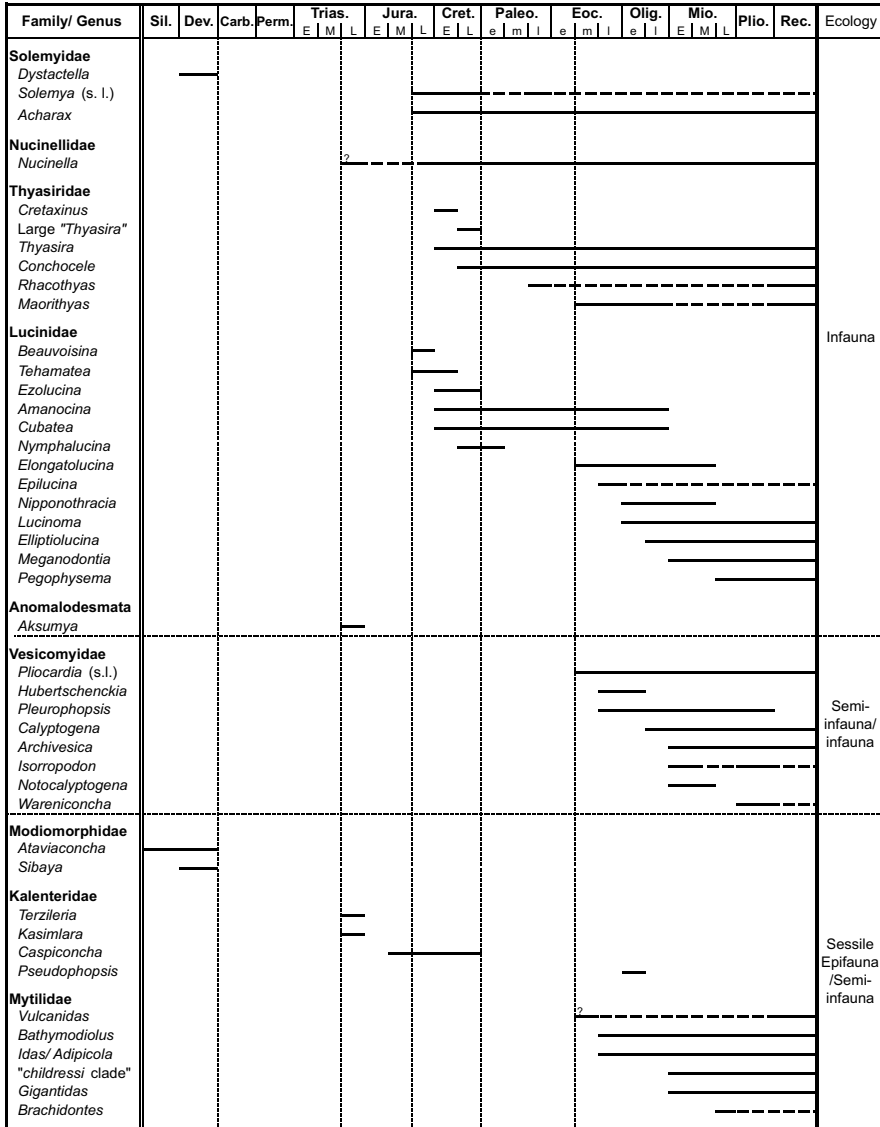


Fig. 10.2 Chronostratigraphic range chart of chemosymbiotic bivalve genera; solid lines show the confirmed fossil record, while dashed lines show the inferred occurrences

observed in the commonest extant chemosymbiotic bivalves (Knight et al. 2014). Hence it seems more plausible that inoceramids were filter-feeder (e.g., Kiel 2010a).

The recent findings of modiomorphid and kalenterid bivalves at Paleozoic and Mesozoic seeps have shed considerable doubt on an earlier hypothesis that brachiopods dominated the seeps in the Paleozoic and Mesozoic and were outcompeted by chemosymbiotic bivalves only from the Late Cretaceous onward (Campbell and

Bottjer 2006). Many of the modiomorphids and kalenterids co-occur with brachiopods at individual seep deposits: the Silurian-Devonian modiomorphid *Ataviaconcha* with the atrypid brachiopod *Septatrypa*, the Triassic kalenterids *Terzileria* and *Kasimlara* with the dimerelloid brachiopod *Halorella*, and the Cretaceous kalenterid *Caspiconcha* with the dimerelloid brachiopod *Peregrinella*. By reviewing the ecology and geochemical settings of these occurrences, Kiel and Peckmann (2019) put forward the new hypothesis that brachiopods and bivalve were partitioning resources: brachiopods relied on methane for nutrition via free-living methanotrophic bacteria, whereas the bivalves relied on sulfide via their sulfide-oxidizing symbionts.

10.2 Family Solemyidae

Krzysztof Hryniewicz

Members of family Solemyidae Gray, 1840, are one of the most basal bivalve clades (Fig. 10.1) with a fossil record going back to the Early Paleozoic. They have a global distribution and are known from the tropics to high latitudes from shallow waters down to ca. 5350 m water depth (Fujiwara 2003; Taylor and Glover 2010; Hansen et al. 2019). All representatives of the two recognized extant genera of *Solemya* and *Acharax* live in obligate symbiosis with sulfur-oxidizing gammaproteobacteria (Coan et al. 2000; Imhoff et al. 2003; Stewart and Cavanaugh 2006; Taylor and Glover 2010). The symbionts are stored intracellularly in bacteriocytes located at the abfrontal zones of ctenidial filaments (Dubilier et al. 2008; Taylor and Glover 2010). Symbiont transmission in solemyid varies depending on the species. For example, symbionts of *Solemya reidi* and *S. velum* are likely transmitted from parent to offspring (vertical transmission; Gustafson and Reid 1988; Cary 1994; Krueger et al. 1996; Russell et al. 2018), while symbionts of *S. pervernicosa* are more alike those of lucinid and thyasirid bivalves than to those of *S. reidi* and *S. velum*, suggesting environmental acquisition (horizontal transmission; Fujiwara et al. 2009).

Solemyids disperse via short-living, actively swimming pericalymma larvae similar to that of other protobranch bivalves (Gustafson and Reid 1986). They occur in a range of habitats, from seeps, vents, and oxygen-minimum zones to other reduced sediments at seagrass beds, sewage outfalls, and around whale carcasses (Reid 1980; Métivier and Cosel 1993; Coan et al. 2000; Neulinger et al. 2006; Kamenev 2009; Fujiwara et al. 2009; Taylor and Glover 2010; Oliver et al. 2011; Sato et al. 2013; Walton 2015). *Solemya* commonly inhabits the shelf and slope depths (e.g., Taylor et al. 2008; Kamenev 2009; Rodrigues et al. 2011; cf. Sato et al. 2013), whereas *Acharax* is commonly associated with deeper settings (e.g., Neulinger et al. 2006). Solemyids are burrowers, often building a U- to Y-shaped burrow extending as deep as 30 cm below the sediment-water interface (Owen 1961; Stanley 1970; Reid 1980; Stewart and Cavanaugh 2006; Seike et al. 2012),

and can be occasionally trapped and killed in their burrows by rapidly deposited sediment cover (Hryniewicz et al. 2020). The species of *Solemya* living in settings with high organic matter content are often gutless (e.g., Reid 1980; Coan et al. 2000), while others have retained their gut and are capable of suspension feeding (e.g., Krueger et al. 1992; Taylor et al. 2008; Simone et al. 2015). Relatively little is known about the biology of *Acharax*, but the available data suggest that at least some species are gutless (Métivier and Cosel 1993). Solemyids are able to thrive at relatively low sulfide levels (Anderson et al. 1987; Conway et al. 1992), and at seeps, they have been recorded from the marginal zones (Sahling et al. 2002; Jenkins et al. 2007). Some species of *Solemya* are able to swim if disturbed (Reid 1980; Taylor et al. 2008).

10.2.1 Fossil Record and Evolution

The oldest known solemyids are *Dystactella ordovicicus* (Pojeta and Runnegar 1985) and *Dystactella aedilis* (Isakar and Sinitsyna 1985) from the Middle Ordovician of Estonia. They belong to the branch of anteroventrally expanded solemyids that has gone extinct in the Paleozoic. The extant genera *Solemya* and *Acharax* belong to the branch of elongated solemyids, known at least since the Devonian (Meek 1873). A possible ancestor of this branch is the anteriorly elongated genus *Psiloconcha* Ulrich, 1894, of Ordovician age. The oldest solemyid from a seep deposit is *Dystactella? eisenmanni* Hryniewicz, Jakubowicz, Belka, Dopieralska, and Kaim, 2017, from a Middle Devonian seep carbonate in Morocco (Aitken et al. 2002; Hryniewicz et al. 2017b). *Solemya* and *Acharax* first appeared at seeps in the Jurassic (Hryniewicz et al. 2014; Kaim et al. 2014). An alleged solemyid species has been found in an early Carboniferous (Viséan) seep in Germany (Peckmann et al. 2001). The oldest undoubted *Solemya* species at seep deposits include *Solemya (Petrasma)* cf. *woodwardiana* from the latest Jurassic-earliest Cretaceous shallow-water seeps in Svalbard (Fig. 10.3a–d¹; Hryniewicz et al. 2014, 2015a), and *Solemya rossiana* has been reported from latest Maastrichtian (Late Cretaceous) shallow-water seeps in Snow Hill Island, Antarctica (Little et al. 2015).

1 Institutional Abbreviations in the Figure Captions

GZG = Geowissenschaftliches Zentrum, University of Göttingen, Germany

JUE = Joetsu University of Education, Japan; collection now at the University Museum of University of Tokyo, Japan

PMO = Natural History Museum, University of Oslo, Norway

PRI = Paleontological Research Institution, Ithaca, USA

UMUT = University Museum of Tokyo University, Japan

UOA = University of Auckland, New Zealand

USNM = Smithsonian Natural History Museum, Washington DC, USA

UWBM = University of Washington, Burke Museum, Seattle, USA

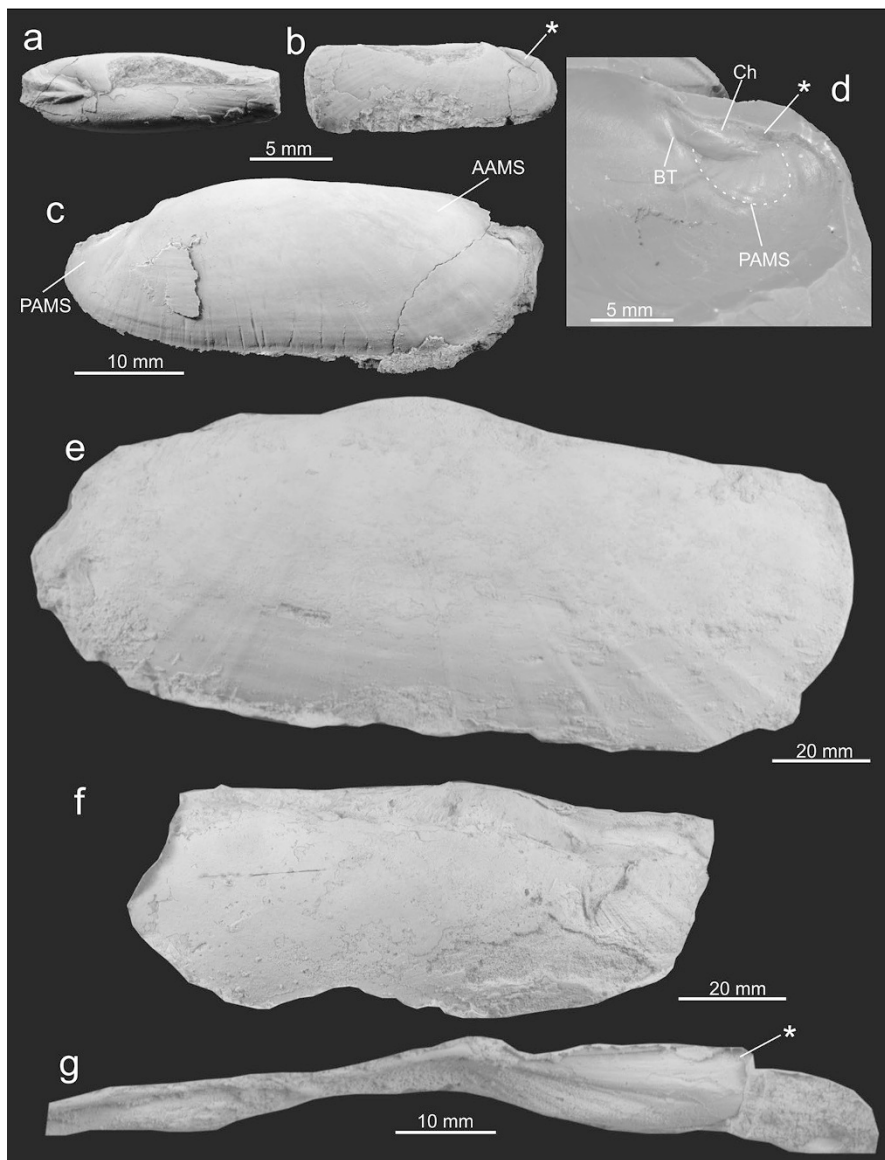


Fig. 10.3 Solemyidae. (a–d) *Solemya (Petrasma)* cf. *woodwardiana* (Leckenby 1859) from a latest Jurassic-earliest Cretaceous seep site on Spitsbergen, Svalbard. (a, b) PMO 224.956: the asterisk indicates the position of the posterior adductor muscle scar (PAMS) extending into the shell dorsally of the chondrophore (Ch). (c, d) PMO 217.249: (c) specimen displaying both the anterior and posterior adductor muscle scars (AAMS and PAMS); (d) rubber cast of an internal mold showing PAMS supported on buttress (BT). (e–g) *Acharax yokosukaensis* (Kanie and Kuramochi, 1995) from Early Miocene seep sites in Ibaraki Prefecture, Honshu, Japan. (e) JUE no. 15887-2; (f) JUE no. 15887-4; (g) JUE no. 15887-2; the asterisk indicates the protruding external ligament attachment. (a–d: Hryniewicz et al. 2014; e–g: Amano and Ando 2011)

Solemya sp. was described from Paleocene wood-fall communities in Spitsbergen Island (Hryniewicz et al. 2019). The oldest species described as *Acharax* is *Acharax stantoni* from the Late Jurassic-Early Cretaceous (Tithonian-Albian) seeps of California (Kaim et al. 2014). Further Cretaceous species of *Acharax* found at seeps are Early Cretaceous (Albian) *Acharax mikasaensis* from the Ponbetsu seep site and the Campanian *Acharax cretacea* from the Yasukawa seep site, both in Hokkaido (Kanie and Nishida 2000; Kiel et al. 2008). Various species of *Acharax* are known also for seeps in the Paleogene (e.g., Amano et al. 2013a, b), the Neogene (e.g. Amano and Ando 2011; Kiel and Taviani 2018), and the late Pleistocene off of Svalbard (Hansen et al. 2019). The largest specimen of *Acharax* at a seep deposit reached at least 296 mm in length and is of the latest Early Miocene age (Fig. 10.3e–g; Amano and Ando 2011). In addition to the seep occurrences listed above, ancient *Solemya* is reported from shelfal siliciclastics, especially those organic-rich (e.g., Roemer 1839; Duff 1978; Kiel 2010a), while *Acharax* is more typical of deep-water environments (e.g., Vokes 1955; Taviani et al. 2011; Kaim et al. 2014).

10.2.2 Classification and Shell Characters

Two extant genera are recognized among Solemyidae, *Solemya* Lamarck, 1818, and *Acharax* Dall, 1908, and are well supported by molecular data (Sharma et al. 2013; Fukasawa et al. 2017). Distinguishing *Solemya* and *Acharax* based on shells requires information on the ligament and the internal radial rib in front of the posterior adductor muscle scar (Taylor et al. 2008; Kamenev 2009; Oliver et al. 2011). Most shell characters, i.e., the elongated shell shape, a thick periostracum, and broad but shallow radial ribs are present in both genera; thus, the easiest way to distinguish *Solemya* from *Acharax* is by the ligament; *Solemya* has an internal ligament set in a chondrophore (Fig. 10.3a–d), whereas *Acharax* has an external ligament supported by a thickened shell margin (Fig. 10.3e–g). Although the difference is noticeable on well-preserved shells, fossils are usually incomplete or partial internal molds lacking the ligament margin (Hryniewicz et al. 2014), rendering a generic identification of the specimens problematic. The internal features of both genera are similar and should not be used for generic distinction (e.g., Vokes 1955; Kamenev 2009; Oliver et al. 2011).

The genus *Solemya* is subdivided into the subgenera *Solemya* s.s.; *Solemyarina* Iredale, 1931; *Petrasma* Dall, 1908a; *Zesolemya* Iredale, 1939; *Austrosolemya* Taylor, Glover, and Williams, 2008; and *Pseudacharax* Huber, 2010, based on the difference in length and character of the anterior ligament extension, relation of the chondrophore to posterior adductor muscle scar, and presence of a buttress, supporting the anterior margin of posterior adductor muscle scar. A detailed discussion and table of the differences between particular subgenera of *Solemya* were presented by Taylor et al. (2008), Kamenev (2009), Oliver and Taylor (2012), and Hryniewicz et al. (2014). The Paleozoic genera *Dystactella* Hall and Whitfield, 1872, and

Clinopistha Meek and Worthen, 1870, have commarginal ornament and an external ligament. They differ by the rate of anterioventral expansion: weak in *Dystactella* and strong in *Clinopistha* (Pojeta 1988).

10.3 Family Nucinellidae

Kazutaka Amano and Krzysztof Hryniewicz

The family Nucinellidae Vokes, 1956, is considered either as the sister taxon to Solemyidae (Fig. 10.4) or at least closely related to it (Sharma et al. 2013). The species of *Nucinella* are shallow burrowers and are not obligate vent and seep inhabitants but also occur in “normal” marine sediments of 6 m to 3500 m in depth (e.g., Matsukuma et al. 1982; La Perna 2005; McLeod et al. 2010; Oliver and Taylor, 2012). Chemosymbiosis has been suggested for some species of *Nucinella* based on their reduced or absent digestive tract (e.g., Kuznetsov and Shileyko 1984; Reid 1998). These suggestions were partially confirmed by the accumulation of light carbon in the tissues of *Nucinella maoriana*, similar in magnitude to that of species of Thyasiridae and Solemyidae with confirmed chemosymbiosis found in their immediate surroundings (McLeod et al. 2010). Oliver and Taylor (2012) found potentially chemoautotrophic bacteria in the gills of the modern species *Nucinella owenensis* and *Huxleyia habooba*, which were recovered from the oxygen-minimum zone in the Arabian Sea off of southern Oman. Thus, *Nucinella* potentially is a member of chemosynthetic communities in seep sites.

10.3.1 Fossil Record and Evolution

The oldest fossil *Nucinella* species are *N. taylori* and *N. nakremi* from earliest Triassic marine sediments in Spitsbergen (Foster et al. 2017). A very small (~2 mm long) *Nucinella?* sp. has been reported from the early Carnian (earliest Late Triassic)

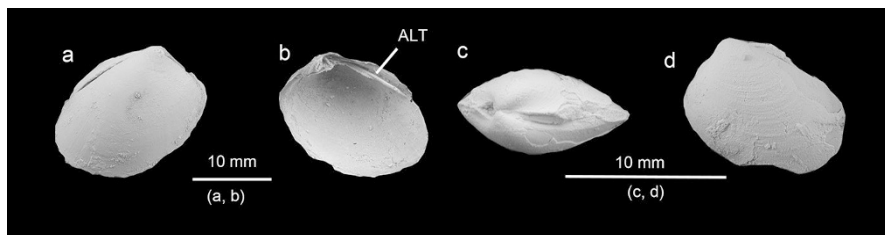


Fig. 10.4 Nucinellidae. (a–d) *Nucinella gigantea* Amano, Jenkins, and Hikida, 2007, from a Campanian seep site in Nakagawa Town, Hokkaido, Japan. (a, b) UMUT MM29245; Holotype; ALT anterior lateral tooth. (c, d) UMUT MM29248; Paratype. (a–d: Amano et al. 2007)

“normal” marine Cassian Formation from Northern Italy (Nützel and Kaim 2014), but the generic assignment of this species is uncertain. Later Mesozoic and Cenozoic non-seep species of *Nucinella* are associated with a variety of shallow to deep marine sediments (e.g., Vokes 1956; Clausen and Wignall 1990; Wignall et al. 2005). Seep species of *Nucinella* are generally larger than their non-seep relatives and are known since the Jurassic and possibly the Triassic. Peckmann et al. (2011) illustrated “a possible *Nucinella*” from a Late Triassic (Norian) seep site in Oregon. However, as the hinge of this species is unknown, it is difficult to judge whether this is the oldest record of this genus from seep deposits. Hammer et al. (2011) illustrated *Nucinella* sp. from uppermost Jurassic-lowermost Cretaceous seep carbonates in Svalbard. This oldest confirmed species of *Nucinella* has been described as *N. svalbardensis* (maximum length = 23 mm) by Hryniewicz et al. (2014). Coeval but smaller species of *Nucinella* have recently been reported from the latest Jurassic seep deposits from Novaya Zemlya in Arctic Russia (Hryniewicz et al. 2015b). As-yet undescribed species of *Nucinella* have been reported from a Barremian (Early Cretaceous) seep site in California (Kaim et al. 2014) and from the mid-Cretaceous Awanui II deposit on the North Island of New Zealand (Kiel et al. 2013). The Late Cretaceous *Nucinella gigantea* (maximum length = 18 mm) was described from Cenomanian and Campanian seep deposits on Hokkaido by Amano et al. (2007a) and Kiel et al. (2008) (Fig. 10.4). Amano et al. (2013b) found one large specimen of *Nucinella* sp. (23 mm in length) in the upper Eocene to lower Oligocene Tanamigawa Formation in Honshu. Moreover, one fossil specimen (14 mm in length) of *Nucinella* sp. was described along with other chemosymbiotic species from the Lower Miocene Kurosedani Formation in Toyama Prefecture, Honshu (Amano et al. 2019b). These records indicate that large *Nucinella* species were common in the latest Jurassic-earliest Cretaceous boreal shallow-water seeps (Hryniewicz et al. 2014, 2015a, b) and the Late Cretaceous Hokkaido seeps (Amano et al. 2007a, b; Kiel et al. 2008) but rather rare in Cenozoic fossil chemosynthetic communities.

10.3.2 Classification and Shell Characters

The genus *Nucinella* Wood, 1851, is characterized by usually small (a few mm in length) nuculiform shell with a smooth surface except for growth lines, a continuous row of taxodont teeth in the cardinal area, a long anterior lateral tooth, and one adductor muscle scar (Fig. 10.4). The largest living species, *N. boucheti* La Perna, 2005, reaches 25 mm in length. *Huxleyia* A. Adams, 1860, differs from *Nucinella* by having cardinal taxodont teeth only anterior to the umbo, posteriorly bound by a deeply sunken resilium. *Nucinella* is easily discriminated from smooth-shelled nuculids such as *Leionucula* by having a long anterior lateral tooth and one adductor scar only and by lacking a nacreous inner layer.

10.4 Family Mytilidae

Steffen Kiel and Kazutaka Amano

Chemosymbiotic species among the Mytilidae occur only in a single subfamily, the Bathymodiolinae. Bathymodiolins range in size from a few mm to approximately 360 mm in length and have colonized a broad range of chemosynthetic environments including vents, seeps, whale fall, and wood fall (Duperron 2010; Lorion et al. 2013). Most bathymodiolins are epifaunal, although some large species live half-buried in the sediment. Typically, methane seeps and hydrothermal vents are inhabited by large species, while wood and bones are colonized by small species. Bathymodiolins disperse via planktotrophic larvae, some of which are able to stay as long as 17 months in surface waters and feed on phytoplankton (Arellano and Young 2009; Arellano et al. 2014; Laming et al. 2015, 2018). After settling on the seafloor and metamorphosis, juveniles undergo a transformation from heterotrophy to chemosymbiosis, via mixotrophy, associated with increasing body size and gill proliferation (Laming et al. 2018). Although juveniles need to attach themselves to hard substrates with byssus threads, larger individuals can cut the byssus and actively move around to find the optimal position for the uptake of reduced compounds (Duperron 2010).

In contrast to all other groups of chemosymbiotic bivalves, bathymodiolins take up the sulfides and other reduced compounds via their inhalant current (Duperron 2010). Also unique among chemosymbiotic bivalves is that the bathymodiolins can harbor methanotrophic symbionts, either exclusively or in addition to the sulfur oxidizers (Childress et al. 1986). All other chemosymbiotic bivalve families rely solely on sulfur-oxidizing symbionts (Dubilier et al. 2008). While the acquisition of sulfur-oxidizing symbionts is considered an apomorphy of the group and is linked to its origin, methanotrophic symbionts were apparently acquired only much later in the evolutionary history of bathymodiolins (Lorion et al. 2013). Bathymodiolins have a wide range of symbiotic associations, with most symbionts being either sulfur or methane oxidizers, although some species are known to host as many as six different symbionts, including methyl and hydrogen oxidizers (Duperron et al. 2008; Duperron 2010; Petersen et al. 2011). The symbionts are housed in the gills, where they are located either extra- or intracellular. The phylogeny of the group suggests that extracellular symbiont location is the ancestral condition, whereas the more integrated, intracellular symbiont location is the derived condition (Lorion et al. 2013). Methanotrophic symbionts are only known from species with intracellular symbiont location, suggesting that the ability to house symbionts intracellularly is an evolutionary prerequisite for the acquisition of methanotrophic symbionts (Lorion et al. 2013). The symbionts are environmentally acquired after metamorphosis (Laming et al. 2018), and both the sulfur oxidizers and the methane oxidizers are gammaproteobacteria (Duperron et al. 2006). The small wood-inhabiting species *Idas argenteus* apparently lost its symbionts and turned to preying on larvae of

xylophagain (wood-feeding) bivalves (Ockelmann and Dinesen 2011; Rodrigues et al. 2015), indicating that chemosymbiosis is not an evolutionary one-way street.

A few non-chemosymbiotic mytilid species have been reported from fossil chemosynthesis-based habitats, including *Musculus?* sp. from Paleocene wood-fall communities in Spitsbergen (Hryniewicz et al. 2019), *Brachidontes* sp. from Miocene seep deposits in Cuba and Venezuela (Kiel and Hansen 2015), and *Samiolus iohannesbaptistae* from a Late Miocene “Calcarei a *Lucina*” seep deposit in northern Italy (Kiel and Taviani 2017).

10.4.1 Fossil Record and Evolution

Bathymodiolins first appear in the fossil record in the middle Eocene (Kiel and Amano 2013). A time-calibrated molecular phylogenetic tree indicated a latest Cretaceous or early Cenozoic origin followed by a major radiation during the late Eocene-early Oligocene, possibly because the increased global circulation of cold deep water after the initial glaciation of Antarctica slowed larval metabolic rates, thereby increasing their longevity and dispersal capabilities (Lorion et al. 2013). Based on the phylogenetically basal position of various wood- and bone-inhabiting species, the “wooden steps” hypothesis was proposed, which claims that bathymodiolins first adapted to the low sulfide concentrations at sunken wood and bones on the seafloor and subsequently adapted to the higher sulfide concentrations at methane seeps and hydrothermal vents (Distel et al. 2000; Smith and Baco 2003). The general pattern of wood- and bone-inhabiting species in basal positions and the vent- and seep-inhabiting species in more derived positions has been confirmed by most subsequent molecular phylogenetic studies (Samadi et al. 2007; Lorion et al. 2008; Miyazaki et al. 2010; Thubaut et al. 2013). However, from the paleontological point of view, the role of whale carcasses as evolutionary stepping stones is less clear. The oldest records of bathymodiolins are from middle Eocene seep deposits, while examples from whale falls (and wood falls) are so far only known from the late Eocene onward (Kiel and Goedert 2006a, b; Kiel 2008). Large marine reptile bones in the late Mesozoic supported a similar suit of taxa as early Cenozoic whale falls, but lack bathymodiolins or other epifaunal chemosymbiotic bivalves (Kaim et al. 2008; Jenkins et al. 2017). Also, wood-fall communities are known from late Mesozoic deep-water deposits, but again, bathymodiolins or other epifaunal chemosymbiotic bivalves are missing from these communities (Kiel et al. 2009; Kaim 2011).

10.4.2 Classification and Shell Characters

Based on molecular phylogenetic work, it is now well established that all chemosymbiotic mytilids inhabiting vents, seeps, bones, and wood form a single monophyletic clade, the bathymodiolins (Distel et al. 2000; Samadi et al. 2007; Miyazaki

et al. 2010; Lorion et al. 2013; Thubaut et al. 2013; Liu et al. 2018). Their closest relative among the Mytilidae is *Modiolus modiolus* (although the sample size is limited), with which bathymodiolins share similarly shaped shells including the morphology of the prodissoconch, as well as a similar shell microstructure (Génio et al. 2012). Within the bathymodiolins, genera are difficult to distinguish based on shell characters, especially among the small taxa. The larger genera may be distinguished using the morphology of muscle attachment scars, although these are typically very weak and are rarely found in fossils older than Miocene.

1. *Bathymodiolus* Kenk and Wilson, 1985: Large mussels with the general shape of the horse mussel *Modiolus* found at hydrothermal vents and methane seeps have initially been assigned to the genus *Bathymodiolus*, based on *B. thermophilus* from the first known vent communities on the Galapagos Ridge (Kenk and Wilson 1985). With increasing numbers of species being discovered at vents and seeps worldwide, molecular work indicated that these large-sized *Bathymodiolus* species belong to at least two distinct clades: *Bathymodiolus* (sensu stricto) and the so-called *childressi* clade, a group of species closely related to *Bathymodiolus childressi* from the Gulf of Mexico. A distinction of the two clades on conchological ground may be possible because they differ by the structure of the posterior retractor muscle scars (see discussion of the “*childressi* clade”). *Bathymodiolus* may be distinguished from *Modiolus* based on its very early juvenile shell, which is triangular in *Bathymodiolus* and more modioliform (more elongate) in *Modiolus*. Based on this character, the Oligocene *Modiolus willapaensis* Squires and Goedert, 1991, was the first fossil species to be identified as belonging to *Bathymodiolus* (Kiel 2006). With the distinction between *Bathymodiolus* (s.s.) and the *childressi* clade being difficult to make in the absence of well-preserved muscle scars, many fossil mussels from methane seep deposits of the Cenozoic age are simply referred to as *Bathymodiolus* (sensu lato). These include several species from the Eocene to Oligocene of Washington State, USA (Kiel and Amano 2013); *Bathymodiolus* (s.l.) *inouei* Amano and Jenkins, 2011, from the late Eocene to Oligocene of Japan (Fig. 10.5c, e, g; Amano et al. 2013b); and *B.* (s.l.) *palmarensis* from the Oligocene of Colombia, as well as several Miocene species from the Caribbean region, Italy, Japan, and New Zealand (Gill et al. 2005; Amano et al. 2010; Kiel et al. 2010; Kiel and Hansen 2015; Kiel and Taviani 2017).
2. *Gigantidas* Cosel and Marshall, 2003: Based on *Gigantidas gladius* Cosel and Marshall, 2003, from extant vents on the Kermadec Ridge north of New Zealand, this genus includes large and very elongate shells and can be separated from *Bathymodiolus* (s.l.) by its elongated shell and strongly concave ventral margin. A single fossil species, *Gigantidas coseli* Saether, Little, Campbell, Marshall, Collins and Alfaro, 2010, has been described from Early to Middle Miocene seep deposits on North Island, New Zealand (Fig. 10.5i; Saether et al. 2010).
3. The “*childressi* clade”: *Bathymodiolus childressi* Gustafson, Turner, Lutz and Vrijenhoek, 1998, from methane seeps in the Gulf of Mexico was only hesitantly assigned to *Bathymodiolus* because molecular phylogenetic data indicated that it

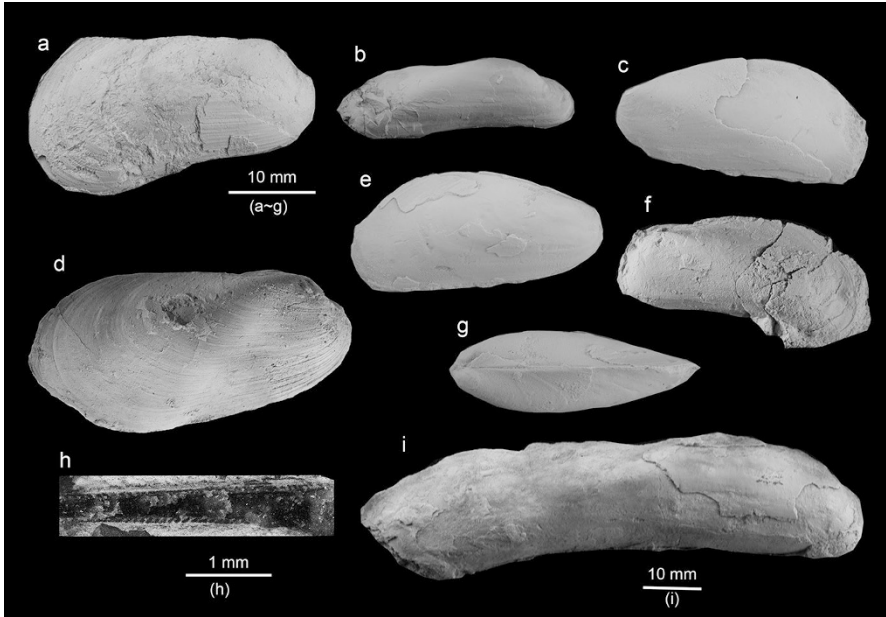


Fig. 10.5 Mytilidae (Bathymodiolinae). **(a)** *Bathymodiolus* (s.l.) *heretaunga* Saether, Little, Campbell, Marshall, Collins, and Alfaro, 2010, from the Middle Miocene Moonlight North seep site in North Island, New Zealand. **(b)** *Adipicola chikubetsuensis* Amano, 1984, from an early Middle Miocene whale-fall site in Shosanbetsu village, Hokkaido, Japan; JUE no. 15002; Holotype. **(c, e, g)** *Bathymodiolus* (s.l.) *inouei* Amano and Jenkins, 2011, from an early Oligocene seep site in Urahoro Town, Hokkaido, Japan; JUE no. 15873; Holotype. **(d)** *Vulcanidas? goederti* Kiel and Amano, 2013, from a middle Eocene seep site in Washington State, USA; UWBM 98890; Holotype. **(f)** *Adipicola* sp. from a Middle Miocene whale-fall site in Nupinai, Hokkaido, Japan. **(h)** *Idas? olympicus* Kiel and Goedert 2007, from an early Oligocene seep site in Washington State, USA; UWBM 98918. **(i)** *Gigantidas coseli* Saether, Little, Campbell, Marshall, Collins, and Alfaro, 2010, from the Middle Miocene Moonlight North seep site in North Island, New Zealand. **(b)**: Amano 1984; **(c, e, g)**: Amano and Jenkins 2011; **(d, h)**: Kiel and Amano 2013; **(f)**: Amano et al. 2007; **(a, i)**: collection by Amano)

belonged to a different clade within the Bathymodiolinae than *B. thermophilus* (Gustafson et al. 1998). Among members of the “*childressi* clade,” the posterior byssal retractors form a continuous scar united with the posterior adductor muscles, reflecting the multibundle posterior byssal retractor complex diagnostic of modern species of this clade (Cosel 2002; Saether et al. 2010). This feature distinguishes the “*childressi* clade” from *Bathymodiolus* (s.s.), in which the anterior and posterior portions of the posterior byssal retractor scars, are well separated. Although several authors suggested establishing a new genus for the “*childressi* clade” (Gustafson et al. 1998; Jones and Vrijenhoek 2006), others suggested including this clade in *Gigantidas* (Thubaut et al. 2013; Xu et al. 2019; Jang et al. 2020). A single fossil species, *Bathymodiolus* (s.l.) *heretaunga* Saether, Little, Campbell, Marshall, Collins and Alfaro, 2010 (Fig. 10.5a), from the

Miocene of New Zealand, has been assigned to the “*childressi* clade” (Saether et al. 2010).

4. *Vulcanidas* Cosel and Marshall, 2010: This phylogenetically basal genus is based on *Vulcanidas insolatus* Cosel and Marshall, 2010, from vents north of New Zealand. Its shell is similar in shape to that of *Bathymodiolus* (s.l.), and it may be distinguished from other bathymodiolins by its distinct ridge running from the beak to the posterior ventral margin, with a concave margin anterior to it and expanding posterior shell portion behind this ridge. The only fossil record so far is *Vulcanidas? goederti* Kiel and Amano, 2013 (Fig. 10.5d), from seep carbonates of the middle Eocene Humptulips Formation in Washington State, which is also the oldest fossil record of the bathymodiolins.
5. *Idas* Jeffreys, 1876/*Adipicola* Dautzenberg, 1927: Numerous small (<20 mm) mussels living on wood, bone, and other organic substrates in deep water have been variously assigned to *Adipicola* and *Idas* (Dell 1987). Molecular phylogenetic work has shown that these species are found within various clades among the bathymodiolins and, furthermore, that they show a wide range of morphologic diversity. This makes it currently very difficult to assign small, fossil bathymodiolins to either of these genera. Two generic names (*Lignomodiolus* and *Nypamodiolus*) have prematurely been applied to these taxa by Thubaut et al. (2013) and have since been used in other publications (Génio et al. 2015; Samadi et al. 2015; Liu et al. 2018; Xu et al. 2019). However, the two genera have not been formally described, and no type species have been designated; hence, the names are *nomen nuda* and are presently not available. Morphologically, *Idas* may be separated from *Adipicola* by small crenulations on its hinge, which are absent in *Adipicola* (Fig. 10.5h). A few fossil records of these taxa are known, the oldest being *Idas? olympicus* Kiel and Goedert, 2007, from late Eocene to Oligocene deep-water whale-fall and wood-fall communities in Washington State, USA (Goedert et al. 1995; Kiel and Goedert 2007). Further records are *Adipicola chikubetsuensis* (Amano, 1984) from an early Middle Miocene whale fall in northern Hokkaido, Japan (Fig. 10.5b; Amano and Little 2005); *Adipicola* sp. from a Middle Miocene whale fall in eastern Hokkaido, Japan (Fig. 10.5f; Amano et al. 2007a, b); and *Adipicola* sp. from a late Middle to early Late Miocene whale fall in central Hokkaido (Jenkins et al. 2018a). *Adipicola apenninica* occurs at a Middle Miocene whale fall (Danise et al. 2016), and *Idas* sp. was reported from Pliocene whale and wood falls in northern Italy (Bertolaso and Palazzi 1994). *Idas* sp. was also illustrated from a Pliocene shallow-water whale fall in northern Italy (Danise et al. 2010). Under certain circumstances, possibly the absence of large bathymodiolins, extant *Idas* colonizes methane seeps, for example, in the Mediterranean Sea (Olu et al. 2004). Fossil seep carbonates with *Idas? olympicus* have been reported from the Oligocene of western Washington State (Kiel and Amano 2013); *Idas* aff. *tauroparva* is known from the Late Miocene “Calcarei a *Lucina*” in northern Italy (Kiel et al. 2018); and a single specimen of *Idas* sp. was found in early Oligocene seep carbonate in northern Peru (Kiel et al. 2020a, b).

10.5 Families Modiomorphidae and Kalenteridae

Robert G. Jenkins, Krzysztof Hryniewicz, and Steffen Kiel

The Modiomorphida is a heterogeneous clade of bivalves ranging from the Ordovician to the Miocene, and both its internal and external phylogenetic relationships are controversial. For the sake of this review of Modiomorphida from fossil vents and seeps, we consider the clade related to Carditida (cf. Kaim and Schneider 2012; Jenkins et al. 2013) rather than to Anomalodesmata (Morris et al. 1991) or to Cardiida (Carter et al. 2011). Among the traditionally defined families of Modiomorphida, only the Modiomorphidae Miller, 1877, and Kalenteridae Marwick, 1953, include taxa at fossil vents and seeps.

Although Modiomorphida are extinct and there is no direct proof for chemosymbiosis in the fossil record, the vent- and seep-inhabiting taxa are generally assumed to have been chemosymbiotic based on the actualistic principle. Modiomorphida at fossil vents and seeps are often large or abundant, and all bivalves with these traits at modern vents and seeps are chemosymbiotic. Hence it seems a fair assumption that also the vent- and seep-inhabiting Modiomorphida were chemosymbiotic (Kelly et al. 2000; Hryniewicz et al. 2017b; Jakubowicz et al. 2017; Jenkins et al. 2013, 2018b; Kiel et al. 2017; Kiel and Peckmann 2019).

Modiomorphida have modioliform shells (hence the name), some species exceed 300 mm in length, and several of the seep-inhabiting taxa are quite elongated, showing a striking resemblance to elongate extant bathymodiolins and vesicomysids (Hryniewicz et al. 2017b). Furthermore, some species of the kalenterid *Caspiconcha* were found in densely packed clusters and positioned at an angle of $\sim 30^\circ$ relative to bedding plane (Kelly et al. 2000; Kiel and Peckmann 2008) and possess a gape at the anterior ventral shell margin (Jenkins et al. 2013). These traits indicate that seep-inhabiting Modiomorphida had a semi-infaunal lifestyle to ensure access to both sulfide from within the sediment and oxygen from the water column, as in extant vesicomysids and some bathymodiolins (Jenkins et al. 2013; Hryniewicz et al. 2017b; Krylova et al. 2010).

10.5.1 Fossil Record and Evolution

Vent- and seep-inhabiting members of the Modiomorphidae are known from the Silurian and Devonian, with the Silurian *Ataviaconcha* sp. from the El-Borj seep deposit in Morocco being the as-yet earliest record of bivalves from chemosynthesis-based ecosystems (Jakubowicz et al. 2017). The Kalenteridae include four genera occurring at fossil seeps, *Terzileria* and *Kasimlara* from the Late Triassic, *Caspiconcha* from the Late Jurassic to Late Cretaceous, and *Pseudophopsis* from the Eocene to the early Oligocene. This stratigraphically patchy distribution of different kalenterid genera inhabiting seeps raised the question if these genera are repeated

radiations of various kalenterid lineages that convergently developed similar morphological adaptations to this habitat (the “repeated colonization hypothesis”), or if they are members of a single phylogenetic lineage that continuously inhabited deep-sea hydrocarbon seeps (the “single lineage hypothesis”) (cf. Kiel 2018). In favor of the first hypothesis, Hryniewicz et al. (2017b) argued that the elongate modioliiform shell shape is a necessary adaptation to reach sulfide deep in the sediment while staying in contact with oxygenated bottom waters, possibly enhanced by competition with infaunal chemosymbiotic species. A possible counter-argument is that the repeated development of elongate shells occurs also among vesicomysids (with very elongate specimens among the genera *Pleurophopsis*, *Archivesica*, and *Abyssogena*) and bathymodiolins (i.e., *Gigantidas* and *Bathymodiolus boomerang*), both of which are largely restricted to chemosynthesis-based ecosystems. However, especially the early Mesozoic, fossil record of seeps is still very patchy, and more data and phylogenetic analyses are needed to solve this issue.

The kalenterid genus *Caspiconcha* has a prominent place in the history of research on the vent and seep fauna. Two Cretaceous members of *Caspiconcha* have been misidentified as vesicomysids or mytilids in the earlier literature, resulting in considerable misinterpretations of the fossil ranges of these modern chemosynthetic bivalve clades (e.g., Little and Vrijenhoek 2003; Kiel and Little 2006). These cases are the alleged mytilid *Modiola major* from seep deposits in California, USA (Fig. 10.6c, d), and the alleged vesicomysid “*Calyptogena* sp.” from Hokkaido, Japan. These two species are now recognized as *Caspiconcha major* and *Caspiconcha lastsamurai*, respectively (Amano and Kiel 2007b; Kiel and Peckmann 2008; Jenkins et al. 2013, 2018b).

10.5.2 Classification and Shell Characters

Family Modiomorphidae

1. *Ataviaconcha* Hryniewicz, Jakubowicz, Belka, Dopieralska, and Kaim, 2017, is based on *A. wendti* (Hryniewicz et al. 2017b) from the Middle Devonian Hollard Mound seep deposit in Morocco. Its shell is elongated and modioliiform with enlarged anterior and posterior lobes and reaches >100 mm in length. Larger specimens have a boomerang-like shape with a deep ventral sinus. Both anterior and posterior adductor muscle scars are present, and it lacks the “caspiconchid process” close to the anterior shell margin (see *Caspiconcha*). A weak socket is present in the cardinal area of the right valve; the shell is otherwise edentulous. At least some of these morphological features, such as large, elongated modioliiform shell with enlarged anterior and posterior lobes, are also seen in the Silurian *Ataviaconcha* sp. from El-Borj (Jakubowicz et al. 2017). The genus hence ranges from the late Silurian to the Middle Devonian.
2. *Sibaya* Little, Maslenikov, Morris, and Gubanov, 1999, is based on the sole species *Sibaya ivanovi*, which is known exclusively from the Devonian Sibay vent

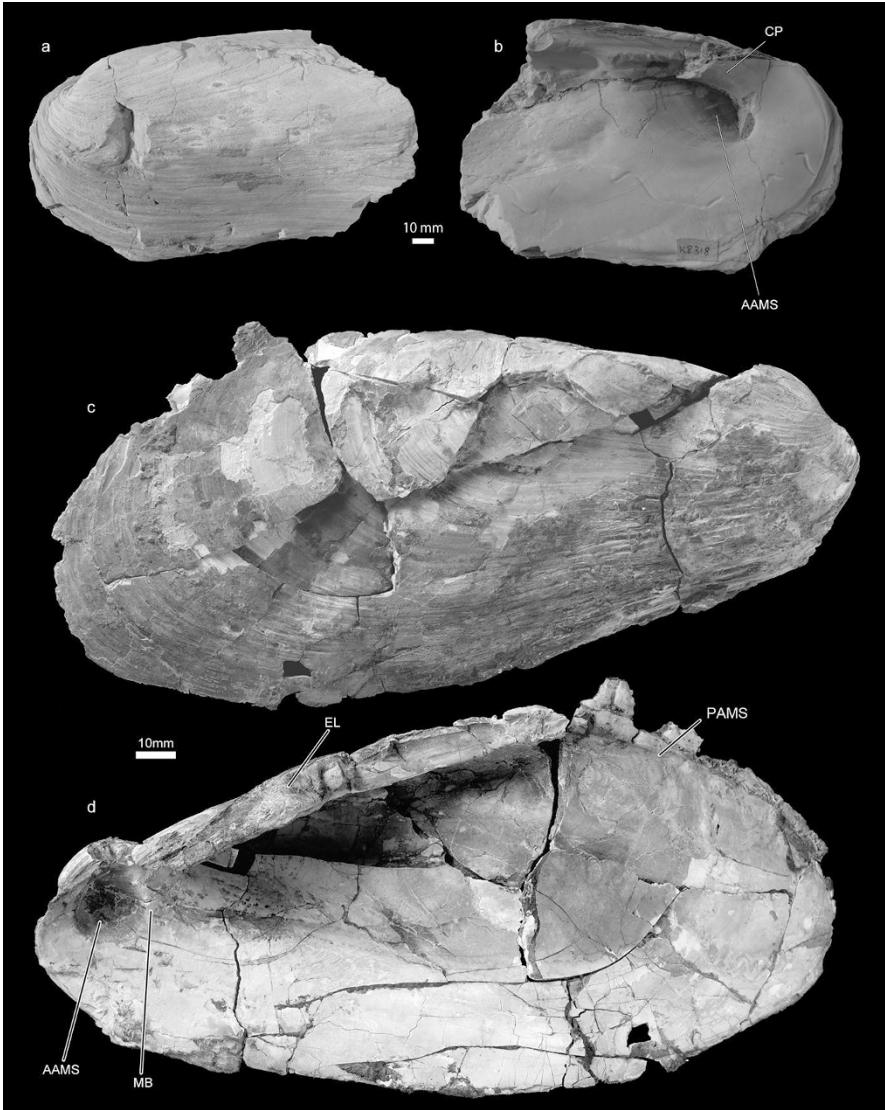


Fig. 10.6 Kalenteridae. (a, b) *Caspiconcha whithami* Kelly, 2000, from an Early Cretaceous seep site in Greenland; K8318 stored at the Sedgwick Museum, the University of Cambridge; Holotype. AAMS anterior adductor muscle scar, CP caspiconchid process. (c, d) *Caspiconcha major* (Gabb, 1869) from the Early Cretaceous Eagle Creek seep site in California, USA; CAS 72527-9 stored at California Academy of Science. AAMS anterior adductor muscle scar, PAMS posterior adductor scar, MB myophoric buttress, EL external ligament. (a, b: Kelly et al. 2000; c, d: Gabb 1869)

site in the Ural Mountains, where it co-occurs with worm tubes (Little et al. 1999). Two specimens of *S. ivanovi* have so far been discovered, one of them incomplete, which in addition to its restricted occurrence, further limits the knowledge on *Sibaya*. A study of limited materials available indicates that *Sibaya* had an ovoid shell reaching 70 mm in length and lacked a ventral sinus. Its external ornament was composed of a series of commarginal growth lines. Ligament was external, the dorsal margin of both valves connected with perios-tracum. Internal structures, like pallial line and muscle scar impressions, are as yet unknown. The genus is known so far only from the Middle Devonian.

Family Kalenteridae

3. *Kasimlara* Kiel, 2018, includes the Upper Triassic type species, *K. kosuni*, and an as-yet undescribed species from the same seep deposits, and can be separated from *Caspiconcha* and *Terzileria* by having a small pallial sinus and a much smaller anterior adductor muscle scar (Kiel 2018).
4. *Terzileria* Kiel, 2018, is known only from its Upper Triassic type species, *T. gregaria* Kiel, 2018, and differs from *Caspiconcha* by having an anterior adductor muscle scar separated from a pedal retractor scar and located at a more ventral position and the pallial line being closer to the shell margin (Kiel 2018).
5. *Caspiconcha* was introduced for *Caspiconcha whithami*, Kelly, in Kelly et al. (2000) (Fig. 10.6a, b) from Early Cretaceous seep deposits in Greenland. It is characterized by a cuneiform to mytiliform shell with a smooth shell surface apart from growth lines, an anterior adductor muscle scar deeply set within the myophoric buttress, which is partially covered by the so-called caspiconchiid process, and an edentulous hinge; the shell has a crossed lamellar shell structure and lacks nacre (Kelly et al. 2000; Jenkins et al. 2013). *Caspiconcha* differs from *Myoconcha* by its caspiconchiid process and its edentulous hinge plate. It presently includes seven named species, the oldest being *Caspiconcha major* from a Upper Jurassic (Tithonian) seep deposit in California, USA. The genus reached its highest diversity and a nearly worldwide geographic distribution in the Albian (Kiel and Peckmann 2008; Jenkins et al. 2013), followed by a rather sudden demise after the end of the Early Cretaceous. One further Late Cretaceous species of *Caspiconcha* is known from the Santonian of Amakusa in southern Japan (Jenkins et al. 2018b) and is awaiting formal description.
6. *Pseudophopsis* Kiel, Hybertsen, Hyžný, and Klompmaker, 2020, is based on *Pleurophopsis peruviana* Olsson, 1931, from the Oligocene of Peru and includes *Unio bitumen* Cooke, 1919, from the Eocene of Cuba (Kiel et al. 2020b). The elongate-oval shells are well inflated, reach 100 mm in length, and are sculptured by rough growth lines only; the hinge plate is either edentulous or bears weak teeth subparallel to the shell margin. *Pseudophopsis* differs from *Caspiconcha* by having a round rather than elongate anterior adductor muscle scar without posterodorsal projection, and the Miocene kalenterid *Madrynomya* Griffin and Pastorino, 2006, has more coiled and more pointed umbones and a much broader but shorter hinge plate.

10.6 Family Lucinidae

Steffen Kiel

Lucinids are the most species-rich group of chemosymbiotic bivalves (Taylor and Glover 2006). The highest diversity is found in shallow water, particularly in sea grass environments, but they are also recorded from the depth of 2500 m, especially from the tropics (Glover and Taylor 2016; Taylor et al. 2014). Lucinids live buried in the sediment, with the umbones orientated upward and the inhalant and exhalant siphons reaching upward in mucus-lined tubes (Allen 1958). Sulfide is taken up by the foot from the sediment pore water and transported to the symbiont-hosting gills. The symbionts are typically gammaproteobacteria, which are environmentally acquired after metamorphosis and are housed intracellularly in the gills (Duperron et al. 2007). The main shell features of lucinids are a roundish to oval shell often with a posterior ridge, an elongate anterior adductor muscle scar that is detached from the pallial line, and the lack of a pallial sinus, and some taxa show an impression of the pallial blood vessel. The hinge often has cardinal and lateral teeth, although groups with reduced dentition or even edentulous forms exist, especially among seep-inhabiting clades (Taylor and Glover 2009; Kiel 2013). Lucinids have a prodissoconch (early ontogenetic shell) with a large initial shell (prodissoconch I) that reflects lecithotrophic development, although some species show indications of a short planktonic larval phase (Glover and Taylor 2007). Shallow-water lucinids have a wide range of shell shapes and ornamentations (Taylor and Glover 2006), whereas seep-inhabiting taxa tend to be smooth, elongate-oval, and flat (Taylor and Glover 2009; Kiel 2013). Exceptions to this are *Nymphalucina* and *Lucinoma* with their strong and sharp ribs, and the very inflated *Meganodontia*.

10.6.1 Fossil Record and Evolution

Lucinidae seem to have originated in the Silurian. *Iliona prisca* from the Silurian of Gotland (Sweden) shares characteristic features with modern lucinids, such as the elongate, detached anterior adductor muscle scar and the scar of the pallial blood vessel. These two characters are thought to be associated with the chemosymbiotic mode of life (Taylor and Glover 2006). Furthermore, *Iliona prisca* was found in a similar life position as Recent lucinids (Liljedahl 1991; Taylor and Glover 2006). Thus, lucinids are considered to have acquired their chemosymbiotic mode of life in the early Paleozoic time.

Diversity among lucinids remained low for most of the Paleozoic and Mesozoic. The rapid and large radiation of the modern groups started in the mid-Cretaceous and was considered related to the rise of sea grasses and mangroves (Stanley 2014). Deep-water groups are known since the Jurassic (Taylor et al. 2014), and the first occurrences at methane seeps are from the Upper Jurassic (Gaillard et al. 1992; Kiel

2013). This late appearance at seeps is peculiar given that lucinids are considered to have acquired their chemosymbiotic mode of life in the Silurian. This may be a sampling artifact because pre-Jurassic seep deposits are scarce (Kiel 2010a) or might reflect the overall diversification of the Lucinidae, which were rare during the Paleozoic and most of the Mesozoic and only started diversifying in the Cretaceous (Stanley 2014; Kiel and Peckmann, 2019).

10.6.2 Classification and Shell Characters

Molecular phylogenetic work conducted during the last decade showed that contrary to previous classifications, neither the Thyasiridae nor the Ungulinidae belong to the lucinids (Williams et al. 2004; Taylor et al. 2007a, b). Seven subfamilies of the Lucinidae are currently recognized based on molecular data – these being the Codakiinae, Leucosphaerinae, Lucininae, Monitilorinae, Myrteinae, and Pegophyseminae; the status of Milthinae is presently equivocal due to the lack of material available for molecular work (Taylor et al. 2011). Members of the Myrteinae have colonized deep-sea methane seeps since the Jurassic and were the most diverse group in this environment during the remainder of the Mesozoic (Kiel 2013). The Codakiinae started colonizing seeps in the Late Cretaceous with the genus *Nymphalucina*, and the most common codakiin at Recent seeps, *Lucinoma*, first appeared in this environment in the Oligocene (Kiel 2013). Among the Pegophyseminae, *Meganodontia* and *Pegophysema* are known from vent/seep environments (Bouchet and Cosel 2004; Kiel and Hansen 2015) and were reported from Miocene seep deposits in both Italy and the Caribbean region (Kiel and Hansen 2015; Kiel and Taviani 2017). Many lucinid genera found in Mesozoic and Cenozoic deep-water seep deposits are restricted to this type of habitat and show morphologies that are unknown from shallow-water environments, with the notable exception of the widespread genus *Lucinoma*. Two species of Lucininae, *Megaxinus ellipticus* (Borson) and *Megaxinus stironensis*, were found at a Pliocene seep site in northern Italy (Kiel and Taviani 2018).

As more fossil seeps are being described, the number of genera living in, and possibly being restricted to, this environment is likely to increase. In the following, the main shell features of the seep-inhabiting lucinid genera are outlined.

Subfamily Myrteinae

The genera *Amanocina*, *Elliptiolucina*, *Elongatolucina*, and *Nipponothracia* are all characterized by an elongate-oval, smooth shell with an edentulous hinge and are considered as a single seep-inhabiting lineage among the Myrteinae (Kiel 2013).

1. *Myrtea* Turton, 1822: The extant *Myrtea amorpha* (Sturany, 1896) occurs at seeps in the Mediterranean Sea (Olu et al. 2004), but in the fossil record, this genus tends to be used as a “trash bin taxon” for various Myrteinae of uncertain affinity and should be treated carefully. In eastern Hokkaido, *Myrtea ezoensis* (Nagao) survived from the Cretaceous to the Paleocene (Amano et al. 2018a).

2. *Beauvoisina* Kiel, Campbell, and Gaillard, 2010: This monotypic genus occurs only in Oxfordian (Late Jurassic) seep deposits at Beauvoisin in southeastern France. Shells are elongate-oval, reach 140 mm in length, are smooth except for rough growth increments, and have two cardinal teeth in each valve and a short ligament nymph. The pallial line and muscle attachment scars are very indistinct to almost indiscernible; the anterior adductor muscle scar is broad and elongated and reaches about half the shell height. A peculiar feature of this genus, which distinguishes it from the otherwise very similar *Tehamatea* and *Cubatea*, is a ridge inside the lunule (Kiel et al. 2010; Kiel 2013).
3. *Cubatea* Kiel, Campbell, and Gaillard, 2010: Based on an Eocene species from Cuba, *Cubatea asphaltica* (Fig. 10.7b) (Cooke, 1919), the genus is now recognized from the Upper Cretaceous of New Zealand to the Neogene of the Caribbean region (Kiel 2013; Kiel and Hansen 2015). Shells are of moderate size (50–100 mm), elongate-oval, with regular rib-like growth increments on the juvenile shell, and a mostly smooth adult shell. The hinge plate is broad, with one strong and often bifid cardinal tooth in the right valve, and two cardinals in the left valve; the lateral teeth are very strong and bifid. The anterior adductor muscle scar is distinctive, relatively short and broad, almost rectangular, is ventrally detached from the pallial line for about 2/3 of its length, and is diverging from the pallial line for about half its own width. The genus *Tehamatea* is very similar and differs mainly in having indistinct (but similarly shaped) muscle attachment scars and weaker lateral teeth. *Ezolucina* differs by having an elongate lunule (Amano et al. 2008; Kiel et al. 2010; Kiel 2013).
4. *Tehamatea* Kiel, 2013: The genus is based on an Early Cretaceous species, *Tehamatea ovalis* (Stanton, 1895), from Tehama County in California, USA (Fig. 10.7a), and reached a worldwide distribution during Late Jurassic to Late Cretaceous time (Agirrezabala et al. 2013; Kiel 2013; Hryniewicz et al. 2014). Its shell characters are essentially those of *Cubatea*; the differences between *Cubatea* and *Ezolucina* are outlined in the discussion of *Cubatea*.
5. *Ezolucina* Amano, Jenkins, Kurihara, and Kiel, 2008: The genus is based on *Vesicomya inflata* Kanie and Nishida, 2000, from the Cenomanian (Upper Cretaceous) of Japan, a large, moderately inflated, veneriform shell with a very elongate lunule. In large specimens, the posterior side has a strong ridge resulting in a somewhat pointed posterior shell margin. The hinge has one strong cardinal tooth in the right valve and two in the left valve. The anterior adductor muscle scar is broad with a rectangular ventral end and reaches just below the midline of the shell (Amano et al. 2008). The type of locality of *Ezolucina inflata* is not a seep deposit, but *Ezolucina* has subsequently been reported from Cretaceous seep deposits in New Zealand (Amano et al. 2008; Kiel et al. 2013).
6. *Cryptolucina* Saul, Squires, and Goedert, 1996: The type species, *Cryptolucina megadyseides* Saul, Squires, and Goedert, 1996, has an elongate-oval shell with a nearly smooth surface; an edentulous hinge; an anterior adductor muscle scar similar to that of *Cubatea*, *Tehamatea*, and *Ezolucina*; and a strongly prosogyrate umbo (Saul et al. 1996). This morphology of the umbo distinguishes *Cryptolucina* from *Beauvoisina*, *Cubatea*, *Ezolucina*, and *Tehamatea*. The type

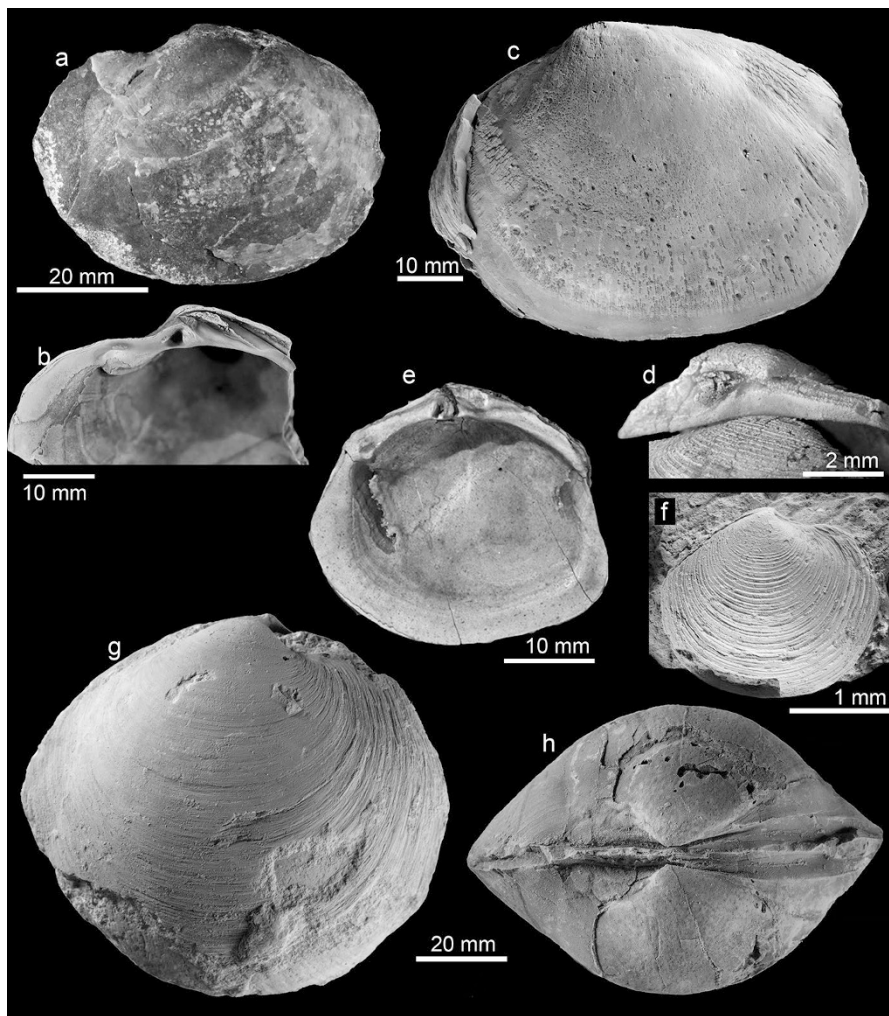


Fig. 10.7 Lucinidae. (a) *Tehamatea ovalis* (Stanton, 1895) from an Early Cretaceous seep site in California, USA; USNM 23056; Holotype. (b) *Cubatea asphaltica* (Cooke, 1919) from an Eocene seep site in Cuba; USNM 533988. (c) *Elliptiolucina washingtonia* Kiel, 2013, from an Oligocene seep site in Washington State, USA; GZG.INV.88327; Holotype. (d) *Amanocina ezoensis* (Kanie and Kuramochi, 1996) from a Late Cretaceous seep site in Hokkaido, Japan; UMUT MM 29541. (e) *Nymhalucina cleburni* (White, 1882) from the Late Cretaceous of Colorado, USA; USNM 9971. (f) *Lucinoma* sp. from the Pliocene Stirone River seep site in northern Italy. (g, h) *Meganodontia* sp. from a Miocene seep site in Cuba. (a–c: Kiel 2013; d: Kiel et al. 2008; e: Kiel and Peckmann 2007; f: collection by Steffen Kiel and Marco Taviani; g, h: PRI collection)

species was described from middle Eocene mudstone of the Humptulips Formation in Washington State, USA, and the assignments of all other species considered as belonging to this genus have been questioned (e.g., Kiel 2013), which may leave *Cryptolucina* as a monotypic genus that is probably not seep-related.

7. *Amanocina* Kiel, 2013: This genus differs from the other three edentulous seep lucinids by lacking the triangular depression in the hinge plate below the umbo and by having a narrower and longer anterior adductor muscle scar. It is based on the Cenomanian (Upper Cretaceous) *Amanocina yezoensis* (Fig. 10.7d) (Kanie and Kuramouchi 1996) and is currently known from the Barremian (Lower Cretaceous) of Greenland, the Albian (Lower Cretaceous) of New Zealand, the Cenomanian (Upper Cretaceous) of Hokkaido, and the Oligocene of Colombia (Kiel 2013).
8. *Nipponothracia* Kanie and Sakai, 1997: The shells of this genus are oval and have the umbo in a subcentral position, in contrast to many species of *Elliptiolucina* and *Elongatolucina* with their umbo displaced toward the anterior. *Nipponothracia* is based on *Thracidora gigantea* Shikama, 1968, and is currently known from the Oligocene of the northern Peru and the Middle Miocene of central Japan and Trinidad (Kase et al. 2007; Kiel 2013; Kiel and Hansen, 2015).
9. *Elongatolucina* Gill and Little, 2013: Shells are large, reaching a length of 180 mm or more, very elongate, and have the umbo in a very anterior position. The anterior adductor muscle scar is detached from the pallial line for most of its length and may reach slightly below the midline of the shell. A character that may distinguish this genus from *Elliptiolucina* is the flattened lateral side of the shell of *Elongatolucina*. The genus is based on *Cryptolucina elassodyseides* Saul, Squires, and Goedert, 1996, and is currently known from the middle Eocene of the Washington State, the Oligocene of Colombia, and the Middle Miocene Venezuela (Gill and Little 2013; Kiel 2013; Kiel and Hansen 2015).
10. *Elliptiolucina* Cosel and Bouchet, 2008: This is the only extant genus of the “edentulous seep lucinids”; shells are elongate-oval and rarely reach beyond 130 mm in length – differences between *Nipponothracia* and *Elongatolucina* are outlined above. Molecular data clearly support its position within the Myrteinae (Kuhara et al. 2014). The currently oldest record is from the late Oligocene of the North American Pacific coast, with further records from the Neogene of the central Indo-West Pacific and New Zealand (Fig. 10.7c; Kiel 2013; Amano et al. 2018b).

Subfamily Codakiinae

11. *Nymphalucina* Speden, 1970: This genus was widespread in the Late Cretaceous Western Interior Seaway, a broad epicontinental sea stretching from the Gulf of Mexico to the Arctic Ocean, where it occurred in seep and non-seep environments (Speden 1970; Kauffman et al. 1996; Kiel et al. 2012). *Lucina scotti*, likely belonging to *Nymphalucina*, has recently been reported from shallow-water seeps in Campanian-Maastrichtian (Late Cretaceous) sediments on Snow

Hill and Seymour islands on the eastern side of the Antarctic Peninsula (Little et al. 2015). The genus thus appears to be widespread. Shells are oval to pentagonal with a distinctive posterior ridge, sharp commarginal ribs and a very elongated lunule. There are two to three cardinal teeth in each valve, which radiate and diverge away from the umbo. The anterior lateral teeth are very strong; the one in the left valve is bifid (Fig. 10.5e). The anterior adductor muscle scar is narrow, detached from the pallial line for most of its length, and reaches just below the midline of the shell (Speden 1970; Kiel 2013). *Lucinoma* differs by having less distinctive anterior lateral teeth, a heart-shaped lunule, and often a slightly longer anterior adductor muscle scar.

12. *Epilucina* Dall, 1901: *Epilucina washingtoniana* (Clark, 1925) occurs in two upper Eocene seep deposits in the Wagonwheel Formation in central California (Squires and Gring 1996), but these are so far the only records of this genus at seeps. The genus is characterized by roundish shells with coarse commarginal ribs; a small, heart-shaped, strongly asymmetrical lunule; a long external ligament; and a weak posterior ridge and/or groove. The hinge plate is moderately broad and bears two cardinal teeth in each valve; anterior and posterior lateral teeth are well developed (Kurihara 2007). The genus differs from *Lucinoma* by its strong lateral teeth, and the anterior adductor muscle scar is further detached from the pallial line in *Lucinoma*.
13. *Lucinoma* Dall, 1901: The origin of this genus might go back to the Paleocene (Petersen and Vedelsby 2000; Taylor et al. 2011), and since the Oligocene time, it can be found at seep deposits worldwide (Goedert and Campbell 1995; Majima et al. 2005; Kiel et al. 2020b). There are at least 24 extant species (Taylor and Glover 2010), and 11 species have been reported from fossil seep deposits alone; most of these records need revision. In contrast to most Mesozoic deep-water lucinids, the genus is not restricted to seeps but is widespread in muddy sediments. Shells are roundish to oval, often with a somewhat pointed anterior margin, a truncate and angular posterior margin, and a posterior ridge. The sculpture consists of distinctive and often sharp-crested commarginal ribs (Fig. 10.7f). The hinge plate is narrow and has two cardinals in each valve, one of which may be bifid; the anterior lateral teeth are not well developed (Salas and Woodside 2002; Holmes et al. 2005; Taylor and Glover 2010). *Nymphalucina* builds similar shells; see *Nymphalucina* section for characters distinguishing the two genera.

Subfamily Pegophyseminae

14. *Meganodontia* Bouchet and Cosel, 2004: The genus is based on the extant species *M. acetabulum* Bouchet and Cosel, 2004, from a possible venting area off of Taiwan. Members of the genus have recently been recognized in Miocene seep deposits in Italy (Kiel and Taviani 2017), New Zealand (Amano et al. 2018b), and the Caribbean region (Fig. 10.7g, h; Kiel and Hansen, 2015). The main shell features include very large (typically > 100 mm) and very inflated shells lacking sculpture except for rough growth increments, a narrow and edentulous hinge plate, a long and thin ligament nymph, and a broad, more-or-

less straight anterior adductor muscle scar that is widely detached from the pallial line and extends for about 2/3 of the shell height toward the ventral shell margin (Bouchet and Cosel 2004). Members of the *Anodontia* clade differ by being smaller and by having a shorter and/or narrower anterior adductor muscle scar (Taylor and Glover 2005).

15. *Pegophysema* Stewart, 1930/*Anodontia* Link, 1807: When Taylor et al. (2011) established a new subfamily Pegophyseminae based on the genus *Pegophysema*, they put *Anodontia* into the subfamily Leucoshaerinae. However, it is very difficult to separate these genera on morphological grounds. Compared to *Meganodontia*, *Pegophysema* and *Anodontia* have a smaller and narrower anterior adductor muscle scar, a more swollen umbo, and a straight hinge (see Amano et al. 2018b). A fossil *Pegophysema* was reported from the Lower Pliocene of the Dominican Republic (Kiel and Hansen 2015); *Anodontia mioinflata* was described from a Late Miocene seep, and *Anodontia* sp. was recorded from a Late Pliocene seep, both in northern Italy (Kiel and Taviani 2018; Kiel et al. 2018).

Subfamily Lucininae

16. *Megaxinus* Brugnone, 1880: The genus is based on *Lucina transversa* Bronn, 1831, from the Italian Pliocene, and its occurrence at seeps is presently restricted to the Upper Pliocene Stirone River seep complex in northern Italy (Kiel and Taviani 2018). Shells reach about 50 mm in length, are roundish to rounded-quadrate in outline, lack sculpture, and have an only weakly developed posterior ridge and a distinct lunule. Internally, they have a mostly edentulous hinge plate, and the long and tapering anterior adductor muscle scar runs very close to the pallial line but is detached from it for about 3/4 of its length.

10.7 Family Thyasiridae

Kazutaka Amano and Krzysztof Hryniewicz

The family Thyasiridae was traditionally classified among Lucinoidea (e.g., Dall 1901; Chavan 1969) until molecular studies have shown that both lucinoids and thyasirids are distinct clades (Taylor et al. 2007a, b). Members of the family Thyasiridae inhabit reduced environments from intertidal mudflats to the deep sea, and many of them harbor sulfur-oxidizing bacteria in or on their gill (Dufour 2005; Oliver and Levin 2006; Oliver and Holmes 2006; Taylor and Glover 2010). In the last decade, six new genera have been proposed from Recent and fossil chemosynthetic communities: *Channelaxinus* Valentich-Scott and Coan, 2012; *Cretaxinus* Hryniewicz, Little, and Nakrem, 2014; *Ochetoctena* Oliver, 2014; *Ascetoaxinus* Oliver and Frey, 2014; *Wallerconcha* Valentich-Scott and Powell, 2014; and *Rhacothyas* Åström and Oliver, 2017.

Thyasirids have a global distribution but are most common in colder waters (Dufour 2018). They include both symbiotic and asymbiotic species;

symbiont-bearing species almost exclusively have gills with two demibranchs, and have by far the highest diversity of symbiont location and integration of symbionts among the bivalves (Dufour 2005). Six gill types have so far been recognized among thyasirids, reflecting progressive integration of symbionts and increasing reliance on chemosymbiosis (Oliver 2014). Symbionts are hosted either on the surface of the gills among the microvilli of the bacteriocytes (Dufour 2005) or in deep invaginations of bacteriocytes, the so-called bacterial chambers (Kharlameko et al. 2016). As far as they have been studied, all symbionts are thiotrophic gammaproteobacteria and are hosted extracellularly (e.g., Imhoff et al. 2003); only symbionts of *Maorithyas hadalis* have been said to be stored intracellularly (Fujiwara et al. 2001). The symbionts are likely acquired from the surrounding environment, at least in the case of *Thyasira* cf. *gouldi* (Batsone et al. 2014).

Most thyasirids are infaunal and burrow in the sediment with the aid of their vermiform foot (Dando and Southward 1986; Oliver and Killeen 2002; Dufour and Felbeck 2003; Dufour 2018), which can be extended up to 30 times the length of the shell (Dufour and Felbeck 2003). Regardless of being symbiotic or asymbiotic, thyasirids construct extensive burrows, likely resulting from pedal feeding combined with the farming of chemosynthetic bacteria along the burrow walls (Zanzer and Dufour 2017). Larger thyasirids have been observed on the sea floor, for example, *Conchocele bisecta* (Conrad 1849) in the Sea of Okhotsk (Sahling et al. 2002; Kharlameko et al. 2016) and *Conchocele novaeguineensis* Okutani, 2002, at a water depth of approximately 470 m off of Papua New Guinea (Okutani 2002). A fragmentary specimen of *C. bisecta*, possibly crushed by a crustacean predator, was obtained from a core sample from the Sea of Japan. These observations were used by Amano et al. (2013a) to infer that *C. bisecta* is a shallow burrower. Earlier works (e.g., Kamenev et al. 2001) claimed that *C. bisecta* uses suspension feeding in addition to chemosymbiosis for nutrition. However, this claim was largely refuted by further studies, which have shown that *C. bisecta* relies almost exclusively on chemosynthetic food source (Kharlameko et al. 2016).

10.7.1 Fossil Record and Evolution

Fossil representatives of the family have been recorded from seep sites and whale-fall and wood-fall sites (e.g., Amano et al. 2007b; Kiel et al. 2009; Kiel 2010a). The oldest thyasirid, *Cretaxinus* Hryniewicz, Little, and Nakrem, 2014, is known from the earliest Cretaceous seep site on Spitsbergen. Then, the following thyasirid genera have been reported from hydrocarbon seep deposits since the Late Cretaceous: *Thyasira* Lamarck, 1818, the large Late Cretaceous “*Thyasira*” *hataii* from the Sada Limestone seep deposit in Japan, which belongs to a new genus; *Conchocele* Gabb, 1866; *Maorithyas* Fleming, 1950; and *Rhacothyas* Åström and Oliver in Åström et al. (2017). *Lucina sculpta* Phillips, 1829, from the Albian Gault Clay in England was illustrated as the “oldest thyasirid” by Taylor et al. (2007a, b); its systematic affiliation is uncertain because its internal morphology is unknown.

As noted by Kiel et al. (2008) and Kaim et al. (2013), *Lucina rouyana* (d'Orbigny, 1844) from Lower Cretaceous (Valanginian-Hauterivian) rocks in Europe could be the oldest species of *Thyasira* (s.s.). The second oldest species is *T.* (s.s.) *tanabei* Kiel, Amano, and Jenkins, 2008 (Fig. 10.8a, b, d, e), from Albian to Campanian

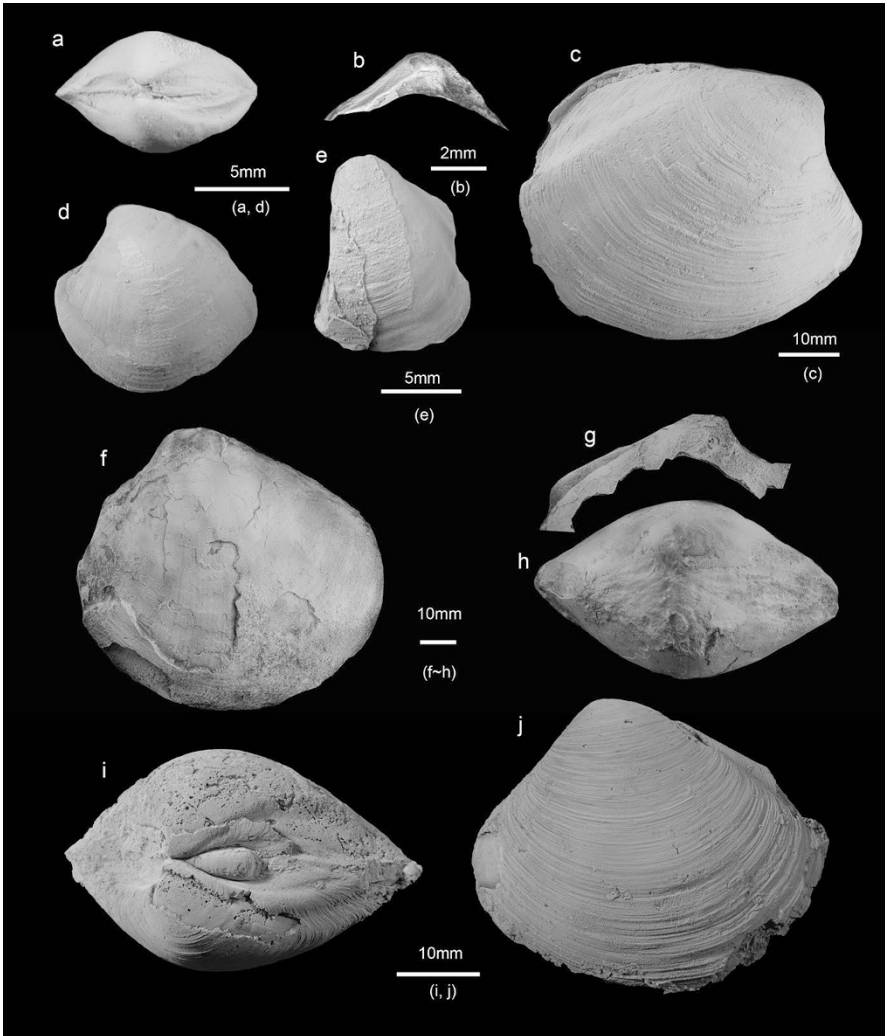


Fig. 10.8 Thyasiridae. *Thyasira* (s.s.) *tanabei* Kiel, Amano, and Jenkins, 2008, from a Late Cretaceous seep site in northern Hokkaido, Japan; (a, b) UMUT MM29533, holotype; (d) UMUT MM 29537, paratype; (e) UMUT MM 29536, paratype. (c) *Conchocele bisecta* (Conrad, 1849) from an early Miocene seep site in Ibaraki Pref., Honshu, Japan. (f, g, h) *Thyasira* sp. from a Late Cretaceous seep site in Kochi Pref., Shikoku, Japan. (i, j) *Cretaxinus hurumi* Hryniewicz, Little, and Nakrem, 2014, from an earliest Cretaceous seep site in Spitsbergen, Svalbard; PMO 217.277, holotype. (a, b, d, e: Kiel et al. 2008; c, f, g, h: collection by Amano; i, j: Hryniewicz et al. 2014)

seep deposits on Hokkaido. In the northern Pacific area, *Thyasira* species are also known from Paleocene deep-water deposits (Kalishevich et al. 1981; Amano et al. 2015). After the late Eocene, *Thyasira* became much less common at hydrocarbon seeps; rare examples include *Thyasira* (s.s.) sp. from Miocene seep sites in New Zealand (Campbell et al. 2008; Amano et al. 2015), *T.* (s.s.) *nakazawai* Matsumoto, 1971, from an Early Miocene seep from the Wappazawa Formation in central Honshu, Japan, and *T.* (s.s.) *montanita* at a seep deposit from the Oligocene-Miocene boundary in Ecuador (Kiel et al. 2021).

The oldest species of *Conchocele*, *Conchocele townsendi* (White, 1890), is known from Maastrichtian seep deposits on Snow Hill Island, Antarctica (Kiel et al. 2008; Little et al. 2015; Hryniewicz et al. 2017a). The next oldest species are *C.* aff. *conradi* (Rosenkranz 1970) from the Danian Kangilia Formation in western Greenland (Rosenkranz 1970) and *C. conradii* from the Thanetian Basilika Formation in Spitsbergen (Hryniewicz et al. 2016, 2017b). *Conchocele* was also reported from Paleocene sediments in New Zealand (Beu and Maxwell 1990). In the northern Pacific, *Conchocele* flourished since late Eocene, and *Thyasira* (s.s.) contemporaneously declined (Amano et al. 2015, 2018a; Hryniewicz et al. 2017a). In the Early Miocene, *Conchocele* invaded the deep-water basin of the Sea of Japan at latest 1 million years after the basin formed (Amano et al. 2019b).

Two species of *Maorithyas* have been found at fossil seep sites, these being *Maorithyas humptulipsensis* Hryniewicz, Amano, Jenkins, and Kiel, 2017a), from the middle Eocene Humptulips Formation (Hryniewicz et al. 2017) and *Maorithyas folgeri* (Wagner and Schilling 1923) from the Eocene Wagonwheel Formation and the Oligocene San Emigdio Formation in Southern California, USA. A single fossil species of *Rhacothyas*, *R. spitzbergensis*, has been described from Paleocene seep and wood-fall communities in Spitsbergen Island (Hryniewicz et al. 2019).

10.7.2 Classification and Shell Characteristics

The size of thyasirids ranges from a few mm to about 200 mm in length (senior author's observation). Most thyasirids are characterized by an edentulous hinge and a sulcated posterodorsal shell area. Molecular phylogenetic work on 13 species of thyasirids divided them into two well-defined clades (Taylor et al. 2007a, b) – *T. flexuosa*/*T. gouldi*/*T. polygonata* from “normal” marine-reduced environments and *T. sarsii*/*T. methanophila* from seeps – and a third clade which lacks strong support and is composed of asymbiotic species including *Mendicula ferruginosa*, *Leptaxinus indusarium*, *Anodontorhina cyclia*, and *Axinulus*.

Several fossil seep thyasirid genera are known, yet due to lack of data and difficulty of identifying thyasirids based on the shell features alone, their taxonomy is only partially resolved. Several taxa are problematic, and more material for further studies is needed. Below we list the main morphological features of ancient seep-inhabiting thyasirids as currently understood.

1. *Cretaxinus* Hryniewicz, Little, and Nakrem, 2014: This genus was proposed for *C. hurumi* from lowermost Cretaceous (uppermost Berriasian) seep carbonates from the Slotsmøya Member in central Spitsbergen, Svalbard. The genus is characterized by a rather large shell reaching 57 mm in length, posterodorsally flattened and poorly pronounced sulci without auricle, and by a thick external ligament (Fig. 10.8i, j). In contrast to other large thyasirids, *Cretaxinus* has a rather weak and short anterior adductor muscle scar and a strong and deep posterior adductor muscle scar. The inner shell surface is covered by dense radial striae, probably resulting from descending mantle muscle scars. The species occurs in small clusters of up to ten specimens, associated with the lucinid *Tehamatea rasmusseni*, the solemyid *Solemya (Petrasma)* cf. *woodwardiana*, and *Nucinella svalbardensis* (Hryniewicz et al. 2014, 2015a).
2. *Thyasira* Lamarck, 1818: This genus includes two subgenera: *Thyasira* (s.s.) and *Philis* Fisher, 1924. *Philis* can be separated from *Thyasira* (s.s.) by having a small tooth-like projection below the umbo. Both subgenera have small shells (up to 30 mm among the Recent species) with two folds and an auricle. Of the two symbiotic clades, the *T. flexuosa*/*T. gouldii*/*T. polygonata* clade differs from the *T. sarsii*/*T. methanophila* clade by having less inflated shells with a medial flattened area (Amano et al. 2015). Huber (2015) splits *Thyasira* into *T.* (s.s.) and eight undescribed groups including the *T. sarsii*/*T. methanophila* clade, for which a new genus may be warranted.
3. Large Cretaceous *Thyasira*: A large species from the Upper Cretaceous Sada Limestone in Shikoku, Japan, was described as *Aphrodina (Aphrodina) hataii* (Fig. 10.8f, g, h) by Katto and Hattori (1964). Tashiro (1992) allocated this species to *Thyasira* (s.l.), but the species differs from the genus *Thyasira* by lacking a distinct auricle and by reaching up to 80 mm in length. Although the size of this species is similar to that of *Conchocele*, its well-rounded posterior margin separates it from *Conchocele* (Nobuhara et al. 2008). Taxonomic work on this species is ongoing.
4. *Conchocele* Gabb, 1866: This genus is characterized by a large shell (up to 200 mm in length) with a long, deeply sunken ligament, a beak situated near the anterior end, a subtruncated anterior margin, and an elongated anterior adductor muscle scar (Fig. 10.8c). The sulci developed in the posterodorsal shell area are strong and deep.
5. *Maorithyas* Fleming, 1950: This genus was proposed on the Recent species, *M. marama* Fleming, 1950, from New Zealand and is characterized by its moderate size (up to 62 mm in length), thin, globose shell with a well-defined lunule.
6. *Rhacothyas* Åström and Oliver in Åström et al., 2017: The genus was introduced for the Recent species *R. kolgae* Åström and Oliver, 2017, from methane seeps off Svalbard. The genus is characterized by a small (up to 25 mm), thin, and luciniform shell with edentulous hinge, a small sunken lunule, and a weak posterior sulcus. Its external surface is sculptured by raised and narrowly spaced commarginal lamellae and weak posterior sulcus. The only fossil record so far is the Paleocene *R. spitzbergensis*, from shallow marine deposits on Svalbard.

10.8 Family Vesicomysidae

Kazutaka Amano and Steffen Kiel

The Vesicomysidae is the second most species-rich family of chemosymbiotic bivalves after the Lucinidae, and they are arguably the most successful radiation into chemosynthetic environments. More than 100 extant species have been described, and there are approximately 30 named fossil species and even more reported in open nomenclature. Vesicomysidae inhabit hydrothermal vents, methane seeps, and whale- and wood-fall sites and are also found in organic-rich deep-sea environments. Geographically they are found worldwide from the Arctic via the tropics to Antarctic waters and in depths from 100 to 9500 m (Krylova and Sahling 2010).

Vesicomysids have a broad size range, ranging from a few mm to more than 300 mm in length. Only the smallest species (belonging to the genus *Vesicomys*) apparently lack symbionts, whereas the larger species host symbionts on which they rely for nutrition. The symbionts are exclusively sulfur-oxidizing gammaproteobacteria that are transmitted mostly from parent to offspring (vertical transmission), resulting in coevolution between host and symbiont lineages (Peek et al. 1998). Sulfide is taken up from the sediment (or in the case of hydrothermal vents, from fluids seeping through crevices between pillow lavas) via the bivalves' extensile foot and is transported to the intracellular symbionts in the gills. Most vesicomysids are semi-infaunal except for species smaller than approximately 20 mm long, which tend to live completely buried in the sediment. The larger species frequently move around at the sediment surface, probably to search for optimal sulfide flux (Krylova and Sahling 2010).

Vesicomysids disperse via lecithotrophic larvae, yet at least some species have wide transoceanic distributions (Kojima et al. 2004; Audzijonyte et al. 2012). The small-scale distribution of vesicomysid species at individual seep sites appears to relate to their sulfide-binding and storage capacity. Species with a high binding and storage capacity (such as *Calyptogena pacifica*) are able to live in areas with lower sulfide flux than species with lower binding and storage capacity (such as *Archivesica kilmeri*), which can only survive in areas with a steady and high supply of sulfide (Barry et al. 1997).

10.8.1 Fossil Record and Evolution

Vesicomysids first appeared in the North Pacific in the middle Eocene, with the earliest record being from the Humptulips Formation in western Washington State, USA (Amano and Kiel 2007b; Hybertsen and Kiel 2018). Another potential middle Eocene record comes from deep-water deposits of the Murotohanto Group in Tokushima Prefecture, Japan (as "*Crassatellites* nov. sp."; Hatae 1960; Suyari and

Yamazaki 1987) but this still needs confirmation. The few middle Eocene seep deposits from the eastern Atlantic and Tethyan region lack vesicomyids (Natalicchio et al. 2015; SK, unpublished). From the late Eocene to Oligocene, vesicomyids occur throughout the Pacific and Caribbean regions (Olsson 1931; Amano and Kiel 2007b; Kiel and Amano 2010; Amano et al. 2013b; Kiel and Hansen 2015; Kiel et al. 2020a, 2020b), but seep deposits are unknown from outside this region, preventing a comprehensive assessment of the biogeography of vesicomyids. From the Miocene onward, seep deposits with vesicomyid bivalves are known from virtually all ocean basins (Beets 1942, 1953; Gill et al. 2005; Majima et al. 2005; Kiel 2007; Amano and Kiel 2007b; Kiel 2010b; Kiel and Amano 2010; Amano and Kiel 2011; Amano and Kiel 2012; Amano et al. 2014a, b; Kiel and Hansen 2015; Kiel and Taviani 2017, 2018; Kase et al. 2019; Amano et al. 2019a, b).

Also, molecular age estimates for the vesicomyids suggest a middle Eocene origin (Baco et al. 1999; Vrijenhoek 2013). Based on the roughly coeval appearance of large whales and vesicomyid bivalves, it was hypothesized that the (geologically) sudden appearance of sulfide-emitting whale carcasses on the seafloor expanded the dispersal capacities of vent and seep-inhabiting species to such an extent that it triggered the radiation of new groups into these habitats (Baco et al. 1999; Smith and Baco 2003).

Other investigations using time-calibrated molecular phylogenetic trees (chronograms) of the vesicomyids indicated that lineages of pliocardiine vesicomyids have accumulated at a regular pace since the Eocene, with no signs of diversification pulses (Valdés et al. 2013; Johnson et al. 2017). The fossil record also provides insights into this issue, but the diversification pattern seen in the fossil record should not be overemphasized because although the genus-level classification of fossil vesicomyids is improving, there are still many uncertainties. Our current understanding of the fossil record of vesicomyid genera is shown in Table 10.2. However, ongoing taxonomic revisions and further discoveries of new taxa and new seep deposits are likely to change this picture. For example, species currently assigned to *Pliocardia* and pre-Miocene species assigned to *Archivesica* are likely to be placed

Table 10.2 Characteristics of the vesicomyid genera having fossil records. + present; – absent; ± basically absent, but sometimes present; ? unknown

Genus	Maximum size (mm)	Elongate shell	Lunular incision	Subumbonal pit	pallial sinus	3a tooth	lined 3a & 3b	nymphal ridge
<i>Isorropodon</i>	47	–	–	+	–	+	+	–
<i>Pliocardia</i>	47	–	+	+	+	+	–	–
<i>Wareniconcha</i>	120	–	–	+	–	+	–	–
<i>Pleurophopsis</i>	180	+	–	–	–	–	–	–
<i>Ectenagena</i>	70	+	–	+	–	–	–	–
<i>Archivesica</i>	250	±	–	+	+	+	–	–
<i>Hubertschenckia</i>	75	-	–	+	+	+	–	+
<i>Calyptogena</i>	90	±	–	–	–	+	–	+
<i>Notocalyptogena</i>	52	+	–	–	–	+	–	–

in new genera as mentioned later. There are many poorly preserved specimens in the fossil record, which may also belong to new genera or may extend the fossil record of described genera further back in time. New genera will continue to be named also for extant species, exemplified by the recent introduction of *Turneroconcha* Krylova and Sahling, 2020, for the iconic giant white clam *Calyptogena magnifica* from the East Pacific Rise hydrothermal vents. Once established, fossil species may be assigned to these new genera. Furthermore, especially the small, thin-shelled genera (e.g., Cosel and Salas 2002) are less likely to be found in the fossil record than large, thick-shelled genera (Valentine et al. 2006).

There is limited fossil evidence for an onshore-offshore pattern, a gradual adaptation to deeper water, in the evolution of the Vesicomysiidae. *Hubertschenckia* appears to have lived in lower sublittoral to upper bathyal depths (Amano and Jenkins 2007). Its probable descendant *Archivesica* now lives in bathyal depth (Kojima 2008). Moreover, extensive work on vesicomysiids in Japan indicates that *Archivesica* and *Calyptogena*, which today live in bathyal depths, took over this ecological niche from the genus *Pleurophopsis* during the Late Miocene (Amano and Kiel 2011; Amano et al. 2019a). A similar onshore-offshore pattern was recognized in molecular phylogenies of the bathymodiolins (Distel et al. 2000; Lorion et al. 2013) with the additional point of an adaptation from low-sulfide environments (wood-falls) to high-sulfide environments (vents/seeps), but this had not been seen in the molecular study of vesicomysiids (Decker et al. 2012).

10.8.2 Classification and Shell Characters

The generic classification of both fossil and recent vesicomysid bivalves is an active, though difficult, field of research suffering from the frequent convergence of many shell characters, resulting in inconsistencies between morphological and molecular data. Krylova and Sahling (2010) distinguish two subfamilies: Vesicomysiinae consists of only the small and asymbiotic type genus *Vesicomysia*; Pliocardiinae includes all other genera. Shell characters used to distinguish species and genera include shell size and shape, presence or absence of a lunule or lunular incision, the point of contact between pallial line and the adductor muscle scars, the presence and shape of a pallial sinus, and the morphology of the right valve hinge area (number and arrangement of teeth, subumbonal pit, posterior nymphal ridge) (Fig. 10.9, Table 10.2). A comprehensive overview of the vesicomysid genera, their characters, and species compositions (although some assignments remain controversial) was provided by Krylova and Sahling (2010); here we discuss only genera with a fossil record.

1. *Pliocardia* Woodring, 1925: The Pliocene type species, *Anomalocardia bowdeniana* Dall, 1903, has a small (~10 mm), oval shell (Fig. 10.9g) with a strong posterior ridge and sulcus, and a lunular incision. It has three cardinal teeth in the right valve, of which 3a is typically thin, while 3b is broad (Fig. 10.9f) and points

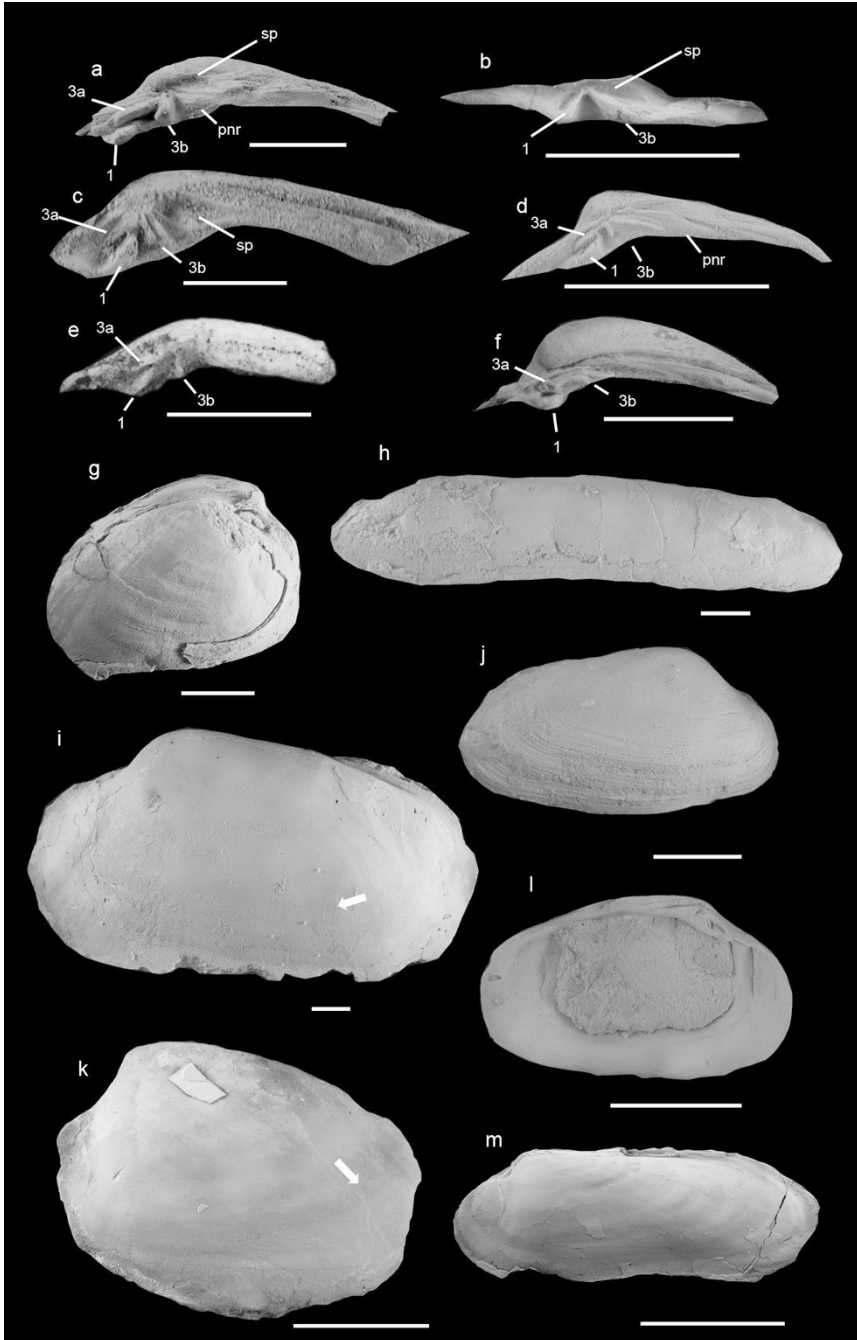


Fig. 10.9 Vesicomiyidae. All scale bars are 10 mm. (a, k) *Hubertschenckia ezoensis* (Yokoyama 1890) from a late Eocene seep site in Hokkaido, Japan: (a) hinge of right valve with subumbonal

in a posteroventral direction (Woodring 1925; Krylova and Janssen 2006; Amano and Kiel 2007b). In molecular phylogenies, extant species with this type of morphology fall within at least two distinct clusters: one with *Vesicomya crenulomarginata* and *V. kuroshimana* and the other with *Calyptogena ponderosa* and *C. cordata* (Kojima et al. 2004; Martin and Goffredi 2011; Audzijonyte et al. 2012; Valdés et al. 2013; Johnson et al. 2017). *Pliocardia* is used for the former group, whereas the latter is typically referred to as ‘*cordata* group’ (Johnson et al. 2017). Apart from their general similarity to *Pliocardia*, these extant species vary greatly in size and also in the presence and shape of the pallial sinus. The same applies to the fossil species currently considered as belonging to *Pliocardia*, including the oldest species of the Vesicomidae, *Pliocardia* aff. *tschudi* from the middle Eocene of Washington State (Amano and Kiel 2007b; Amano et al. 2014a), *Vesicomya tschudi* from the lower Oligocene of Peru (Kiel et al. 2020b), and *Pliocardia?* *tanakai* from the Middle Miocene Bessho Formation in central Honshu (Miyajima et al., 2017). Clearly, the species currently assigned to *Pliocardia* are in need of taxonomic revision, and the introduction of one or more new genera may be necessary (Amano et al. 2014a; Martin and Goffredi 2011; Kiel et al. 2020b).

2. *Wareniconcha* Cosel and Olu, 2009: This genus is based on the Recent species *Wareniconcha guineensis* (Thiele and Jaekel 1931) living in the Gulf of Guinea. It is characterized by having a veneriform, medium-sized shell, a narrow hinge plate with a strong middle cardinal tooth (1) in the right valve and a subumbonal pit, and the lack of a pallial sinus. One large fossil species, *Wareniconcha mercenarioides*, occurs at a Pliocene methane-seep deposit at Liog-Liog Point on Leyte Island, Philippines (Kase et al. 2019).
3. *Pleurophopsis* Van Winkle, 1919: This is an exclusively fossil genus based on *P. unioides* Van Winkle, 1919, from Miocene seep deposits in Trinidad. It is characterized by an elongate shell with two cardinal teeth in the right valve

pit (sp) and posterior nymphal ridge (pnr); JUE no. 15837-12; (k) inner surface of left valve with pallial sinus (indicated by white arrow), JUE no. 15837-10. (b, m) *Pleurophopsis hokkaidoensis* (Amano and Kiel 2007b) from the early Middle Miocene whale-fall site in Shosanbetsu Village, Hokkaido, Japan; (b) rubber cast of right valve hinge with subumbonal pit (sp), JUE no. 15851, paratype; (m) JUE no. 15848, holotype. (c, i) *Archivesica kawamurai* (Kuroda, 1943) from Pliocene seep sites in Kanagawa Pref. (c) and Chiba Prefecture (i), Honshu, Japan; (c) right valve hinge with subumbonal pit (sp); JUE no. 15877-2; (i) inner surface of left valve with pallial sinus (indicated by white arrow); JUE no. NSM no. 4409. (d, l) *Calyptogena pacifica* Dall, 1891, from a Late Miocene seep site in Aomori Prefecture, Honshu, Japan; (d) right valve hinge with subumbonal pit (sp) and posterior nymphal ridge (pnr), JUE no. 15884-5; (l) JUE no. 15884-1. (e, j) *Notocalyptogena neozelandica* Amano, Saether, Little, and Campbell, 2014, from the Early Miocene Ugly Hill seep site, North Island, New Zealand; (e) UOA L4593, paratype; (j) UOA L4591, holotype. (f, g) *Pliocardia kawadai* (Aoki, 1954) from an Early Miocene seep site in Fukushima Pref., Honshu, Japan; (f) JUE no. 15895-2; (g) JUE no. 15895-3. (h) *Pleurophopsis uchimuraensis* (Kuroda 1931) from a Middle Miocene seep site in Nagano Prefecture, Honshu, Japan; JUE no. 15865-1. (a, b, k, m: Amano and Kiel 2007b; c, i: Amano and Kiel, 2010; d, l: Amano and Jenkins 2011b; e, j: Amano et al. 2014b; f, g: Amano and Kiel 2012; h: Amano and Kiel 2011)

(a strong cardinal 1 and a short 3b, cardinal 3a is reduced; Fig. 10.9b). The anterior adductor muscle scar and pedal retractor muscle scar are separate, and the pallial line starts at the posteroventral margin of the anterior adductor muscle scar. A synonym is *Adulomya* Kuroda, 1931, with the Miocene type species *A. uchimuraensis* Kuroda, 1931 (see also Amano et al. 2019a; Fig. 10.9h). *Pleurophopsis* shares its elongated shell and two cardinal teeth in the right valve with the Recent genus *Ectenagena* Woodring, 1938, but differs by the absence of a deep umbonal pit. The oldest fossil record of *Pleurophopsis* may be *P. chinookensis* (Squires and Goedert 1991) from upper Eocene seep deposits of western Washington State, USA (Amano and Kiel 2007b).

4. *Calyptogena* Dall, 1891: Based on the extant *Calyptogena pacifica* (Fig. 10.9d, l), this genus includes species with moderately sized shells, characterized by having a posterior nymphal ridge on the hinge plate, three cardinal teeth in the right valve of which cardinal 3b typically points in an antero-ventral direction, and the absence of a pallial sinus, subumbonal pit, and lunular incision (Krylova and Sahling 2006). In particular, the posterior nymphal ridge is unusual among vesicomysids and clearly distinguishes this genus from all others. The oldest fossil record is *Calyptogena katallaensis* from the Oligocene of Alaska (Kiel and Amano 2010); the oldest record of an extant species is *Calyptogena pacifica* from the Upper Miocene of Japan (Amano and Jenkins 2011b).
5. *Notocalyptogena* Amano, Saether, Little, and Campbell, 2014: This is so far a monospecific genus based on *N. neozelandica* (Fig. 10.9e, j), from the Early and Middle Miocene of New Zealand (Amano et al. 2014b). *Notocalyptogena* and *Calyptogena* share elongate ovate shells (maximum length = 90 mm; Krylova and Sahling 2006), three cardinal teeth in the right valve, and the lack of a subumbonal pit and a pallial sinus. *Notocalyptogena* differs from *Calyptogena* by lacking a stout posterior cardinal tooth (3b) and a posterior nymphal ridge.
6. *Hubertschenckia* Takeda, 1953: This is an exclusively fossil genus based on *Tapes ezoensis* Yokoyama, 1890, from the late Eocene to Oligocene of northern and central Japan (Amano et al. 2013b; Amano and Kiel 2007b; Takeda 1953). Its shell is elongate ovate, has three cardinal teeth in the right valve, a subumbonal pit, and a shallow pallial sinus (Fig. 10.9a, k). *Hubertschenckia* differs from *Archivesica* by having a smaller shell (about 75 mm versus up to 300 mm in *Archivesica*; Krylova and Sahling, 2010), a long anterior cardinal tooth (3a), a middle tooth (1) that runs parallel to the hinge margin, and a vertical posterior cardinal tooth (3b) (Amano and Kiel 2007b).
7. *Archivesica* Dall, 1908b: The extant type species *A. gigas* (Dall, 1896) is characterized by an elongate, broad, ovate shell with three cardinal teeth in the right valve; a subumbonal pit; and a shallow pallial sinus. The cardinals are thin; cardinal 1 starts below the umbo, is curved, and points to the anterior; 3a runs roughly parallel to the posterior shell margin and is fused with 3b, which points to the posterior. The oldest record of the genus is *Archivesica sakoi* Amano, Jenkins, Ohara, and Kiel, 2014, from the Lower Miocene Shikiya Formation in Wakayama Prefecture, southern Honshu, followed by several species in the Middle to Late Miocene species of Italy (Kiel and Taviani 2017), the Late Miocene of Japan (Amano and Kiel, 2010; Amano and Suzuki 2010), and the

Pliocene-Pleistocene of California (Squires 1991). Problematics are the relationships to, or synonymies with, the three genera *Phreagena*, *Laubiericoncha*, and *Akebiconcha*. *Phreagena* Woodring, 1938, is based on the Pliocene species *Phreagena lasia* Woodring and may be distinguishable from *Archivesica* by having a thicker shell with narrower subumbonal pit, a longer ligament, and a deeper anterior pedal retractor scar (Krylova and Janssen 2006). *Laubiericoncha* Cosel and Olu, 2008, based on the extant *L. myriamae* Cosel and Olu was separated from *Archivesica* by having a tapering posterior part of shell, a short and broad pallial sinus, and a deep anterior pedal retractor scar. *Akebiconcha* Kuroda, 1943, based on the extant *A. kawamurai* Kuroda (Fig. 10.9c, i) was not compared with *Archivesica* at its proposal. The concept of the generic composition of the pliocardiids as outlined by Krylova and Sahling (2010) was not entirely supported by recent molecular phylogenetic work (Audzijonyte et al. 2012; Johnson et al. 2017); thus, *Phreagena* and *Akebiconcha* are regarded as a synonym of *Archivesica* (Amano and Kiel 2007b). Moreover, *Laubiericoncha* Cosel and Olu, 2008, based on *L. myriamae* Cosel and Olu, 2008 falls within a large cluster including the type species of *Archivesica* (Audzijonyte et al. 2012; Decker et al. 2012; Johnson et al. 2017), and also based on shell characters, it is difficult to distinguish from *Archivesica* (Amano and Kiel 2007b; Amano and Suzuki 2010). Although Johnson et al. (2017) referred to a large clade including all these taxa as “*gigas* group,” it has to be referred to as *Archivesica* because *A. gigas* is the type species of *Archivesica*.

8. *Isorropodon* Sturany, 1896: The type species, *Isorropodon perplexum*, is extant in the Mediterranean Sea. This genus comprises species with small, thin, ovate shells that may or may not have a posterior ridge, lack a lunular incision, and have a *Vesicomya*-like dentition with the cardinals in the right valve all arranged roughly in one line and undulating sub-parallel to the dorsal shell margin. *Pliocardia* differs by having a lunular incision and a more *Archivesica*-like hinge dentition with a thick posterior cardinal tooth (3b) in the right valve that points postero-ventrally. *Vesicomya* has a more globular, roundish shell with a lunular incision (Cosel and Salas 2001). Fossil species includes *Isorropodon frankfortensis* Amano and Kiel, 2007b, from the Lower Miocene in southwestern Washington State, USA (Amano and Kiel 2007b), and *Isorropodon* sp. from the Pliocene Stirone River deposit in Italy (Kiel and Taviani 2018).

10.9 The Anomalodesmata

Steffen Kiel

Anomalodesmatan bivalves have not been reported from modern seeps, and only a few are known from the older fossil record. A single cuspidariid species, *Thermomya sulcata* Chen, Okutani, Watanabe, and Kojima, 2018, was reported from a back-arc vent site in the Southern Mariana Trough (Chen et al. 2018), but although the

anatomy of the available specimens are too poorly preserved to assess the potential of chemosymbiosis, this seems unlikely as all other cuspidariids are carnivore (e.g., Morton and Machado 2019).

A definitive anomalodesmatan, *Aksumya* Kiel, 2018, occurs in Upper Triassic seep deposits in Turkey and is restricted to seeps (Kiel et al. 2017). Its shells reach up to 82 mm in length, are oval-elongate with a drawn-out and somewhat pointed posterior margin, are apparently edentulous, sculptured by irregular growth lines, and have microscopic spines, which clearly identify them as members of the Anomalodesmata (Sartori and Harper 2009). The feeding habits of *Aksumya* is unknown, and chemosymbiosis can only be inferred from its relatively large size, its abundance at seeps, and its restriction to the seep environment.

Several taxa previously reported as anomalodesmatans from Paleozoic seeps (i.e., from the Hollard Mound; Aitken et al. 2002) are now considered as belonging to the modiomorphids (see above; Hryniewicz et al. 2017a). From the Permian of Brazil, members of three genera of presumed anomalodesmatans (*Anhemia*, *Tambaquyra*, and *Maackia*) were reported from concretionary limestone deposits, interpreted as cold seep deposits (Matos et al. 2017). If this interpretation is correct, anomalodesmatans would have reached a remarkable diversity at late Paleozoic-early Mesozoic seeps. However, the figured outcrops and rock samples look unlike those of other, confirmed, seep deposits, and lack the typical “seep cements” such as banded and botryoidal rim cements (cf. Peckmann and Thiel 2004). In addition, the reported carbon isotope values are only as low as -7.6‰ and thus well within the range of septarians and other concretions resulting from the oxidation of organic matter (Irwin et al. 1977). Furthermore, the interpretation of Matos et al. (2017) of these bivalves as chemosymbiotic relies partly on a questionable comparison of shell characters of non-chemosymbiotic bivalves and partly on the negative isotope signature of the shells themselves. However, studies on extant and fossil bivalves have shown that metabolic carbon (which would carry a signal for chemosymbiosis) is not incorporated into the shell (Paull et al. 1989; Kiel and Peckmann 2007). Moreover, the Permian shells from Brazil are recrystallized and hence do not carry the original isotopic signature of the shell but rather of the dissolved carbon incorporated during their recrystallization. A single specimen of *Pleuromya?* has been collected from the Paleocene seep fauna of the Basilika Formation on Spitsbergen Island (Hryniewicz et al. 2019).

10.10 Conclusions

Kazutaka Amano

The chronostratigraphic ranges of all genera of mainly seep-inhabiting chemosymbiotic bivalves are shown in Fig. 10.2; records from hydrothermal vent, whale fall and wood fall are also included. This shows an overall increase in bivalve diversity at seeps since the Paleozoic, a pattern that was linked earlier to the general increase of bivalve biodiversity through the Phanerozoic (Kiel and Peckmann 2019). Forsey

(2013) emphasized a large increase in seep bivalve diversity starting in the Jurassic and considered this increase as being part of the “Mesozoic Marine Revolution” (Vermeij 1977, 1987). Remarkably, apart from the Devonian solemyid *Dystactella*, many infaunal chemosymbiotic bivalve taxa such as the solemyids, thyasirids, and lucinids appeared in the Late Jurassic and diversified in the Cretaceous. This timing is synchronous with the increasing infaunality of bivalves as an antipredatory strategy, known as one of the effects of the “Mesozoic Marine Revolution.” However, these patterns and their potential causes should be treated cautiously because the fossil record of seeps and seep communities beyond the Cretaceous is still very sparse (Campbell 2006; Kiel 2009, 2015; Hryniewicz et al. 2017b; Kiel and Peckmann 2019).

Drill holes made by predatory gastropods have been reported from chemosymbiotic bivalves soon after the first appearance of these gastropods in the mid-Cretaceous (Taylor et al. 1983): in Cenomanian nucinellids; Eocene thyasirids and vesicomysids; Oligocene thyasirids and bathymodiolins; and Miocene thyasirids, vesicomysids, and bathymodiolins (Amano 2003; Amano and Jenkins 2007; Amano and Kiel 2007a; Kiel et al. 2008, 2016). The fossil record of these drill holes thus suggests increasing predation pressure since the Late Cretaceous. Remarkably, this coincides roughly with a “mid-Cretaceous faunal turnover” from pre- to post-Albian seep faunas (Kiel et al. 2012; Jenkins et al. 2013, 2018b; Kiel 2015). Although this faunal change is not readily apparent in terms of genus richness or extinction and origination pattern (Fig. 10.2), the lifestyle of the dominant bivalves at seeps changed from epifaunal to infaunal. Kiel (2015) suggested that this “mid-Cretaceous faunal turnover” resulted from a decrease in seawater sulfate concentrations but did not consider drilling predation in this context. However, drill holes in the main epifaunal bivalve at seeps at that time, *Caspiconcha*, have never been reported. Disentangling the biological, chemical, and physical environmental changes leading to the described changes in seep bivalve diversity and life habits in the late Mesozoic requires further research.

Many clades of the modern vent and seep fauna, including the dominant bathymodiolins and vesicomysids with their semi-infaunal or epifaunal lifestyles, appeared in the Eocene (Fig. 10.2). Jacobs and Lindberg (1998) and Vrijenhoek (2013) claimed that deep-water anoxia during the Paleocene-Eocene Thermal Maximum (PETM) caused the extinction of the deep-sea fauna, including that at vents and seeps. Furthermore, also molecular age estimates indicate an early Cenozoic origin of many of the major groups at vents and seeps, and the PETM extinction is considered to have played a major role in this pulse of origination, by extinguishing old groups and making room for new ones (Chelvodonné et al. 2002; Jones et al. 2006; Vrijenhoek. 2013). However, the (admittedly patchy) fossil record during this time interval (Fig. 10.2) does not show any extinctions (Hryniewicz et al. 2017a, 2019). Kiel (2015) argued that the mid-Eocene appearance of semi-infaunal and epifaunal bivalves such as bathymodiolins and vesicomysids was linked to a dramatic rise in seawater sulfate concentrations (Wortmann and Paytan 2012), which resulted in increased sulfide availability at vents and seeps, and organic substrates. New and more detailed fossil records across the end-Cretaceous and PETM extinction events are needed to test these competing hypotheses.

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References

- Adams A (1860) On some new genera and species of Mollusca from Japan. *Ann Mag Nat Hist (ser 3)* 5:299–303
- Agirrezabala LM, Kiel S, Blumenberg M et al (2013) Outcrop analogues of pockmarks and associated methane-seep carbonates: a case study from Lower Cretaceous (Albian) of the Basque-Cantabrian Basin, western Pyrenees. *Palaeogeogr Palaeoclimatol Palaeoecol* 390:94–115
- Aitken SA, Henderson CM, Collom CJ et al (2002) Stratigraphy, paleoecology and origin of Lower Devonian (Emsian) carbonate mud buildups, Hamar Laghdad, eastern Anti-Atlas, Morocco. *Bull Can Petrol Geol* 50:217–243
- Allen JA (1958) On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Philos Trans R Soc Lond B* 241:421–484
- Amano K (1984) Two species of Mytilidae (Bivalvia) from the Miocene deposits in Hokkaido, Japan. *Venus* 43:183–189
- Amano K (2003) Predatory gastropod drill holes in Upper Miocene cold seep Bivalves, Hokkaido, Japan. *Veliger* 46:90–96
- Amano K, Ando H (2011) Giant fossil *Acharax* (Bivalvia: Solemyidae) from the Miocene of Japan. *Nautilus* 125:207–212
- Amano K, Jenkins RG (2007) Eocene drill holes in cold-seep bivalves of Hokkaido, northern Japan. *Mar Ecol* 28:108–114
- Amano K, Jenkins RG (2011a) New fossil *Bathymodiolus (sensu lato)* (Bivalvia: Mytilidae) from Oligocene seep-carbonates in eastern Hokkaido, Japan, with remarks on the evolution of the genus. *Nautilus* 125:29–35
- Amano K, Jenkins RG (2011b) Fossil record of extant vesicomylid species from Japan. *Venus* 69:163–176
- Amano K, Kiel S (2007a) Drill holes in bathymodiolin mussels from a Miocene whale-fall community in Hokkaido, Japan. *Veliger* 49:265–269
- Amano K, Kiel S (2007b) Fossil vesicomylid bivalves from the North Pacific region. *Veliger* 49:270–293
- Amano K, Kiel S (2010) Taxonomy and distribution of fossil *Archivesica* (Bivalvia: Vesicomylidae) in Japan. *Nautilus* 124:155–165
- Amano K, Kiel S (2011) Fossil *Adulomya* (Vesicomylidae, Bivalvia) from Japan. *Veliger* 51:76–90
- Amano K, Kiel S (2012) Two fossil vesicomylid species (Bivalvia) from Japan and their biogeographic implications. *Nautilus* 126:79–85
- Amano K, Little CTS (2005) Miocene whale-fall community from Hokkaido, northern Japan. *Palaeogeogr Palaeoclimatol Palaeoecol* 215:345–356
- Amano K, Suzuki A (2010) Redescription of ‘*Calyptogena shiretokensis Uozumi* (Bivalvia: Vesicomylidae) from the Miocene Rurua Formation on the Shiretoko Peninsula, eastern Hokkaido, Japan. *Venus* 68:165–171
- Amano K, Jenkins RG, Hikida Y (2007a) A new gigantic *Nucinella* (Bivalvia: Solemyoidea) from the Cretaceous cold-seep deposit in Hokkaido, northern Japan. *Veliger* 49:84–90
- Amano K, Little CTS, Inoue K (2007b) A new Miocene whale-fall community from Japan. *Palaeogeogr Palaeoclimatol Palaeoecol* 247:236–242

- Amano K, Jenkins RG, Kurihara Y et al (2008) A new genus for *Vesicomya inflata* Kanie and Nishida, a lucinid shell convergent with that of vesicomysids, from Cretaceous strata of Hokkaido, Japan. *Veliger* 50:255–262
- Amano K, Jenkins RG, Aikawa M et al (2010) A Miocene chemosynthetic community from the Ogaya Formation in Joetsu: evidence for depth-related ecologic control among fossil seep communities in the Japan Sea back-arc basin. *Palaeogeogr Palaeoclimatol Palaeoecol* 286:164–170
- Amano K, Hasegawa S, Ishihama S (2013a) (Molluscan fossils from core sample collected from off Joetsu during MD 179 cruise.) *J Jpn Ass Petrol Technol* 78:92–96 (In Japanese)
- Amano K, Jenkins RG, Sako Y et al (2013b) A Paleogene deep-sea methane-seep community from Honshu, Japan. *Palaeogeogr Palaeoclimatol Palaeoecol* 387:126–133
- Amano K, Jenkins RG, Ohara M et al (2014a) Miocene vesicomysid species (*Bivalvia*) from Wakayama in southern Honshu, Japan. *Nautilus* 128:9–17
- Amano K, Saether KP, Little CTS et al (2014b) Fossil vesicomysid bivalves from Miocene hydrocarbon seep sites, North Island, New Zealand. *Acta Palaeontol Pol* 59:421–428
- Amano K, Little CTS, Campbell KA et al (2015) Paleocene and Miocene *Thyasira sensu stricto* (*Bivalvia*: Thyasiridae) from chemosynthetic communities from Japan and New Zealand. *Nautilus* 129:43–53
- Amano K, Jenkins RG, Kurita H (2018a) New and Mesozoic-relict mollusks from Paleocene wood-fall communities in Urahoro Town, eastern Hokkaido, northern Japan. *J Paleontol* 92:634–647
- Amano K, Little CTS, Campbell KA (2018b) Lucinid bivalves from Miocene hydrocarbon seep sites of eastern North Island, New Zealand, with comments on Miocene New Zealand seep faunas. *Acta Palaeontol Pol* 63:371–382
- Amano K, Miyajima Y, Jenkins RG et al (2019a) Miocene to Recent biogeographic history of vesicomysid bivalves in Japan, with two new records of the family. *Nautilus* 133:48–56
- Amano K, Miyajima Y, Nakagawa K et al (2019b) Chemosymbiotic bivalves from the lower Miocene Kurosedani Formation in Toyama Prefecture, central Honshu, Japan. *Paleontol Res* 23:208–219
- Anderson AE, Childress JJ, Favuzzi JA (1987) Net uptake of CO₂ driven by sulfide and thiosulphate oxidation in the bacterial symbiont-containing bivalve *Solemya reidi*. *J Exp Biol* 133:1–31
- Aoki S (1954) Mollusca from the Miocene Kabeya Formation, Joban coal-field, Fukushima Prefecture, Japan. *Sci Rep Tokyo Kyoiku Daigaku (Sec C)* 3:23–41
- Arellano SM, Young CR (2009) Spawning, development, and the duration of larval life in a deep-sea cold-seep mussel. *Biol Bull* 216:149–162
- Arellano SM, Van Gaest AL, Johnson SB et al (2014) Larvae from deep-sea methane seeps disperse in surface waters. *Proc R Soc B* 281:20133276
- Asato K, Kase T (2019) (Paleoecology of *Shikamaia*, the Permian giant bivalves (Alatoconchidae: Ambonychioidea) from Japan.) Abstracts of the annual meeting of the Malacological Society of Japan 2019:20 (In Japanese)
- Åström EKL, Oliver PG, Carroll ML (2017) A new genus and two new species of Thyasiridae associated with methane seeps off Svalbard. *Arctic Ocean Mar Biol Res* 13(4):402–416
- Audzijonyte A, Krylova EM, Sahling H et al (2012) Molecular taxonomy reveals broad trans-oceanic distributions and high species diversity of deep-sea clams (*Bivalvia*: Vesicomysidae: Pliocardiinae) in chemosynthetic environments. *Syst Biodivers* 10:403–415
- Baco AR, Smith CR, Peek AS et al (1999) The phylogenetic relationships of whale-fall vesicomysid clams based on mitochondrial COI DNA sequences. *Mar Ecol Prog Ser* 182:137–147
- Barry JP, Kochevar RE, Baxter CH (1997) The influence of pore-water chemistry and physiology on the distribution of vesicomysid clams at cold seeps in Monterey Bay: implications for patterns of chemosynthetic community organization. *Limnol Oceanogr* 42:318–328
- Batstone RT, Laurich JR, Salvo F et al (2014) Divergent chemosymbiosis-related characters in *Thyasira* cf. *gouldi* (*Bivalvia*, Thyasiridae). *PLoS One* 9(3):e92856
- Beets C (1942) Beiträge zur Kenntnis der angeblich oberoligocänen Mollusken-Fauna der Insel Buton, Niederländisch-Ostindien. *Leidse Geol Meded* 13:255–328

- Beets C (1953) Reconsideration of the so-called Oligocene fauna in the asphaltic deposits of Buton (Malay Archipelago). *Leidse Geol Meded* 17:237–258
- Bertolaso L, Palazzi S (1994) La posizione sistematica di *Delphinula bellardii* Michelotti, 1847. *Boll Malacol* 29:291–302
- Beu AG, Maxwell PA (1990) Cenozoic Mollusca of New Zealand. New Zealand Geological Survey Palaeontological Bulletin 58. New Zealand Department of Scientific and Industrial Research, Lower Hutt
- Bieler R, Mikkelsen PM, Collins TM et al (2014) Investigating the bivalve tree of life—an exemplar-based approach combining molecular and novel morphological characters. *Invertebr Syst* 28:32–115
- Bouchet P, Cosel RV (2004) The world's largest lucinid is an undescribed species from Taiwan (Mollusca: Bivalvia). *Zool Stud* 43:704–711
- Bron HG (1831) Italiens Tertiär-gebide und deren organische Einschlüsse. Heidelberg.
- Brugnone G (1880) Le conchiglie plioceniche nelle vicinanze di Caltasetta. *Boll Soc Malacol Ital* 6:85–158
- Campbell KA (2006) Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: past developments and future research directions. *Palaeogeogr Palaeoclimatol Palaeoecol* 232:362–407
- Campbell KA, Bottjer DJ (2006) Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold-seep paleoenvironments. *Geology* 23:321–324
- Campbell KA, Francis DA, Collins M et al (2008) Hydrocarbon seep carbonates of a Miocene forearc (East Coast Basin), North Island, New Zealand. *Sediment Geol* 204:83–105
- Carter JG, Altaba CR, Anderson LC et al (2011) A synoptical classification of the Bivalvia (Mollusca). *Paleontol Contrib* 4:1–47
- Cary SC (1994) Vertical transmission of a chemoautotrophic symbiont in the protobranch bivalve, *Solemya reidi*. *Mol Mar Biol Biotechnol* 3:121–130
- Chavan A (1969) Superfamily Lucinacea Fleming, 1828. In: Moore RC (ed) *Mollusca* 6, Bivalvia 2. Treatise on invertebrate paleontology, part N. Geological Society of America and University of Kansas, Boulder, pp N491–N518
- Chen C, Okutani T, Watanabe HK et al (2018) The first cuspidariid bivalve associated with a hydrothermal vent discovered from the southern Mariana Trough. *Venus* 76:39–44
- Chevaldonné P, Jollivet D, Desbruyères D et al (2002) Sister-species of eastern Pacific hydrothermal-vent worms (Ampharetidae, Alvinelidae, Vestimentifera) provide new mitochondrial clock calibration. *Cah Biol Mar* 43:367–370
- Childress JJ, Fisher CR, Brooks JM et al (1986) A methanotrophic marine molluscan (Bivalvia Mytilidae) symbiosis: mussels fueled by gas. *Science* 233:1306–1308
- Clark BL (1925) Pelecypoda from the marine Oligocene of western North America. *Univ Calif Publ Geol Sci* 15:69–136
- Clausen CK, Wignall PB (1990) Early Kimmeridgian bivalves of southern England. *Meso Res* 2:97–149
- Coan EV, Scott PV, Bernard FR (2000) Bivalve seashells of western North America: marine bivalve molluscs from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History monograph 2. Santa Barbara Museum of Natural History, Santa Barbara
- Combosch JD, Collins TM, Glover EM et al (2017) A family-level tree of life for bivalves based on a Sanger-sequencing approach. *Mol Phylogenet Evol* 107:191–208
- Conrad TA (1849) Fossils from northwestern America. In: Dana JD (ed) *United States exploring expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N., atlas, geology, vol 10*. Sherman, Philadelphia, pp 722–728
- Conway NM, Howes BL, McDowell Capuzzo JE et al (1992) Characterization and site description of *Solemya borealis* (Bivalvia; Solemyidae), another bivalve-bacteria symbiosis. *Mar Biol* 112:601–613
- Cooke CW (1919) Contributions to the geology and paleontology of the West Indies IV: Tertiary mollusks from the Leeward Islands and Cuba. *Carnegie Inst Wash Publ* 291:103–156

- Cosel RV (2002) A new species of bathymodioline mussel (Mollusca, Bivalvia, Mytilidae) from Mauritania (West Africa), with comments of the genus *Bathymodiolus* Kenk and Wilson, 1985. *Zoosystema* 24:259–271
- Cosel RV, Bouchet P (2008) Tropical deep-water lucinids (Mollusca: Bivalvia) from the Indo-Pacific: essentially unknown, but diverse and occasionally gigantic. In: Héros V, Cowie R, Bouchet P (eds) Tropical deep sea benthos, vol 25. *Mém Mus Natl Hist Nat*, Paris 196:115–213
- Cosel RV, Marshall BA (2003) Two new species of large mussels (Bivalvia Mytilidae) from active submarine volcanoes and a cold seep off the eastern North Island of New Zealand, with descriptions of a new genus. *Nautilus* 117:31–46
- Cosel RV, Marshall BA (2010) A new genus and species of large mussel (Mollusca: Bivalvia: Mytilidae) from the Kermadec Ridge. *Tuhinga* 21:59–73
- Cosel RV, Olu K (2008) A new genus and new species of Vesicomidae (Mollusca, Bivalvia) from cold seeps on the Barbados accretionary prism, with comments on other species. *Zoosystema* 30:929–944
- Cosel RV, Olu K (2009) Large Vesicomidae (Mollusca: Bivalvia) from cold seeps in the Gulf of Guinea off the coasts of Gabon, Congo and northern Angola. *Deep-Sea Res Part II* 56:2350–2379
- Cosel RV, Salas C (2001) Vesicomidae (Mollusca: Bivalvia) of the genera *Vesicomya*, *Waisiuconcha*, *Isorropodon* and *Callogonia* in the eastern Atlantic and the Mediterranean. *Sarsia* 86:333–366
- d'Orbigny AD (1844) *Paléontologie Française, terrains Crétacés*, vol 3. Mollusques. G. Masson, Paris
- Dall WH (1891) Scientific results of explorations by the U.S. Fish Commission Steamer Albatross XX: on some new or interesting West American shells obtained from dredgings of the U.S. Fish Commission steamer Albatross in 1888. *Proc US Natl Mus* 14:174–191
- Dall WH (1896) Diagnoses of new species of mollusks from the west coast of America. *Proc US Natl Mus Nat Hist* 18:7–20
- Dall WH (1901) Synopsis of the Lucinacea and of the American species. *Proc US Natl Mus Nat Hist* 23:779–833
- Dall, WH (1903) Contributions to the Tertiary of Florida with especial reference to the Siliceous-bed of Tampa and the Pliocene beds of the Caloosahatchee River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species, Part VI: concluding the work. *Trans Wagner Free Inst Sci Phila* 3:1219–1654
- Dall WH (1908a) A revision of the Solenomyacidae. *Nautilus* 22:1–2
- Dall WH (1908b) Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the US Fish Commission Steamer 'Albatross,' during 1891, Lieut. Commander Z. L. Tanner, USN, commanding, XXXVII: reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer 'Albatross,' from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, USN, commanding, XIV: the Mollusca and the Brachiopoda. *Bull Mus Comp Zool Harvard Univ* 43:205–487
- Dando PR, Southward AJ (1986) Chemoautotrophy in bivalve molluscs of the genus *Thyasira*. *J Mar Biol Assoc UK* 66:915–929
- Danise S, Dominici S, Bertolaso L (2010) Mollusk species at a Pliocene shelf whale fall (Orciano Pisano, Tuscany). *Plaios* 25:449–456
- Danise S, Bertolaso L, Dominici S (2016) Bathymodioline mussel dominated Miocene whale fall from Italy. *Boll Soc Paleontol Ital* 55:47–53
- Dautzenberg PH (1927) Mollusques provenant des campagnes scientifiques du Prince Albert Ier de Monaco dans l'Océan Atlantique et dans le Golfe de Gascogne. *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier Prince Souverain de Monaco LVVII*. Impri Monaco, Monaco

- Decker C, Olu K, Cunha RL et al (2012) Phylogeny and diversification patterns among vesicomid bivalves. *PLoS One* 7:1–8
- Dell RK (1987) Mollusca of the family Mytilidae (Bivalvia) associated with organic remains from deep water off New Zealand, with revisions of the genera *Adipicola* Dautzenberg, 1927 and *Idasola* Iredale, 1915. *Natl Mus NZ Rec* 3:17–36
- Distel DL, Baco AR, Chuang E et al (2000) Do mussels take wooden steps to deep-sea vents? *Nature* 403:725–726
- Distel DL, Altamia MA, Lin Z et al (2017) Discovery of chemoautotrophic symbiosis in the giant shipworm *Kuphus polythalamia* (Bivalvia: Teredinidae) extends wooden-steps theory. *Proc Natl Acad Sci USA* 114(18):E3652–E3658
- Dubilier N, Bergin C, Lott C (2008) Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nat Rev Microbiol* 6:725–740
- Duff KL (1978) Bivalvia from the English lower Oxford Clay (Middle Jurassic). *Palaeontol Soc Monogr* 132(1–137):pls 1–13
- Dufour SC (2005) Gill anatomy and evolution of symbiosis in the bivalve family Thyasiridae. *Biol Bull* 208:200–212
- Dufour SC (2018) Bivalve chemosymbioses on mudflats. In: Beninger PG (ed) *Mudflat ecology*. Springer, Heidelberg, pp 169–184
- Dufour SC, Felbeck H (2003) Sulphide mining by the superextensible foot of symbiotic thyasirid bivalves. *Nature* 426:65–67
- Duperron S (2010) The diversity of deep-sea mussels and their bacterial symbioses. In: Kiel S (ed) *The vent and seep biota, Topics in geobiology* 33. Springer, Heidelberg, pp 137–167
- Duperron S, Bergin C, Zielinski F et al (2006) A dual symbiosis shared by two mussel species, *Bathymodiolus azoricus* and *Bathymodiolus puteoserpentis* (Bivalvia: Mytilidae), from hydrothermal vents along the northern Mid-Atlantic Ridge. *Environ Microbiol* 8:1441–1447
- Duperron S, Fiala-Médoni A, Caprais JC et al (2007) Evidence for chemoautotrophic symbiosis in a Mediterranean cold seep clam (Bivalvia: Lucinidae): comparative sequence analysis of bacterial 16S rRNA, APS reductase and RubisCO genes. *FEMS Microbiol Ecol* 59:64–74
- Duperron S, Halary S, Lorion J et al (2008) Unexpected co-occurrence of six bacterial symbionts in the gills of the cold seep mussel *Idas* sp. (Bivalvia: Mytilidae). *Environ Microbiol* 10:433–445
- Fischer P (1861) Description d'une genre nouveau. *J Conchyliol* 9:345–347
- Fleming CA (1950) New Zealand Recent Thyasiridae (Mollusca). *Trans R Soc NZ* 78:251–254
- Forsey GF (2013) Fossil evidence for the escalation and origin of marine mutualisms. *J Nat Hist* 47:1833–1864
- Foster WJ, Danise S, Twitchett R (2017) A silicified early Triassic marine assemblage from Svalbard. *J Syst Palaeontol* 15:851–877
- Fujiwara Y (2003) Endosymbioses between invertebrates and chemosymbiotic bacteria. *Jpn J Benthol* 58:26–33
- Fujiwara Y, Kato C, Masui N et al (2001) Dual symbiosis in a cold seep thyasirid clam *Maorithyas hadalis* from the hadal zone in the Japan Trench, western Pacific. *Mar Ecol Prog Ser* 214:151–159
- Fujiwara Y, Okutani T, Yamanaka T et al (2009) *Solemya pervernicosa* lives in sediment underneath submerged whale carcasses: its biological significance. *Venus* 68:27–37
- Fukasawa Y, Matsumoto H, Beppu S et al (2017) Molecular phylogenetic analysis of chemosymbiotic Solemyidae and Thyasiridae. *Open J Mar Sci* 7:124–141
- Gabb WM (1866) Description of the Tertiary invertebrate fossils. *Calif Geol Surv Palaeontol* 2:1–38
- Gaillard C, Rio M, Rolin Y (1992) Fossil chemosynthetic communities related to vents or seeps in sedimentary basins: the pseudobioherms of southeastern France compared to other world examples. *Palaios* 7:451–465
- Génio L, Kiel S, Cunha MR et al (2012) Shell microstructures of mussels (Bivalvia: Mytilidae: Bathymodiolinae) from deep-sea chemosynthetic sites: do they have a phylogenetic significance? *Deep-Sea Res Part I* 64:86–103

- Génio L, Rodrigues CF, Guedes IF et al (2015) Mammal carcasses attract a swarm of mussels in the deep Atlantic: insights into colonization and biogeography of a chemosymbiotic species. *Mar Ecol* 36:71–81
- Gill FL, Little CTS (2013) A new genus of lucinid bivalve from hydrocarbon seeps. *Acta Palaeontol Pol* 58:573–578
- Gill FL, Harding IC, Little CTS et al (2005) Palaeogene and Neogene cold seep communities in Barbados, Trinidad and Venezuela: an overview. *Palaeogeogr Palaeoclimatol Palaeoecol* 227:191–209
- Glover EA, Taylor JD (2007) Diversity of chemosymbiotic bivalves on coral reefs: Lucinidae (Mollusca, Bivalvia) of New Caledonia and Lifou. *Zoosystema* 29:109–181
- Glover EA, Taylor JD (2016) Lucinidae of the Philippines: highest known diversity and ubiquity of chemosymbiotic bivalves from intertidal to bathyal depths (Mollusca: Bivalvia: Lucinidae). *Mém Mus Natl Hist Nat* 208:65–234
- Goedert JL, Campbell KA (1995) An early Oligocene chemosynthetic community from Makah Formation, northeast Olympic Peninsula, Washington. *Veliger* 38:22–129
- Goedert JL, Squires RL, Barnes LG (1995) Paleocology of whale-fall habitats from deep-water Oligocene rocks, Olympic Peninsula, Washington State. *Palaeogeogr Palaeoclimatol Palaeoecol* 118:151–158
- Gray JE (1840) Shells of molluscan animals. In: *Synopsis of the contents of the British Museum*, ed. 42. Woodfall & Son, London, pp 105–152
- Griffin M, Pastorino G (2006) *Madrynomys bruneti* n. gen. and sp. (Bivalvia: ?Modiomorphidae): a Mesozoic survivor in the Tertiary of Patagonia? *J Paleontol* 80:272–282
- Grossman EL (1993) Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts: comment and reply. *Geology* 21:94–96
- Gustafson RG, Reid RGB (1986) Development of the pericalymma larva of *Solemya reidi* (Bivalvia: Cryptodonta: Solemyidae) as revealed by light and electron microscopy. *Mar Biol* 93:411–427
- Gustafson RG, Reid RGB (1988) Association of bacteria with larvae of gutless protobranch bivalve *Solemya reidi* (Cryptodonta: Solemyidae). *Mar Biol* 97:389–401
- Gustafson RG, Turner RD, Lutz RA et al (1998) A new genus and five new species of mussels (Bivalvia: Mytilidae) from deep-sea sulfide/hydrocarbon seeps in the Gulf of Mexico. *Malacologia* 40:63–112
- Hall J, Whitfield RP (1872) Descriptions of new species of fossils from the vicinity of Louisville, Kentucky, and the falls of the Ohio; from the collection of Dr. James Knapp, of Louisville (continued). Preprint, Published in advance of the Report of the New York State Museum, Albany
- Hammer Ø, Nakrem HA, Little CTS et al (2011) Hydrocarbon seeps from close to the Jurassic–Cretaceous boundary, Svalbard. *Palaeogeogr Palaeoclimatol Palaeoecol* 306:15–26
- Hansen J, Ezat MM, Åström EKL et al (2019) New late Pleistocene species of *Acharax* from Arctic methane seeps off Svalbard. *J Syst Palaeontol* 18(2):197–212
- Hatae N (1960) (The geology and the geological structure of Amakusa-Shimo-shima, Kumamoto Prefecture.) *Sci Rep Kagoshima Univ* 9:61–107 (In Japanese)
- Holmes AM, Oliver PG, Sellanes J (2005) A new species of *Lucinoma* (Bivalvia: Lucinoidea) from a methane gas seep off the southwest coast of Chile. *J Conchol* 38:673–681
- Hryniewicz K, Little CTS, Nakrem HA (2014) Bivalves from the latest Jurassic–earliest Cretaceous hydrocarbon seep carbonates from central Spitsbergen, Svalbard. *Zootaxa* 3859:1–66
- Hryniewicz K, Nakrem HA, Hammer Ø et al (2015a) Palaeocology of the latest Jurassic–earliest Cretaceous hydrocarbon seep carbonates from central Spitsbergen, Svalbard. *Lethaia* 48:353–374
- Hryniewicz K, Hagström J, Hammer Ø et al (2015b) Late Jurassic–Early Cretaceous hydrocarbon seep boulders from Novaya Zemlya and their faunas. *Palaeogeogr Palaeoclimatol Palaeoecol* 436:231–244
- Hryniewicz K, Bitner MA, Durska E et al (2016) Paleocene methane seep and wood-fall marine environments from Spitsbergen, Svalbard. *Palaeogeogr Palaeoclimatol Palaeoecol* 462:41–56

- Hryniewicz K, Amano K, Jenkins RG et al (2017a) Thyasirid bivalves from Cretaceous and Paleogene cold seeps. *Acta Palaeontol Pol* 62:705–728
- Hryniewicz K, Jakubowicz M, Belka Z et al (2017b) New bivalves from a Middle Devonian methane seep in Morocco: the oldest record of repetitive shell morphologies among some seep bivalve molluscs. *J Syst Palaeontol* 15:19–41
- Hryniewicz K, Amano K, Bitner MA et al (2019) A late Paleocene fauna from shallow-water chemosynthesis-based ecosystems, Spitsbergen, Svalbard. *Acta Palaeontol Pol* 64:101–141
- Hryniewicz K, Bakayeva S, Heneralova L et al (2020) Taphonomy and palaeoecology of deep-water chemosymbiotic bivalves from the Eocene of Outer Eastern Carpathians, Ukraine. *Palaeogeogr Palaeoclimatol Palaeoecol* 553:109782
- Huber M (2010) Compendium of bivalves. ConchBooks, Hackenheim
- Huber M (2015) Compendium of bivalves 2. ConchBooks, Harxheim
- Hybertsen F, Kiel S (2018) A middle Eocene seep deposit with silicified fauna from the Humptulips Formation in western Washington State, USA. *Acta Palaeontol Pol* 63:751–768
- Imhoff JF, Sahling H, Sülting J et al (2003) 16s rDNA-based phylogeny of sulphur-oxidising bacterial endosymbionts in marine bivalves from cold-seep habitats. *Mar Ecol Prog Ser* 249:39–51
- Iredale T (1931) Australian Molluscan notes, no. 1. *Rec Aust Mus* 18:201–235
- Iredale T (1939) Mollusca, part I. Scientific Reports of the Great Barrier Reef Expedition 1928–1929, 5. British Museum (Natural History), London, pp 209–245
- Irwin H, Curtis C, Coleman M (1977) Isotopic evidence for source of diagenetic carbonates formed during burial of organic-rich sediments. *Nature* 269:209–213
- Isakar M, Sinityna I (1985) (Redescription of E. Eichwald's Ordovician bivalve species.) *Proc Acad Sci Estonian SSR Geol* 34:46–54 (In Russian)
- Jacobs DK, Lindberg DR (1998) Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas. *Proc Natl Acad Sci USA* 95:9396–9401
- Jakubowicz M, Hryniewicz K, Belka Z (2017) Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Sci Rep* 7:14292
- Jang S-J, Ho P-T, Jun S-Y et al (2020) A newly discovered *Gigantidas* bivalve mussel from the Onnuri Vent Field on the northern Central Indian Ridge. *Deep-Sea Res Part I* 161:103299
- Jeffreys JG (1876) New and peculiar Mollusca of the Pecten, Mytilus and Arca families, procured in the Valorous expedition. *Ann Mag Nat Hist* 18:424–436
- Jenkins RG, Kaim A, Hikida Y et al (2007) Methane-flux-dependent lateral faunal changes in a Late Cretaceous chemosymbiotic assemblage from the Nakagawa area of Hokkaido, Japan. *Geobiology* 5:127–139
- Jenkins RG, Kaim A, Little CTS et al (2013) Worldwide distribution of the modiomorphid bivalve genus *Caspiconcha* in late Mesozoic hydrocarbon seeps. *Acta Palaeontol Pol* 58:357–382
- Jenkins RG, Kaim A, Sato K et al (2017) Discovery of chemosynthesis-based association on the Cretaceous basal leatherback sea turtle from Japan. *Acta Palaeontol Pol* 62:683–690
- Jenkins RG, Kaim A, Amano K et al (2018a) A new Miocene whale-fall community dominated by the bathymodiolin mussel *Adipicola* from the Hobetsu area, Hokkaido, Japan. *Paleontol Res* 22:105–111
- Jenkins RG, Kaim A, Hikida Y et al (2018b) Four new species of the Jurassic to Cretaceous seep-restricted bivalve *Caspiconcha* and implications for the history of chemosynthetic communities. *J Paleontol* 92:596–610
- Johnson SB, Krylova EM, Audzijonyte A et al (2017) Phylogeny and origins of chemosynthetic vesicomyid clams. *Syst Biodivers* 15:346–360
- Jones WJ, Vrijenhoek RC (2006) Evolutionary relationships within the '*Bathymodiolus*' *childressi* group. *Cah Biol Mar* 47:403–407
- Jones WJ, Won YJ, Maas PAY et al (2006) Evolution of habitat use by deep-sea mussels. *Mar Biol* 148:841–851
- Kaim A (2011) Non-actualistic wood-fall associations from Middle Jurassic of Poland. *Lethaia* 44:109–124

- Kaim A, Schneider S (2012) A conch with a collar: early ontogeny of the enigmatic fossil bivalve *Myoconcha*. *J Paleontol* 86:652–658
- Kaim A, Kobayashi Y, Echizenya H et al (2008) Chemosynthesis-based associations on Cretaceous plesiosaurid carcasses. *Acta Paleontol Pol* 53:97–104
- Kaim A, Skupien P, Jenkins RG (2013) A new Lower Cretaceous hydrocarbon seep locality from the Czech Carpathians and its fauna. *Palaeogeogr Palaeoclimatol Palaeoecol* 390:42–51
- Kaim A, Jenkins RG, Tanabe K et al (2014) Mollusks from late Mesozoic seep deposits, chiefly in California. *Zootaxa* 3861:401–440
- Kalishevich TG, Zalinskaja ED, Serova MY (1981) (Development of organic world of the Pacific Belt on the Mesozoic and Cenozoic boundary: foraminifers, molluscs and palynoflora of the Northwestern Sector) Nauka Publishing House, Moscow (In Russian)
- Kamenev GM (2009) North Pacific species of the genus *Solemya* Lamarck, 1818 (Bivalvia: Solemyidae) with notes on *Acharax johnsoni* (Dall, 1891). *Malacologia* 51:233–261
- Kamenev GM, Nadochy VA, Kuznetsov AP (2001) *Conchocele bisecta* (Conrad, 1849) (Bivalvia: Thyasiridae) from cold-water methane-rich areas of the sea of Okhotsk. *Veliger* 44:84–94
- Kanie Y, Kuramouchi T (1996) Description on possibly chemosynthetic bivalves from the Cretaceous deposits of Obira-cho, northwestern Hokkaido. *Sci Rep Yokosuka City Mus* 44:63–68
- Kanie Y, Nishida T (2000) New species of chemosynthetic bivalves, *Vesicomya* and *Acharax*, from the Cretaceous deposits of northwestern Hokkaido. *Sci Rep Yokosuka City Mus* 47:79–84
- Kanie Y, Sakai T (1997) Chemosynthetic bivalve *Nipponothracia*, gen. nov. from the Lower Cretaceous and middle Miocene mudstones in Japan. *Venus* 56:205–220
- Kase T, Kurihara Y, Hagino K (2007) Middle Miocene chemosynthetic thraaciid *Nipponothracia gigantea* (Shikama, 1968) from central Japan is a large lucinid bivalve (Lucinoidea; Mollusca). *Veliger* 49:294–302
- Kase T, Isaji S, Aguilar YM et al (2019) A large new *Wareniconcha* (Bivalvia: Vesicomidae) from a Pliocene methane seep deposit in Leyte, Philippines. *Nautilus* 133:26–30
- Katto J, Hattori M (1964) Some Veneridae from the Shimantogawa Group in the Outer Zone of Shikoku, Japan. *Res Rep Kochi Univ Nat Sci I* 13:7–10
- Kauffman EG, Arthur MA, Howe B et al (1996) Widespread venting of methane-rich fluids in Late Cretaceous (Campanian) submarine springs (Tepee Buttes), Western Interior Seaway, U.S.A. *Geology* 24:799–802
- Kauffman EG, Harries PJ, Meyer C et al (2007) Paleocology of giant Inoceramidae (*Platyceramus*) on a Santonian (Cretaceous) seafloor in Colorado. *J Paleontol* 81:64–81
- Kelly SRA, Blanc E, Price SP et al (2000) Early Cretaceous giant bivalves from seep-related limestone mounds, Wollaston Foreland, northeast Greenland. In: Harper EM, Taylor JD, Crame JA (eds) *The evolutionary biology of the Bivalvia*. Geological Society of London Special Publication 177. Geological Society, London, pp 227–246
- Kenk VC, Wilson BR (1985) A new mussel (Bivalvia, Mytilidae) from hydrothermal vents in the Galapagos Rift Zone. *Malacologia* 26:253–271
- Kharlameko VI, Kamenev GM, Kalachev AV et al (2016) Thyasirid bivalves from the methane seep community off Paramushir Island (Sea of Okhotsk) and their nutrition. *J Molluscan Stud* 82:391–402
- Kiel S (2006) New records and species of mollusks from Tertiary cold-seep carbonates in Washington State, USA. *J Paleontol* 80:121–137
- Kiel S (2007) Status of the enigmatic fossil vesicomid bivalve *Pleurophopsis*. *Acta Paleontol Pol* 52:639–642
- Kiel S (2008) Fossil evidence for micro- and macrofaunal utilization of large nekton-falls: examples from early Cenozoic deep-water sediments in Washington State, USA. *Palaeogeogr Palaeoclimatol Palaeoecol* 267:161–174
- Kiel S (2009) Global hydrocarbon seep-carbonate precipitation correlates with deep-water temperatures and eustatic sea-level fluctuations since the Late Jurassic. *Terra Nova* 21:279–284

- Kiel S (2010a) The fossil record of vent and seep mollusks. In: Kiel S (ed) *The vent and seep biota. Topics in Geobiology 33*. Springer, Heidelberg, pp 255–278
- Kiel S (2010b) On the potential generality of depth-related ecologic structure in cold-seep communities: Cenozoic and Mesozoic examples. *Palaeogeogr Palaeoclimatol Palaeoecol* 295:245–257
- Kiel S (2013) Lucinid bivalves from ancient methane seeps. *J Molluscan Stud* 79:346–363
- Kiel S (2015) Did shifting seawater sulfate concentrations drive the evolution of deep-sea vent and seep ecosystems? *Proc R Soc B* 282:20142908
- Kiel S (2018) Three new bivalve genera from Triassic hydrocarbon seep deposits in southern Turkey. *Acta Palaeontol Pol* 63:221–234
- Kiel S, Amano K (2010) Oligocene and Miocene vesicomyid bivalves from the Katalla district in southern Alaska, USA. *Veliger* 51:76–84
- Kiel S, Amano K (2013) The earliest bathymodiolin mussels: evaluation of Eocene and Oligocene taxa from deep-sea methane seep deposits in western Washington State, USA. *J Paleontol* 87:589–602
- Kiel S, Goedert JL (2006a) Deep-sea food bonanzas: early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. *Proc R Soc B* 273:2625–2631
- Kiel S, Goedert JL (2006b) A wood-fall association from late Eocene deep-water sediments of Washington State, USA. *Palaios* 21:548–556
- Kiel S, Goedert JL (2007) Six new mollusk species associated with biogenic substrates in Cenozoic deep-water sediments in Washington State, USA. *Acta Palaeontol Pol* 52:41–52
- Kiel S, Hansen BT (2015) Cenozoic methane-seep faunas of the Caribbean region. *PLoS One* 10:e0140788
- Kiel S, Little TCS (2006) Cold-seep mollusks are older than the general marine mollusk fauna. *Science* 313:1429–1431
- Kiel S, Peckmann J (2007) Chemosymbiotic bivalves and stable carbon isotopes indicate hydrocarbon seepage at four unusual Cenozoic fossil localities. *Lethaia* 40:345–357
- Kiel S, Peckmann J (2008) Paleocology and evolutionary significance of an Early Cretaceous *Peregrinella*-dominated hydrocarbon-seep deposit on the Crimean Peninsula. *Palaios* 23:751–759
- Kiel S, Peckmann J (2019) Resource partitioning among brachiopods and bivalves at ancient hydrocarbon seeps: a hypothesis. *PLoS One* 14:e0221887
- Kiel S, Taviani M (2017) Chemosymbiotic bivalves from Miocene methane-seep carbonates in Italy. *J Paleontol* 91:444–466
- Kiel S, Taviani M (2018) Chemosymbiotic bivalves from the late Pliocene Stirone River hydrocarbon seep complex in northern Italy. *Acta Palaeontol Pol* 63:557–568
- Kiel S, Amano K, Jenkins RG (2008) Bivalves from Cretaceous cold seep deposits on Hokkaido, Japan. *Acta Palaeontol Pol* 53:525–537
- Kiel S, Amano K, Hikida Y et al (2009) Wood-fall associations from Late Cretaceous deep-water sediments of Hokkaido, Japan. *Lethaia* 42:74–82
- Kiel S, Campbell KA, Gaillard C (2010) New and little known mollusks from ancient chemosynthetic environments. *Zootaxa* 2390:26–48
- Kiel S, Wiese F, Titus AL (2012) Shallow-water methane-seep faunas in the Cenomanian Western Interior Seaway: no evidence for onshore-offshore adaptations to deep-sea vents. *Geology* 40:839–842
- Kiel S, Birgel D, Campbell KA et al (2013) Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeogr Palaeoclimatol Palaeoecol* 390:17–34
- Kiel S, Birgel D, Lu Y et al (2021) A thyasirid-dominated methane-seep deposit from Montañita, Ecuador, from the Oligocene-Miocene boundary. *Palaeogeogr Palaeoclimatol Palaeoecol* 247: 110477
- Kiel S, Amano K, Jenkins RG (2016) Predation scar frequencies in chemosymbiotic bivalves at an Oligocene seep deposit and their potential relation to inferred sulfide tolerances. *Palaeogeogr Palaeoclimatol Palaeoecol* 453:139–145

- Kiel S, Krystyn L, Demirtaş F et al (2017) Late Triassic mollusk-dominated hydrocarbon-seep deposits from Turkey. *Geology* 45:751–754
- Kiel S, Sami M, Taviani M (2018) A serpulid-*Anodontia*-dominated methane-seep deposit from the Miocene of northern Italy. *Acta Palaeontol Pol* 63:569–577
- Kiel S, Altamirano AJ, Birgel D et al (2020a) Fossiliferous methane-seep deposits from the Cenozoic Talara Basin in northern Peru. *Lethaia* 53:166–182
- Kiel S, Hybertsen F, Hyžný M et al (2020b) Mollusks and a crustacean from early Oligocene methane-seep deposits in the Talara Basin, northern Peru. *Acta Palaeontol Pol* 65:109–138
- Knight RI, Morris NJ, Todd JA et al (2014) Exceptional preservation of a novel gill grade in large Cretaceous inoceramids: systematic and palaeobiological implications. *Palaeontology* 57:37–54
- Kojima S (2008) (Evolution and phylogeny of vesicomysids.) In: Fujikura K, Okutani T, Maruyama T (eds) Deep-sea life-Biological observations using research submersibles. Tokai University Press, Hatano, pp 143–145 (In Japanese)
- Kojima S, Fujikura K, Okutani T (2004) Multiple trans-Pacific migrations of deep-sea vent/seep-endemic bivalves in the family Vesicomysidae. *Mol Phylogenet Evol* 32:396–406
- Krueger DM, Dubilier N, Cavanaugh CM (1992) Chemoautotrophic symbiosis in the tropical clam *Solemya occidentalis* (Bivalvia: Protobranchia): ultrastructural and phylogenetic analysis. *Mar Biol* 126:55–64
- Krueger DM, Gustafson RG, Cavanaugh CM (1996) Vertical transmission of chemoautotrophic symbionts in the bivalve *Solemya velum* (Bivalvia: Protobranchia). *Biol Bull* 190:195–202
- Krylova EM, Janssen R (2006) Vesicomysidae from Edison Seamount (south west Pacific: Papua New Guinea: New Ireland fore-arc basin). *Arch Molluskenkd* 135:231–261
- Krylova EM, Sahling H (2006) Recent bivalve molluscs of the genus *Calyptogena* (Vesicomysidae). *J Molluscan Stud* 72:359–395
- Krylova EM, Sahling H (2010) Vesicomysidae (Bivalvia): current taxonomy and distribution. *PLoS One* 5:e9957
- Krylova EM, Sahling H (2020) A new genus *Turneroconcha* (Bivalvia: Pliocardiinae) for the giant hydrothermal vent clam '*Calyptogena*' *magnifica*. *Zootaxa* 4808(1):79–100
- Kuhara T, Kano Y, Yoshikoshi K et al (2014) Shell morphology, anatomy and gill histology of the deep-sea bivalve *Elliptiolucina ingens* and molecular phylogenetic reconstruction of the chemosynthetic family Lucinidae. *Venus* 72:13–27
- Kurihara Y (2007) Occurrence of *Epilucina californica* (Conrad) (Bivalvia: Lucinidae) from the Neogene of Japan, with notes on the biogeographic history of *Epilucina*. *Paleontol Res* 11:29–39
- Kuroda T (1931) (Fossil Mollusca.) In: Homma F (ed) *Geology of the central part of Shinano*, part 4. Kokin Shoin, Tokyo, pp 1–90 (In Japanese)
- Kuroda T (1943) (*Akebiconcha*, a new pelecypod genus.) *Venus* 13:14–18 (In Japanese)
- Kuznetsov AP, Shileyko AA (1984) (On gutless Protobranchia (Bivalvia).) *Biol Nauki* 1984: 39–40 (In Russian)
- La Perna R (2005) A gigantic deep-sea Nucinellidae from the tropical West Pacific (Bivalvia: Protobranchia). *Zootaxa* 881:1–10
- Lamarck JB (1818) *Histoire naturelle des animaux sans vertèbres*, vol 5. Deterville, Paris
- Laming SR, Duperron S, Gaudron SM et al (2015) Adapted to change: the rapid development of symbiosis in newly settled, fast-maturing chemosymbiotic mussels in the deep sea. *Mar Environ Res* 112(B):100–112
- Laming SR, Gaudron SM, Duperron S (2018) Lifecycle ecology of deep-sea chemosymbiotic mussels: a review. *Front Mar Sci* 5(282):1–15
- Leanza A (1940) *Myoconcha neuquena* n. sp. Del Lias de Piedra Pintada en El Neuquén. *Paleontologia* 22:123–131
- Leckenby J (1859) On the Kelloway Rock of Yorkshire coast. *Q J Geol Soc* 15:4–15
- Liljedahl L (1991) Contrasting feeding strategies in bivalves from the Silurian of Gotland. *Palaeontology* 34:219–235

- Link HF (1807) Beschreibung der Naturalien-Sammlung der Universität Rostock. Universität Rostock, Rostock
- Little CTS, Vrijenhoek RC (2003) Are hydrothermal vent animals living fossils? *Trends Ecol Evol* 18:582–588
- Little CTS, Maslennikov VV, Morris NJ et al (1999) Two Paleozoic hydrothermal vent communities from the southern Ural Mountains, Russia. *Palaeontology* 42:1043–1078
- Little CTS, Birgel D, Boyce AJ et al (2015) Late Cretaceous (Maastrichtian) shallow water hydrocarbon seeps from Snow Hill and Seymour Islands James Ross Basin, Antarctica. *Palaeogeogr Palaeoclimatol Palaeoecol* 418:213–228
- Liu J, Liu H, Zhang H (2018) Phylogeny and evolutionary radiation of the marine mussels (Bivalvia: Mytilidae) based on mitochondrial and nuclear genes. *Mol Phylogenet Evol* 126:233–240
- Lorion J, Duperron S, Gros O et al (2008) Several deep-sea mussels and their associated symbionts are able to live both on wood and on whale falls. *Proc R Soc B* 276:177–185
- Lorion J, Kiel S, Faure B et al (2013) Adaptive radiation of chemosymbiotic deep-sea mussels. *Proc R Soc B* 280:20131243
- MacLeod KG, Hoppe KA (1992) Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts. *Geology* 20:117–120
- Majima R, Nobuhara T, Kitazaki T (2005) Review of fossil chemosynthetic assemblages in Japan. *Palaeogeogr Palaeoclimatol Palaeoecol* 227:86–123
- Martin AM, Goffredi SK (2011) '*Pliocardia krylovata*', a new species of vesicomimid clam from cold seeps along the Costa Rica margin. *J Mar Biol Assoc UK* 92:1127–1137
- Marwick J (1953) Divisions and faunas of the Hokonui System (Triassic and Jurassic). *Paleontol Bull* 21:1–141
- Matos SA, Warren LV, Fürsich FT et al (2017) Paleocology and paleoenvironments of Permian bivalves of the Serra Alta Formation, Brazil: ordinary suspension feeders or late Paleozoic Gondwana seep organisms? *J S Am Earth Sci* 77:21–41
- Matsukuma A, Okutani T, Tsuchi R (1982) Three new species of the Nucinellidae (Bivalvia: Protobranchia) from Pacific coast of Japan. *Venus* 40:177–186
- Matsumoto E (1971) Oligocene mollusks from the Setogawa Group in central Japan. *Bull Natl Sci Mus (Jpn)* 14:661–669
- McLeod RJ, Wing SR, Skilton JE (2010) High incidence of invertebrate-chemoautotroph symbioses in benthic communities of the New Zealand fjords. *Limnol Oceanogr* 55:2097–2106
- Meek FB (1873) Descriptions of invertebrate fossils of the Silurian and Devonian systems. *Geol Surv Ohio Rep* 1:1–243
- Meek FB, Worthen AH (1870) Description of new species and genera of fossils from the Palaeozoic rocks of the western states. *Proc Acad Natl Sci Phila* 1870:22–45
- Métivier B, Cosel RV (1993) *Acharax alinae* n. sp., Solemyidae (Mollusca: Bivalvia) géante du Bassin de Lau. *CR Acad Sci Ser III Sci Vie* 316:229–237
- Miller SA (1877) The American Palaeozoic fossils, a catalogue of the genera and species. Cincinnati, Ohio
- Miyajima Y, Nobuhara T, Koike H (2017) Taxonomic reexamination of three vesicomimid species (Bivalvia) from the middle Miocene Bessho Formation in Nagano Prefecture, central Japan, with notes on vesicomimid diversity. *Nautilus* 131:51–66
- Miyazaki JI, Martins LDO, Fujita Y et al (2010) Evolutionary process of deep-sea *Bathymodiolus* mussels. *PLoS One* 5:e10363
- Morris NJ, Dickins JM, Astafieva-Urbaitis K (1991) Upper Palaeozoic anomalodesmatan Bivalvia. *Bull Br Mus (Nat Hist) Geol* 47:51–100
- Morton B, Machado FM (2019) Predatory marine bivalves: a review. In: Sheppard C (ed) *Advances in marine biology* 84. Academic/Elsevier, London
- Natalicchio M, Peckmann J, Birgel D et al (2015) Seep deposits from northern Istria, Croatia: a first glimpse into the Eocene seep fauna of the Tethys region. *Geol Mag* 152:444–459

- Neulinger SC, Sahling H, Süling J et al (2006) Presence of two phylogenetically distinct groups in the deep-sea mussel *Acharax* (Mollusca: Bivalvia: Solemyidae). *Mar Ecol Prog Ser* 312:161–168
- Nobuhara T, Onda D, Kikuchi N et al (2008) (Lithofacies and fossil assemblages of the Upper Cretaceous Sada Limestone, Shimanto City, Kochi Prefecture, Shikoku, Japan.) *Fossils* 84:47–60 (In Japanese)
- Nützel A, Kaim A (2014) Diversity, palaeoecology and systematics of a marine fossil assemblage from the late Triassic fossil Cassian Formation at Settsass Scharte, N Italy. *Palaeontol Z* 88:405–431
- Ockelmann KW, Dinesen GE (2011) Life on wood—the carnivorous deep-sea mussel *Idas argenteus* (Bathymodiolinae, Mytilidae, Bivalvia). *Mar Biol Res* 7:71–84
- Okutani T (2002) A new thyasirid *Conchocele novaeguineensis* n. sp. from thanatocoenosis associated with a possible cold seep activity off New Guinea. *Venus* 61(3/4):141–145
- Oliver PG (2013) Description of *Atopomya dolobrata* gen. et sp. nov.: first record of bacterial symbiosis in the Saxicavellinae (Bivalvia). *J Conchol* 41:359–367
- Oliver PG (2014) ‘Tubular gills’: extreme gill modification in the Thyasiroidea with the description of *Ochetoctena tomasi* gen. et sp. nov. (Bivalvia: Thyasiroidea). *Zoosyst Evol* 90:121–132
- Oliver PG, Frey MA (2014) *Ascetoaxinus quatsinoensis* sp. et gen. nov. (Bivalvia: Thyasiroidea) from Vancouver Island, with notes on *Conchocele* Gabb, 1866, and *Channelaxinus* Valentich-Scott & Coan, 2012. *Zootaxa* 3869:452–468
- Oliver PG, Holmes AM (2006) A new species of Thyasiridae (Bivalvia) from chemosynthetic communities in the Atlantic Ocean. *J Conchol* 39:175–183
- Oliver PG, Killeen IJ (2002) The Thyasiridae (Mollusca: Bivalvia) of the British continental shelf and North Sea oilfields: an identification manual. *Studies of Marine Biodiversity and Systematics from the National Museum of Wales, BIOMÔR Reports* 3. National Museum of Wales, Cardiff
- Oliver PG, Levin L (2006) A new species of the family Thyasiridae (Mollusca: Bivalvia) from the oxygen minimum zone of the Pakistan Margin. *J Mar Biol Assoc UK* 86:411–416
- Oliver PG, Taylor JD (2012) Bacterial symbiosis in the Nucinelidae (Bivalvia: Solemyida) with descriptions of two new species. *J Molluscan Stud* 78:81–91
- Oliver PG, Rodrigues CF, Cunha MR (2011) Chemosymbiotic bivalves from the mud volcanoes of the Gulf of Cadiz, NE Atlantic, with descriptions of new species of Solemyidae, Lucinidae and Vesicomomyidae. *ZooKeys* 113:1–38
- Oliver PG, Southward EC, Dando PR (2012) Bacterial symbiosis in *Syssitomya pourtalesiana* Oliver, 2012 [Galeommatoidea, Montacutidae]: a bivalve commensal with the deep-sea echinoid *Pourtalesia*. *J Molluscan Stud* 79:30–41
- Olsson AA (1931) Contributions to the Tertiary paleontology of northern Peru, Part 4: the Peruvian Oligocene. *Bull Am Paleontol* 17:97–264
- Olu-Le Roy K, Sibuet M, Fiala-Médioni A et al (2004) Cold seep communities in the deep eastern Mediterranean Sea: composition, symbiosis and spatial distribution on mud volcanoes. *Deep-Sea Res Part I* 51:1915–1936
- Owen G (1961) A note on the habits and nutrition of *Solemya parkinsoni* (Protobranchia: Bivalvia). *Q J Microsc Sci* 102:15–21
- Paull CK, Martens CS, Chanton JP et al (1989) Old carbon in living organisms and young CaCO₃ cements from abyssal brine seeps. *Nature* 342:166–168
- Peckmann J, Thiel V (2004) Carbon cycling at ancient methane-seeps. *Chem Geol* 205:443–467
- Peckmann J, Gischler E, Oschmann W et al (2001) An Early Carboniferous seep community and hydrocarbon-derived carbonates from the Harz Mountains, Germany. *Geology* 29:271–274
- Peckmann J, Kiel S, Sandy MR et al (2011) Mass occurrences of the brachiopod *Halorella* in late Triassic methane-seep deposits, eastern Oregon. *J Geol* 119:207–220
- Peek AS, Feldman RA, Lutz RA et al (1998) Cospeciation of chemoautotrophic bacteria and deep sea clams. *Proc Natl Acad Sci USA* 95:9962–9966

- Petersen GH, Vedelsby A (2000) An illustrated catalogue of the Paleocene Bivalvia from Nuussuaq, northwest Greenland: their paleoenvironments and the paleoclimate. *Steenstrupia* 25:25–120
- Petersen JM, Zielinski FU, Pape T et al (2011) Hydrogen is an energy source for hydrothermal vent symbioses. *Nature* 476:176–180
- Phillips J (1829) Illustrations of the geology of Yorkshire, 1st edn. John Murray, York
- Pojeta J (1988) The origin and Paleozoic diversification of solemyoid pelecypods. *NM Bur Mines Mineral Resour Mem* 44:201–271
- Pojeta J, Runnegar B (1985) The early evolution of diasome molluscs. In: Trueman ER, Clarke MR (eds) *Evolution. The mollusca*, vol 10. Academic, Orlando, pp 295–336
- Reid RGB (1980) Aspects of biology of a gutless species of *Solemya* (Bivalvia: Protobranchia). *Can J Zool* 58:386–393
- Reid RGB (1998) Order Solemyoidea. In: Beesley PL, Ross GJB, Wells A (eds) *Mollusca Southern Synthesis, Fauna of Australia*, part A, vol 5. CSIRO Publishing, Melbourne, pp 241–247
- Rodrigues CF, Duperron S, Gaudron SM (2011) First documented record of a living solemyid bivalve in a pockmark of the Nile Deep-Sea Fan (eastern Mediterranean Sea). *Mar Biodivers Rec* 4:e10. <https://doi.org/10.1017/s175526721100008x>
- Rodrigues CF, Laming SR, Gaudroni SR et al (2015) A sad tale: has the small mussel *Idas argenteus* lost its symbionts? *Biol J Linn Soc* 114:398–405
- Roemer FJ (1839) Die Versteinerungen des norddeutschen Oolithen-Gebirges: ein Nachtrag. Hahn, Hannover
- Rosenkranz A (1970) Marine Upper Cretaceous and lowermost Tertiary deposits in west Greenland. *Bull Geol Soc Den* 19:406–453
- Russell SL, McCartney E, Cavanaugh CM (2018) Transmission strategies in a chemosynthetic symbiosis: detection and quantification of symbionts in host tissues and their environment. *Proc Biol Sci* 285:20182157
- Saether KP, Little CTS, Campbell KA et al (2010) New fossil mussels (Bivalvia: Mytilidae) from Miocene hydrocarbon seep deposits, North Island, New Zealand, with general remarks on vent and seep mussels. *Zootaxa* 2577:1–45
- Sahling H, Rickert D, Lee RW et al (2002) Macrofaunal community structure and sulfide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. *Mar Ecol Prog Ser* 231:121–138
- Salas C, Woodside J (2002) *Lucinoma kazani* n. sp (Mollusca: Bivalvia): evidence of a living benthic community associated with a cold seep in the Eastern Mediterranean Sea. *Deep-Sea Res Part I* 49:991–1005
- Samadi S, Quémeré E, Lorion J et al (2007) Molecular phylogeny in mytilids supports the wooden steps to deep-sea vents hypothesis. *C R Biol* 330:446–456
- Samadi S, Puillandre N, Pante E et al (2015) Patchiness of deep-sea communities in Papua New Guinea and potential susceptibility to anthropogenic disturbances illustrated by seep organisms. *Mar Ecol* 36(Suppl 1):109–132
- Sartori AF, Harper EM (2009) Sticky bivalves from the Mesozoic: clues to the origin of the anomalodesmatan arenophilic system. *Lethaia* 42:486–494
- Sato K, Watanabe H, Sasaki T (2013) A new species of *Solemya* (Bivalvia: Protobranchia: Solemyidae) from a hydrothermal vent in the Iheya Ridge in the mid-Okinawa Trough, Japan. *Nautilus* 123(3):93–100
- Sato K, Kano Y, Setiamarga DHE et al (2020) Molecular phylogeny of protobranch bivalves and systematic implications of their shell microstructure. *Zool Scr* 49(4):458–472
- Saul LR, Squires RL, Goedert JL (1996) A new genus of cryptic lucinid? bivalve from Eocene cold seeps and turbidite-influenced mudstone, western Washington. *J Paleontol* 70:788–794
- Seike K, Jenkins RG, Watanabe H et al (2012) Novel use of burrow casting as a research tool in deep-sea ecology. *Biol Lett* 8:648–651
- Sharma PP, Zardus JD, Boyle EE et al (2013) Into the deep: a phylogenetic approach to the bivalve subclass Protobranchia. *Mol Phylogenet Evol* 69:188–204

- Shikama T (1968) On a giant *Thracidora* from the Hayama Group, Miura Peninsula. *Sci Rep Yokohama Natl Univ (sec 2)* 14:13–16, pl 2
- Simone LRL, Mikkelsen PM, Bieler R (2015) Comparative anatomy of selected marine bivalves from the Florida Keys, with notes on Brazilian congeners (Mollusca: Bivalvia). *Malacologia* 58:1–127
- Smith CR, Baco AR (2003) Ecology of whale falls at the deep-sea floor. *Oceanogr Mar Biol Annu Rev* 41:311–354
- Speden IG (1970) The type Fox Hills Formation, Cretaceous (Maestrichtian), South Dakota, part 2, systematics of the Bivalvia. *Peabody Mus Nat Hist Yale Univ Bull* 33:1–222
- Squires RL (1991) New morphologic and stratigraphic information on *Calypptogena* (*Calypptogena gibbera* Crickmay, 1929, (Bivalvia: Vesicomidae), from the Pliocene and Pleistocene of southern California. *Veliger* 34:73–77
- Squires RL, Goedert JL (1991) New late Eocene mollusks from localized limestone deposits formed by subduction-related methane seeps, southwestern Washington. *J Paleontol* 65:412–416
- Squires RL, Gring MP (1996) Late Eocene chemosynthetic? bivalves from suspect cold seeps, Wagonwheel Mountain, central California. *J Paleontol* 70:63–73
- Stanley SM (1970) Relation of shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America Memoir* 125. Geological Society of America, Boulder
- Stanley SM (2014) Evolutionary radiation of shallow-water Lucinidae (Bivalvia with endosymbionts) as a result of the rise of seagrasses and mangroves. *Geology* 42:803–806
- Stanton TW (1895) Contributions to the Cretaceous paleontology of the Pacific coast: the fauna of the Knoxville beds. *US Geol Surv Bull* 133:1–132
- Stewart RB (1930) Gabb's California Cretaceous and Tertiary type lamellibranchs. *Acad Nat Sci Phila Spec Pub* 3(3):1–314
- Stewart FJ, Cavanaugh CM (2006) Bacterial endosymbioses in *Solemya* (Mollusca: Bivalvia)-Model systems for studies of symbiont-host adaptation. *Antonie Van Leeuwenhoek* 90:343–360
- Sturany R (1896) Zoologische Ergebnisse VII, Mollusken I (Prosobranchier und Opisthobranchier; Scaphopoden; Lamellibranchier) gesammelt von S.M. Schiff 'Pola' 1890–1894. *Denkschr Kaiserl Akad Wiss Math-Naturwiss Cl* 63:1–36
- Suyari K, Yamazaki T (1987) (Boundary between the north and south Shimanto subbelts in Tokushima Prefecture.) *J Sci Univ Tokushima* 20:37–46 (In Japanese)
- Takeda H (1953) The Poronai Formation (Oligocene Tertiary) of Hokkaido and South Sakhalin and its fossil fauna. *Stud Coal Geol* 3:1–103
- Tashiro M (1992) (Fossil monograph—Japanese Cretaceous bivalves). Jono Printing, Japan (In Japanese)
- Taviani M, Angeletti L, Ceregato A (2011) Chemosymbiotic bivalves of the family Solemyidae (Bivalvia, Protobranchia) in the Neogene of the Mediterranean Basin. *J Paleontol* 85:1067–1076
- Taylor JD, Glover EA (2005) Cryptic diversity of chemosymbiotic bivalves: a systematic revision of worldwide Anodontia (Mollusca: Bivalvia: Lucinidae). *Syst Biodivers* 3:281–338
- Taylor JD, Glover EA (2006) Lucinidae (Bivalvia) – the most diverse group of chemosymbiotic molluscs. *Zool J Linnean Soc* 148:421–438
- Taylor JD, Glover EA (2009) New lucinid bivalves from hydrocarbon seeps of the western Atlantic (Mollusca: Bivalvia: Lucinidae). *Steenstrupia* 30:111–124
- Taylor JD, Glover EA (2010) Chemosymbiotic bivalves. In: Kiel S (ed) *The vent and seep biota*. Springer, Heidelberg, pp 107–133
- Taylor JD, Cleavelly RJ, Morris NJ (1983) Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. *Palaeontology* 26:521–553
- Taylor JD, Williams ST, Glover EA (2007a) Evolutionary relationships of the bivalve family Thyasiridae (Mollusca: Bivalvia), monophyly and superfamily status. *J Mar Biol Assoc UK* 87:565–574
- Taylor JD, Williams ST, Glover EA et al (2007b) A molecular phylogeny of heterodont bivalves (Mollusca: Bivalvia: Heterodonta): new analyses of 18S and 28S rRNA genes. *Zool Scr* 36:587–606

- Taylor JD, Glover EA, Williams ST (2008) Ancient chemosynthetic bivalves: systematics of Solemyidae from eastern and southern Australia. In: Davie PJF, Phillips JA (eds) Proceedings of the 13th international marine biological workshop: the marine fauna and flora of Moreton Bay, Queensland. Mem Qld Mus – Nature 54:75–104
- Taylor JD, Glover EA, Smith L et al (2011) Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). Zool J Linn Soc 163:15–49
- Taylor JD, Glover EA, Williams ST (2014) Diversification of chemosymbiotic bivalves: origins and relationships of deeper water Lucinidae. Biol J Linn Soc 11:401–420
- Thiele J, Jaeckel S (1931) Muscheln der Deutschen Tiefsee-Expedition, II Teil. Deutsche Tiefsee-Expedition 1898–1899 21. G. Fischer, Jena, pp 159–268
- Thubaut J, Puillandre N, Faure BM et al (2013) The contrasted evolutionary fates of deep-sea chemosynthetic mussels (Bivalvia, Bathymodiolinae). Ecol Evol 3:4748–4766
- Turton W (1822) *Conchylia dithyra Insularum britannicarum*: the bivalve shells of the British Islands. Natali, London
- Ulrich EO (1894) The Lower Silurian Lamellibranchiata of Minnesota. Minnesota Geol Nat Hist Surv Final Rep 3:475–628
- Valdés F, Sellanes J, D’Elía G (2013) Phylogenetic position of vesicomid clams from a methane seep off central Chile (~36°S) with a molecular timescale for the diversification of the Vesicomidae. Zool Stud 51:1154–1164
- Valentich-Scott P, Coan EV (2012) Thyasiroidea. In: Coan EV, Valentich-Scott P (eds) Bivalve seashells of tropical West America: marine bivalve mollusks from Baja California to northern Peru, part 1. Santa Barbara Museum of Natural History, Santa Barbara, pp 362–372
- Valentich-Scott P, Powell CL II, Lorenson TD et al (2014) A new genus and species of Thyasiridae (Mollusca, Bivalvia) from deep-water, Beaufort Sea, northern Alaska. ZooKeys 462:11–26
- Valentine JW, Jablonski D, Kidwell SM et al (2006) Assessing the fidelity of the fossil record by using marine bivalves. Proc Natl Acad Sci USA 103:6599–6604
- Van Winkle K (1919) Remarks on some new species from Trinidad. Bull Am Paleontol 8:19–27
- Vermeij GJ (1977) The Mesozoic marine revolution: evidence of snails, predators and grazers. Paleobiology 3:245–258
- Vermeij GJ (1987) Evolution and escalation: an ecological history of life. Princeton University Press, Princeton, New Jersey
- Vokes HE (1955) Notes on Tertiary and Recent Solemyacidae. J Paleontol 29:534–545
- Vokes HE (1956) Notes on Nucinellidae (Pelecypoda) with description of a new species from the Eocene of Oregon. J Paleontol 30:652–671
- Vrijenhoek RC (2013) On the instability and evolutionary age of deep-sea chemosynthetic communities. Deep-Sea Res Part II 92:189–200
- Wagner CM, Schilling KH (1923) The San Lorenzo Group of the San Emigdio region, California. Univ Calif Publ Bull Dep Geol Sci 14:235–276
- Walliser EO, Mertz-Kraus R, Schöne BR (2018) The giant inoceramid *Platyceramus platinus* as a high-resolution paleoclimate archive for the Late Cretaceous of the Western Interior Seaway. Cretac Res 86:73–90
- Walliser EO, Tanabe K, Hikida Y et al (2019) Sclerochronological study of the gigantic inoceramids *Sphenoceramus schmidti* and *S. sachalinensis* from Hokkaido, northern Japan. Lethaia 52:410–428
- Walton K (2015) New Zealand living Solemyidae (Bivalvia: Protobranchia). Molluscan Res 35:246–261
- White CA (1882) On certain Cretaceous fossils from Arkansas and Colorado. Proc US Natl Mus 4:136–138
- White CA (1890) On certain Mesozoic fossils from the islands of St. Paul’s and St. Peter’s in the Straits of Magellan. Proc US Natl Mus 13:13–14
- Wignall PB, Newton RJ, Little CTS (2005) The timing of paleoenvironmental change and cause-and effect relationships during the early Jurassic mass extinction in Europe. Am J Sci 305:1014–1032

- Williams ST, Taylor JD, Glover EA (2004) Molecular phylogeny of the Lucinoidea (Bivalvia): non-monophyly and separate acquisition of bacterial chemosymbionts. *J Molluscan Stud* 70:187–202
- Wood SV (1851) Monograph of the Crag Mollusca with descriptions of shells from the upper Tertiaries of the British Isles, part 2, bivalves. *Palaeontogr Soc Monogr* 4:1–150
- Woodring WP (1925) Miocene Mollusca from Bowden Jamaica: pelecypods and scaphopods. *Carnegie Inst Wash Publ* 336:1–564
- Woodring WP (1938) Lower Pliocene mollusks and echinoids from the Los Angeles Basin, California, and their inferred environment. *US Geol Surv Prof Pap* 190:1–67
- Wortmann UG, Paytan A (2012) Rapid variability of seawater chemistry over the past 130 million years. *Science* 337:334–336
- Xu T, Feng D, Tao J et al (2019) A new species of deep-sea mussel (Bivalvia: Mytilidae: *Gigantidas*) from the South China Sea: morphology, phylogenetic position, and gill-associated microbes. *Deep-Sea Res Part I* 146:79–90
- Yokoyama M (1890) Versteinerungen aus der japanischen Kreide. *Palaeontographica* 36:159–202
- Zanzerl H, Dufour SC (2017) The burrowing behavior of symbiotic and asymbiotic thyasirid bivalves. *J Conchol* 42:299–308