Thyasirid bivalves from Cretaceous and Paleogene cold seeps

KRZYSZTOF HRYNIEWICZ, KAZUTAKA AMANO, ROBERT G. JENKINS, and STEFFEN KIEL

We present a systematic study of thyasirid bivalves from Cretaceous to Oligocene seep carbonates worldwide. Eleven species of thyasirid bivalves are identified belonging to three genera: *Conchocele*, *Maorithyas*, and *Thyasira*. Two species are new: *Maorithyas humptulipsensis* sp. nov. from middle Eocene seep carbonates in the Humptulips Formation, Washington State, USA, and *Conchocele kiritachiensis* sp. nov. from the late Eocene seep deposit at Kiritachi, Hokkaido, Japan. Two new combinations are provided: *Conchocele townsendi* (White, 1890) from Maastrichtian strata of the James Ross Basin, Antarctica, and *Maorithyas folgeri* (Wagner and Schilling, 1923) from Oligocene rocks from California, USA. Three species are left in open nomenclature. We show that thyasirids have Mesozoic origins and appear at seeps before appearing in "normal" marine environments. These data are interpreted as a record of seep origination of thyasirids, and their subsequent dispersal to non-seep environments. We discuss the age of origination of thyasirids in the context of the origin of the modern deep sea fauna and conclude that thyasirids could have deep sea origins. This hypothesis is supported by the observed lack of influence of the Cretaceous and Paleogene Oceanic Anoxic Events on the main evolutionary lineages of the thyasirids, as seen in several other members of the deep sea fauna.

Key words: Bivalvia, Thyasiridae, cold seeps, deep sea, ecology, evolution, Cretaceous, Paleogene.

Krzysztof Hryniewicz [krzyszth@twarda.pan.pl], Institute of Paleobiology, Polish Academy of Sciences, ul. Twarda 51/55, 00-818 Warszawa, Poland.
Kazutaka Amano [amano@juen.ac.jp], Department of Geoscience, Joetsu University of Education, 1Yamayashiki Joetsu City, Niigata 943-8512, Japan.
Robert G. Jenkins [robertgj@staff.kanazawa-u.ac.jp], School of Natural System, College of Science and Engineering, Kanazawa University, Kanazawa City, Ishikawa 920-1192, Japan.
Steffen Kiel [steffen.kiel@nrm.se], Swedish Museum of Natural History, Department of Palaeobiology, Box 500 07, 104 05 Stockholm, Sweden.

Introduction

Marine chemosynthesis-based ecosystems comprise hydrothermal vents (e.g., Van Dover 2000), hydrocarbon seeps (e.g., Sibuet and Olu 1998; Levin 2005) and wood and nekton falls (Smith and Baco 2003; Bernardino et al. 2010). Hydrocarbon seeps are submarine edifices where low-temperature fluids are released to the water column (Judd and Hovland 2007). These environments are populated by faunas dominated by macroinvertebrate species living in symbiosis with chemoautotrophic bacteria (Levin 2005), among which the most iconic are epifaunal and semi-infaunal groups like vestimentiferan tubeworms (Bright and Lallier 2010), vesicomyid clams and bathymodiolin mussels (Taylor and Glover 2010) and large abyssochrysoid gastropods (Sasaki et al. 2010). Infaunal groups, among them lucinid and thyasirid bivalves, have received less attention, although often being dominant in some Recent cold seeps (Kharlamenko et al. 2016). Fossil lucinid bivalves are relatively well known, commonly comprising the main faunal element of Cretaceous and Paleogene seeps (Kiel 2013).

The focus of this study are the less well known fossil thyasirid seep faunas. Many species are known from Cretaceous to Pleistocene seep deposits worldwide (e.g., Van Winkle 1919; Yabe and Nomura 1925; Kauffman 1967; Squires and Gring 1996; Goedert et al. 2003; Kiel et al. 2008; Amano et al. 2013). Although thyasirids are rarely common in ancient seep settings, the genus *Cretaxinus* Hryniewicz, Little, and Nakrem, 2014, was reported to be restricted to ancient seep environments, and it is possible that one more thyasirid genus occurs at fossil seeps only (Nobuhara et al. 2008). Despite a growing volume of data
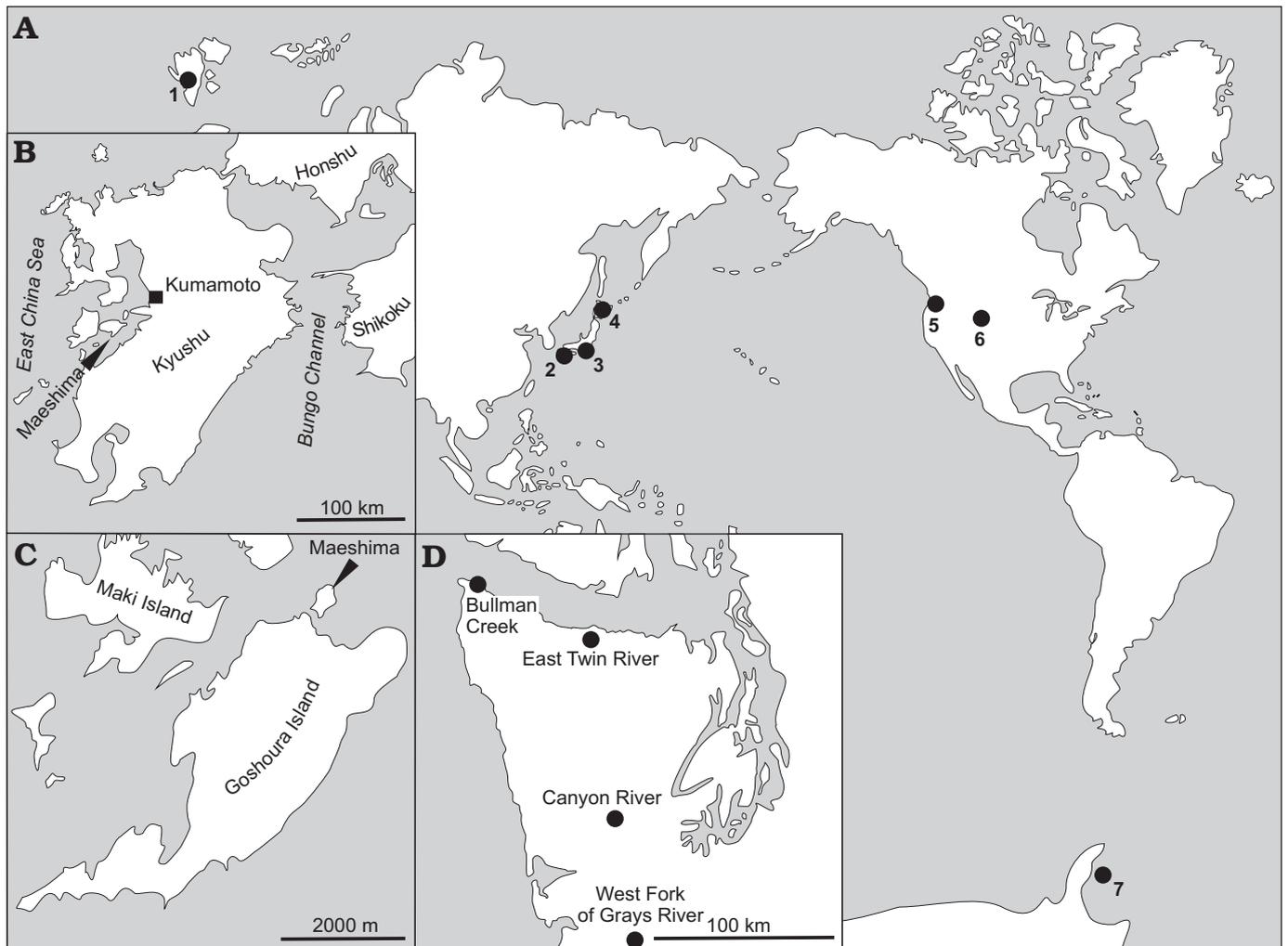
Fig. 1. **A**. Map showing some of the fossil seep localities bearing thyasirids examined in this study. Detailed maps of Amakusa area, Kyushu, Japan (**B**, **C**), Washington State, USA (**D**). 1, Colesbukta area, Spitsbergen, Svalbard; 2, Maeshima, Amakusa area, Kyushu, Japan; 3, Tanami, Honshu, Japan; 4, Hokkaido, Japan; 5, Washington State, USA; 6, Montrose, Nebraska, USA; 7, James Ross Basin, Seymour Island, Antarctica. After Campbell 2006 (A) and Goedert and Benham 1999 (D). For detailed list of localities discussed, the reader is refered the Material section, and references therein.

on fossil seeps, the taxonomy of thyasirids in these habitats remains poorly understood. The purpose of this paper is to improve the current knowledge of fossil seep-inhabiting thyasirids using newly collected material and museum collections. Due to an overwhelming number of Neogene seep deposits, especially in Japan and the Russian Far East, the current study is restricted to more manageable Cretaceous and Paleogene occurrences.

Institutional abbreviations.—CSUN, California State University at Northridge, USA; GPIBo, Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Germany; JUE, Joetsu University of Education, Japan; LACMIP, Natural History Museum of Los Angeles County, Los Angeles, USA; MMH; Natural History Museum of Denmark, Geological Museum, Copenhagen, Denmark; NRM, Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm, Sweden; PMO, Natural History Museum, University of Oslo, Norway; UCMP,

University of California Museum of Paleontology, Berkeley, USA; UMUT, University Museum, University of Tokyo, Tokyo, Japan; USNM, United States National Museum of Natural History, Washington, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material

This study is based on a collection of specimens from Cretaceous−Oligocene localities worldwide (Figs. 1, 2). The majority of these localities have already been described; therefore we only briefly outline the localities and provide references to more detailed descriptions. The localities are listed below in an alphabetical order.

Bear River, southwestern Washington State, USA.— Large seep deposit in an abandoned quarry on the south side of Bear River in Pacific County, western Washington State, embedded in upper Eocene strata of "Siltstone of Cliff Point"
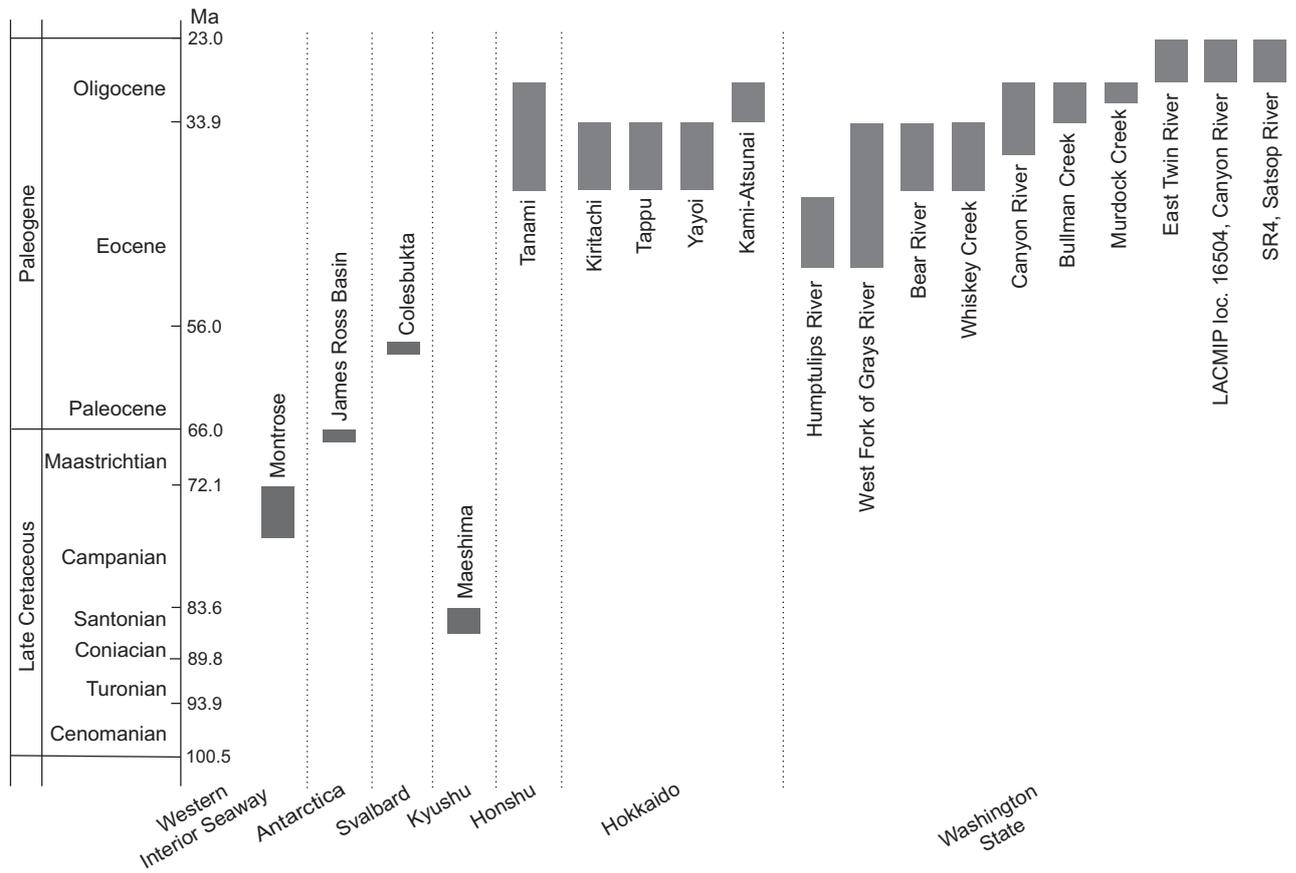
Fig. 2. Geological ages of the fossil seep localities bearing thyasirids examined in this study.

(LACMIP loc. 5802). It contains a diverse fauna dominated by *Bathymodiolus willapaensis*; the thyasirids reported herein are quite rare (Goedert and Squires 1990; Squires and Goedert 1991; Goedert and Benham 2003; Kiel 2010).

Bullman Creek, northwestern Washington State, USA.—Cold seep limestone found as float on beach terrace approximately 1 km east of the mouth of Bullman Creek in Clallam County, northwestern Washington State, derived from the lower Oligocene Jansen Creek Member of the Makah Formation; coordinates: 48°20.798' N, 124°31.223' W.

Canyon River, western Washington State, USA.—Large cold seep carbonate block with large thyasirid bivalves exposed by natural etching. Found as float on gravel bar, east bank of Canyon River, approximately 100 m upstream from bridge, coordinates: 47°18.166' N, 123°30.567' W; SE ¼ of Section 13, T. 21 N., R. 7 W according to US public land description system, Grays Harbor County, Washington State. The outcrop is surrounded by uppermost Eocene to lower Oligocene deposits of the Lincoln Creek Formation.

Colesbukta area, Spitsbergen, Svalbard.—Thyasirids identified as *Conchocele conradii* by Rosenkrantz (1970) come from prodelta and offshore sandstone and siltstone of the Paleocene Basilika Formation cropping out in several localities on the western shore of Colesbukta. The majority of the specimens described herein comes from Fossildalen and were first mentioned by Hägg (1925), with some of those

occurrences later identified as seep deposits and wood-rich sediments (Hryniewicz et al. 2016). The fauna is dominated by *C. conradii* associated with diverse background species, chiefly mollusks.

East Twin River, northwestern Washington State, USA.—Block of cold-seep limestone found as float along base of bluff approximately 110 m north and 490 m west of the southeast corner of Section 24, T. 31 N., R. 10 W according to US public land description system, approx. 1.6 km east of East Twin River, Clallam County, Washington State. The block comes from the upper part of the Pysht Formation and is of late Oligocene age (Nesbitt et al. 2013).

Humptulips Formation, western Washington State, USA.—Our material comes from two distinct localities from the middle Eocene Humptulips Formation in western Washington State, USA. LACMIP loc. 12385 is a large seep deposit in an abandoned meander on the East Fork of the Humptulips River in Grays Harbor County, hosting a diverse mollusk fauna including the bathymodiolin *Vulcanidas*? *goederti*, the vesicomyid "*Pliocardia*" cf. *tschudi*, and the thyasirid described herein, previously identified as *Thyasira* (*Conchocele*) *folgeri* (Goedert and Squires 1990; Kiel and Amano 2013). The second site is a small seep deposit found in the river bed of the Humptulips River (CSUN loc. 1583) with the main taxa being the lucinid bivalve *Elongatolucina elassodyseides* and the abyssochrysoid gastro-
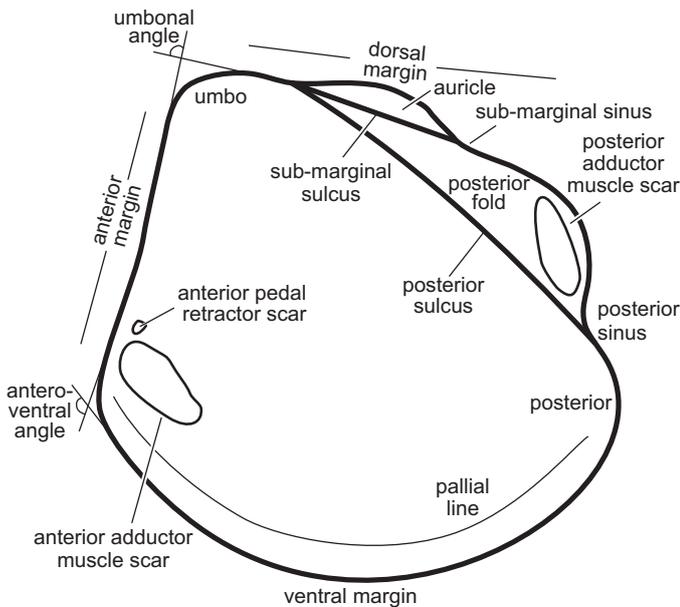
Fig. 3. Schematic drawing of a model thyasirid bivalve with explanations of the main morphological terms used herein.

pod *Humptulipsia raui* (Goedert and Kaler 1996; Kiel 2008; Gill and Little 2013).

James Ross Basin, Western Antarctica.—Specimens of the large thyasirid "*Thyasira*" *townsendi* are common throughout Maastrichtian strata of Snow Hill and López de Bertodano formations of Snow Hill and Seymour islands, respectively (Wilckens 1910). Some of the sites have recently been identified as seep-related (Little et al. 2015). Here we re-illustrate two specimens previously figured by Wilckens (1910).

Kami-Atsunai, Hokkaido, Japan.—Large, lower Oligocene seep deposit found in deep-water strata of the Nuibetsu Formation along the Atsunai River, 1.5 km east of the Kami-Atsunai railway station in Urahoro-cho in eastern Hokkaido, Japan. The main taxa found at this locality are the vesicomyid *Hubertschenckia ezoensis*, the bathymodiolin *Bathymodiolus inouei*, and a species of *Conchocele* discussed herein (Amano and Jenkins 2011).

Kiritachi, Hokkaido, Japan.—Articulated specimens of *Conchocele kiritachiensis* sp. nov. described herein come from an upper Eocene seep deposit of Sakasagawa Formation, cropping out at the cliff along the Kotanbetsu River, 2 km west of Seiryu Bridge in Kiritachi, Tomamae Town, northwestern Hokkaido (Loc. SK 15 of Noda [1992]; 44°13'22" N, 141°53'8" E). The locality also contains buccinid gastropods (Amano and Oleinik 2016).

LACMIP loc. 16504, western Washington State, USA.—An upper Oligocene seep deposit, found in the bathyal siltstone of the Lincoln Creek Formation (Squires 1995). The deposit contains a diverse fauna of mollusks (Squires and Goedert 1995; Goedert and Benham 1999) and sponges (Rigby and Goedert 1996).

Maeshima, Kyushu, Japan.—Small blocks of heavily in-

durated, grey seep carbonates found at the beach within a Santonian submarine slump deposits of the Himenoura Group at Maeshima, Goshoura Island, Kumamoto Prefecture, southern Kyushu, Japan. The carbonates contain small molluscan fossils, among them low-spired gastropods and small thyasirid bivalves here identified as *Thyasira tanabei*. Details for this locality will be provided in a separate publication.

Montrose, Nebraska, USA.—The material described in this paper comes from the Upper Cretaceous (Campanian; Jamie Brezina, personal communication 2017) offshore Pierre Shale of the Western Interior Seaway. It was collected in 2014 by Andrzej Kaim (Institute of Paleobiology, Warsaw) near the Warbonnet Battlefield Memorial, close to Montrose, Nebraska, USA. The memorial is located on top of a seep deposit with numerous bivalves, mostly lucinids, and less common gastropods, including well preserved naticiform gastropods (Andrzej Kaim, personal communication 2017).

Murdock Creek, northwestern Washington State, USA.—Several small blocks of seep carbonate float found on the beach platform west of the mouth of Murdock Creek, Clallam County, Washington State, derived from the upper lower Oligocene deep-water strata of the lower part of the Pysht Formation (LACMIP loc. 6295). These blocks include a diverse but scattered fauna including protobranch, vesicomyid, and bathymodiolin bivalves, provannid gastropods, and serpulid worm tubes (Goedert and Squires 1993; Kiel and Amano 2013; Vinn et al. 2013).

SR4, western Washington State, USA.—Seep deposit with a diverse fauna found along the bank of Satsop River at 47°16'18.0" N, 123°28'56.2" W, in the upper Oligocene part of the Lincoln Creek Formation (Peckmann et al. 2002; Zwicker et al. 2015).

Tanami, Honshu, Japan.—A medium-sized seep deposit found in upper Eocene to lower Oligocene submarine fan deposits of the Tanamigawa Formation near Tanami, Kushimoto Town in Wakayama Prefecture, southern Honshu, Japan (Amano et al. 2013). The main invertebrate species at this locality is a species of *Conchocele*, accompanied by less numerous specimens of the bathymodiolin *Bathymodiolus* aff. *inouei* (Amano and Jenkins 2011), and the vesicomyid *Hubertschenkia ezoensis*. A complete list of invertebrate macrofauna from this locality is given by Amano et al. (2013).

Tappu, Hokkaido, Japan.—Four carbonate blocks derived from dark grey mudstone found 130 m and 150 m upstream from Eikou Bridge at Tappu, along the Shimokinebetsu River in Obira Town in northwestern Hokkaido. The fauna of these upper Eocene sites consists of the thyasirid *Conchocele taylori* documented herein, the vesicomyid *Hubertschenckia ezoensis*, the malletiid *Malletia poronaica*, and the carditid *Cyclocardia elliptica*, in association with some other taxodont bivalves and some turrid gastropods (Ohara and Kanno 1969, 1973; Amano et al. 2013).

Yayoi, Hokkaido, Japan.—Cold-seep deposit located in a high cliff along the Ikushunbetsu River to the west of Yayoi Town in Mikasa City in central Hokkaido, Japan, that is enclosed in dark grey mudstone of the upper Eocene Poronai Formation. The fauna of this site consists mainly of a species of *Conchocele* and the vesicomyid *Hubertschenckia ezoensis*, along with a few gastropods (Yokoyama 1890; Amano and Jenkins 2007).

West Fork of Grays River, western Washington State, USA.—Blocks of cold seep carbonate on gravel bar approximately 30 m upstream from the old bridge over the West Fork of Grays River, approximately 800 m east and 950 m south of the northwest corner of Section 28, T. 11 N., R. 7 W, according to US public land description system; Pacific County, Washington State; coordinates: 46.404230°N, 123.553867°W The rocks in this area were mapped as middle to upper Eocene "Siltstone of Unit B" (Wolfe and McKee 1968).

Whiskey Creek, northwestern Washington State, USA.— Large limestone boulders eroded from a landslide west of the mouth of Whiskey Creek in Clallam County on the north side of the Olympic Peninsula in Washington State, USA. They appear to be derived from upper Eocene strata of the Pysht Formation; the most common taxa are the lucinid bivalve *Cryptolucina megadyseides* and the vesicomyid *Adulomya chinookensis*, whereas the thyasirid reported here is uncommon (Goedert et al. 2003).

Systematic palaeontology

Class Bivalvia Linnaeus, 1758

Subclass Heterodonta Neumayr, 1884

Order Lucinida Gray, 1854

Family Thyasiridae Dall, 1900 (1895)

Genus *Conchocele* Gabb, 1866

Type species: *Thyasira bisecta* Conrad, 1849; Miocene, Astoria Formation, Astoria, Oregon, USA.

Remarks.—Various species concepts have been applied to the extant members of *Conchocele*. In some cases smaller and more rounded specimens were referred to as *Conchocele bisecta* (Conrad, 1849), whereas larger and more quadrangular specimens were referred to as *Conchocele disjunta* (Gabb, 1866) (e.g., Tegland 1928; Habe 1964; Boss 1967; Bernard 1972). The current approach is to treat both morphospecies as a variation of the same biological species, and to refer to the extant species as *C. bisecta* due to the rule of priority (Kamenev et al. 2001; Oliver and Frey 2014). The more extensive discussion of this problem is beyond the scope of this paper, however, we would like to point out that both *C. bisecta* and *C. disjuncta* are based on fossil rather than extant material, and each fossil species was erected based on material of different age (Miocene and Pliocene, respectively). Caution should be applied when synonymizing these two fossil species, and when applying these names to extant material. The only name for a North Pacific *Conchocele* that has been applied to a living species, as far as we are aware of, is *Thyasira disjuncta* var. *ochotica* Krishtofovich, 1936 (locality: sea shore). It might be worth to carefully check this "variation" for conchological differences to *C. disjuncta*; if there are notable differences, *C.* "*ochotica*" might be used for extant North Pacific species.

Conchocele townsendi (White, 1890)

Fig. 4.

1890 *Lucina? townsendi* sp. nov.; White 1890: 14, pl. 3: 1, 2.
1903 *Lucina? townsendi* White, 1890; Weller 1903: 67, pl. 11: 2, 3.
1910 *Thyasira townsendi* (White, 1890); Wilckens 1910: 53–56, pl. 2: 31, 32, pl. 3: 1.
1988 *Thyasira townsendi* (White, 1990) (sic!); Zinsmeister and Macellari 1988: 273, 276, figs. 9.7, 9.8.
2008 "*Thyasira*" *townsendi* (White, 1890); Kiel et al. 2008: 535.
2015 "*Thyasira*" *townsendi* (White, 1890); Little et al. 2015: fig. 5G–I.

Type material: Holotype unknown; hypotypes NRM Mo 1560; USNM 405773 (Zinsmeister and Macellari 1988).

Type locality: Saint Paul's and Saint Peter's islands, Magellan Strait.

Type horizon: Cretaceous (details unknown).

Material.—Two specimens (NRM Mo 1552, 1560) from Maastrichtian cold seep carbonates of Seymour Island, Antarctica.

Remarks.—The species was initially described as a possible species of *Lucina* by White (1890) from St. Paul's and St. Peter's islands in the Straits of Magellan, both of which we could not locate. It was thereafter noted from Antarctic strata by Weller (1903), who mentioned it from outcrops of the Admiralty Sound area, Weddell Sea. The first precise locality information comes from the work of Wilckens (1910), who mentions numerous occurrences on Snow Hill and Seymour Islands, western Weddell Sea. Wilckens (1910) formally transferred the species to *Thyasira*. This interpretation was followed in a description of Zinsmeister and Macellari (1988), who noticed that the species is similar to *Conchocele disjuncta* Gabb, 1869, from the Pliocene of California. However, they considered a closer relationship between the two species unlikely due to the significant temporal and spatial distance between them.

Doubts about including "*Thyasira*" *townsendi* in *Thyasira* were expressed by Kiel et al. (2008) and Little et al. (2015). Here we formally transfer the species to *Conchocele* based on the beaks located close to the anterior of the shell, a steeply sloping anterior margin bound by a keel, the lack of a distinct submarginal and deep posterior sulcus, and a posterior margin indented by a deep sinus. This is the only Cretaceous thyasirid which we can confidently place in the genus *Conchocele*. The Coniacian "*Thyasira*" *cretacea* Whiteaves, 1874, from Enos Canyon, California (Anderson 1958) is not figured well enough for a more detailed comparison. The same applies to "*Thyasira*" *cretacea* from the Late Cretaceous of Vancouver Island (Whiteaves 1874), and to "*Thyasira*" *collignoni* from Campanian of New Caledonia
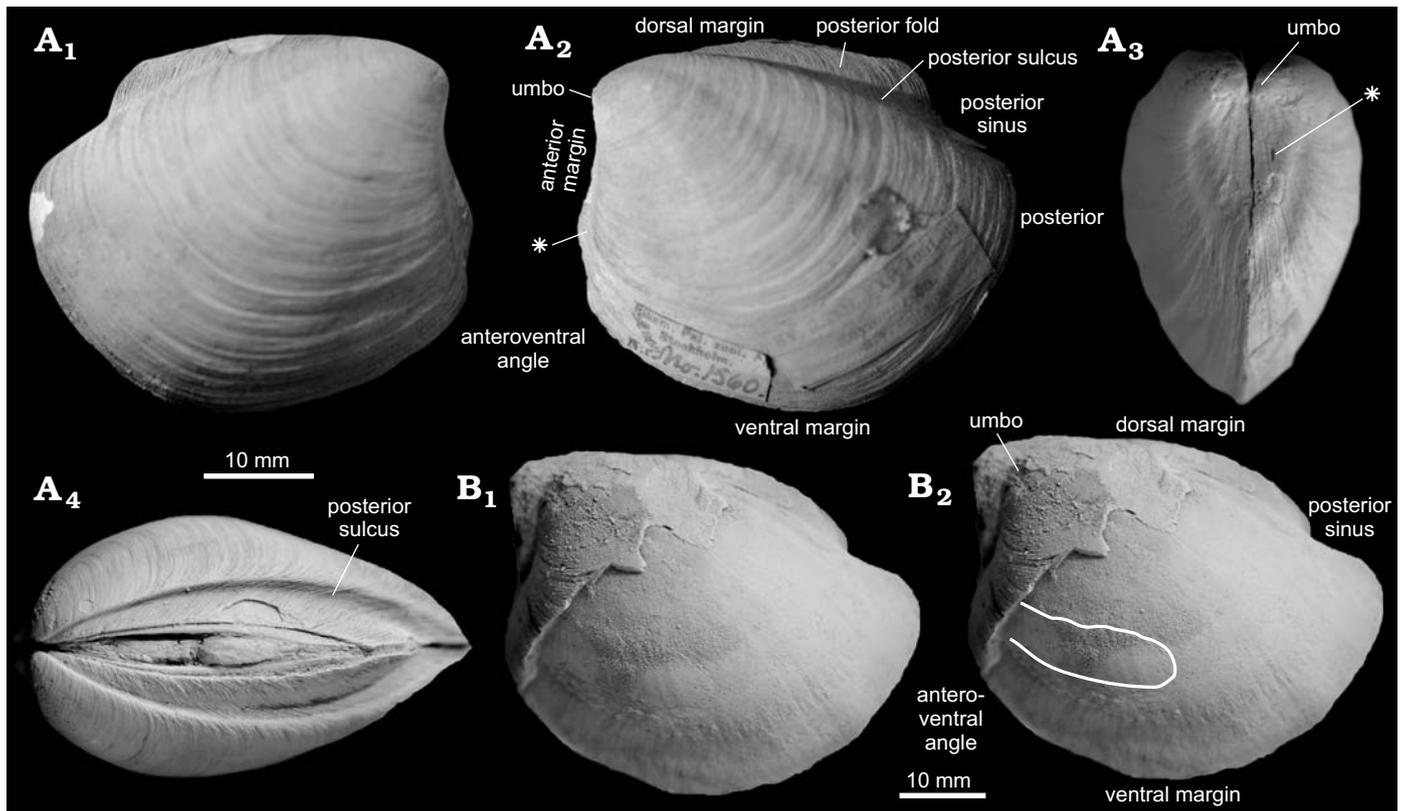
Fig. 4. Thyasirid bivalve *Conchocele townsendi* (White, 1890) from Maastrichtian cold seep carbonates of Seymour Island, James Ross Basin, Antarctica. **A**. NRM Mo 1560; a complete shell in right (A_1) and left (A_2) lateral view, showing outline and fine commarginal ornament; in anterior view (A_3), showing two ridges running from the umbo towards the anteroventral angle; in dorsal view (A_4), showing narrow and sharp posterior sulcus and posterior fold and weak furrow possibly representing accessorial ligament attachment surface. **B**. NRM Mo 1552; an internal mold in left lateral view with fragments of the shell adhering to the anterior and umbonal area (B_1) and with outline of the anterior adductor muscle scar visible (B_2).

(Freneix 1980), the figured specimens of which lack a well preserved posterior margin. "*Aphrodina*" *hataii* Katto and Hattori, 1965, from the Campanian–Maastrichtian Sada Limestone seep deposit in Shikoku, Japan (Nobuhara et al. 2008) has a deep posterior sulcus but lacks a characteristic posterior sinus (KH personal observation) as well as a truncated anterior margin and should not be included in *Conchocele*.

Stratigraphic and geographic range.—Maastrichtian of the James Ross Basin and possibly the Magellan Strait area.

Conchocele conradii (Rosenkrantz, 1942)
Fig. 5.

1925 *Thyasira bisecta* Conrad, 1849; Hägg 1925: 46–48, pl. 4: 14–17, pl. 5: 18, 19, non 20.
1942 *Thyasira conradii* n. sp.; Rosenkrantz 1942: 277–278.
1970 *Thyasira* (*Conchocele*) *conradi* Rosenkrantz, 1942 (sic!); Rosenkrantz 1970: 427, fig. 7.1, non fig. 7.2.
1970 *Conchocele conradii* (Rosenkrantz, 1942); Vonderbank 1970: pl. 10: 2a, b.
?1980 *Conchocele conradii* (Rosenkrantz, 1942); Thiedig et al. 1980: 143, pl. 1: 1, 3, non 4.
2016 *Conchocele conradii* (Rosenkrantz, 1942); Hryniewicz et al. 2016: fig. 12A.

Type material: Holotype unknown; lectotype MMH 10792 (Rosenkrantz 1970).

Type locality: South-western side of Colesbukta, Spitsbergen, Svalbard.

Type horizon: Paleocene, Basilika Formation.

Material.—All of the material studied comes from Paleocene Basilika Formation, Colesbukta area, Spitsbergen, Svalbard. Two specimens from GPIBo, including one figured by Vonderbank (GPIBo Nr. 159) (1970); 14 unnumbered specimens from PMO; 37 specimens from NRM, including one figured (NRM PZ Mo 182204; Fig. 5A), this comprises five specimens (Mo PZ 149148–152) illustrated by Hägg (1925) and one (NRM PZ Mo 182204) by Hryniewicz et al. (2016); 121 unnumbered specimens from the collections of ZPAL, and one numbered and figured specimen (ZPAL L.16/1). The material from GPIBo contains only specimens with sandstone matrix which are unlikely to be of seep origin. The specimens from PMO are all of seep origin; the material from NRM and ZPAL contains a mixture of seep and non-seep specimens, with seep specimens prevailing.

Remarks.—*Conchocele conradii* from the south-western side of Colesbukta on Spitsbergen, Svalbard, was first described as *Thyasira bisecta* Conrad, 1849, by Hägg (1925), who noticed that the specimens from Svalbard are larger than the largest specimens of *C. bisecta* from the Miocene Astoria Formation type locality in Oregon, USA (Moore
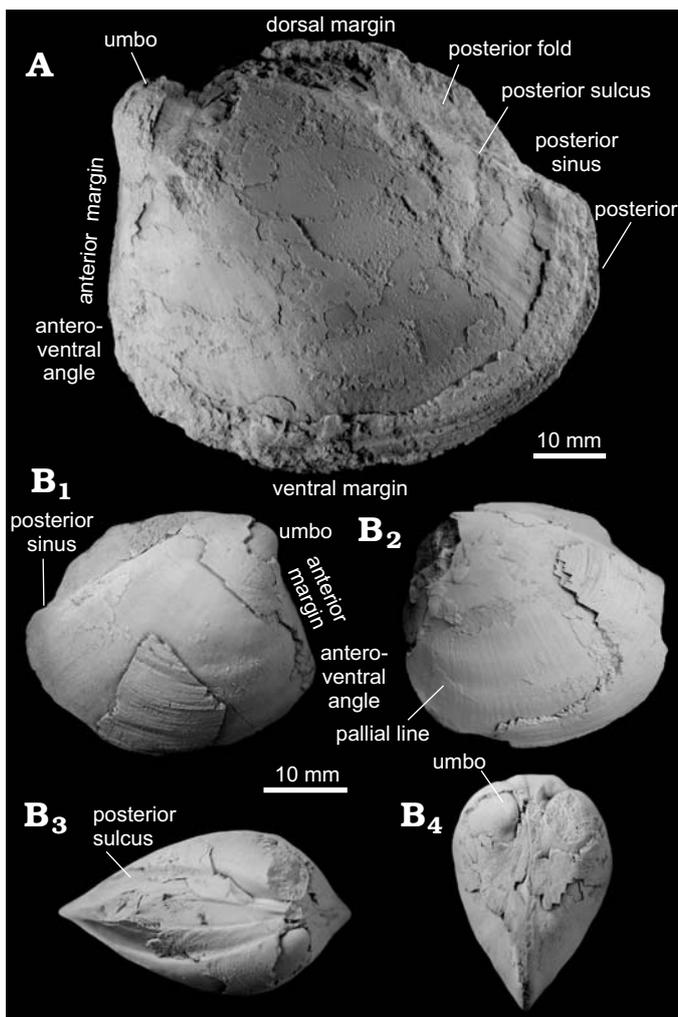
Fig. 5. Thyasirid bivalve *Conchocele conradii* (Rosenkrantz, 1942) from Paleocene strata of the Basilika Formation, Colesbukta, Spitsbergen, Svalbard. **A**. NRM PZ Mo 182204; a medium sized internal mold in left lateral view with no clear outline of an anterior adductor muscle scar visible. **B**. ZPAL L.16/1; an internal mold in right (B₁) and left (B₂) views with fragments of the shell adhering (no clear anterior adductor muscle scar visible); in dorsal view (B₃) showing fragments of a posterior sulcus; anterior fragments of the shell (B₄) showing flat anterior margin without ridges.

1963). He also noticed that the Svalbard specimens are closely related to *C. townsendi* from the Cretaceous of the James Ross Basin, Antarctica, discussed above. A new species name, *Thyasira conradii,* was thereafter proposed for the Svalbard species by Rosenkrantz (1942). Its generic affinity was later revisited by Rosenkrantz (1970) and by Vonderbank (1970), who formally moved it to *Conchocele*.

An allegedly similar species, *Conchocele* aff. *conradii*, was mentioned to occur in the lower Paleocene Kangilia Formation in West Greenland (Rosenkrantz 1970). The illustration provided therein (Rosenkrantz 1970: fig. 7.2) is insufficient for a more detailed comparison; the overall shell outline presented there is somewhat different from that of *C. conradii*, and is more reminiscent of *C. townsendi*. Therefore, until more material is available for study, we do not include the specimens from the Kangilia Formation in

C. conradii. Conchocele conradii differs from *C. townsendi* by its somewhat shorter shell, more rounded ventral margin, broader posterior sulcus, and the lack of two ridges on the anterior margin of the shell. The specific significance of the latter character is unknown, however, as not all specimens of *C. townsendi* have the two ridges mentioned. All other Paleogene species of *Conchocele* that we have investigated have more quadrangular shells than *C. conradii*.

Stratigraphic and geographic range.—Paleocene cold seep carbonates and associated sunken driftwood environments of the Basilika Formation, Colesbukta, Spitsbergen, Svalbard. Possibly also upper Eocene–lower Oligocene strata of the Renardodden Formation, Renardoden, Belsund area, Spitsbergen, Svalbard (Thiedig et al. 1980). A similar species *Conchocele* aff. *conradii* was reported from lower Paleocene Kangilia Formation from West Greenland (Rosenkrantz 1942, 1970).

Conchocele taylori Hickman, 2015

Fig. 6, 7.

1979 *Conchocele* cf. *nipponica* (Yabe and Nomura, 1925); Katto and Masuda 1979: pl. 2: 12a, b, 13a, b.
2003 *Conchocele bisecta* (Conrad, 1849); Goedert et al. 2003: pl. 42: 9.
2007 *Conchocele bisecta* (Conrad, 1849); Amano and Jenkins 2007: fig. 2A, D–F.
2013 *Conchocele bisecta* (Conrad, 1849); Amano et al. 2013: fig. 6E, I.
2015 *Conchocele taylori* sp. nov.; Hickman 2015: 12, fig. 4E–G.
2016 *Conchocele bisecta* (Conrad, 1849); Nobuhara et al. 2016: figs. 2–15.

Type material: Holotype UCMP 110688, paratype UCMP 110689 (Hickman 2015).

Type locality.—Rock Creek seep carbonate (for details, see Hickman 2015: 14).

Type horizon.— Keasey Formation, upper Eocene.

Material.—The material examined comprises at least 13 specimens from Canyon River (uppermost Eocene–lower Oligocene, western Washington State, USA), including two figured specimens (ZPAL L.16/3–4; Fig. 7C, E); nine specimens from Bullman Creek (lower Oligocene, northwestern Washington State, USA), including one figured specimen (ZPAL L.16/5; Fig. 7F); three specimens from Murdock Creek (upper lower Oligocene, northwestern Washington State, USA); and three specimens from Whiskey Creek (upper Eocene, northwestern Washington State, USA), and three specimens from LACMIP loc. 16504 (upper Oligocene, western Washington State, USA). The collection from Japan comprises 66 specimens from Tanami (upper Eocene–early Oligocene, Honshu); 199 specimens from Tappu (upper Eocene, Hokkaido); and 82 specimens from Yayoi (upper Eocene, Hokkaido), all housed in JUE; 14 specimens from Kami-Atsunai (lower Oligocene, Hokkaido) housed at ZPAL, including two figured (ZPAL L.16/2 and ZPAL L.16/6; Fig. 7B, G); and 226 specimens from Kami-Atsunai housed at JUE. The original description of Hickman (2015) was based on small specimens < 25 mm long, in this study we figure and describe specimens up to 69 mm long.
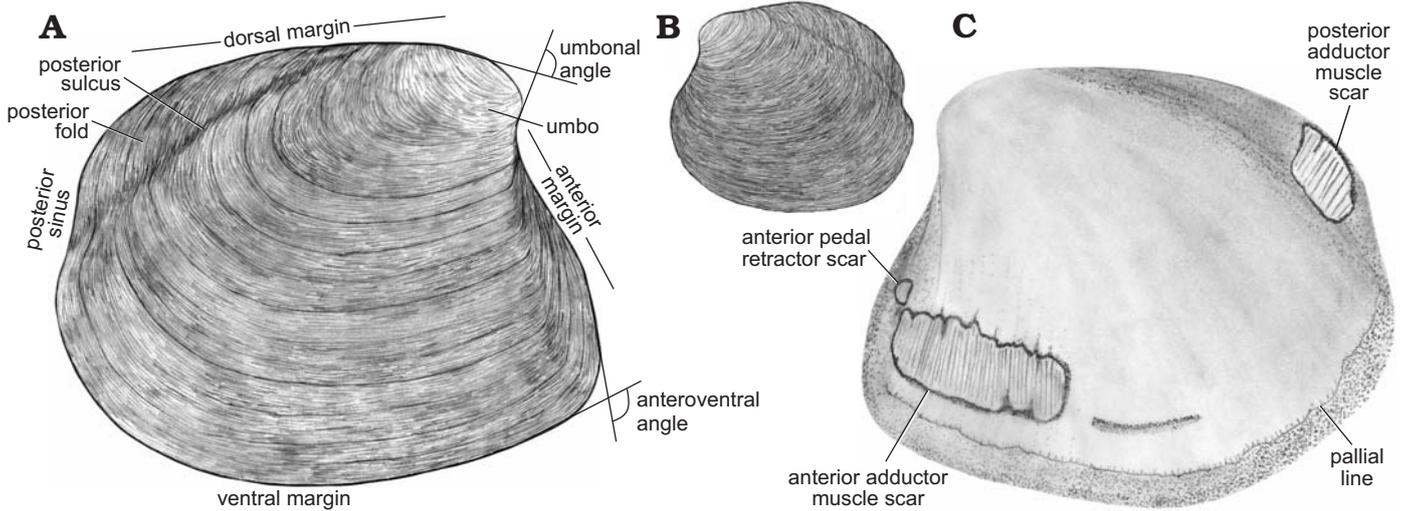
Fig. 6. Schematic illustration of the thyasirid bivalve *Conchocele taylori* Hickman, 2015, highlighting its main morphological features. **A**. Based on JUE 16038, a larger, presumably adult shell, exterior of the right valve. **B**. Based on ZPAL L.16/6, a small, presumably juvenile shell, exterior of the left valve. **C**. Based on ZPAL L.16/6, an internal mold of a larger presumably adult specimen, left valve. Not to scale.

Emended diagnosis.—Shell up to 69 mm long, equivalve. Smaller specimens ovate, larger specimens ovate-triangular; posterior sulcus on smaller specimens weak, progressively stronger on larger specimens; umbones prominent; anterior dorsal margin protruding and concave on specimens smaller than approximately 30 mm; anterior margin of larger specimens with protruding anteroventral angle. Shell surface with numerous, fine prominent growth lines; ligament sunken in deep groove; lunule broad and shallow; dentition unknown.

Description.—Umbo incurved, moderately prominent. Umbonal angle close to 90°. Lunule lanceolate, moderately deep. Anteroventral angle broad and convex, bound by two indistinct ridges. On largest specimens lunule absent, anterior margin weakly convex in dorsalmost part, straight in the remaining part. Ventral margin convex, broadly arcuate, with deepest point posterior to mid-line. Posterior of the shell moderately pointed in specimens, rounded in larger specimens. Posterior shell margin indented by a moderately deep

sinus, posterior sulcus rather shallow and weakly convex. Posterior fold prominent and well visible, some specimens have an additional, weak ridge mid-fold. Dorsal margin arcuate. Ligament sunken, occupying approximately 2/3 of the dorsal margin. Anterior adductor muscle scar relatively well impressed, elongated but shorter than that of other *Conchocele* species, occupying ca. 1/4 of the shell length. Anterior pedal retractor muscle scar small, separated from anterior adductor muscle scar. Posterior adductor muscle scar small, elongated, located inside posterior fold.

Remarks.—*Conchocele taylori* differs from the late Eocene–early Oligocene *C. bathyaulax* Hickman, 2015, from several non-seep localities from the Keasey Formation in Oregon, USA, by its greater umbonal angle, a less prominent umbo, a more prominent posterior fold, and by having a concave anterior margin (Hickman 2015). The Miocene *Conchocele bisecta* (Conrad, 1849) from the Astoria Formation in Oregon differs from *Conchocele taylori* by its more pronounced umbo in smaller specimens, and more quadran-

Fig. 7. Thyasirid bivalve *Conchocele taylori* Hickman, 2015. **A**. JUE 16038 from a upper Eocene seep carbonate of the Poronai Formation, Yayoi Town, →
Hokkaido, Japan; a partially preserved smaller specimen in right (A_1) and left (A_2) lateral views, showing a relatively rounded shell outline; dorsal aspect with relatively weak posterior sulcus (A_3); an anterior view (A_4), showing relatively flat anterior area with weak ridges running towards the anteroventral angle. **B**. ZPAL L16/2 from a lower Oligocene seep carbonate of the Nuibetsu Formation, Kami-Atsunai, Hokkaido, Japan; an internal mold of a smaller specimen in left lateral view, showing the anterior adductor muscle scar, and its more angular outline compared to the specimen illustrated in A. **C**. ZPAL L16/3 from an upper Eocene–lower Oligocene seep carbonate from Canyon River, Lincoln Creek Formation, western Washington State, USA; a medium-sized, well preserved shell in right (C_1) and left (C_2) lateral views, showing external ornament of fine commarginal growth lines and shell outline; dorsal view (C_3) shows shallow posterior sulcus similar to that of JUE 16038; anterior view (C_4) shows lunule. **D**. JUE 16039 from a lower Oligocene seep carbonate from Nuibetsu Formation, Kami-Atsunai, Hokkaido, Japan; a partially preserved shell of a medium-sized individual in right lateral view, showing the well-developed anteroventral angle similar to the specimen shown in C. **E**. ZPAL L.16/4 from an upper Eocene–lower Oligocene seep carbonate from Canyon River, Lincoln Creek Formation, western Washington State, USA; a large specimen in left lateral view, with poorly incurved umbo (the anteroventral angle was covered with matrix during the preparation of this figure). **F**. ZPAL L.16/5 from a lower Oligocene seep carbonate from Makah Formation, Bullman Creek, northwestern Washington State, USA; an internal mold with slightly damaged posterior showing right (F_1) and left (F_2) lateral views and left anterior adductor muscle scar; anterior view (F_3) shows incurved umbones and shallow lunule; dorsal view (F_4) shows shallow posterior sulcus. **G**. ZPAL L.16/6 from a lower Oligocene seep carbonate of the Nuibetsu Formation, Kami-Atsunai, Hokkaido, Japan; a partially preserved internal mold in left lateral view of showing anterior adductor muscle scar; note that the anteroventral angle, the curvature of the umbones, and the shape of the preserved dorsal and ventral margins is very similar to that of F.
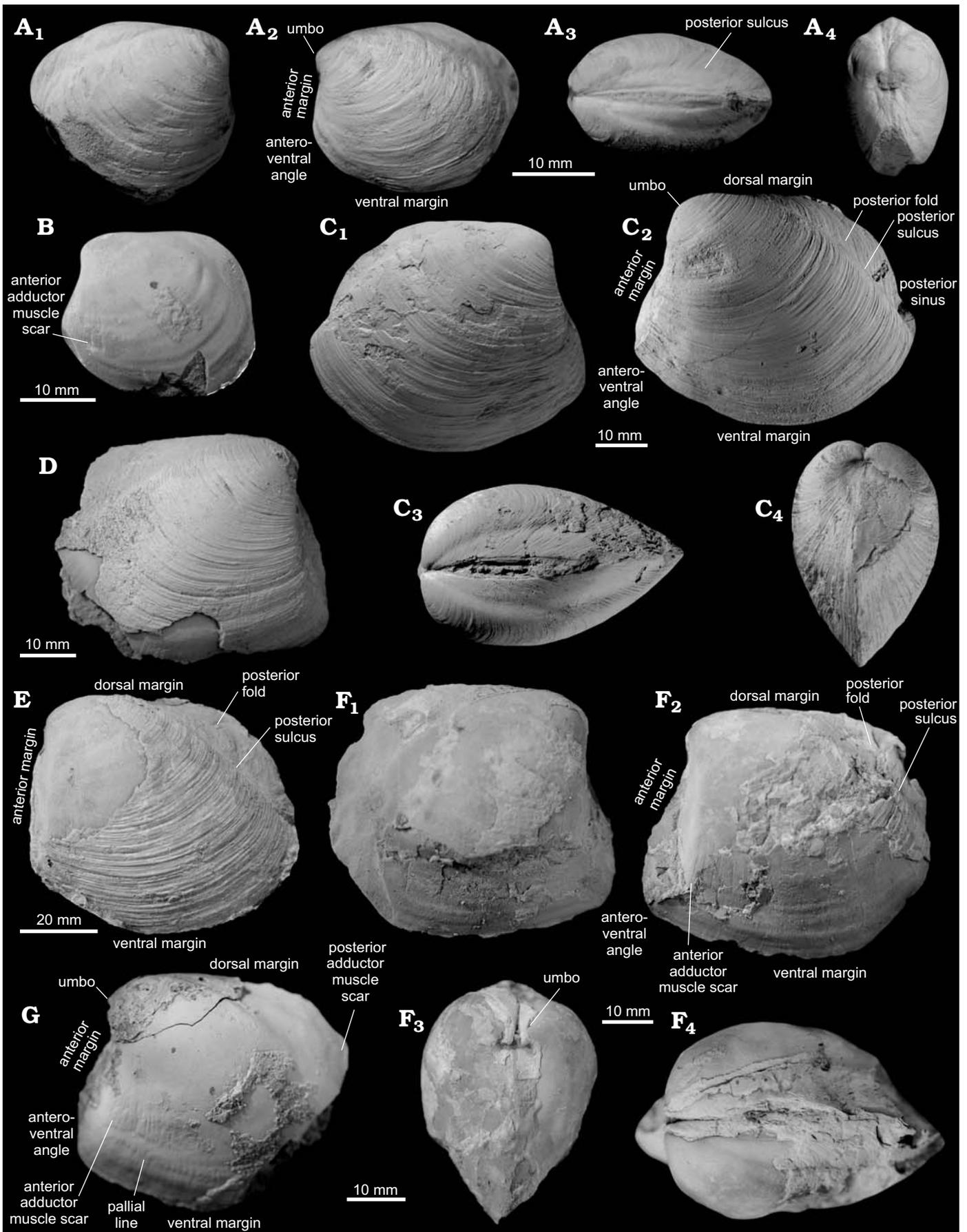
gular shell shape in larger specimens. The anteroventral margin of smaller specimens of *Conchocele taylori* is less pointed than that of *C. bisecta*. The anterior adductor muscle scar of *Conchocele taylori* is shorter than that of *C. bisecta*. *Conchocele townsendi* has much more elongated shell, and deeper posterior sulcus as compared to *C. taylori*.

Stratigraphic and geographic range.—Late Eocene–Oligocene, North Pacific margin from Oregon to southern Honshu.

Conchocele kiritachiensis sp. nov.

Figs. 8, 9.

Etymology: Named for the type locality (Kiritachi).

Type material: Holotype: JUE 16036; an articulated and undeformed specimen with most of the shell preserved. Other figured specimens designated as paratypes (JUE 16037-1 to 16037-7), all from the type locality.

Type locality: A hydrocarbon seep deposit at Kiritachi, Tomamae Town, Hokkaido, Japan.

Type horizon: Sakasagawa Formation, upper Eocene.

Material.—Type material and 10 unnumbered specimens from the type locality, all stored in JUE paleontological collections.

Dimensions.—The holotype is 45.5 mm long and 41.1 mm high.

Diagnosis.—Medium-size species of *Conchocele* with umbones displaced strongly towards anterior, straight anterior shell margin, pointed beaks and obtuse anteroventral angle. Posterior sinus deep and obtuse. Posterior fold broad but short.

Description.—Shell medium-sized, up to 62.1 mm long, equivalve, moderately inflated, rhomboidal in outline. External ornament composed of densely spaced, low commarginal growth lines. Umbones terminal, umbonal angle around 95°, beaks prosogyrous, not incurved, anteroventral angle around 120°. Lunule absent, but anterior area demarcated with crude ridge running from umbo toward anteroventral angle. Ventral margin nearly straight close to anteroventral angle, well rounded in median and posterior part, with deepest curvature located posterior to mid-line. Posterior angle around 95°, posterior sinus deep, forming an obtuse angle. Posterior sulcus dorsally convex, sharp. Posterior dorsal margin rounded. Anterior adductor muscle scar well-impressed, striated, elongate ovate. Posterior adductor muscle scar rather small, weakly impressed, visible in both side of posterior sulcus. Ligament sunken but hinge structure unknown.

Remarks.—This species belongs to a group of *Conchocele* species with rhomboidal shells with pointed beaks and straight anterior shell margin. A similar and coeval species from Eastern Pacific is *Conchocele bathyaulax* Hickman, 2015 from non-seep deposits of the upper Eocene–lower Oligocene Keasey Formation, Oregon, which has narrower and longer posterior fold than *C. kiritachiensis*. *Conchocele* cf. *bathyaulax* from upper Eocene–Oligocene seeps in Washington State is also similar to *C. kiritachiensis*, but differs by having a more inflated and shorter shell and an overall larger size.
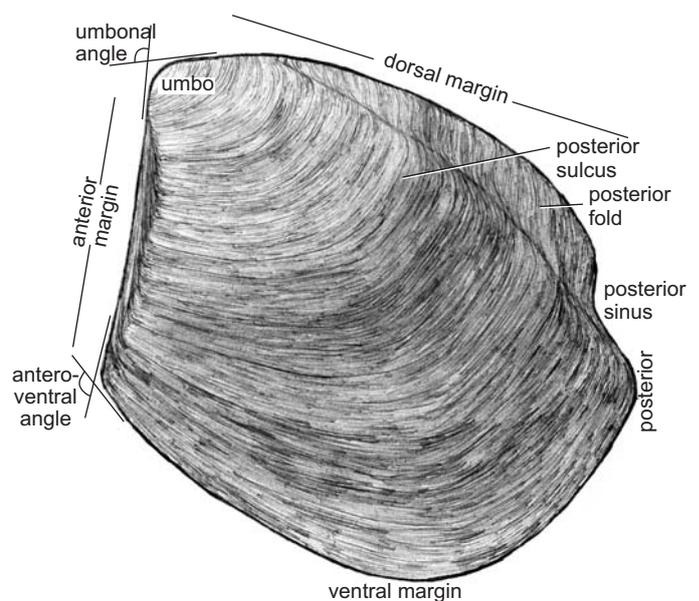
Fig. 8. Schematic illustration of the external shell of the thyasirid bivalve *Conchocele kiritachiensis* sp. nov. highlighting its main morphological features.

There are several similar species known in the Cenozoic of the Northwestern Pacific. Yabe and Nomura (1925: pl. 23: 8, 10a) figured "*Thyasira*" *bisecta* from the Neogene of Sakhalin. Similar specimens from the upper Pliocene of south-western Sakhalin were later figured and designated by Kristofovich (1936: 29, pl. 1: 3, 4) as "*Thyasira*" *bisecta* var. *alta*. In the following work, Kristofovich (1964: 213, pl. 53: 5) mentions "*Thyasira*" *disjuncta* var. *alta* to occur in the upper Miocene of Sakhalin, Kamchatka and Pliocene of Sado Island. The age of the Sakhalin occurrence was later found by Khudik (1989) to be Miocene–Pliocene. This species is more elongated, has a smaller apical angle, and narrower posterior fold than *C. kiritachiensis*, but is otherwise similar and belongs to the same species group. Some specimens described by Kristofovich (1936) as new species "*Thyasira*" *pervulgata* (Kristofovich 1936: 45, pl. 6: 4, 6) from the Eocene? and "*Thyasira*" *wajampolkana* (Kristofovich 1936: 44, pl. 6: 3, 3a) from the Miocene of western Kamchatka could also belong to the same species group as *Conchocele kiritachiensis*. However, both species are not sufficiently well described and figured to allow a more detailed comparison.

Stratigraphic and geographic range.—Type locality and horizon only.

Conchocele cf. *bathyaulax* Hickman, 2015

Fig. 10.

Material.—Six specimens from Canyon River (upper Eocene–lower Oligocene, western Washington State, USA), including one figured (ZPAL L.16/8; Fig. 10B); and three specimens from East Twin River (upper Oligocene, northwestern Washington State, USA), including two figured (ZPAL L.16/7, 9; Fig. 10A, C).
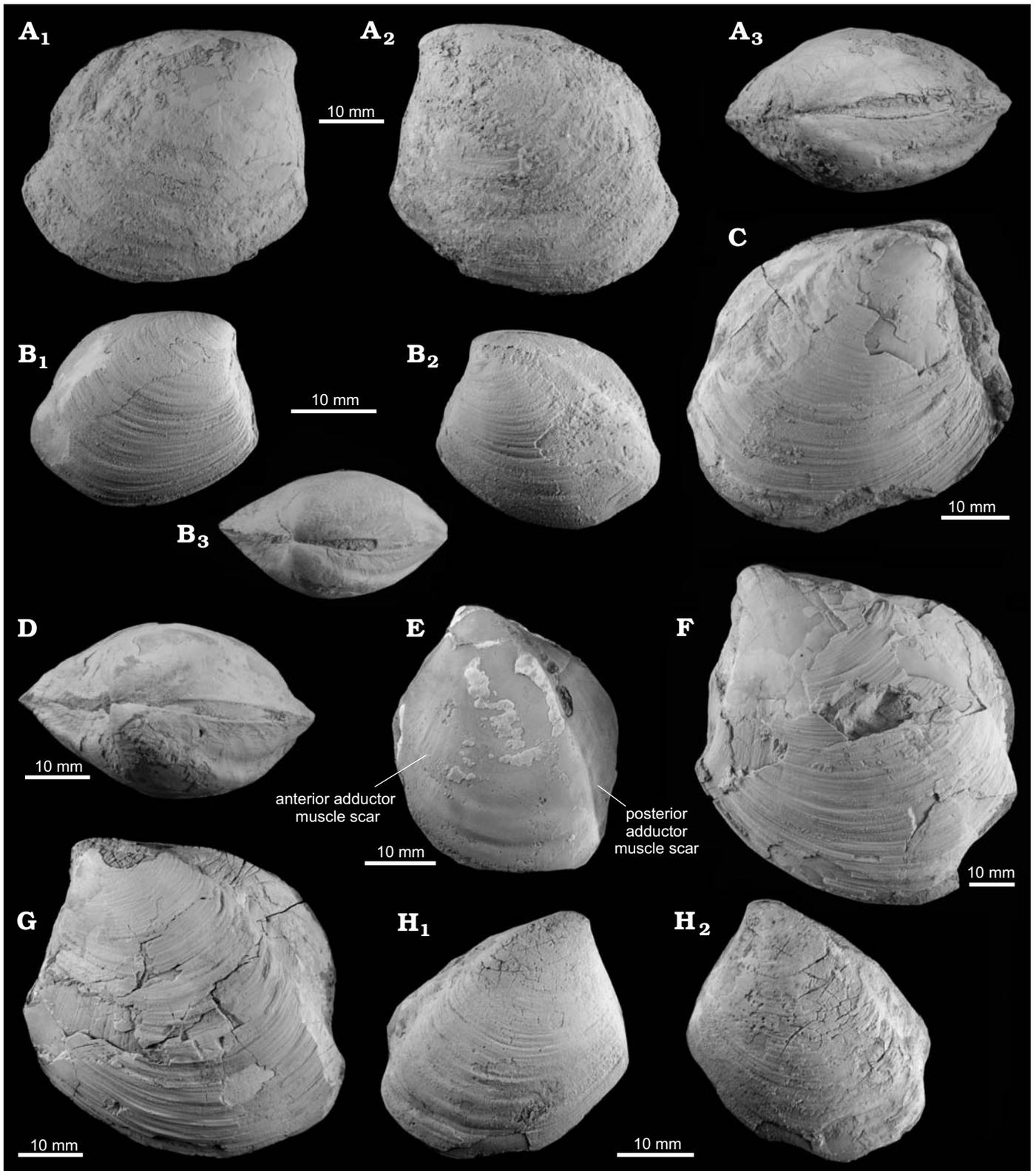
Fig. 9. Thyasirid bivalve *Conchocele kiritachiensis* sp. nov. from an upper Eocene seep carbonate of the Sakasagawa Formation, Kiritachi, Hokkaido, Japan. **A**. JUE 16036, holotype in right (A₁) and left lateral (A₂) views; dorsal view (A₃) showing anterior flat area demarcated by rude ridge and a posterior fold. **B**. JUE 16037-3, paratype, young shell in right (B₁) and left (B₂) lateral and dorsal (B₃) views. **C**. JUE 16037-2, paratype in right lateral view. **D**. JUE 16037-4, paratype in dorsal view, showing distinct anterior flat area demarcated by rude ridge and a distinct posterior sulcus. **E**. JUE 16037-7, inner side of paratype in left lateral view, showing both anterior and posterior adductor muscle scar. **F**. JUE 16037-6, paratype in left lateral view, the largest specimen of this species, having a pointed umbo and a wide posterior fold. **G**. JUE 16037-1, paratype, large specimen in left lateral view, showing a pointed umbo and a wide posterior fold. **H**. JUE 16037-5, paratype in right (H₁) and left (H₂) lateral views, showing narrow apical angle, instead posterior fold partly broken.
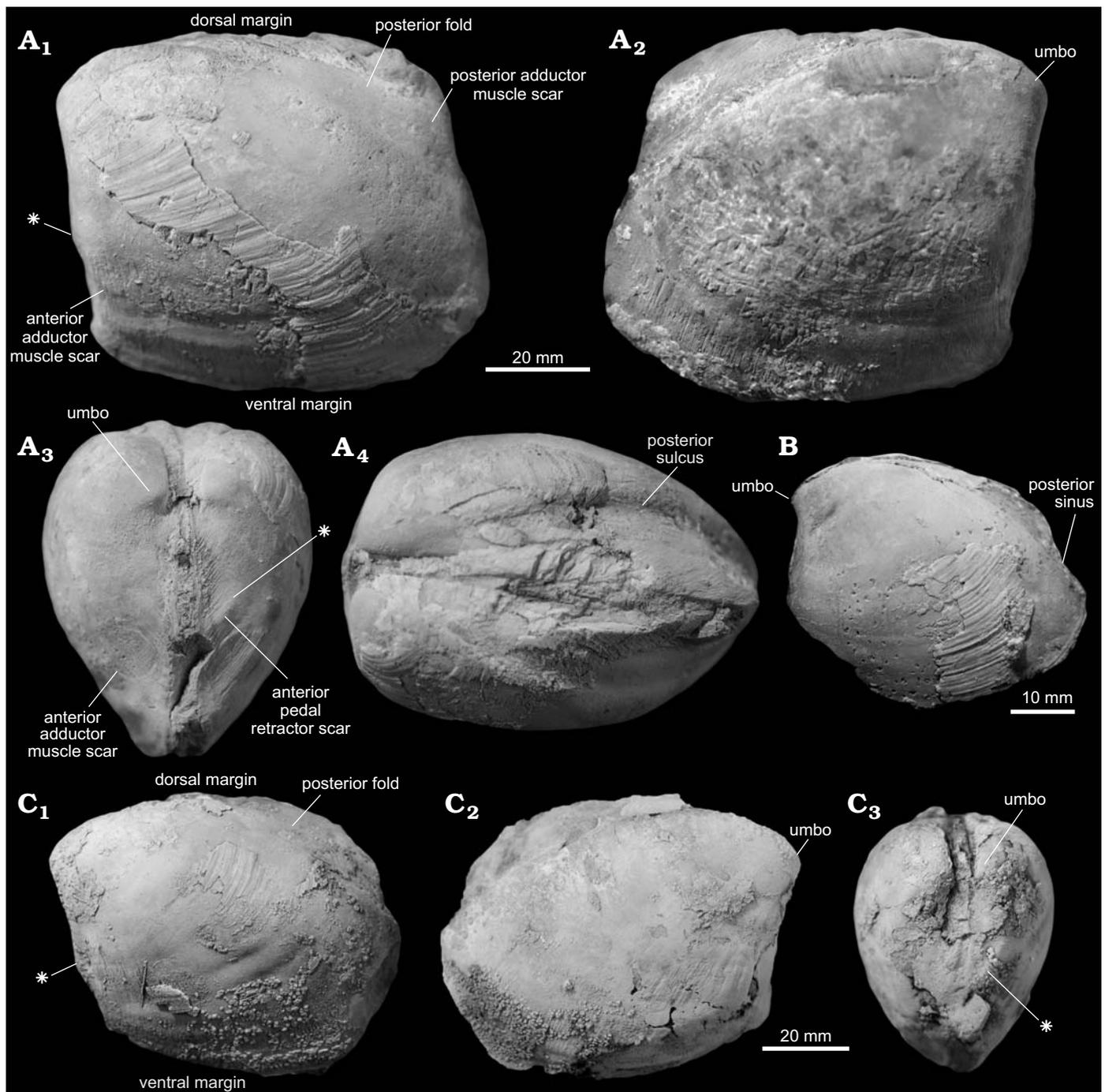
Fig. 10. Thyasirid bivalve *Conchocele* cf. *bathyaulax* Hickman, 2015. **A**. ZPAL L.16/7 from an upper Oligocene seep carbonate of the Pysht Formation, East Twin River, northwestern Washington State, USA; an articulated specimen in left (A_1) and right (A_2) views, showing characteristic rhomboidal shape with roughly parallel, convex dorsal and ventral margins, and roughly parallel anterior and posterior margins, asterisk shows a lateral aspect of a secondary ridge (A_1); anterior view (A_3), showing anterior pedal and adductor muscle scars, weakly incurved umbones and inflated shells, asterisk shows a frontal aspect of a secondary ridge shown in A_1; dorsal view (A_4), shows moderately deep posterior sulcus. **B**. ZPAL L.16/8 from an upper Eocene–lower Oligocene of the Canyon River, Lincoln Creek Formation, western Washington State, USA; a medium-sized specimen in left lateral view, showing incurved umbo. **C**. ZPAL L.16/9 from an upper Oligocene of the Pysht Formation, East Twin River, northwestern Washington State, USA; a large specimen in left (C_1) and right (C_2) lateral views with umbo more protruding than ZPAL L.16/7, 8 (A, B), asterisk shows a lateral aspect of a secondary ridge shown in C_3; anterior view (C_3) showing weak secondary ridge running from umbo towards the anteroventral angle (asterisked).

Description.—Shell large, up to 80 mm long, thin, equivalve, inflated, subquadrate to rhomboidal. External ornament composed of densely spaced, commarginal growth lines. Umbones terminal and prosogyrous, not incurved. Lunule absent, anterior of shell flattened with a weak anterior ridge running from the umbo towards anteroventral shell angle. Anterior margin straight, anteroventral angle obtuse. Ventral margin rounded, with deepest point located

posterior to mid-line. Posterior shell extremity weakly pointed. Posterior sulcus straight to weakly dorsally convex. Posterior fold high, with weak ridge running amidst. Inner shell surface covered with thin radial striae. Anterior adductor muscle scar well impressed, elongated, striated, covering ca. 1/3 of shell length, separated from pallial line. Anterior pedal retractor muscle scar medium-sized, striated. Posterior adductor muscle scar weaker than anterior one, striated, restricted to posterior fold. Ligament unknown.

Remarks.—*Conchocele bathyaulax* and *Conchocele* cf. *bathyaulax* share a characteristic inflated shell with projecting umbo and straight anterior margin. They differ by the width of the posterior fold, which is narrower in *C. bathyaulax* compared to *C.* cf. *bathyaulax*, and *C. bathyaulax* is shorter than *C.* cf. *bathyaulax*. Due to the large intraspecific morphological variability exhibited by many thyasirids (e.g., Oliver and Killeen 2002; Oliver and Sellanes 2005; Rodrigues et al. 2008), we prefer to leave *C.* cf. *bathyaulax* species in open nomenclature and compare it to *C. bathyaulax* until material warranting a more coherent systematic statement is available. Another similar fossil species is *Conchocele kiritachiensis* sp. nov., which is less inflated than *C.* cf. *bathyaulax* and has a longer shell with more deeply incised posterior sulcus (cf. Fig. 9). All previously mentioned species are similar to the extant *C. scarlatoi* Ivanova and Moskaletz, 1984, from shallow waters of the Sea of Japan (Kharlamenko et al. 2016), with which they share shells with projecting umbones and straight anterior margin lacking a lunular incision. *Concocele taylori* from uppermost Eocene–Oligocene seep carbonates of paleo-Northern Pacific margin has more rounded shell, with more dorsally convex posterior fold and protruding anteroventral angle (cf. Fig. 7). The Miocene *C. bisecta* has a more rounded shell with a concave anterior margin, a lunular incision, and a rectangular anteroventral margin (Moore 1963).

Genus *Maorithyas* Fleming, 1950

Type species: *Maorithyas marama* Fleming, 1950; Recent, Fiordland, New Zealand.

Species included: *Maorithyas humptulipsensis* sp. nov. from middle Eocene seep carbonates at LACMIP loc. 12385 and CSUN loc. 1583, Humptulips Formation, Humptulips River, Washington State, *Maorithyas folgeri* (Wagner and Schilling, 1923), from the San Emigdio (Oligocene) and Wagonwheel (Eocene) formations, Kern County, Southern California, USA; *Maorithyas marama* Fleming, 1950, Recent, southern New Zealand and *Maorithyas flemingi* Powell, 1955, Recent, southern New Zealand. Possibly also *Maorithyas*? sp. from the late Eocene Bear River seep deposit in western Washington State, USA.

Maorithyas humptulipsensis sp. nov.

Figs. 11, 12.

Fig. 11. Schematic illustration of the thyasirid bivalve *Maorithyas humptulipsensis* sp. nov., highlighting its main morphological features. **A**. Outer surface of the right valve in lateral view. **B**. Internal surface of the right valve in lateral view. **C**. Outer surface of the right valve in dorsal view and internal mold of the left valve view. **D**. Outer surface of the right valve in anterior view and internal mold of the left valve view.
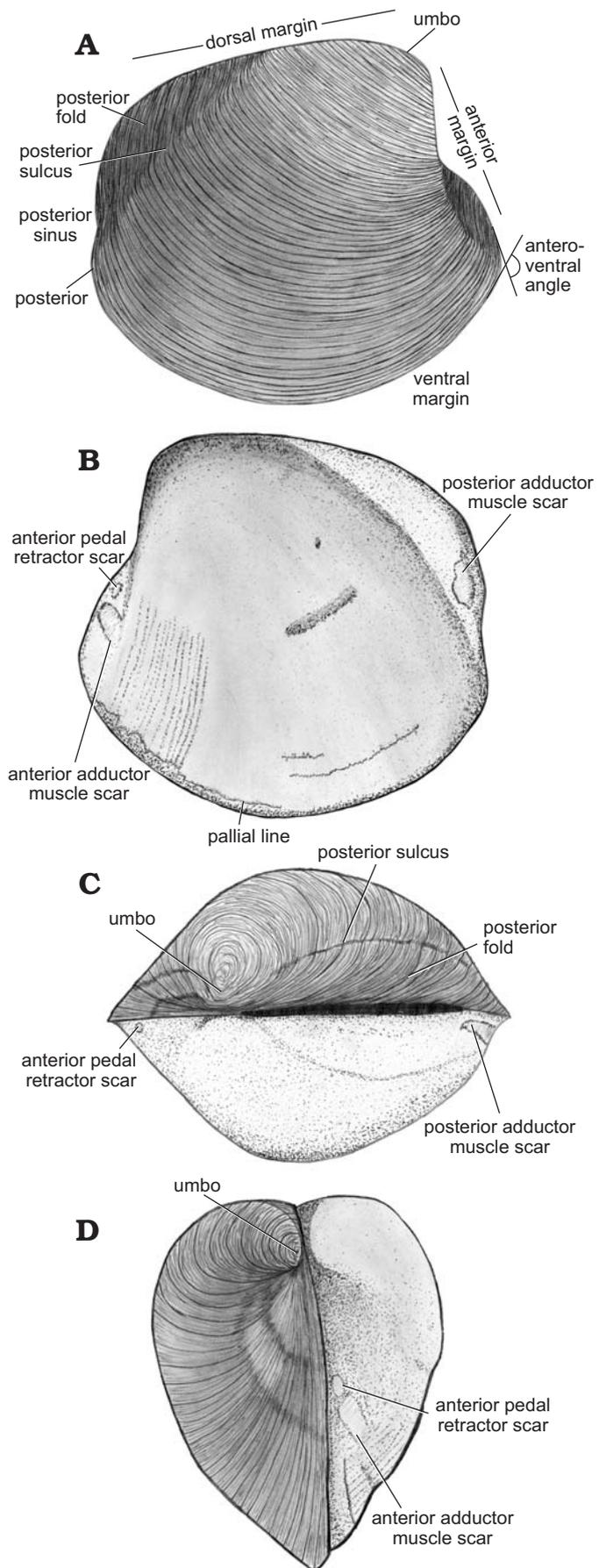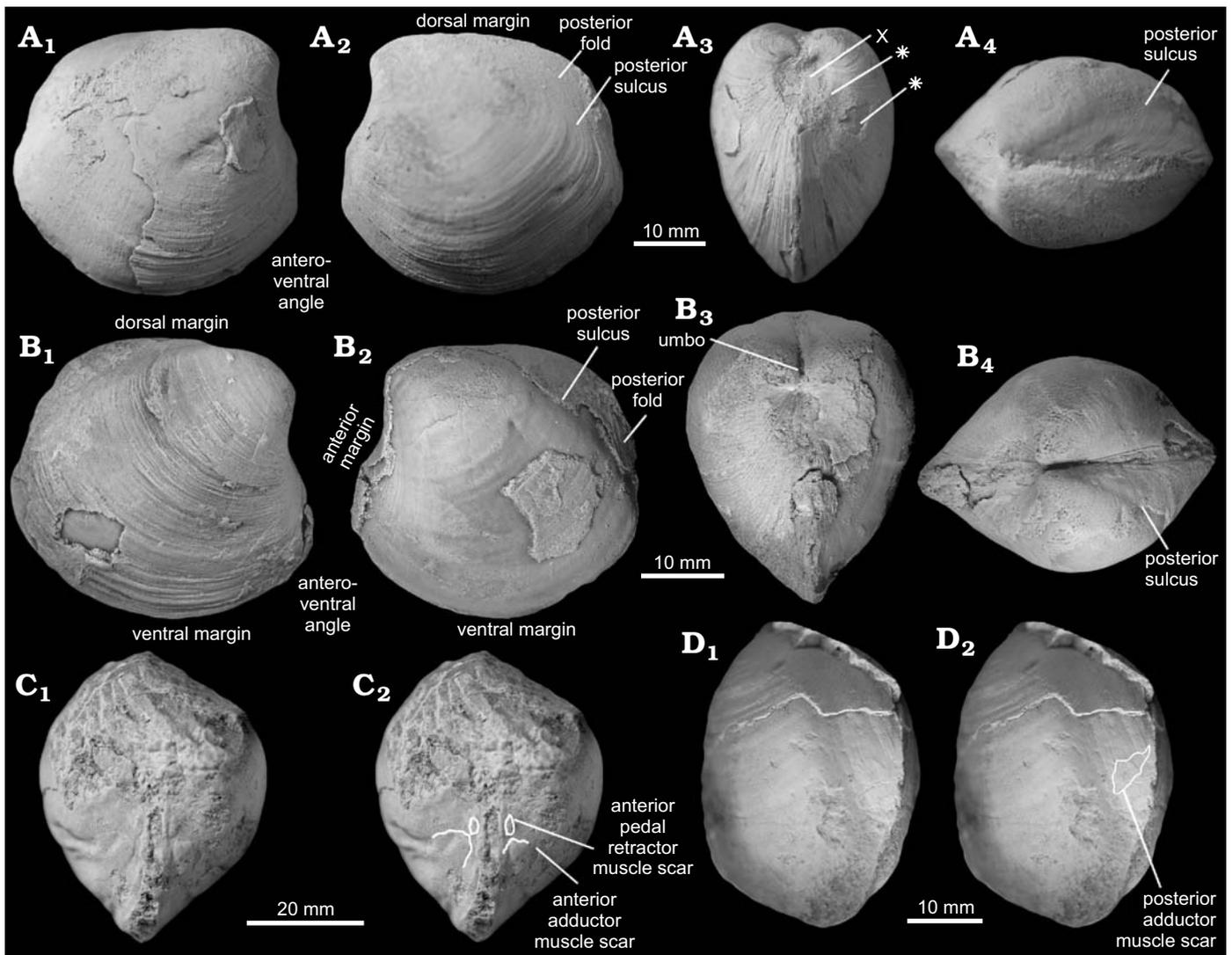
Fig. 12. Thyasirid bivalve *Maorithyas humptulipsensis* sp. nov. from a middle Eocene seep carbonate of the Humptulips Formation, LACMIP loc. 12385, Washington State, USA. **A**. ZPAL L.16/10, holotype in right (A$_1$) and left (A$_2$) lateral views; anterior view (A$_3$), showing two ridges running from umbo towards the anterioventral angle (asterisks), bounding weak lunule (×). **B**. NRM Mo 182388, a partially preserved specimen in right (B$_1$) and left (B$_2$) lateral views; the shape similar to that of the specimen shown in A, although the dorsal margin is more convex; the anterior view (B$_3$) shows inflated shell with incurved umbo; dorsal view (B$_4$) shows weak posterior sulcus. **C**. ZPAL L.16/11, a partially preserved internal mold in anterior view (C$_1$); the interpretative drawing (C$_2$) shows the position of anterior adductor and anterior pedal retractor muscle scars. **D**. ZPAL L.16/12, specimen in oblique posterior view (D$_1$), the interpretative drawing (D$_2$) shows the posterior adductor muscle scar.

1990 *Thyasira* (*Conchocele*) *folgeri* Wagner and Schilling, 1923; Goedert and Squires 1990: fig 2a.

Etymology: Named after the Humptulips River.

Type material: Holotype: ZPAL L.16/10 (Fig. 12A); an articulated specimen with most of the shell preserved. Other figured (Fig. 12B–D) specimens designated as paratypes (NRM Mo 182388, ZPAL L.16/11, ZPAL L.16/12), all from the type locality.

Type locality: LACMIP loc. 12385, Humptulips River, Washington State, USA.

Type horizon: Seep carbonates of the Humptulips Formation, middle Eocene.

Material.—From the type locality: type material and 5 unnumbered specimens housed at ZPAL, 32 housed at NRM from CSUN loc. 1583 (middle Eocene, Humptulips River, western Washington State, USA): 10 unnumbered specimens, the largest of which reaches 45 mm in length, housed at NRM.

Dimensions.—The holotype is 35 mm long and 35 mm high.

Diagnosis.—Bulbous species of *Maorithyas* with pointed anteroventral angle and weak posterior fold not extending beyond outline of shell.

Description.—Shell up to 62 mm long, thin, equivalve, very inflated, subrounded to pentagonal. External ornament composed of very fine, commarginal growth lines. Umbones subcentral, anterior of midline of the shell, prosogyrous, strongly incurved. Lunule present, heart-shaped, shallow. Anterior margin straight and short, bound by two indistinct ridges running from umbo, anteroventral angle obtuse. Ventral margin rounded, with deepest point around

mid-line. Posterior margin straight with very weak sinus. Posterior fold not projecting beyond posterior margin of the shell, posterior sulcus shallow and broad, with weak secondary sulcus sometimes visible amidst fold. Posterodorsal margin weakly concave. Escutcheon absent. Ligament narrow, sunken. Interior of shell covered with thinly spaced, radial striae, more common in anterior. Anterior adductor muscle scar weak and small, visible only in its anterior part. Anterior pedal retractor muscle scar shallow, small and oval. Posterior adductor muscle scar small and weak, restricted to posterior fold.

Remarks.—*Maorithyas humptulipsensis* differs from the Recent *Maorithyas marama* Fleming, 1950, and *Maorithyas flemingi* Powell, 1955, by its more rhomboidal shell, more anteriorly situated umbo and less pronounced posterior fold, which does not extend beyond the posterior margin of the shell (cf. Fleming 1950: pl. 25: 2; Powell 1955: pl. 1: 1). However, the degree of extension of the posterior fold seems to have some range of variation in the type species. For example, three specimens identified as *M. marama*, collected at Stewart Island and stored at the Museum of New Zealand Te Papa Tongarewa (M 26537) show a narrower posterior fold than the type. The Recent "*Maorithyas*" *hadalis* from the Japan Trench figured by Fujikura et al. (1999: fig. 3) and Okutani et al. (1999) differs in characters of the hinge plate, nymph and anterior adductor muscle scar from *Maorithyas humptulipsensis*, and may not even belong to *Maorithyas* (Valentich-Scott et al. 2014: 17).

Maorithyas is a poorly known genus, comprising only two named and one unnamed extant species (Fleming 1950; Powell 1955; Spencer 2009: 199). In addition to a single fossil species *M. humptulipsensis*, it is possible that "*Thyasira*" *folgeri* Wagner and Schilling, 1923, from upper Eocene seep carbonates in the Wagonwheel Mountains in central California (Squires and Gring 1996; Kiel and Peckmann 2007) belongs to *Maorithyas*. The holotype of "*Thyasira*" *folgeri* (UCMP 11434, UCMP loc. 3195; Oligocene, San Emigdio Formation, Devil's Kitchen, Kern County, southern California, USA; Moore 1988: pl. 7: 9; Fig. 13) is simi-
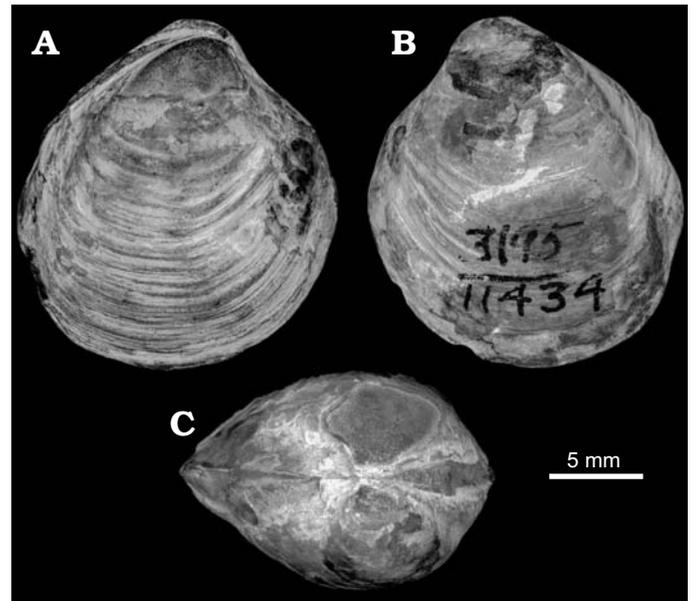
Fig. 13. Thyasirid bivalve *Maorithyas folgeri* (Wagner and Schilling, 1923) from Oligocene strata of the San Emigdio Formation, Devil's Kitchen, California, USA. UCMP 11434, holotype in right (**A**), left (**B**) lateral, and dorsal (**C**) views.

larly rounded and inflated as *M. humptulipsensis*, and also has a very weak to no distinct posterior sinus. It has, however, a less pronounced posterior fold different from that of *M. humptulipsensis*, and a less pronounced anteroventral angle. *Thyasira folgeri* from the Wagonwheel Mountain seep (Squires and Gring 1996: fig. 4.8) is very similar to the holotype in general outline and the lack of a posterior sinus, and is also unlikely to belong to *Conchocele* as classified by Squires and Gring (1996). In our opinion, "*Thyasira*" *folgeri* from both mentioned localities in Kern County should be considered a species of *Maorithyas*, thus being *Maorithyas folgeri* (Wagner and Schilling, 1923). The holotype of *T. folgeri* was found together with lucinids in "limy concretions in the black shale member" (Wagner and Schilling 1923: 243) and might hence also be from a seep deposit.
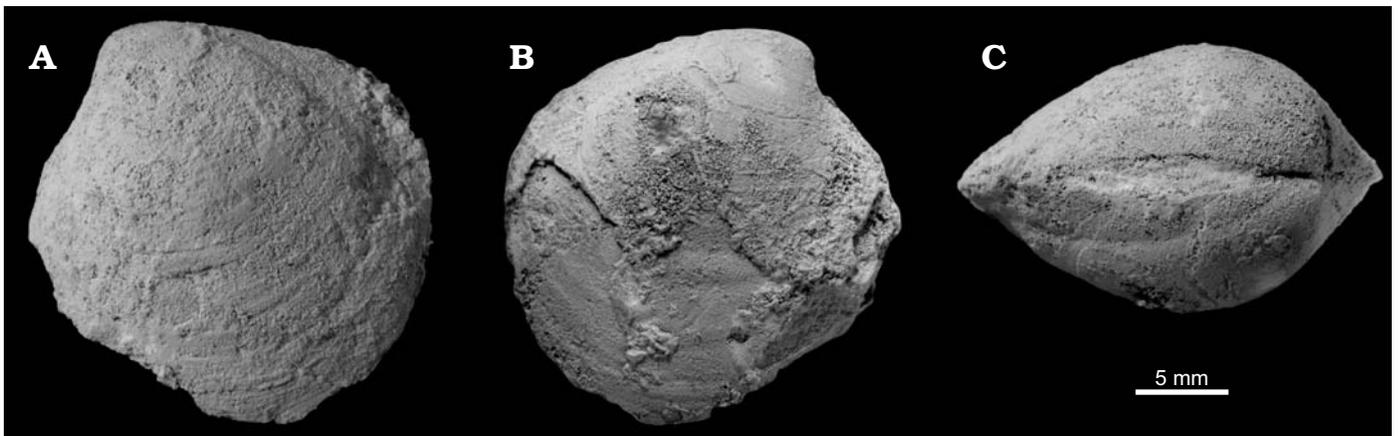
Fig. 14. Thyasirid bivalve *Maorithyas*? sp. from upper Eocene cold seep carbonates in the "Siltstone of Cliff Point", Bear River, western Washington State, USA. ZPAL L.16/13, a poorly preserved specimen in left (**A**), right (**B**) lateral, and dorsal (**C**) views.
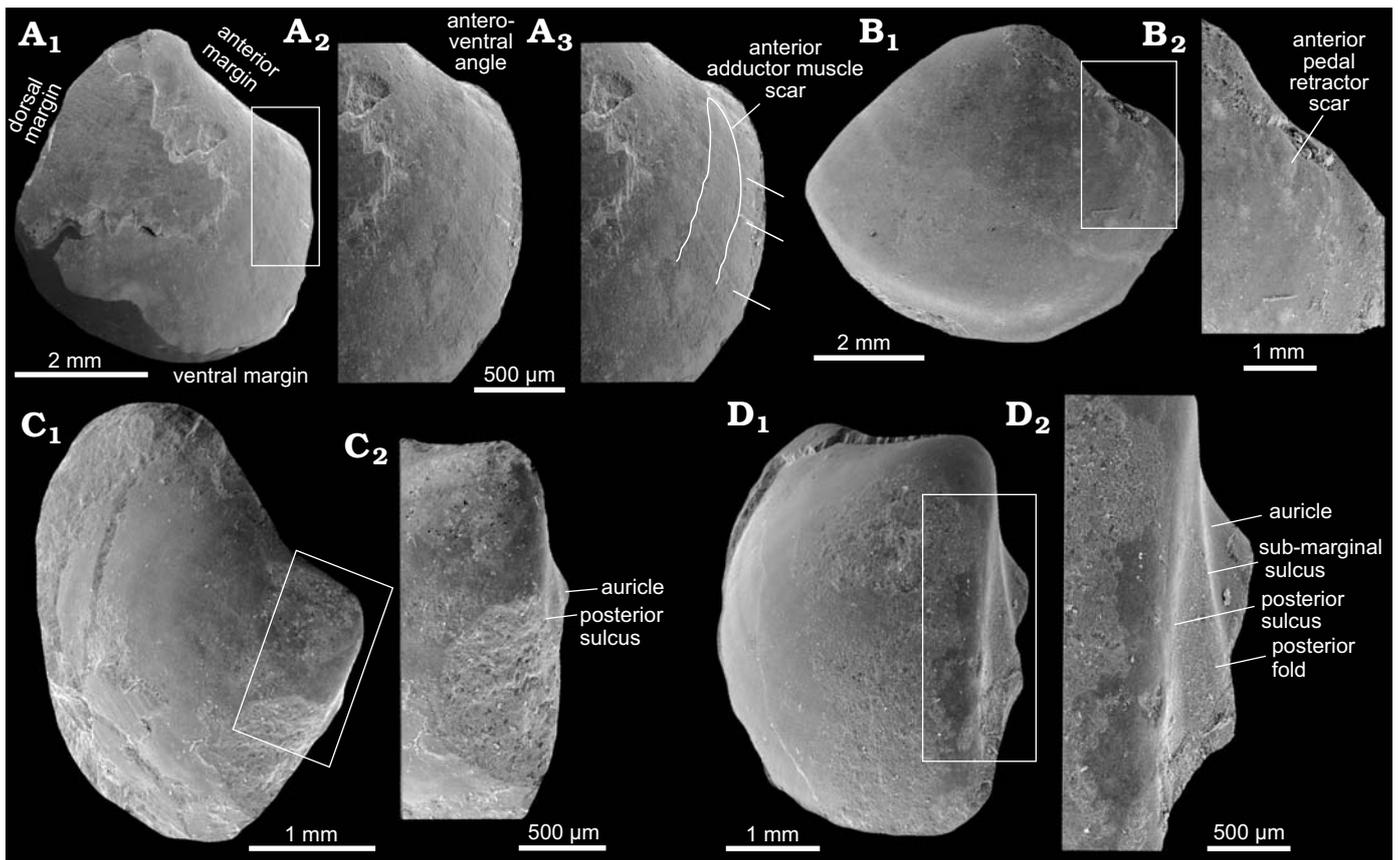
Fig. 15. Thyasirid bivalve *Thyasira tanabei* Kiel, Amano, and Jenkins, 2008, from Santonian seep carbonates from the Himenoura Group, Maeshima, Goshoura Island, Kumamoto Prefecture, southern Kyushu, Japan. **A**. ZPAL L.16/14, a partial internal mold in oblique right lateral view (A_1); detail with indicated radial striae and anterior adductor muscle scar (A_2, A_3). **B**. ZPAL L.16/15, a partial internal mold in oblique right lateral view (B_1); probably anterior pedal retractor muscle scar (B_2). **C**. ZPAL L.16/16, a specimen in oblique dorsal view (C_1); a very weak posterior sulcus and posterior fold, with minute auricle visible (C_2). **D**. ZPAL L.16/17, a specimen in oblique posterodorsal view (D_1); posterodorsal shell margin with posterior sulcus, posterior fold, submarginal sulcus and auricles indicated (D_2).

Stratigraphic and geographic range.—Middle Eocene seep deposits (LACMIP loc. 12385 and CSUN loc. 1583) from the Humptulips Formation, Washington State, USA.

Maorithyas? sp.

Fig. 14.

Material.—One specimen (ZPAL L.16/13) from the upper Eocene Bear River site from the "Siltstone of Cliff Point" in western Washington State, USA.

Remarks.—The specimen from the Bear River site is incomplete and weathered, therefore its systematic assignment is only tentative. Its inflated shell and very shallow posterior sulcus somewhat resembles that of *Maorithyas humptulipsensis* from the middle Eocene Humptulips River site in Washington State. However, the Bear River specimen is 21 mm long and shorter than the majority of the specimens of *Maorithyas humptulipsensis* available for comparison. Also, it has a somewhat less pronounced posterior fold than *M. humptulipsensis*, and a less pronounced umbo, suggesting that the Bear River specimen does not belong to *M. humptulipsensis*. Any further discussion of the Bear River species

has to be postponed until more material from this locality is available.

Genus *Thyasira* Lamarck, 1818

Type species: *Thyasira flexuosa* (Montagu, 1803); Recent, Falmouth Harbour, Cornwall, UK.

Thyasira tanabei Kiel, Amano, and Jenkins, 2008

Fig. 15.

1993 *Conchocele*? sp.; Kanie et al. 1993: fig. 2.
2008 *Thyasira tanabei* sp. nov.; Kiel et al. 2008: 530, fig. 5A–G, fig. 6A.
?2009 Thyasirid bivalve; Kiel et al. 2009: fig. 3L, M.
2017 *Thyasira tanabei* Kiel, Amano, and Jenkins, 2008; Jenkins et al. 2017: fig. 3H, I.

Type material: Holotype (UMUT MM 29533) and paratypes (UMUT MM 29534–29537, 29539) (Kiel et al. 2008).

Type locality: Yasukawa seep site in Nakagawa Town, Hokkaido.

Type horizon: Omagari Formation, Yezo Group, lower Campanian, Upper Cretaceous.

Material.—Three illustrated specimens (ZPAL L.16/14–17; Fig. 15) and 3 unnumbered from Santonian cold seep carbonates from Maeshima, Kyushu, Japan.

Remarks.—The specimens from Santonian cold seep carbonates of Himenoura Group, Maeshima, Kyushu, are similar in their general appearance to *Thyasira tanabei* specimens from Cretaceous cold seep, sunken leatherback turtle carcass and possibly sunken wood associations from Yezo Group, Hokkaido, previously described and figured by Kiel et al. (2008, 2009) and Jenkins et al. (2017). The specimens from Maeshima (max. 5 mm in length) are smaller than their conspecifics from cold seeps of Hokkaido, which approach 12 mm in length (Kiel et al. 2008: table 2), and are also less inflated and have more pronounced posterior folds. In shape, the Maeshima specimens resemble an undescribed thyasirid species from the Akita River wood fall in Hokkaido, which are in the size range of the Maeshima specimens (4 mm in length; Kiel et al. 2009: 78, fig. 3L, M) and are also only slightly inflated. However, due to poor preservation of the material from the Akita River wood fall, a more detailed comparison between the specimens of the two sites is currently not possible.

Stratigraphic and geographic range.—Cretaceous of Japan; known from Albian–Campanian cold seeps of Hokkaido (the Ponbetsu, Kanajirisawa, and Yasukawa sites; Kiel et al. 2008), Santonian cold seeps of Maeshima, Kyushu, Campanian turtle fall from Nio Creek, Hokkaido, and questionably the Coniacian Akita River wood-fall on Hokkaido (Kiel et al. 2009).

Thyasira becca Kauffman, 1967

Fig. 16.

1967 *Thyasira becca becca* subsp. nov.; Kauffman 1967: 126, pl. 4:1–21, pl. 5: 28, 33, 37, 38.
1967 *Thyasira becca cobbani* subsp. nov.; Kauffman 1967: 132, pl. 1: 28, pl. 5: 34–36.

Type material: Holotype: USNM 153512; paratypes listed by Kauffman (1967).

Type locality: USGS Mesozoic locality D1410, Fall River County, South Dakota.

Type horizon: Middle *Baculites scotti* Zone, Pierre Shale, upper Campanian, Upper Cretaceous.

Material.—Three illustrated specimens (ZPAL L.16/18–20; Fig. 16) from Campanian seep carbonate at Warbonnet Battlefield Monument, Montrose, Nebraska.

Remarks.—The specimens from Montrose fit the description of *Thyasira becca* from the Campanian of the Western Interior Seaway (Kauffman 1967). *Thyasira becca* was initially subdivided into two subspecies: the rounded *T. becca becca*, and the subrectangular *T. becca cobbani* (Kauffman 1967: 126); however we hesitate to include our specimens in any of those subspecies due to the small number of available specimens. *Thyasira becca* is significantly larger and more rounded than *T. tanabei* from the Albian–Campanian cold seeps and sunken wood from Japan (Kiel et al. 2008). *Thyasira xylodia* from Eocene–Miocene whale and wood falls in Washington State is, at a length of approximately 10 mm, more triangular and higher than the Montrose speci-
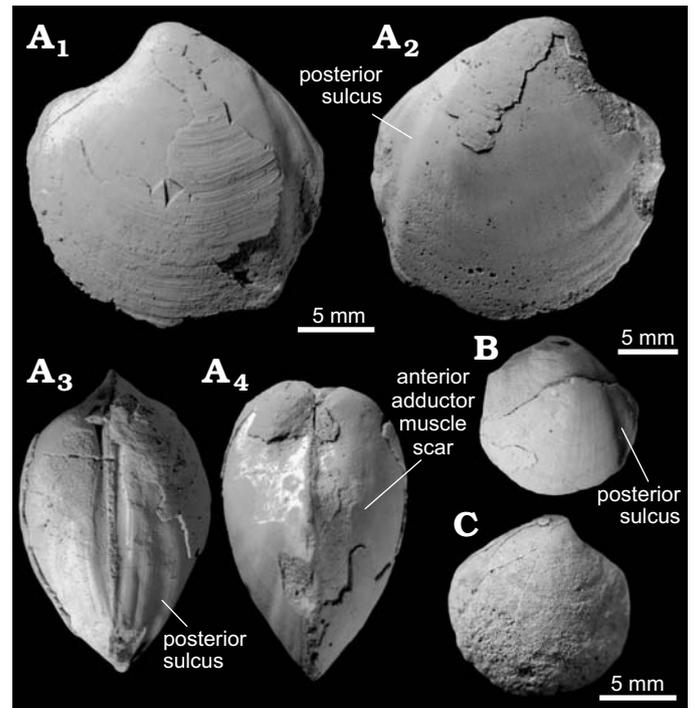
Fig. 16. Thyasirid bivalve *Thyasira becca* Kauffman, 1967, from a Campanian seep carbonate at Warbonnet Battlefield Monument, Montrose, Nebraska, USA. **A**. ZPAL L.16/18, a partial internal mold in left (A_1) and right (A_2) lateral views, with fragments of the shell preserved and weak radial striation on the surface of the mold; dorsal view (A_3) shows broad posterior sulcus; anterior view (A_4) shows poorly preserved anterior adductor muscle scar. **B**. ZPAL L.16/19, a partial internal mold in left lateral view, showing broad posterior sulcus and posterior part of the posterior adductor muscle scar. **C**. ZPAL L.16/20, of a complete internal mold in right lateral view showing the shell outline.

mens, and it also differs by having a much lower posterior fold (Kiel and Goedert 2007: fig. 7A).

Thyasirid species from the Western Interior Seaway belong to the *Thyasira advena–Thyasira becca* species complex, comprising large, rounded to oval species of *Thyasira* with protruding umbones. The group comprises *T. advena* sensu lato, *T. becca* sensu lato, and *T. cantha* (Kauffman 1967). The species complex is contrasted with the *Thyasira rostrata* complex, comprising smaller, thin-shelled and triangular species with weakly protruding umbones. This group is composed of *T. beauchampi* sensu lato, *T. quadrula*, *T. rostrata*, and *T. triangulata*. Shape and size-wise, the species from the *T. advena–T. becca* complex resemble Recent rounded species from the *T. sarsi–T. southwardae–T. methanophila* complex, comprising chemosymbiotic opportunists (*T. sarsi*) and seep-restricted specialists (*T. methanophila*) (Taylor et al. 2007; Amano et al. 2015).

Stratigraphic and geographic range.—Campanian of the Western Interior Seaway, North America. The species has been recorded from cold seep carbonates known as "Tepee Buttes" (Kauffman et al. 1996) and from non-seep localities in Colorado, South Dakota and potentially Canada (Kauffman 1967). Here we report the species from a Campanian "Tepee
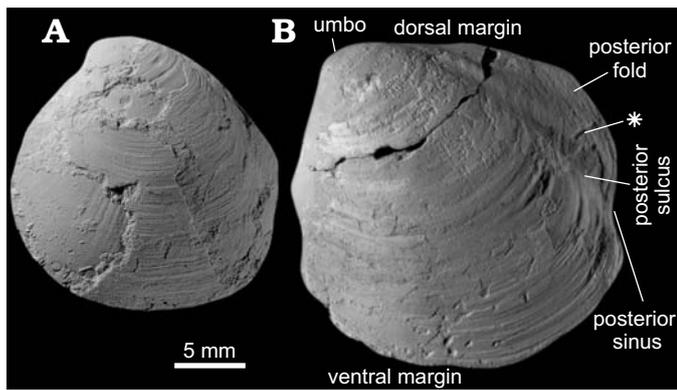
Fig. 17. Thyasiridae gen. et sp. indet A and B, respectively. **A**. ZPAL L.16/21 from middle to upper Eocene cold seep carbonates of West Fork of Grays River, "Siltstone of Unit B", western Washington State, USA; a poorly preserved specimen in left lateral view with partially preserved shell. **B**. ZPAL L.16/22 from an upper Oligocene, SR4 seep carbonate, Satsop River area, Lincoln Creek Formation, western Washington State, USA; a specimen in left left lateral view showing shell outline, external ornament, and secondary ridge running amidst posterior fold (asterisk).

Butte" seep carbonate from Warbonnet Battlefield Monument, Montrose, northwestern Nebraska.

Thyasiridae gen. et sp. indet. A

Fig. 17A.

Material.—One illustrated specimen (ZPAL L.16/21; Fig. 17A) from middle to upper Eocene cold seep carbonates of the "Siltstone of Unit B" from the West Fork of Grays River, western Washington State, USA.

Description.—Shell ovate, the available specimen is 18.9 mm long and 19.3 mm high with preserved surface covered with fine commarginal growth lines. Sulcus well visible, moderately deep and straight. Umbo poorly incurved. Anterior and posterior adductor muscle scars unknown.

Remarks.—This species is in rather poor condition and we leave it in open nomenclature. It could represent a juvenile specimen of an unidentified species of *Conchocele* (e.g., Kharlamenko et al. 2016: fig. 4D–F), a specimen of an unidentified species of *Maorithyas* or of *Thyasira*.

Thyasiridae gen. et sp. indet. B

Fig. 17B.

Material.—One illustrated specimen (ZPAL L.16/22; Fig. 17B) from upper Oligocene cold seep carbonates (Lincoln Creek Formation) of SR4 locality, from the Satsop River area, western Washington State, USA.

Description.—Shell quadrangular-oval, 29 mm long, 26.8 mm high. Umbo poorly incurved. Posterior sinus shallow but present, posterior sulcus shallow, broad. Posterior fold high, sculptured by radial ridge running from the umbo towards the posterior end of fold. Surface sculptured by commarginal growth line. Muscle scars unknown.

Remarks.—This specimen resembles smaller individuals of *Conchocele taylori* in outline and the height of the posterior

fold, and *C.* cf. *bathyaulax* in the presence of secondary radial ridge amidst posterior fold. However this assignment cannot be confirmed due to the damage of the only specimen available from SR4. More specimens are needed before this species can be assigned to any genus of thyasirids.

Discussion

The origins and evolutionary history of the thyasirids and their adaptation to the chemosymbiotic life style are arguably the most obscure among all chemosymbiotic bivalve families. In better-studied examples such as the bathymodiolins, there is a trend from a low degree to a high degree of structural integration of the symbionts (Lorion et al. 2013). Likewise, the pliocardiin vesicomyids, which rely almost exclusively on nutrition from their symbionts, appear to be derived from the asymbiotic vesicomyins (Johnson et al. 2017). Furthermore, bathymodiolins appear to have colonized low-sulfide habitats first and subsequently adapted to high-sulfide environments (Distel 2000). The current understanding of the phylogeny of the thyasirids, however, seems to indicate the opposite pattern: symbiotic species with highly integrated gill endosymbionts appear to be basal and live mostly in sulfide-rich environments such as pockmarks, cold seeps, and fjords rich in organic matter (e.g., Dando and Southward 1986; Dando and Spiro 1993; Dando et al. 1994; Fujiwara et al. 2001; Oliver and Killeen 2002; Dufour 2005; Batstone et al. 2014; Kharlamenko et al. 2016; Åstrom et al. 2017). There is some molecular evidence that smaller, asymbiotic thyasirids (i.e., *Axinulus* Verrill and Bush, 1898; *Mendicula* Iredale, 1924; *Leptaxinus* Verrill and Bush, 1898; *Adontorhina* Berry, 1947) may form a separate subfamily Axinopsidinae which is derived with respect to the genus *Thyasira* (i.e., Bernard 1972; Coan et al. 2000); these thyasirids are found mainly in colder waters in polar or deep sea settings (e.g., Payne and Allen 1991; Zelaya 2009, 2010) and do not show a particular association with seep environments.

The fossil record as outlined herein indicates that the thyasirids first appeared in the late Mesozoic, with the oldest species, *Cretaxinus hurumi* Hryniewicz, Little, and Nakrem, 2014, coming from the earliest Cretaceous cold seep carbonates in Spitsbergen (Berriasian; ca. 140 Ma; Fig. 18; Hryniewicz et al. 2014). This relatively young origin is surprising considering their basal position among heterobranch bivalves (Taylor et al. 2007)—the slightly more derived lucinids have a fossil record dating back to at least the Silurian (ca. 430 million years ago; Liljedahl 1992). Furthermore, as we will discuss below, most thyasirid genera with a fossil record first appear at hydrocarbon seeps and apparently colonized "normal" soft sediments only later in their geological history. It should be kept in mind, though, that the thyasirids could potentially have a much longer fossil record but due to their typically small and thin-shelled nature and their preference for deep water, they have a low fossilization potential (cf. Valentine et al.
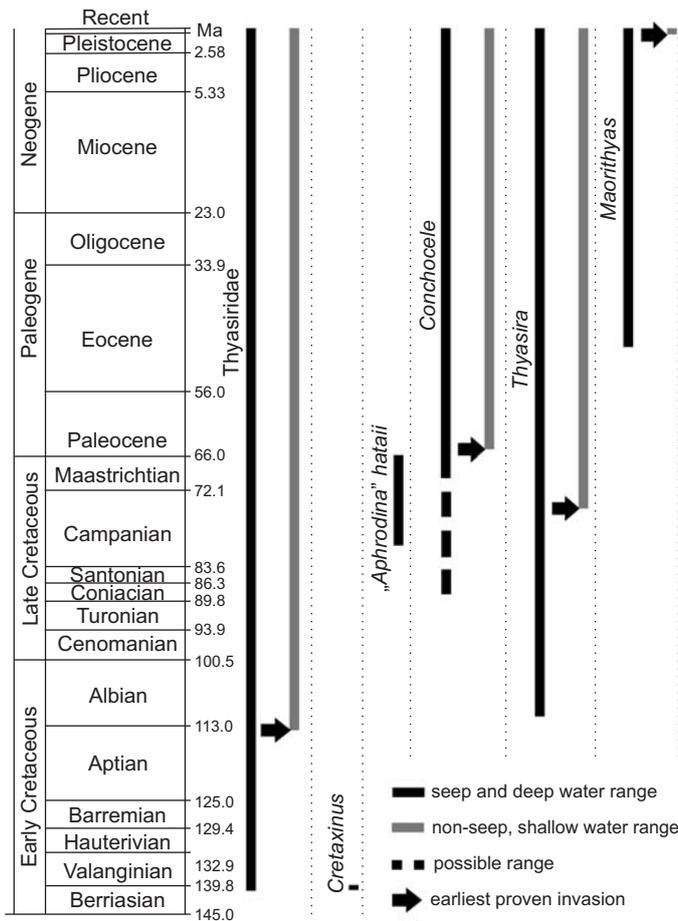
Fig. 18. Geological ranges of Thyasiridae and the discussed thyasirid genera at seeps and non-seep environments.

2006) and may simply have been overlooked. In contrast, their apparent abundance at fossil seep deposits might be a result of the rapid in situ carbonate precipitation at seeps, which facilitates the preservation of shells, including small and thin-shelled ones (Kiel and Little 2006). Although several large species of modern thyasirids are known from seep environments, thyasirids generally peak in diversity in normal, deep sea benthic environments (Payne and Allen 1991), which likely reflects their deep sea origins.

Even if earlier thyasirids have been overlooked for the reasons outlined above, or because they looked very different from the modern ones, we feel confident that the fossil record as outlined here reflects the history of the radiation of the modern thyasirids. Therefore it should be a valuable baseline for the interpretation of molecular phylogenetic data on this group. We will now go through the relevant clades:

– *Cretaxinus hurumi* is the oldest known thyasirid, occurs only in earliest Cretaceous seep deposits in Spitsbergen, and has not been seen in the surrounding mudstone (Hryniewicz et al. 2014).

– *Thyasira* clade 1 consists of the extant species *Thyasira flexuosa* Lamarck, 1818, *Thyasira gouldii* Philippi, 1845a, and *Thyasira polygona* (Jeffreys, 1864), all known chiefly from non-seep environments (e.g., López-Jamar et al.

1987; Oliver and Killeen 2002; Taylor et al. 2007; Batstone et al. 2014; Amano et al. 2015). Their shells are characterized by being higher than long, and by having a median flattened area (Amano et al. 2015). The oldest fossil species of this clade is *T. tanabei* from Cretaceous deep-water seep deposits in Japan (Albian–Campanian, 113–72 Ma) and possibly also from Cretaceous wood-fall environments from Japan (Kiel et al. 2008, 2009; this study). Thus the *T. flexuosa–T. polygona–T. gouldii* clade appears to have initially inhabited cold seeps from which they are now absent. A similar pattern is known from the protobranch bivalve *Nucinella* Wood, 1851, which has been reported from seeps as old as late Triassic and until Oligocene time (Peckmann et al. 2011; Amano et al. 2013; Hryniewicz et al. 2014), but is not known from such environments today. Alternatively, *T. tanabei* may represent a member of an extinct, seep-specialized *Thyasira* clade with a shell convergent to that of the *T. flexuosa–T. polygona–T. gouldii* clade.

– *Thyasira* clade 2, consisting of the extant *Thyasira methanophila* Oliver and Sellanes, 2005, *T. sarsi* (Philippi 1845b) and most likely also *T. capitanea* Åstrom and Oliver in Åstrom et al., 2017, *T. oleophila* Clarke, 1989, *T. scotiae* Oliver and Drewery, 2013; *T. southwardae* Oliver and Holmes, 2006 and *T. volcolutre* Rodrigues and Oliver in Rodrigues et al., 2008 (Taylor et al. 2007). A likely early Miocene member of this clade is *Thyasira nakazawai* from deep-water seep deposits in central Honshu, Japan (ca. 23–16 Ma; Amano et al. 2015) and we suggest that *Thyasira becca* Kauffman, 1967, from shallow-water seeps and non-seep environments in the Western Interior Seaway could potentially represent a Late Cretaceous member of the *T. methanophila–T. sarsi* clade. Even older species of this clade include an as-yet unnamed species of *Thyasira* from Albian (113–100 Ma) deep-water cold seeps from the Ellef Ringnes Island in Canadian Arctic Archipelago (Williscroft et al. 2017), and "*Lucina*" *rouyana* d'Orbigny, 1844, from deep-water cold seep carbonates of Czech Carpathians (Valanginian–Hauterivian, ca. 140–130 myr old; Ascher 1906), which has been interpreted as a species of *Thyasira* (Kiel et al. 2008; Kaim et al. 2013). The latter species need further taxonomic work, but it appears likely that the *T. methanophila–T. sarsi* clade has been inhabiting seeps since the Cretaceous.

– "*Aphrodina*" *hataii* from the Campanian–Maastrichtian "Sada Limestone" seep deposit (Katto and Hattori 1965; Nobuhara et al. 2008) may represent an independent genus (Takami Nobuhara, KH, and SK, unpublished material) and is only known from this seep locality.

– *Conchocele* Gabb, 1866, arguably represents the most successful radiation of a thyasirid bivalve at seeps, at least in the Pacific Ocean. The oldest documented occurrence of *Conchocele* is *C. townsendi* from Maastrichtian (latest Cretaceous; 72–66 Ma) shallow-water seep carbonates and other marine sediments in the James Ross Basin, Antarctica (Little et al. 2015). A potentially older record is "*Thyasira*" *cretacea* from Coniacian (89–86 Ma) possible

seep carbonates from Enos Canyon, California (Anderson 1958). Within *Conchocele*, we distinguish two morphologically distinct subclades. The first comprises species with straight anterior margin, and pointed, anteriorly placed beaks, with *C. kiritachiensis* from the upper Eocene seep carbonates from eastern Pacific margin (Kiritachi, Tomamae-cho, Hokkaido) and *Conchocele* cf. *bathyaulax* from the upper Eocene–Oligocene seep carbonates and non-seep environments from western Pacific margin (Washington State). This subclade likely comprises also the extant *C. scarlatoi* from shallow waters of the Sea of Japan. The second subclade comprises species with protruding anterior margin and incurved, moderately pointed umbones. This group comprises *C. taylori*, broadly distributed in the seep environments of northern circum-Pacific area, and extant *Conchocele* species known from seep environments of northern circum-Pacific area and the Caribbean (Kharlamenko et. al 2016). Due to the scarcity of data especially on the younger taxa, the precise relationships between Cretaceous, Paleocene, Neogene, and extant seep *Conchocele* remain to be characterized.

– *Maorithyas* Fleming, 1950, is a poorly known genus with only two extant species known from rather shallow water environments off New Zealand (Fleming 1950; Powell 1955). The oldest fossil species is the middle Eocene *Maorithyas humptulipsensis* reported here from a deep-water (ca. 2000–2500 m; cf. Kiel and Amano 2013) seep carbonate in western Washington State, USA. A remarkably similar case of a deep-water origin of a modern shallow-water clade is the bathymodiolin mussel *Vulcanidas*, whose oldest fossil record is from the very same deep-water seep deposit as *M. humptulipsensis* (Kiel and Amano 2013).

– The genus *Channelaxinus* Valentich-Scott and Coan, 2012, was recently reported from a Miocene deep-water seep carbonate in Italy (Kiel and Taviani 2017).

In general, major evolutionary novelties are considered to have developed in shallow water throughout the Phanerozoic, and have then moved offshore over geologic time scales, making the deep sea a refuge for relict taxa (Jablonski et al. 1983; Jablonski and Bottjer 1991). However, some counter examples of deep-water origins and subsequent colonization of shallower water exist, indicating that the deep sea could also act as a source of biodiversity because it is larger, more stable and not (or at least less) affected by large extinction events as are shallower water habitats (Thuy et al. 2012). Examples of such offshore-onshore pattern include several groups of corals, mollusks and crustaceans (e.g., Hessler and Wilson 1983; Jablonski and Bottjer 1991; Jablonski 2005; Lindner et al. 2008), and, as outlined here, the modern thyasirids appear to be another such example.

The Cretaceous rise of the modern thyasirids might be linked to their sulfide requirements. Extant thyasirids show a preference for relatively low sulfide concentrations compared to other chemosymbiotic bivalve families (e.g., Oliver et al. 2013) and this appears to have also been the case for their Paleogene relatives (Kiel et al. 2016). Marine sulfate concentrations appear to control sulfide availability at methane seeps (Wortmann and Paytan 2012) and extremely low sulfate concentrations during the Cretaceous did indeed have a major impact on the evolution of the seep fauna (Kiel 2015). This low sulfide availability during the Cretaceous might have favored the adaptation of thyasirids to the methane seep environment.

There is a remarkable coincidence between the rise of large thyasirids at seeps and the disappearance of the semi-infaunal, seep-restricted bivalve *Caspiconcha*. *Caspiconcha* was abundant at seeps during the early Cretaceous and significantly decreased in abundance after the drop in marine sulfate concentrations about 120 million years ago (Kiel 2015). Its last record is from the Campanian (Omagari seep carbonate; Jenkins et al. 2013) roughly coeval with the appearance of the large thyasirids *Conchocele* and "*Thyasira*" *hataii* at seeps. A possible connection between the two events might be deduced from an observation made on extant chemosymbiotic mytilids and thyasirids colonizing piles of oil-rich (and hence sulfide-rich) drill-hole cuttings underneath oil rigs in the North Sea. The first colonizer of these piles is the epifaunal bathymodiolin mussel *Idas*, which relies on sulfide emitting from the cuttings. *Idas* declines in abundance after about a year when infaunal thyasirids become abundant within the cuttings and take up the majority of the sulfide (Dando and Hartley 2005). Analogously, we speculate that the large infaunal thyasirids that appeared at seeps during the late Cretaceous were essentially mining most of the available sulfide at seeps from within the sediment, and thus depriving the semi-infaunal *Caspiconcha* of its source of nutrition. With sulfide levels already being low during the late Cretaceous low-sulfide interval (cf. Kiel 2015), *Caspiconcha* was already in decline, and increased sulfide mining by the large thyasirids might have been the final blow that drove *Caspiconcha* to extinction.

The fossil history of the thyasirids as outlined here indicates that the so-called Oceanic Anoxic Events during the Cretaceous and early Cenozoic, including the Paleocene/Eocene Thermal Maximum, had little (if any) effect on the diversity and the taxonomic composition of thyasirids at seeps. Instead, they show a slow rise in diversity in terms of genera and clades within genera throughout the Cretaceous and Cenozoic (Fig. 18). The major rise in marine sulfate concentration after the early Eocene and the concomitant rise in sulfide availability at seeps (cf. Wortmann and Paytan 2012; Kiel 2015) likely created high sulfide niches at seeps, which the low sulfide-adapted thyasirids were unable to exploit. Therefore the thyasirids do not show a major radiation in the early Cenozoic, in contrast to bathymodiolin mussels (Lorion et al. 2013) and vesicomyid clams (Johnson et al. 2017). Remarkably, the genus *Thyasira* is the only seep-inhabiting genus that showed a decrease in mean body size after the Eocene rise in sulfide availability, in contrast to all others, which show an increase in mean body size (Kiel 2015).

Conclusions

This paper presents a study of thyasirid bivalves from Cretaceous and Paleogene cold seep deposits. Eleven species, belonging to three long-lasting genera (*Conchocele* Gabb, 1866, *Thyasira* Lamarck, 1818, and *Maorithyas* Fleming, 1950) have been identified. The fossil record suggests that modern thyasirids originated at seeps in the earliest Cretaceous and persisted in this environment for 140 Ma until the present day. The "deep-to-shallow" origination patterns exhibited by thyasirids is similar to that observed among some other invertebrate groups, such as corals and crustaceans, showing that the deep sea may be a source of some evolutionary novelties. Likewise, similar to other deep sea and seep-inhabiting invertebrates, thyasirids show no significant diversity changes around major Mesozoic and Cenozoic Oceanic Anoxic Events, analogously to various other members of the deep sea fauna and raises doubts about the global character of these events.

Acknowledgements

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