



LUCINID BIVALVES FROM ANCIENT METHANE SEEPS

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ABSTRACT

Twelve species of lucinid bivalves are reported from late Jurassic to late Miocene methane-seep deposits worldwide. Among them, eight species and two genera are new. *Amanocina* n. gen. includes *Nipponothracia yezoensis* from the Cenomanian of Japan as type species, *Cryptolucina kuhnpassetensis* Kelly, 2000 from the Berriasian of Greenland, *A. raukumara* n. sp. from the Albian of New Zealand and *A. colombiana* n. sp. from the Oligocene of Colombia. *Tehamatea* n. gen. includes *Lucina ovalis* Stanton, 1895 and *Lucina colusaensis* Stanton, 1895 from the late Jurassic to early Cretaceous of California, *T. vocontiana* n. sp. from the Hauterivian of southern Europe and *T. agirrezabalai* n. sp. from the Albian of northern Spain. The new species are: *Cubatea awanuiensis* from the Albian and Cenomanian of New Zealand, *Nymphalucina panochensis* from the early Palaeocene of California, *Elliptiolucina washingtonia* from the late Oligocene of Washington State, USA, and *Elongatolucina peckmanni* from the Oligocene of Colombia. New combinations are provided for *Nipponothracia lomilensis* (Olsson, 1931) from the Oligocene of Peru and *Elliptiolucina hetzeli* (Martin, 1933) from the late Miocene of Indonesia. The anterior adductor muscle scar of *Beauvoisina carinata* is documented for the first time. The lucinids found at Jurassic and Cretaceous deep-water methane seeps belong to the subfamily Myrteinae and within this to genera that are restricted to the seep environment (*Beauvoisina*, *Tehamatea*, *Amanocina* and *Cubatea*); shallow-water seeps were inhabited by the codakiine genus *Nymphalucina*, which is not seep-restricted. *Amanocina*, *Cubatea* and *Nymphalucina* survived into the Cenozoic. Genera that newly colonized deep-water seeps during the Cenozoic include members of both Myrteinae (*Elongatolucina*, *Nipponothracia* and *Elliptiolucina*) and Codakiinae (*Epilucina* and *Lucinoma*); the latter are clearly not seep-restricted.

INTRODUCTION

Methane seeps in the deep sea are inhabited by unusual faunal communities that are dominated by taxa living in symbiosis with chemoautotrophic bacteria (Paull *et al.*, 1985; Levin, 2005). The most intensely studied groups of chemosymbiotic bivalves are the epifaunal bathymodioline and the semi-infaunal vesicomyids. Lucinids have received less attention, likely due to their infaunal mode of life that makes them invisible in the common video observations of these habitats (Taylor & Glover, 2010). In fact, the fossil record of seep communities, where infaunal taxa may be more likely to be preserved than epifaunal taxa, is rich in lucinids. Numerous species, some exceeding 200 mm in length, have been reported from Late Jurassic to Pliocene seep deposits worldwide. A few genera such as *Beauvoisina* Kiel, Campbell & Gaillard, 2010, *Elongatolucina* Gill & Little, 2013, and *Nipponothracia* Kanie & Sakai, 1997 are considered as being restricted to methane-seep deposits (Kase *et al.*, 2007; Kiel, 2010a; Kiel *et al.*, 2010; Gill & Little, 2013), while other genera like *Cryptolucina*, *Ezolucina* and *Lucinoma* occur in a wider range of habitats (Saul *et al.*, 1996; Kiel & Goedert, 2006; Amano *et al.*, 2008). However, the taxonomy of many

lucinids at fossil seep deposits remains poorly understood. The purpose of the present study is to use newly collected material and museum collections to revise systematically as many lucinid bivalves as possible (except *Lucinoma*) that are known to occur in Jurassic to Miocene seep deposits.

MATERIAL

Most of the material described here is from fossil methane-seep deposits that have been described in detail elsewhere. Hence, only brief locality descriptions are provided here, in stratigraphic order, along with the relevant references.

Institutional abbreviations

GZG = Geowissenschaftliches Museum der Universität Göttingen, Germany; GNS = Geological and Nuclear Sciences, Lower Hutt, New Zealand; LACMIP = Los Angeles County Museum of Natural History, Invertebrate Paleontology; PRI = Paleontological Research Institution, Ithaca, USA; RMNH = Netherlands Centre for Biodiversity Naturalis, Leiden, The

Netherlands; USGS = United States Geological Survey; USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Buton asphalt deposits

These are fossiliferous asphalt deposits cropping out at several places in the southern half of the small island of Buton, just off southeastern Kalimantan, Indonesia (Martin, 1933); the pteropod fauna indicates a late Miocene age (Janssen, 1999). The unusual mode of fossil preservation in this deposit has long prompted speculations on its origin, including the suggestion that it might be a mud volcano (Martin, 1937). Due to the occurrence of vesicomid bivalves and large, oval lucinids, it has been considered as an ancient seep deposit (Goedert *et al.*, 2003). Potentially seep-related taxa include the vesicomids *Waisiuconcha albertinae* and *W. margotae*, and the lucinids *Elliptiolucina hetzeli* and *Lucina (Myrtea) butonensis* (which most likely is a *Lucinoma*) (Beets, 1942, 1953). Beets' original material was studied at RMNH.

Lincoln Creek Formation

These late Eocene to Oligocene deep-water sediments in western Washington State, USA, have yielded numerous seep deposits, especially in outcrops along the Canyon and Satsop rivers (Goedert & Squires, 1990, 1993; Peckmann *et al.*, 2002; Kiel, 2006). *Elliptiolucina washingtonia* n. sp. reported here was found at two outcrops of the late Oligocene part of the formation exposed along the Canyon River (one is LACMIP loc. 17747 and the other is about 500 m upstream from it at 47°16.593'N, 123°31.390'W) and was collected by James L. Goedert in summer 2002.

Lomitos chert

Cherty limestones presumably of Oligocene age that are exposed south of Talara in northern Peru contain a diverse fauna including lucinid, thyasirid and vesicomid bivalves (Olsson, 1931; Kiel & Peckmann, 2007). Olsson's type material was investigated at PRI.

Palmar-Molinera road

This is a presumably Oligocene seep deposit in Colombia (USGS loc. 11253); the material was collected by Axel Olsson and deposited in USNM. The fauna includes *Bathymodiulus palmarensis*, two lucinids and a solemyid bivalve, and a few poorly preserved gastropods (Kiel & Peckmann, 2007; Kiel *et al.*, 2010).

Panoche Hills

Numerous seep deposits crop out over a distance of about 3000 m from N to S in the Cima Sandstone lens of the Moreno Formation in the western slope of the San Joaquin Valley in central California, USA (Schwartz *et al.*, 2003). The material reported here was collected by the author and James L. Goedert in autumn 2011 from the southernmost deposits reported by Schwartz *et al.* (2003) (36°37'59.44"N, 120°41'32.61"W). The lucinid described here is by far the most common species at this deposit, followed by aporrhaid gastropods, scaphopods and rare solitary corals. The alleged 'vestimentiferan tube worms' at these deposits (cf. Schwartz *et al.*, 2003) are, based on my own field observations, fluid conduits and were not made by tube-dwelling annelids. Kaim *et al.* (2008) suggested that the 'provannid gastropods' reported by Schwartz *et al.* (2003) from the Panoche Hills seep deposits may be aporrhaid gastropods; this can be confirmed

because I have found specimens with the expanded wing-like outer lip typical of aporrhoids.

Port Awanui

Three mid-Cretaceous seep deposits are reported from Port Awanui, North Island, New Zealand, and a new species is here described from two of them, called Awanui II (Albian-Cenomanian) and Awanui GS 688 (Cenomanian) (37°49'58.62"S, 178°27'06.45"E). The fauna includes the two lucinids described herein, and *Caspiconcha*, *Nucinella*, thyasirids and solemyids among the other bivalves, and *Hokkaidoconcha* and *Retiskenea?* among the gastropods (Kiel *et al.*, in press). The material was collected by the author and James S. Crampton in autumn 2010.

Cold Fork of Cottonwood Creek

This large, fossiliferous seep deposit in the Lodoga Formation of the Great Valley Group in Tehama County, California, USA (40°10'01.25"N, 122°40'55.43"W), contains a diverse fauna including the bivalves *Caspiconcha major*, *Tehamatea ovalis* and *Aucellina*, and the gastropods *Bathypurpurinopsis stantoni*, *Atresius liratus*, *Retiskenea kieli* and a large, as yet undescribed abyssochrysoid; the age is Early Cretaceous, Aptian/Albian (Stanton, 1895; Campbell *et al.*, 1993, 2008a; Campbell & Bottjer, 1995; Kiel *et al.*, 2008a; Jenkins *et al.*, 2013). The present material was collected by the author and James L. Goedert in autumn 2011.

Rottier

The seep deposits near Rottier in the Department Drôme, southern France (44°28'13.20" N, 5°25'22.00" E), are dominated either by the brachiopod *Peregrinella multicastrata* or by the gastropod *Humptulipsia macsotayi* and the here-described lucinid bivalve *Tehamatea vocontiana* n. sp.; the deposit is dated by ammonite biostratigraphy as Hauterivian (Early Cretaceous) (Thieuloy, 1972; Kiel *et al.*, 2010). The material was collected in spring 2006 and summer 2010 by the author, Christian Gaillard and Luc Bulot.

Curnier

This is an isolated limestone block dominated by the brachiopod *Peregrinella multicastrata* found as a float in a dry creek bed near Curnier in the Department Drôme in southern France (44°23.393'N, 05°15.299'E) not far from Rottier and in the same strata. Additional taxa include the lucinid *Tehamatea vocontiana* n. sp. described here and the abyssochrysoid gastropod *Humptulipsia macsotayi*. This locality is considered as an ancient seep deposit due to the occurrence of the brachiopod *Peregrinella* and due to the overall similarity with the seep deposit at Rottier (cf. Thieuloy, 1972; Campbell & Bottjer, 1995; Kiel *et al.*, 2010). The material was collected in summer 2010 by the author and Luc Bulot.

Planerskoje

This is a small limestone deposit in presumed Hauterivian (Early Cretaceous) mud and siltstones near Planerskoje in the eastern Crimean peninsula, Ukraine (44°58'08.13"N, 35°12'01.50"E). The fauna lived in an environment of slow and diffuse methane seepage and is dominated by the brachiopod *Peregrinella multicastrata* that often hosted parasitic polychaetes; the bivalve *Caspiconcha rubani* is not uncommon, while the gastropod *Paskentana anistratenkorum* is rare (Kiel, 2008; Kiel & Peckmann, 2008; Peckmann *et al.*, 2009; Kiel *et al.*, 2010). The material was collected by the author in summer 2007.

Rocky Creek

Isolated limestones occur on a small knoll near Rocky Creek in Morgan Valley, Lake County, CA, USA (38°53'57.80"N, 122°28'35.27"W), probably of Valanginian age (Early Cretaceous). The fauna includes the lucinid *Tehamatea colusaensis* and astartid and pectinid bivalves, while among the gastropods are *Atresius liratus*, *Amberleya morganensis* and *Lithomphalus enderlini* (Campbell *et al.*, 1993; Kiel & Campbell, 2005). The present material was collected by the author and James L. Goedert in autumn 2011.

Bear Creek

Numerous small limestone blocks are exposed and/or scattered near the end of Hamilton Canyon and the surrounding hillsides, East of Bear Creek in Colusa County, CA, USA (39°03'07.70"N, 122°24'31.25"W), and are dated as Valanginian (Early Cretaceous). They preserve a rich fauna including *Caspiconcha major*, solemyid and astartid bivalves, and the gastropods *Lithomphalus enderlini*, *Paskentana paskentaensis*, *Triassurella goederti* and *Puncturella mcleani*, among others (Campbell *et al.*, 1993; Kiel & Campbell, 2005; Kiel *et al.*, 2008a, 2010). The present material was collected by the author and James L. Goedert in autumn 2011.

Paskenta

This consists of two small carbonate lenses within turbidites of the Stony Creek Formation of the Great Valley Group in Tehama County, CA, USA (39°54'15.42"N, 122°35'49.16"W), dated as Tithonian (Late Jurassic). The fauna is dominated by solemyid and 'Buchia' bivalves; lucinids and nuculids are rare; gastropods include *Amberleya dilleri*, *Hokkaidoconcha occidentalis*, *Paskentana paskentaensis* and the slit-limpet *Puncturella mcleani*; the brachiopod *Cooperrhynchia schucherti* is locally common (Campbell *et al.*, 1993, 2002; Sandy & Campbell, 1994; Kiel *et al.*, 2010). The present material was collected by the author and James L. Goedert in autumn 2011 and Stanton's (1895) type material was studied at USNM.

Beauvoisin

Several isolated carbonate lenses occur within deep-basinal deposits of the Terres Noires Formation near Beauvoisin in the Department Drôme in southeastern France (44°18'N, 5°12'E) and are of Oxfordian (Late Jurassic) age. The lucinid bivalve *Beauvoisina carinata* is by far the most common taxon, while gastropods include *Paskentana umbilicata*, *Hokkaidoconcha novacula* and a neritid and an aporrhaid; in addition, there are two different types of crustacean coprolites, sponge spicules and the irregular echinoid *Tithonia oxfordiana* (Gaillard *et al.*, 1985, 1992, 2011; Senowbari-Daryan *et al.*, 2007; Kiel *et al.*, 2010). The material was collected by the author and Christian Gaillard in spring 2006.

METHODS

Specimens were coated with ammonium chloride prior to photography, except where indicated. Specimens used for serial-grinding tomography and digital reconstruction of the hinge area were first embedded in epoxy resin, then *c.* 0.1-mm-thick layers were abraded repeatedly using a GMN MPS2 120 manual grinding machine. After each step, the surface was scanned at 1200 dpi on a flatbed scanner with a custom-built water bath with a glass bottom placed on the scanner's surface. The images were converted to 8-bit greyscale jpeg files and aligned using the 'auto align' function in Adobe Photoshop

CS3. Areas of interest were extracted from the complete set of images using the 'image stacks' function in ImageJ v. 1.45 s (Abramoff *et al.*, 2004) and the shells were redrawn to enhance their visibility. Digital reconstructions were produced from these subsamples in Voreen v. 2.6.1. Due to the low number of images per hinge (17–20), these reconstructions had a very step-like appearance and were smoothed using the 'grain' and 'rough pastel' filters in Adobe Photoshop CS3.

SYSTEMATIC DESCRIPTIONS

Family Lucinidae Fleming, 1828

Subfamily Myrteinae Chavan, 1969

Genus *Beauvoisina* Kiel, Campbell & Gaillard, 2010

Type species: Beauvoisina carinata Kiel, Campbell & Gaillard, 2010, from late Jurassic seep deposits at Beauvoisin, southeastern France (Kiel *et al.*, 2010).

Included species: Type species only.

Remarks: The anterior adductor muscle scar of *Beauvoisina carinata* is very indistinct and is here described for the first time. Among the tens of investigated specimens, only a single one shows a scar that is broad, elongate and reaches about half the shell height (Fig. 1) and is thus overall very similar to that of *Tehamatea*. The main difference between *Tehamatea* and *Beauvoisina* is the strong ridge in the lunule in *Beauvoisina*, which is lacking in *Tehamatea*. However, the two genera appear to be very closely related. *Ezolucina* and *Cubatea* also differ from *Beauvoisina* by the lack of the strong ridge in the lunule. In addition, the anterior adductor muscle scar of *Ezolucina* is much more distinctive and more quadrate than *Beauvoisina*, and *Cubatea* has very distinctive lateral teeth. Overall, these four genera, *Beauvoisina*, *Cubatea*, *Ezolucina* and *Tehamatea*, are very similar to each other and likely represent a single radiation of the Myrteinae into the seep environment. The genus *Nymphalucina*, also reported herein, differs from these four genera by having a distinct posterior ridge and truncation, and by having distinctive commarginal sculpture.

Genus *Cubatea* Kiel, Campbell & Gaillard, 2010

Type species: Myrtaea(?) asphaltica Cooke, 1919; Oligocene?, from the Almira asphalt mine near Bejucal, Cuba; OD.

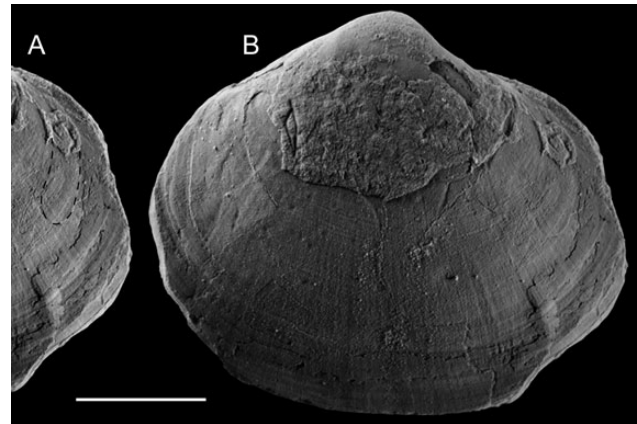


Figure 1. *Beauvoisina carinata* Kiel, Campbell & Gaillard, 2010, from a late Jurassic (Oxfordian) seep deposit at Beauvoisin, France; anterior adductor muscle scar indicated by stippled line (A) and complete specimen (B) (GZG.INV.88311). Scale bar = 10 mm.

Included species: *Cubatea awanuiensis* n. sp. from Albian to Cenomanian of New Zealand described below.

***Cubatea awanuiensis* new species**

(Fig. 2)

Ezolucina sp. 'Awanui' Kiel *et al.*, in press: figs 13G–J.

Types: Holotype GNS TM8836 and paratypes GNS TM8909 and TM8911 from Awanui II, paratype GNS TM8910 from Awanui GS688.

Type locality: Awanui II; Seep carbonate on the beach platform near Port Awanui on the east coast of the Raukumara Peninsula, North Island, New Zealand.

Etymology: After the type locality.

Material examined: 15 specimens from Awanui II and 15 specimens from Awanui GS688.

Diagnosis: Oval shell with prominent, subcentral, only slightly prosogyrate beak; lunule short, shallow, slightly asymmetrical, broader in right valve; escutcheon lanceolate, narrow; external sculpture on early shell of thin, regular, commarginal ribs with fine growth lines in between; on shells >10 mm length irregular growth lines only. Hinge plate strong and thick, ligament nymph short; one strong cardinal tooth in right valve, two cardinals in left valve; right valve with one elongate anterior lateral and one elongate posterior lateral tooth, left valve with corresponding sockets. Anterior adductor muscle short, broad, reaching about half of shell height, detached from pallial line for about half its length (up to 2/3 in very large specimens) at an angle of *c.* 30°, detached part straight; posterior adductor muscle scar broad, roundish; pedal retractor scar distinct from adductor muscle scar, triangular, oval or bean-shaped, situated underneath lateral tooth. Interior of shell covered by irregular radial grooves, in large specimens also by distinct round tubercles; pallial line entire, marked by distinct, undulating band, area beyond pallial line with broad, radial grooves. Largest specimen 60 mm high.

Distribution: Albian to Cenomanian of North Island, New Zealand.

Remarks: *Cubatea awanuiensis* differs from the type species *C. asphaltica* mainly by its more prominent umbo, slightly more slender lunule, and its more prominent anterior cardinal tooth in the left valve.

Genus *Tehamatea* new genus

Type species: *Lucina ovalis* Stanton, 1895.

Etymology: Combined from Tehama County, CA, USA, where the type species was found, and *Myrtea*, a potentially related lucinid genus.

Diagnosis: Large oval shells, moderately inflated; beak subcentral, elevated, slightly prosogyrate; lunule and escutcheon present; early shell (up to *c.* 10 mm length) sculptured by widely spaced, fine commarginal lamellae, remaining shell with fine, irregular commarginal growth lines only; ligament thick; one or two cardinal teeth in right valve, anterior tooth sometimes reduced; one cardinal in left valve; lateral teeth present; anterior adductor muscle scar

commonly indistinct, elongate, reaching about half shell height, detached from pallial line for about half its length, deviating from pallial line at low angle and not more than its own width; posterior adductor muscle scar oval to elongate-oval; pallial line entire, thin.

Included species: *Lucina colusaensis* Stanton, 1895 from late Jurassic to early Cretaceous seep deposits in California, USA, *Tehamatea agirrezabalai* n. sp. from the Albian of northern Spain, and *T. vocontiana* n. sp. from the early Cretaceous of southern France and the Ukraine. Another potential member is '*Myrtea* sp.' from the Campanian (Late Cretaceous) Omagari seep deposit in Hokkaido, Japan (Hikida *et al.*, 2003).

***Tehamatea ovalis* (Stanton, 1895)**

(Figs 3, 4)

Lucina ovalis Stanton, 1895: 59–60, pl. 12, fig. 1.

Material examined: The type material from Paskenta (USNM 23056), five specimens from the Bear Creek site, and one specimen from CFCC (22 × 18 × 5 mm, single valve).

Distribution: Late Jurassic (Tithonian) to Early Cretaceous (Albian), Great Valley Group, CA, USA.

Remarks: Stanton (1895: 59–60) noted that “the hinge has two rather large cardinal teeth, and the laterals are also well developed. [...] The ligament is large and prominent.” These features have indeed been seen on Stanton’s type material by the present author. Tate (1867: 303) mentioned a *Lucina ovalis* from the Jurassic of Ireland. I have not found any other reference to this species in the literature and assume that this was in error; Tate possibly intended to refer to *Cardinia ovalis*, which is frequently mentioned elsewhere in his paper.

***Tehamatea colusaensis* (Stanton, 1895)**

(Fig. 5)

Lucina colusaensis Stanton, 1895: 60, pl. 11, figs 4, 5.

Material examined: Stanton’s two type specimens: USNM 23057 from Paskenta and 23058 from Wilbur Springs; nine specimens from the Rocky Creek seep deposit.

Remarks: Amano *et al.* (2008) suggested that '*Lucina*' *colusanensis* might be an *Ezolucina*, based on its veneroid shell shape. But its internal features differ from those of *E. inflata*: it has two cardinal teeth in the right valve, while *E. inflata* has only one, the anterior adductor muscle scar is not quadrate as in *E. inflata* (i.e. the scar is not angular on its ventral side) and in general internal features such as muscle scars and pallial line are very distinct in *E. inflata*, but rather indistinct in '*Lucina*' *colusanensis*. Instead, the species fits well into the diagnosis of *Tehamatea*. It differs from the other Californian *Tehamatea* species, *T. ovalis*, by having the beak in a more anterior position and by its pointed posterior margin.

The very large ligament noted by Stanton (1896) is documented here in several specimens (Fig. 5D–F) and Stanton (1895: 60) further noted that the “hinge and muscular impressions have not been seen...”. Anterior adductor muscle scars are here documented for two species and can actually also be seen on one of Stanton’s type specimens; the hinge of two specimens is also documented here and consists of two thick cardinal teeth in the right valve and one thick tooth in the left valve (Fig. 5B, C, G).

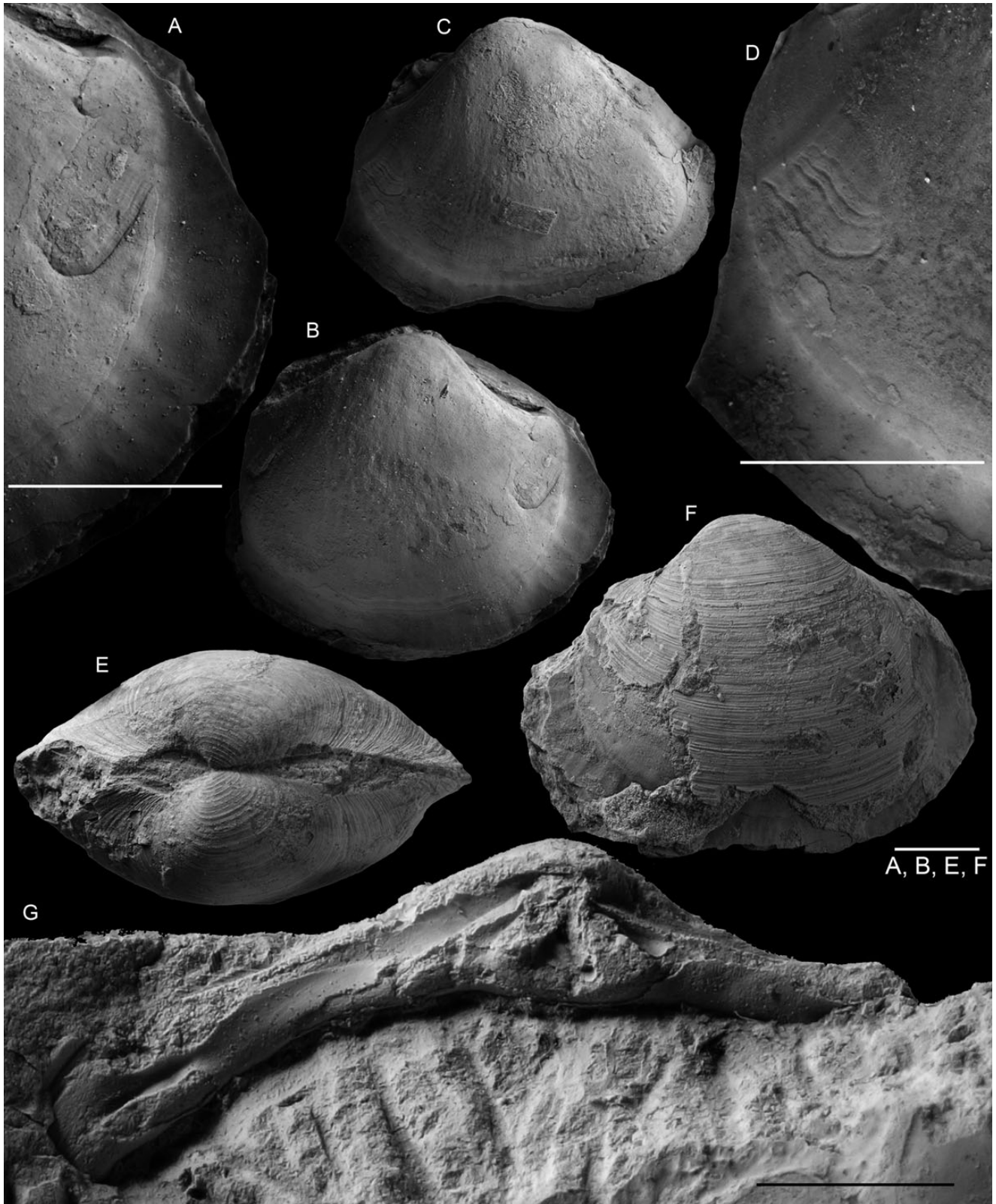


Figure 2. *Cubatea avanuiensis* n. sp., from Albian-Cenomanian seep deposits at Port Awanui, North Island, New Zealand. **A, B.** Right valve of an internal mould showing pallial line and anterior adductor muscle scar (paratype GNS TM8909). **C, D.** Left valve of an internal mould showing pallial line and anterior adductor muscle scar (paratype GNS TM8910). **E, F.** Specimen with shell (holotype TM8836). **G.** Hinge area of a right valve (paratype GNS TM8911). Scale bars **A–F** = 10 mm, **G** = 5 mm.

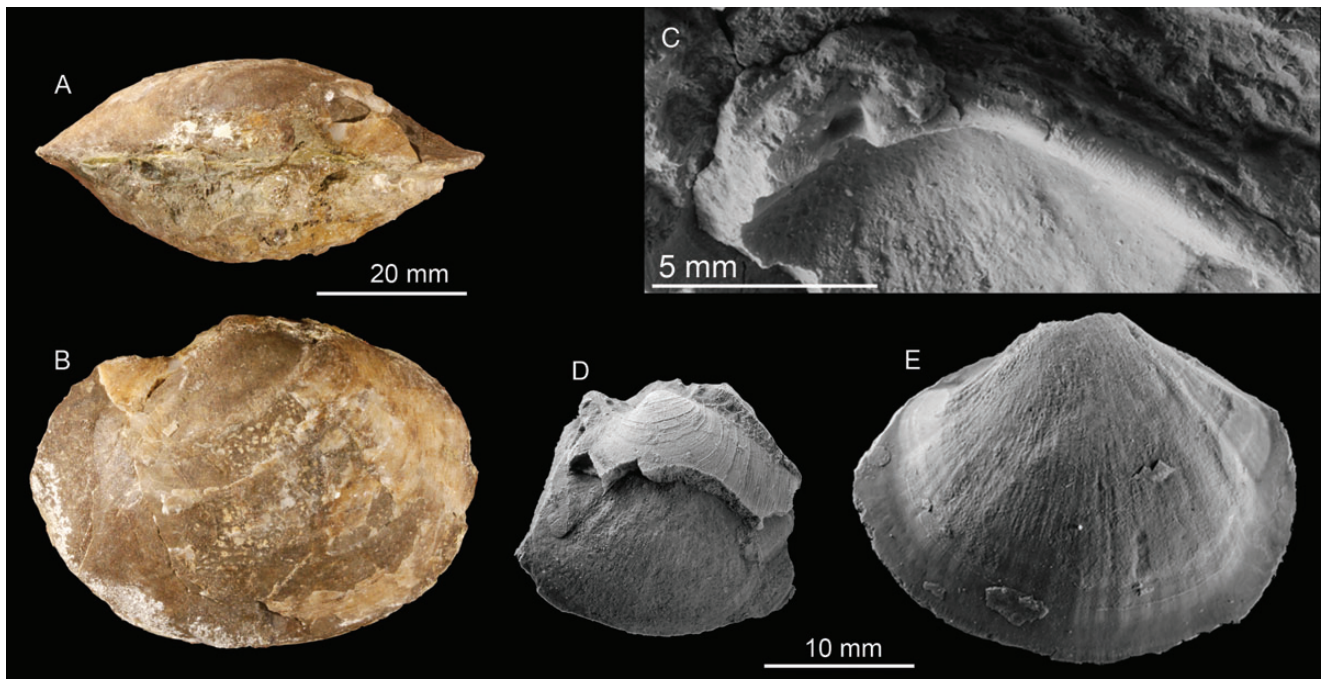


Figure 3. *Tehamatea ovalis* (Stanton, 1895) from late Jurassic to early Cretaceous seep deposits in California, USA. **A, B.** Holotype (USNM 23056) from the Tithonian Paskenta site; not whitened. **C, D.** Specimen from the Valanginian Bear Creek site showing the hinge of a right valve (**C**), and regular commarginal ornament on the early whorl and the anterior adductor muscle scar (**D**) (GZG.INV.88319). **E.** Internal mould showing internal features of a left valve (GZG.INV.88320). Scale bars **A, B** = 20 mm; **C** = 5 mm; **D, E** = 10 mm.

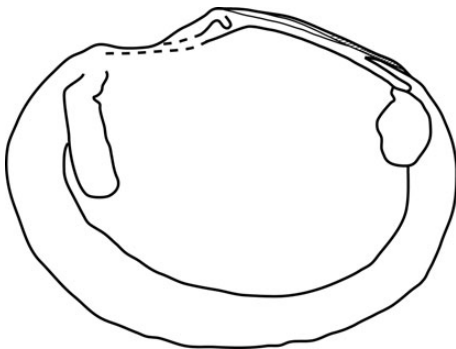


Figure 4. Sketch reconstruction of *Tehamatea ovalis* (Stanton, 1895). Not to scale.

***Tehamatea agirrezabalai* new species**

(Figs 6, 7)

Lucinid bivalve Agirrezabala *et al.*, in press: figs 15D, 16B.

Types: Holotype GZG.INV.88321, paratype GZG.INV.88322.

Type locality: Seep carbonates on the beach platform near Ispaster, northern Spain.

Etymology: For Luis M. Agirrezabala, who discovered the Cretaceous seep deposits along the Basque coast.

Material examined: Three specimens (including types) and several fragments.

Diagnosis: Large (up to 140 mm in length) slightly oval shell with elevated umbo; external sculpture of fine, commarginal

growth lines only; anterior adductor muscle scar distinct, detached from pallial line for almost half its length, deviation from pallial line variable from 10 to almost 30°; pallial line distinct, slightly undulating; hinge in each valve with two strong cardinal teeth nearly at right angle to each other.

Distribution: Type locality only.

Remarks: This is by far the largest of the three *Tehamatea* species reported here and differs from *T. ovalis* and *T. vocontiana* n. sp. also by being less elongate. It further differs from *T. vocontiana* in have two strong cardinal teeth in the right valve, whereas *T. vocontiana* has only one.

***Tehamatea vocontiana* new species**

(Figs 8, 9)

Bivalvia gen. indet. Thieuloy, 1972: 21, pl. 1, fig. 10; pl. 2, fig. 3; pl. 3, fig. 1.

Pseudomiltha aff. *germani* (Pictet & Campiche 1865)—Macsotay, 1980: 146. Lemoine *et al.*, 1982: 645.

Lucinid bivalve Kiel & Peckmann, 2008: 754, fig. 6G–I.

Types: Holotype GZG.INV.88323 and paratype GZG.INV.88325 from Rottier, paratypes GZG.INV.88323 and GZG.INV.88326 from Planerskoje.

Type locality: Seep deposits near Rotter, Department Drôme, southeastern France.

Etymology: For the Vocontian Basin, southern France.

Material examined: Three specimens from the type locality, five from Curnier and eight from Planerskoje, including types.

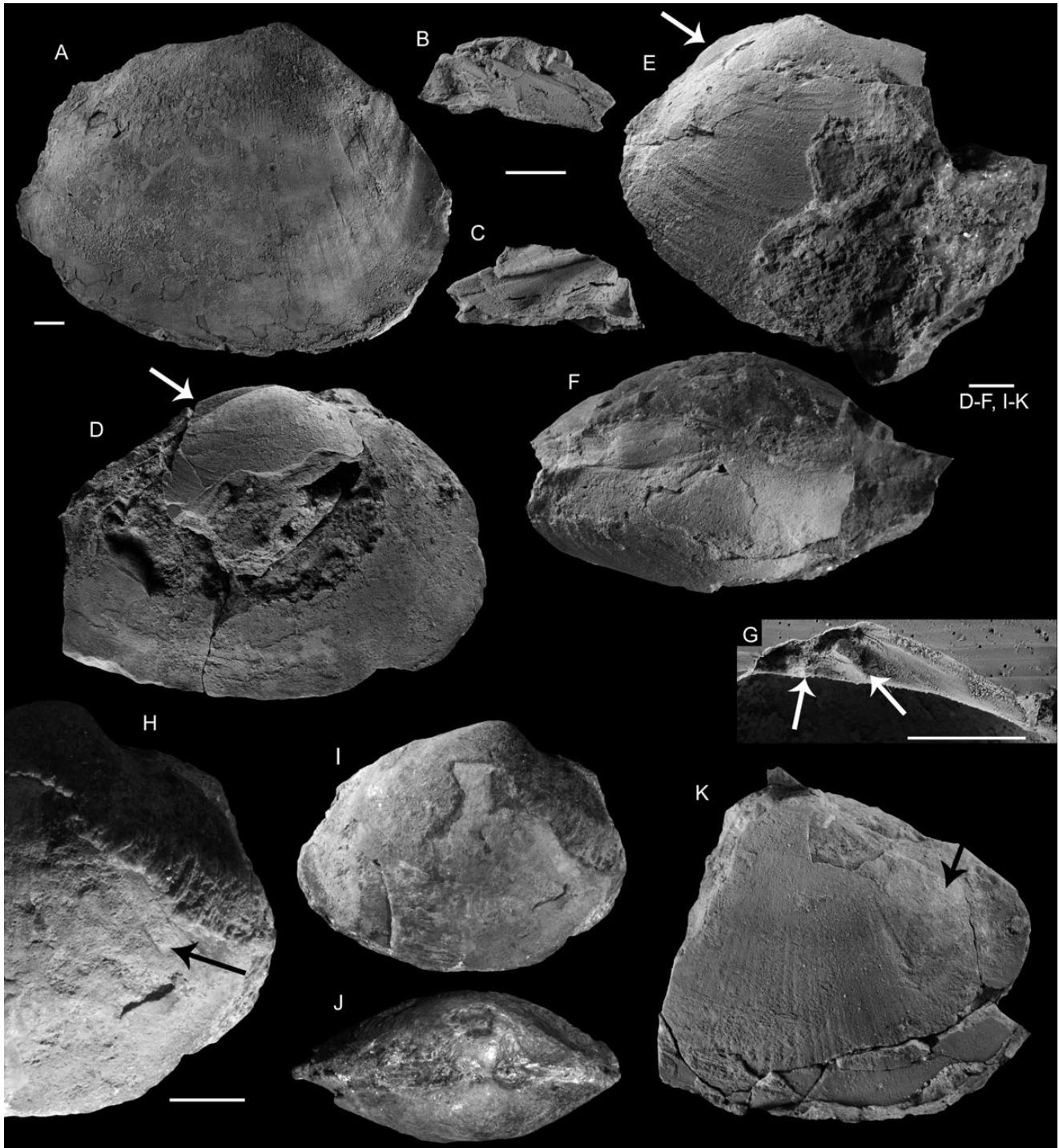


Figure 5. *Tehamatea colusaensis* (Stanton, 1895) from early Cretaceous seep deposits in California, USA; all but the holotype (I–K) are from the Rocky Creek seep deposit. **A.** Large internal mould showing the angular anterior adductor muscle scar and the regular radial striation (GZG.INV.88312). **B., C.** Moulds of the hinge of the same specimen as **A.** **D.** Internal mould showing large ligament (arrow) (GZG.INV.88314). **E., F.** Specimen with shell remains, showing the large ligament (GZG.INV.88315). **G.** Rubber cast of a right valve hinge; arrows indicate the two cardinal teeth (GZG.INV.88315). **H–J.** Holotype (USNM 23058) from Wilbur Springs, arrow indicates the anterior adductor muscle scars; specimen not whitened. **K.** Internal mould showing regular radial striation. Scale bars = 10 mm.

Diagnosis: Large, oval shell, up to 210 mm long; umbo prominent, elevated, slightly prosogyrate; lunule short, escutcheon lanceolate; sculpture of rough growth increments. Anterior adductor muscle scar narrow, elongate, detached from pallial

line for more than half its length, deviation from pallial line $c. 20^\circ$. Internal shell surface with regular radial striation or pits. Right valve hinge with one strong, vertical cardinal tooth.

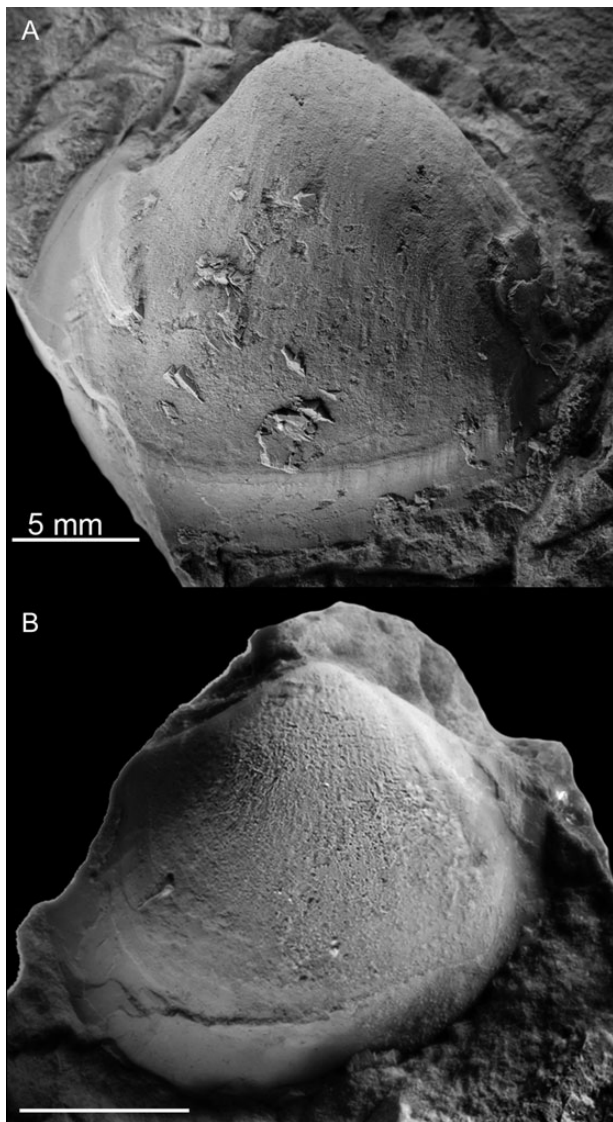


Figure 6. *Tehamatea agirrezabalai* n. sp. from Albian seep deposits near Ispaster, northern Spain. **A.** Internal mould showing anterior adductor muscle scar and pallial line (holotype GZG.INV.88321). **B.** Internal mould showing fine radial striation (paratype GZG.INV.88322). Scale bars = 5 mm.

Distribution: Methane seep deposits of Hauterivian age in the Vocontian Basin, southern France and the Planerskoje section on the Crimean peninsula, Ukraine.

Remarks: Macsotay (1980) and Lemoine *et al.* (1982) identified this species as *Pseudomiltha* aff. *germani*. The original *Lucina germani* Pictet & Campiche 1865 is based on a single specimen, represented by an internal mould, from an early Cretaceous environment dominated by large aporrhaid and nerineid gastropods (“*facies à ptérocères et à nérinées*”; Pictet & Campiche, 1865: 286). Such an assemblage is typical for a Mesozoic tropical shallow-water or lagoonal setting and thus very different from the methane-seep settings from which the here-reported specimens were collected. In addition, the specimen illustrated by Pictet & Campiche (1865: pl. 122, fig. 5) is flatter than the specimens from the seep deposits. The seep-related species is therefore considered as distinct from *Lucina germani* and is here described as *Tehamatea vocontiana* n. sp. It is similar in outline to the

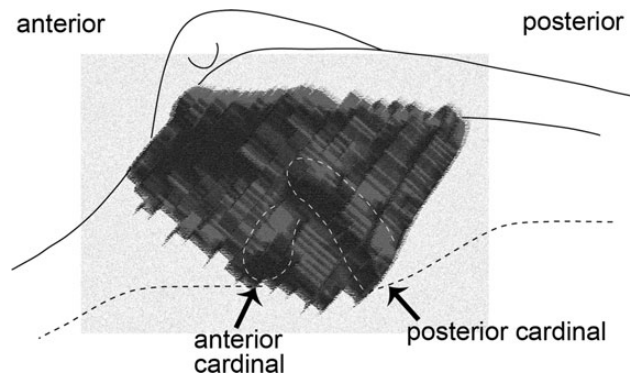


Figure 7. *Tehamatea agirrezabalai* n. sp., reconstruction of the hinge region of a right valve using serial grinding tomography and digital photo editing.

Californian-type species, *T. ovalis*, from which it differs mainly by its more prominent beak and the reduced anterior cardinal tooth.

The largest specimen reported from Rottier was 210 mm long (Thieuloy, 1972), the largest specimen that I collected at Rottier is a cross section of 128 mm height. From the Ukrainian locality near Planerskoje, Kiel & Peckmann (2008) figured a small specimen with only a single cardinal tooth in the right valve. The same hinge configuration is shown here also for a specimen from Curnier, France, by digital reconstruction of its hinge using serial grinding tomography (Fig. 9).

‘The edentulous seep lucinids’

Remarks: The four genera dealt with below, *Amanocina* n. gen., *Elliptiolucina* Cosel & Bouchet, 2008, *Elongatolucina* Gill & Little, 2013, and *Nipponothracia* Kanie & Sakai, 1997, form a group of closely related taxa that share large, smooth and edentulous shells which probably represents a single radiation into the seep environment. The latter three genera are in fact very difficult to distinguish—an increased knowledge of the morphological variation among species of the extant *Elliptiolucina* may even render them synonymous. When Cosel & Bouchet (2008) introduced *Elliptiolucina*, they did not discuss differences from *Nipponothracia*, and Okutani (2011: 116) considered that the “smaller but thicker shell with a smoother surface and characteristic concavity in the posterior adductor scar” distinguished *Elliptiolucina* from *Nipponothracia*, although the posterior adductor scar of the type species of *Nipponothracia* has actually never been shown in the published illustrations (i.e. Kanie & Sakai, 1997; Kase *et al.*, 2007). In their introduction of *Elongatolucina*, Gill & Little (2013) suggested that the straight ventral margin, the more elongate shell and the greater angle of divergence of the anterior adductor muscle scar of *Elongatolucina* distinguished it from *Elliptiolucina*. While the latter two characters probably do not distinguish those genera (*Elliptiolucina virginiae* Cosel & Bouchet, 2008, their fig. 17C, is just as elongate as *Elongatolucina elassodyseides* and its anterior adductor muscle scar has an angle of divergence approaching 40°, a value considered typical for *Elongatolucina* by Gill & Little, 2013), the ventral margin of *Elongatolucina* species is indeed nearly straight, unlike in *Elliptiolucina*. Furthermore, *Elongatolucina* has flattened sides, a feature that I have not seen in the published illustrations of species of *Elliptiolucina*. The new genus *Amanocina* clearly differs from these genera by having a longer anterior adductor muscle scar with a narrower angle of divergence, and by lacking the triangular excavation in the hinge plate.

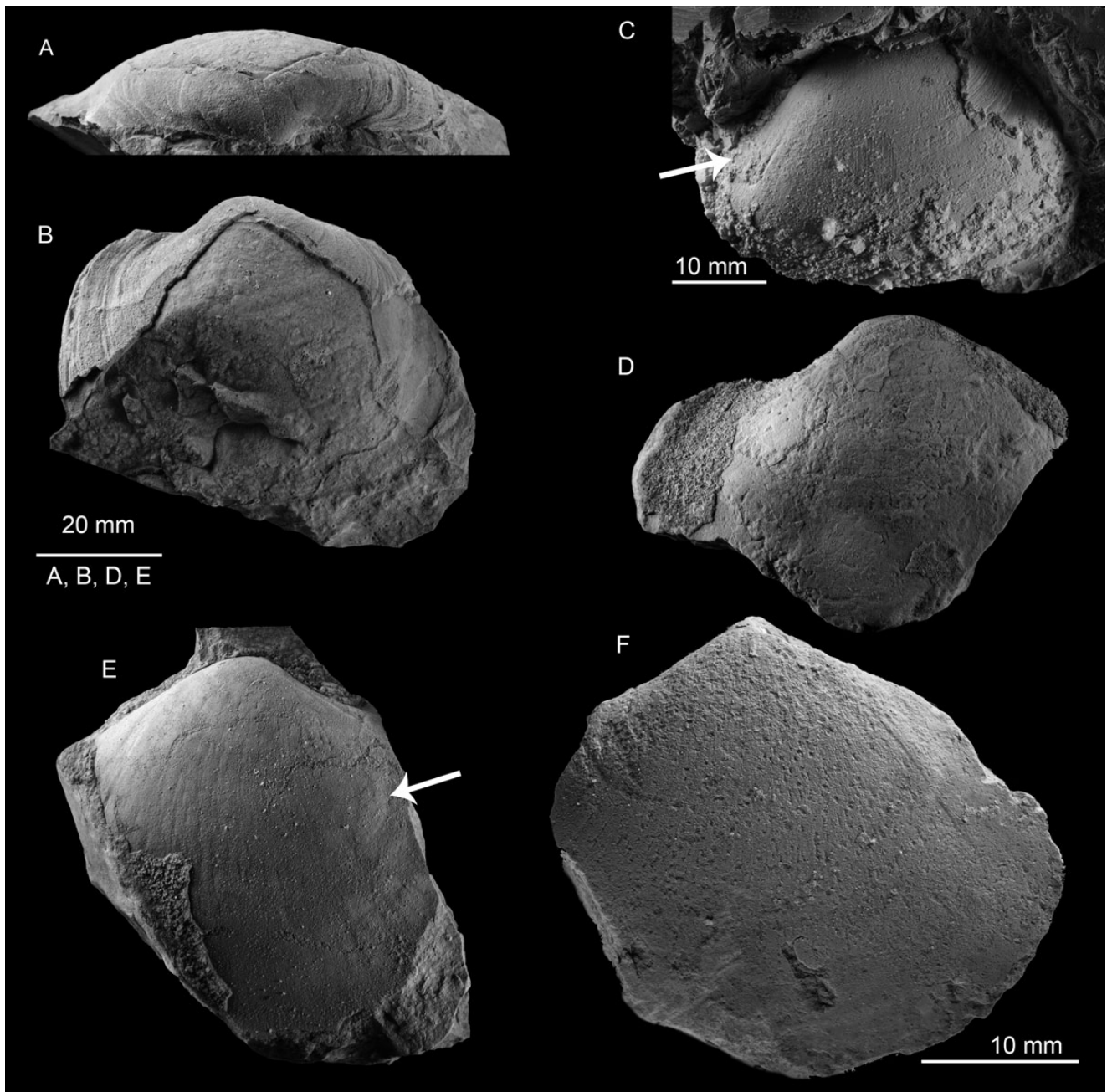


Figure 8. *Tehamatea vocontiana* n. sp. from early Cretaceous seep deposits in southern and southeastern Europe. **A, B.** Specimen from Rottier, France, with partially preserved shell (holotype GZG.INV.88323). **C.** Specimen used for serial grinding tomography, from Curnier, France, arrow indicates anterior adductor muscle scar. **D.** Specimen with partially preserved shell from the Planerskoje site, Ukraine, showing the elevated beak (GZG.INV.88324). **E.** Internal mould from Rottier, France, arrow indicating anterior adductor muscle scar (GZG.INV.88325). **F.** Internal mould from the Planerskoje site, Ukraine, with pitted internal striation (GZG.INV.88326). Scale bars **A, B, D, E** = 20 mm; **C, F** = 10 mm.

Genus *Elliptiolumcina* Cosel & Bouchet, 2008

Type species: *Elliptiolumcina magnifica* Cosel & Bouchet, 2008; OD; Recent, central Indo-West Pacific.

Included species: The Recent *E. labeyriei* Cosel & Bouchet, 2008 and *E. virginiae* Cosel & Bouchet, 2008 from Indonesia and the Philippines, *E. ingens* Okutani, 2011 from southern Japan, the late Miocene to early Pliocene *E. hetzeli* (Martin, 1933) from Indonesia and the Philippines, and *E. washingtonia* n. sp. from the late Oligocene of western Washington.

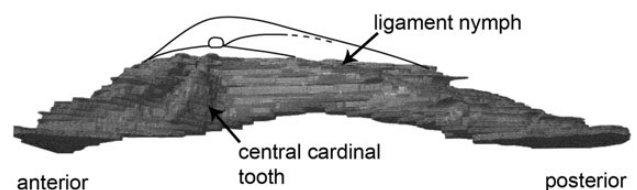


Figure 9. *Tehamatea vocontiana* new species, reconstruction of the hinge area of a right valve using serial grinding tomography and digital photo editing. Same specimen as Figure 8C, from Curnier, France.

***Elliptiolumina hetzeli* (Martin, 1933)**

(Fig. 10)

Lucina (*Miltha*) *hetzeli* Martin, 1933: 9, pl. 1, fig. 5.*Lucina* (*Pseudomiltha*) *hetzeli*—Beets, 1942: 313, pl. 30, figs 152–153.

Material examined: Two specimens from the asphalt deposits on Buton Island (Kalimantan, Indonesia, from stations 15204 and 42527) were studied at RMNH.

Remarks: Both investigated specimens show the ‘characteristic concavity in the posterior adductor scar’, a character that is thought to distinguish *Elliptiolumina* from *Nipponothracia* (Okutani, 2011: 116). In addition to the late Miocene Indonesian material, *E. hetzeli* has been reported from early Pliocene seep deposits on Leyte, Philippines, where they reach a length of up to 91 mm (Kase *et al.*, 2007; Majima *et al.*, 2007). This is considerably larger than the up to 58 mm long specimens from Buton Island.

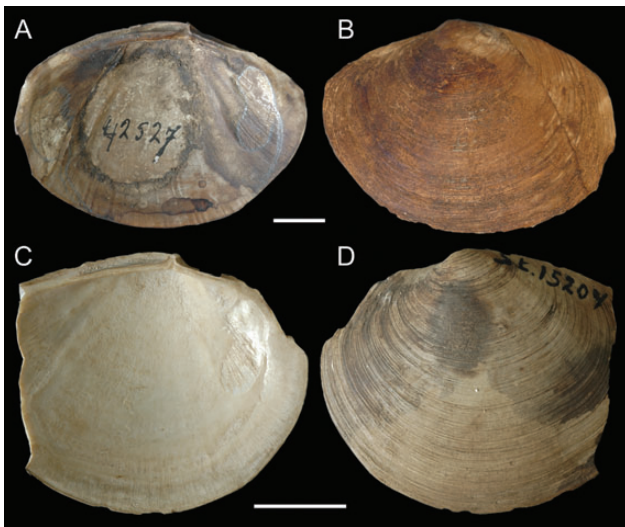


Figure 10. *Elliptiolumina hetzeli* (Martin, 1933) from the late Miocene asphalt deposit on Buton, Indonesia (RMNH); specimens not whitened. **A, B.** Almost entire left valve. **C, D.** Specimen with posterior part broken off. Scale bars = 10 mm.

***Elliptiolumina washingtonia* new species**

(Fig. 11)

Types: Holotype GZG.INV.88327, paratype GZG.INV.88328.

Type locality: LACMIP loc. 17747 in the Canyon River, western Washington State, USA.

Etymology: For Washington State.

Material examined: Six specimens from two localities along the Canyon River, western Washington State.

Diagnosis: Large, oval to elongate-oval shell, anterior margin somewhat pointed, posterior and ventral margins rounded, posterior sulcus indistinct; beak slightly elevated and prosogyrate, displaced anteriorly at about 37% of total shell length; surface sculpture of fine commarginal growth increments only. Interior with radial striation that becomes quite strong near the ventral shell margin, but fades quickly at pallial line; area beyond pallial line smooth; hinge area smooth, with triangular excavation below umbo; anterior adductor muscle scar broad and moderately elongate, reaching about half shell height, deviating from pallial line for about half its length, at an angle of about 35°; posterior adductor muscle scar small, quadrate.

Distribution: Late Oligocene of the Lincoln Creek Formation in western Washington State, USA.

Remarks: *Elliptiolumina washingtonia* n. sp. differs from the extant *E. labeyriei* Cosel & Bouchet, 2008 by its much larger size (135 mm in length) while *E. labeyriei* reaches only 53 mm in length (Cosel & Bouchet, 2008) and by its anterior adductor muscle scar, which has a larger angle of deviation from the pallial line than in *E. labeyriei*.

Genus *Elongatolumina* Gill & Little 2013

Type species: *Cryptolumina elassodysseides* Saul, Squires & Goedert, 1996, middle Eocene, Washington State, USA; OD.

Included species: *Elongatolumina* aff. *elassodysseides* from the Miocene of Venezuela and *E. peckmanni* n. sp. from the Oligocene of Colombia.

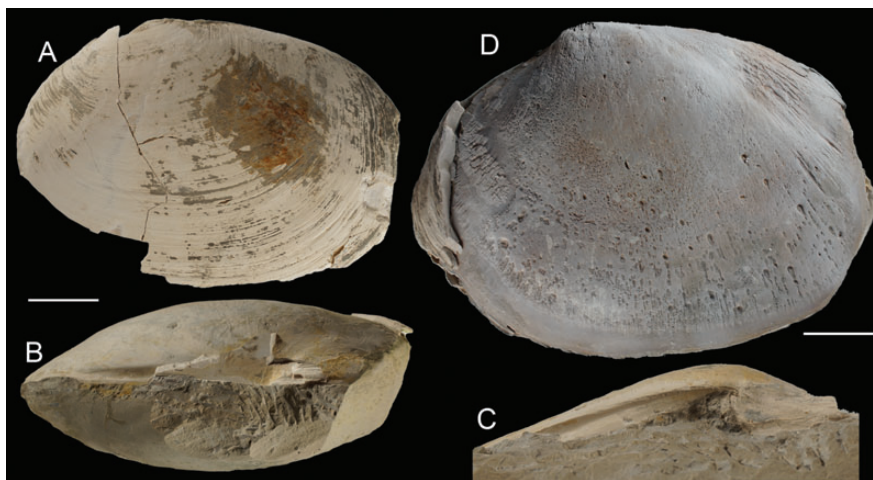


Figure 11. *Elliptiolumina washingtonia* n. sp. from the late Oligocene Lincoln Creek Formation in western Washington, USA. **A–C.** Paratype, not whitened (GZG.INV.88328), exterior of shell (**A**), dorsal view (**B**), hinge (**C**). **D.** Holotype (GZG.INV.88327), interior of left valve. Scale bars **A, B, D** = 20 mm; **C** = 10 mm.

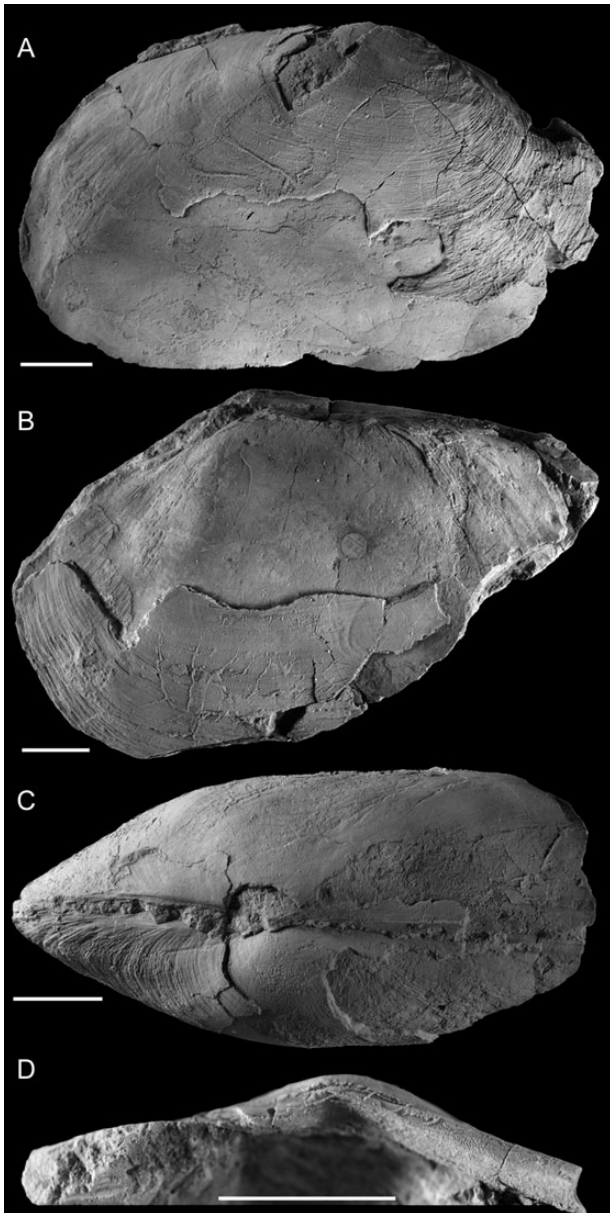


Figure 12. *Elongatolucina peckmanni* n. sp. from a presumably Oligocene seep deposit in Colombia. **A.** Holotype (USNM 558827). **B.** View of left valve of specimen showing the anterior adductor muscle scar (paratype, USNM 558828). **C.** Dorsal view of specimen with intact shell (paratype, USNM 558829). **D.** Specimen showing the edentulous hinge and the triangular excavation below the umbo (USNM 533985). Scale bars **A–C** = 20 mm; **D** = 10 mm.

***Elongatolucina peckmanni* new species**
(Fig. 12)

Lucinid Kiel & Peckmann, 2007: 351, fig. 5A, B.

Types: Holotype USNM 558827, paratypes USNM 533985, 558828, 558829.

Type locality: Seep deposit on the Palmar-Molinera road, Colombia.

Etymology: For Jörn Peckmann, Vienna, who was involved in the initial description of the type locality.

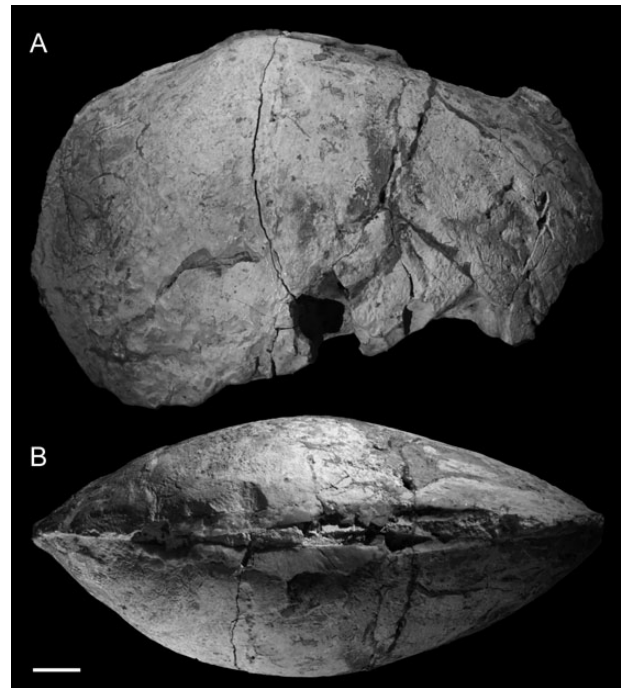


Figure 13. Holotype of *Nipponothracia lomitensis* (Olsson, 1931) from an Oligocene seep deposit in northern Peru (PRI); not whitened. Scale bar = 10 mm.

Material examined: Four specimens from the presumably Oligocene Palmar-Molinera-road site in Colombia.

Diagnosis: Large, elongate-oval shell, anterodorsal, posterodorsal and ventral margins straight, anterior side somewhat pointed, posterior margin rounded, shell laterally flattened, sculptured by fine growth lines; beak very low and nearly orthogyrate, in anterior position at 34.4–37.5% of total shell length; hinge edentulous, with triangular excavation below beak; anterior adductor muscle scar moderately long, reaching down to 36% of total shell height; posterior adductor muscle scar nearly round; pallial line entire, close to shell margin; shell interior with radial striation, especially strong on posterodorsal side.

Remarks: *Elongatolucina peckmanni* n. sp. is regarded here as distinct from both the Eocene *E. elassodyseides* from western Washington and from the Miocene *E. aff. elassodyseides* from Venezuela because (1) it is larger (length 175 mm or more versus only up to 135 mm in *E. elassodyseides*), (2) it has the umbo in a less anterior position (at 34.4–37.5% of total shell length versus 28.2–32.6% in the Venezuelan specimens and 27–32% in the Washington specimens of *E. elassodyseides*), (3) the anterior adductor muscle scar reaches lower (36% of total shell height versus 45–50% in the Venezuela specimens and 45–58% in the Washington specimens of *E. elassodyseides*) and (4) it appears to be broader (all measurements from the illustrations of Gill & Little, 2013, and own material from Washington).

Genus *Nipponothracia* Kanie & Sakai, 1997

Type species: *Thracidora gigantea* Shikama, 1968; OD; Middle Miocene, central Japan.

Included species: *N. lomitensis* (Olsson, 1931) from the Oligocene of northern Peru.

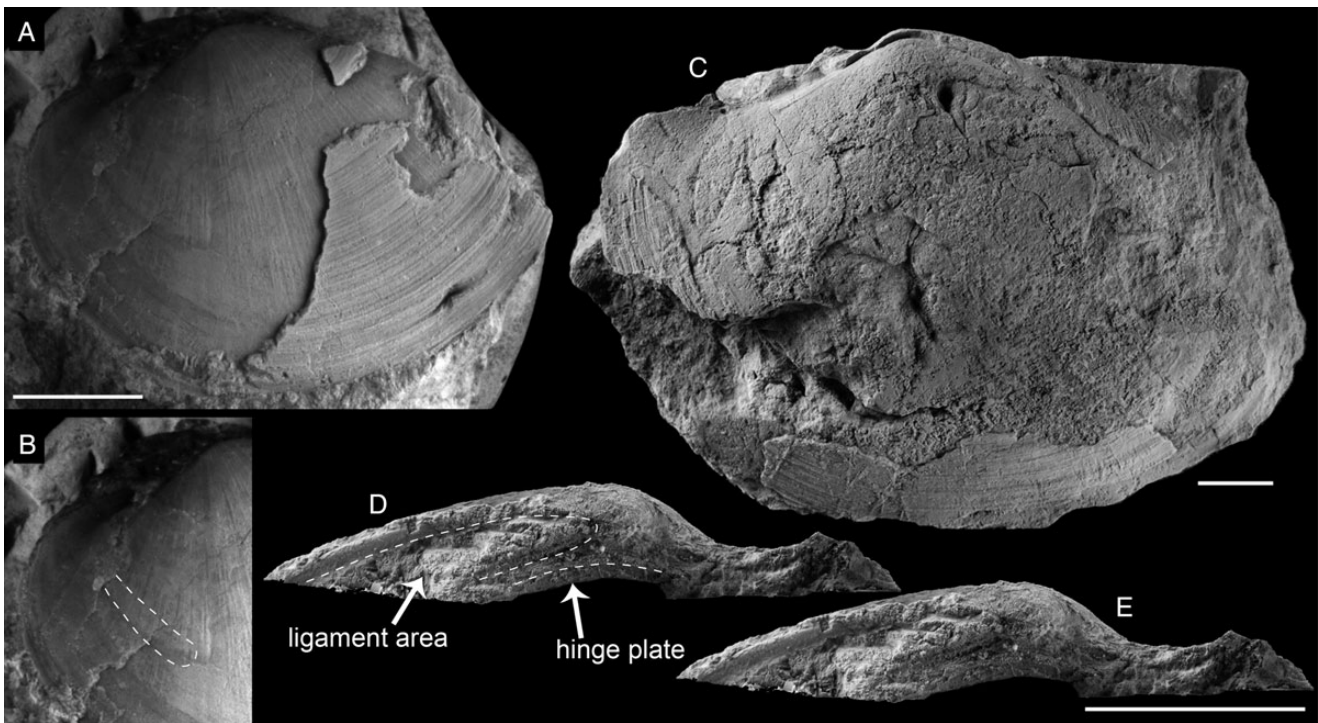


Figure 14. *Amanocina colombiana* n. sp. from a presumably Oligocene seep deposit in Colombia. **A, B.** Holotype (USNM 533986), view of exterior surface (**A**) and detail with anterior adductor muscle scar indicated by stippled line (**B**). **C–E.** Large specimen (paratype, USNM 558830); **C.** outline; **D.** view of hinge with ligament area and hinge plate indicated by stippled line; **E.** same view as **D** but without annotations. Scale bars = 10 mm.

***Nipponothracia lomitensis* (Olsson, 1931)**

(Fig. 13)

Lucina? *lomitensis* Olsson, 1931: 48, pl. 5, figs 1, 4.

Material examined: The two type specimens figured by Olsson (1931).

Remarks: The smaller of the two specimens (Olsson, 1931: fig. 1) has an evenly convex shell and the umbo in an anterior position at *c.* 32% of the total shell length. It shows a broad, elongate anterior adductor muscle scar that reaches just below the midline of the shell and is detached from the pallial line for about half its length, deviating from it by *c.* 20°. The larger specimen (Olsson, 1931: fig. 4) is poorly preserved but the cast of the hinge indicates that it is edentulous. It thus shows most characteristics of *Nipponothracia* and is therefore transferred here to this genus.

Genus *Amanocina* new genus

Type species: *Thracia yezoensis* Kanie & Kuramochi, 1996; Cenomanian, Hokkaido, Japan (Kanie & Kuramochi, 1996; Kiel *et al.*, 2008b).

Etymology: For Kazutaka Amano, Joetsu.

Diagnosis: Large, oval, little to moderately inflated shells with surface sculpture consisting only of fine growth lines. Beak sub-central or displaced slightly towards the anterior; hinge plate narrow, edentulous, without triangular excavation below umbo; pallial line distant from shell margin, marked by a fine groove; anterior adductor muscle scar narrow, elongate, reaching well below midline, detached from pallial line for most of its length, by only a very narrow angle; posterior adductor muscle scar small, round to slightly oval.

Included species: *Cryptolucina kuhnpassetensis* Kelly, 2000 from the Berriassian of Greenland (in Kelly *et al.*, 2000), *A. raukumara* n. sp. from the Albian of New Zealand and *A. colombiana* n. sp. from the Oligocene of Colombia.

Remarks: *Amanocina* differs from the other edentulous seep-related lucinids by its more slender and longer anterior adductor muscle scar, which stays close to the pallial line and reaches well below the midline of the shell. In the type species of *Nipponothracia*, *Elongatolucina* and *Elliptiolucina*, the anterior adductor muscle scar is broader, extends to about the shell's midline and deviates from the pallial line at a broader angle than in *Amanocina yezoensis* and its congeners (Saul *et al.*, 1996; Kase *et al.*, 2007; Cosel & Bouchet, 2008; Gill & Little, 2013). Furthermore, the hinge plate of *A. yezoensis* is smooth and narrow (Kiel *et al.*, 2008b), whereas in the type species of *Nipponothracia*, *N. gigantea*, the hinge plate is deeply excavated below the umbo. Also the hinge plate of *A. kuhnpassetensis* does not seem to be excavated (Kelly *et al.*, 2000), which might thus be another distinguishing character between the two genera; unfortunately, the hinge line of *A. raukumara* n. sp. described below is insufficiently preserved and does not show this character. Whether *Nipponothracia ponbetensis* from the Albian of Hokkaido, Japan, also belongs to *Amanocina* remains unclear, because internal features such as the anterior adductor muscle scar and the hinge are still unknown.

***Amanocina colombiana* new species**

(Fig. 14)

Lucinid Kiel & Peckmann, 2007: 351, fig. 5C, D.

Types: Holotype USNM 533986; paratype USNM 558830.

Type locality: Seep deposit on the Palmar-Molinera Road, Colombia.

Etymology: After Colombia.

Material examined: Four specimens including the types.

Diagnosis: Large, oval-venereoid shell with somewhat pointed posterior side; beak elevated, very slightly prosogyrate, displaced anteriorly at about 43% of total shell length; surface sculpture of fine commarginal growth increments only. Interior with fine radial striation; hinge plate narrow, edentulous, not excavated; ligament area broad; anterior adductor muscle scar, narrow, elongate, reaching well below midline of shell, detached from pallial line for about 70% of its length, deviation from pallial line about 15%.

Distribution: Type locality only.

Remarks: In a first report on the Colombian seep deposit (Kiel & Peckmann, 2007) two lucinid specimens were illustrated, one of which is here designated as holotype of *A. colombiana*. The other specimen was an isolated beak showing an edentulous hinge with a triangular excavation below the umbo. An additional specimen from this locality with an outline identical to the holotype, however, shows a hinge without triangular excavation below the umbo. The isolated beak figured in Kiel & Peckmann (2007: fig. 5A, B) thus does not belong to *A. colombiana*, but in fact to *Elongatolucina peckmanni* n. sp. described above. The largest intact specimen (Fig. 14C) is 96 mm long, 70 mm high and 15 mm wide (single valve). Two poorly preserved internal moulds in USNM from the same locality, which presumably also belong to *A. colombiana*, reach 140 mm in diameter.

***Amanocina raukumara* new species**

(Fig. 15)

Nipponothracia? sp. Kiel *et al.*, 2012: fig. 13M.

Types: Holotype TM8840, paratypes GNS TM8912, TM8913.

Type locality: Seep deposit 'Awanui 688' at Port Awanui, New Zealand.

Etymology: After the Raukumara Peninsula, North Island, New Zealand.

Material examined: Type material only.

Diagnosis: Large and oval but only slightly inflated shell with low and only slightly prosogyrate beak in an anterior position at 42–45% of total shell length; shell thin, sculptured by indistinct growth lines; hinge edentulous; anterior adductor muscle scar narrow, elongate, reaching well below midline to about 32% of total shell height, detached from pallial line for about 72% of its length, at an angle of no more than 12 degrees; posterior adductor muscle scar indistinct, oval, with two grooves radiating from the umbo to its dorsal and ventral sides. Hinge plate narrow, edentulous; interior of shell with irregular, indistinct radial striations. Largest specimen 80 mm long, 64 mm high and 16 mm thick.

Remarks: I attempted to prepare the hinge area of two specimens, which was difficult due to carbonate precipitates and recrystallization in this area. Although the hinges were clearly edentulous, they were impossible to photograph. *Amanocina raukumara* n. sp. differs from the type species, *A. yezoensis*, in its more oval outline, less distinct interior striation, and less elevated beaks. Also *A. kuhnpassetensis* has more elevated beaks than *A. raukumara* and is more inflated.

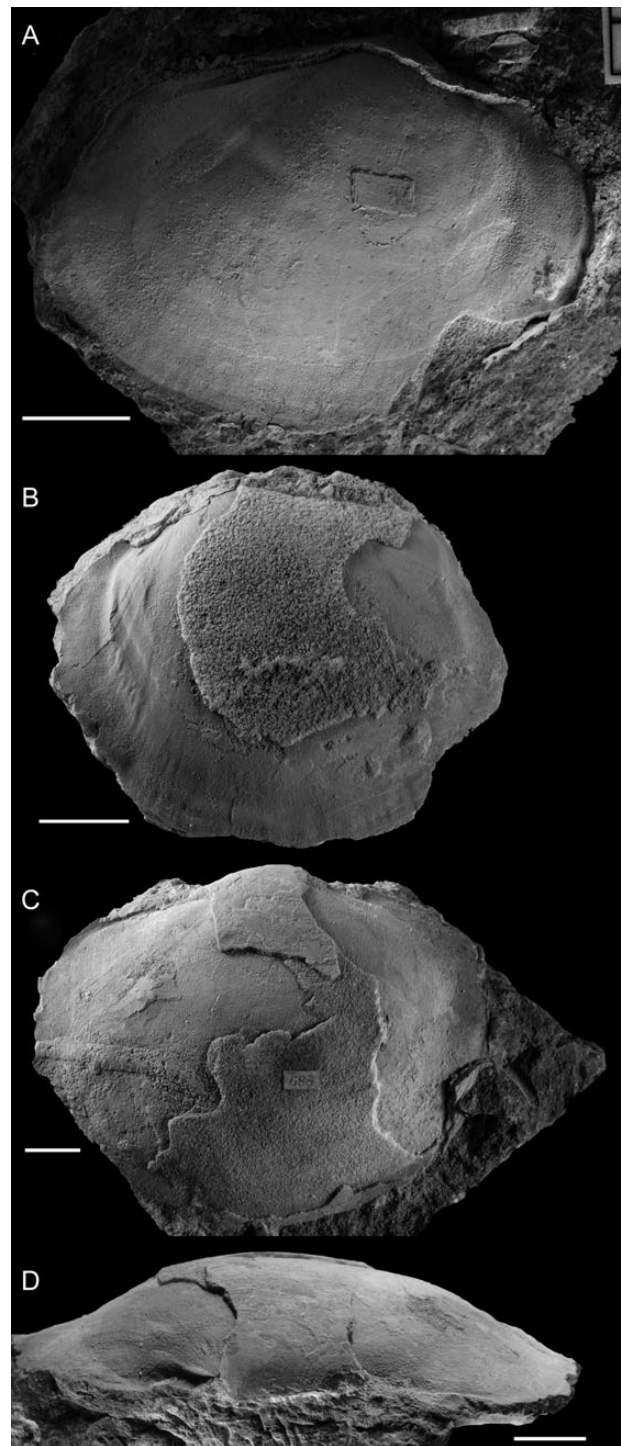


Figure 15. *Amanocina raukumara* n. sp. from a Cenomanian seep deposit at Port Awanui on the Raukumara Peninsula, North Island, New Zealand (site Awanui GS688). **A.** Holotype showing outline, anterior adductor muscle scar and other internal features (GNS TM8840). **B.** View of left valve showing anterior adductor muscle scar (paratype GNS TM8912). **C, D.** Large specimen, lateral view of right valve (**C**) and dorsal view (**D**) (paratype GNS TM8913). Scale bars = 10 mm.

Subfamily Codakiinae Korobokov, 1954

Remarks: This subfamily has recently been redefined based on molecular phylogenetic evidence to include mainly *Codakia* Scopoli, 1777, *Ctena* Mörch, 1861, and *Lucinoma* Dall, 1901,

which share shells with regularly spaced, commarginal lamellae, prominent cardinal teeth, and long, narrow, anterior adductor muscle scars (Taylor *et al.*, 2011). These characters are also seen in the Cretaceous to Palaeocene genus *Nymphalucina*, which is therefore here included in Codakiinae.

Genus *Nymphalucina* Speden, 1970

Type species: *Tellina occidentalis* Morton, 1842; Maastrichtian of the Western Interior Seaway, North America.

Nymphalucina panochensis new species (Fig. 16)

Lucinid bivalve Schwartz *et al.*, 2003: 344, fig. 5f.

Types: Holotype GZG.INV.88317, paratypes GZG.INV.88316 and GZG.INV.88318.

Type locality: Seep deposits in the Panoche Hills, central California.

Etymology: For the Panoche Hills.

Material examined: Six specimens including types.

Diagnosis: Subquadrate, flat shell, slightly longer than high, posterior margin strongly truncate, anteroventral margin well rounded, beak pointed, slightly elevated; sculpture of fine, sharp, regular lamellae; hinge of left valve with two moderately strong cardinals that radiate away from each other, and a socket

about the width of the teeth between them; interior of shell with radial grooves and pits; anterior adductor muscle scar elongate, moderately narrow, straight to slightly undulating, detached from pallial line for most of its length, at an angle of *c.* 15°. Largest specimen 47 mm long and 38 mm high.

Distribution: Early Palaeocene seep deposits in the Panoche Hills, central California.

Remarks: Species of *Nymphalucina* are common at shallow-water methane seeps in the Late Cretaceous Western Interior Seaway in North America (Kauffman *et al.*, 1996; Kiel *et al.*, 2012). *Nymphalucina panochensis* n. sp. can easily be distinguished from all other species of *Nymphalucina* by its extremely truncate posterior margin. Furthermore, its cardinals in the left valve point in a more anterior direction than in the other species of *Nymphalucina*. Specimens of *N. cleburni* (White, 1882) are here illustrated (Fig. 17) for comparison; this species was hesitantly considered as synonym of the type species *N. occidentalis* by Speden (1970).

With its truncate posterior margin and distinct commarginal ribs, *N. panochensis* is very similar to species of *Plastomiltha* Stewart, 1939. The type species, *P. claibornensis* (Conrad), as figured by Harris (1919: pl 39, figs 8, 9) is very similar externally, just a little more rounded, but on the inner side of the shell *P. claibornensis* has a much thinner and more elongate anterior adductor muscle scar than *N. panochensis* and a distinct ridge running from the umbo to the anterior side of the posterior adductor muscle scar, a feature not seen in *N. panochensis*. Also similar is the Eocene *Plastomiltha? odontota* Woodring, 1982 from Panama (Woodring, 1982: pl. 84, figs 4–6), but this species also has a thinner and more elongate anterior adductor muscle scar than *N. panochensis*. Although the preservation of the specimens of *N. panochensis* is poor, a deep lunule that would affect the hinge dentition, as described for members of *Plastomiltha* (Harris, 1919; Gardner, 1926; Stewart, 1930) was not seen. Lastly, species of *Plastomiltha* have a roundish outline while in *N. panochensis* the ventral margin is posteriorly almost straight or only slightly convex, and the transition to the posterior margin is abrupt.

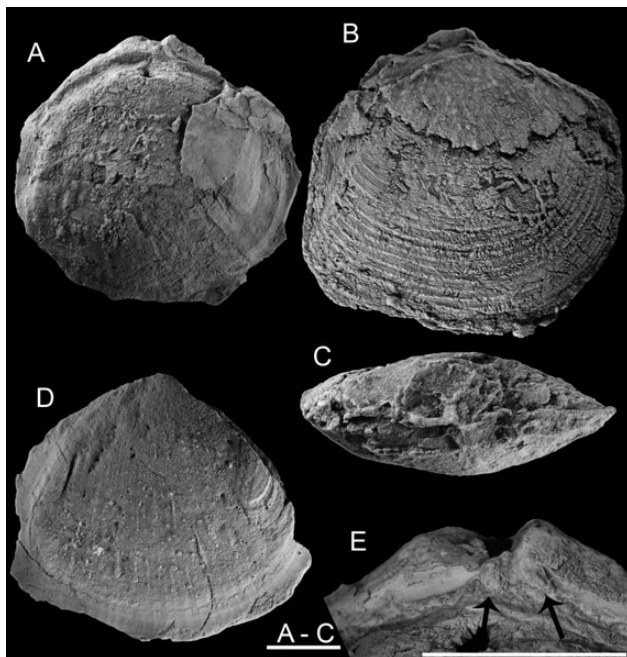


Figure 16. *Nymphalucina panochensis* n. sp. from early Palaeocene (Danian) seep deposit in Panoche Hills, California, USA. **A.** Paratype showing anterior adductor muscle scar (GZG.INV.88316). **B.** **C.** Holotype showing outline and external sculpture (**B**) and the convexity of the shell (**C**) (GZG.INV.88317). **D.** Internal mould showing pallial line and internal striation (paratype GZG.INV.88318). **E.** Close-up of the left valve hinge of specimen in **A**, after some preparation; arrows indicate the two cardinal teeth. Scale bars = 10 mm.

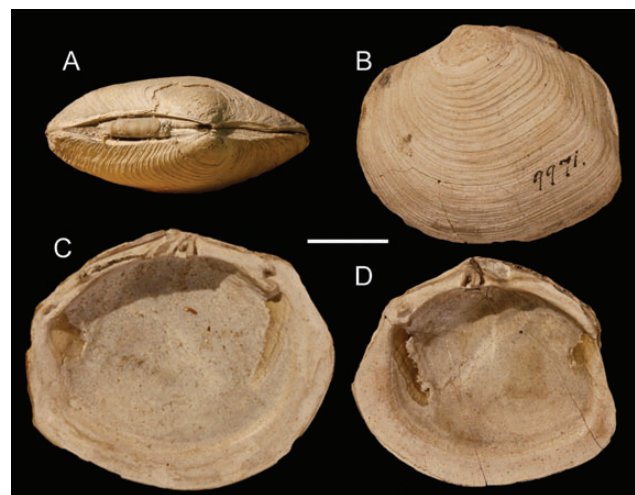


Figure 17. *Nymphalucina cleburni* (White, 1882) from Late Cretaceous sediments "50 miles East of Greeley, Colorado" (USNM 9971); specimens not whitened. Specimen in dorsal view (**A**) showing thick ligament and asymmetrical lunule, and a view of the external surface (**B**) showing sculpture and the posterior ridge. **C.** Interior features of left valve. **D.** Interior features of right valve. Scale bar = 10 mm.

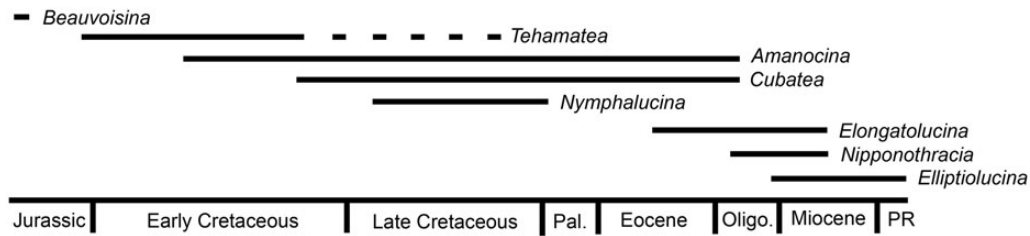


Figure 18. Geologic ranges of the lucinid genera reported here. Abbreviations: Pal., Palaeocene; Oligo., Oligocene; PR, Pliocene to Recent.

Nymphalucina panochensis is the most common macrofaunal element at the seep deposits at Right Angle Canyon in the Panoche Hills.

Notes on fossil seep lucinids for which no new data are available

Epilucina washingtoniana (Clark, 1925) was found at two late Eocene seep deposits in southern California by Squires & Gring (1996) who briefly discussed other reports of this species in late Eocene sediments along the North American west coast, which are potential seeps or other sulphide-rich habitats. Taylor *et al.* (2011) tentatively placed *Epilucina* in the subfamily Codakiinae.

An unnamed species of *Ezolucina* has been reported from a Campanian seep deposit on the North Island of New Zealand (Kiel *et al.*, in press). This species indeed has a general shell shape resembling that of the Cenomanian-type species of *Ezolucina*, *Vesicomya inflata* Kanie & Nishida, 2000, from Hokkaido, Japan (Amano *et al.*, 2008). But such veneroid shells with pointed posterior margin can also be seen in other genera of seep-related lucinids, for example *Tehamatea colusaensis* and to some extent in *Amanocina colombiana*, and thus a reliable identification of '*Ezolucina*' sp. from New Zealand must await specimens with preserved internal features.

Members of the genus *Lucinoma* are very common at Cenozoic seep deposits in the North Pacific realm (see reviews by Majima *et al.*, 2005 and Kiel, 2010b). For those in western Washington, Goedert *et al.* (2003) suggested that they are more common at seeps from shallower paleodepths. A thorough treatment of the many records of *Lucinoma* at fossil seep deposits, however, would go beyond the scope of the present study.

The taxonomic affinities of *Myrtea?* sp. from the Campanian-Maastrichtian (Late Cretaceous) Sada Limestone seep deposits in Japan (Nobuhara *et al.*, 2008) is still unclear due to its poor preservation. *Myrtea cooki* Olsson, 1931 was reported from a seep deposit in the Peruvian Oligocene (Olsson, 1931; Kiel & Peckmann, 2007) and is based on a single specimen from Belen near Lagunitos in the Piura Department in northern Peru. Externally it has the same oval outline and smooth surface as most of the lucinids documented here, and there is no chance to prepare the specimen in a way to reveal hinge dentition and muscle scars. Clarifying the systematic affinities of this species will require the collection of additional material, but *Myrtea* seems an unlikely genus for this species due to the lack of distinct sculpture. *Myrtea amorpha* (Sturany, 1896) was reported from modern seeps in the eastern Mediterranean Sea (Olu *et al.*, 2004).

Lucinids tentatively identified as *Miltha* have been reported from Late Cretaceous seep deposits of Japan (Hikida *et al.*, 2003; Jenkins *et al.*, 2007) and the Miocene of New Zealand (Campbell *et al.*, 2008b). No further material or information are available for these species and their taxonomic affinities remain uncertain.

Saxolucina (*Megaxinus*) *matsushitai* Matsumoto, 1971 from lower Miocene limestones within mudstone of the Wappazawa Formation in central Japan (Matsumoto, 1971) has a strong

prosogyrate beak, unlike most species described here, and both Majima *et al.* (2005) and Kase *et al.* (2007) suggested that it may belong to *Cryptolucina* Saul, Squires & Goedert, 1996. The type species of *Cryptolucina*, *C. megadyseides* Saul, Squires & Goedert, 1996, was described from middle Eocene mudstone of the Humpulips Formation in western Washington (Saul *et al.*, 1996) and may actually not be seep-related.

Lastly, there are a few reports of undetermined 'lucinid bivalves' from ancient seep deposits. Among these, an illustrated specimen from the late Jurassic-early Cretaceous Sassenfjorden seeps on Svalbard (Hammer *et al.*, 2011: fig. 7D, E) shows an anterior adductor muscle scar resembling that of *Tehamatea*, but its hinge is as yet unknown and its classification remains uncertain. A few 'lucinid' specimens from the late Jurassic Gateway Pass seep deposits on Alexander Island, Antarctica (Kelly *et al.*, 1995), were investigated by the author in the collection of the British Antarctic Survey, but they were poorly preserved and fragmentary, and impossible to determine. Also the Cenozoic lucinids from seeps on Barbados and Trinidad (Gill *et al.*, 2005) require further work.

DISCUSSION

The Lucinidae are the most diverse family of chemosymbiotic bivalves and have a wide bathymetric range, although the vast majority of species live in shallow water (Taylor & Glover, 2006). The late Jurassic to Miocene seep-related lucinids reported here, however, show an interesting history of adaptation to this environment from deep-water ancestors. All except *Nymphalucina panochensis* appear to belong to the subfamily Myrteinae, as defined by Taylor *et al.* (2011), based on their oval to elongate-oval shells, their short to moderately long anterior adductor muscle scars and their overall lack of sculpture. The Myrteinae are essentially a deep-water subfamily and, indeed, none of the species reported here belongs to coeval shallow water genera but instead to genera that are restricted to hydrocarbon seeps or at least areas enriched in decaying terrestrial plant matter.

The seep-related genera reported here fall within two groups, the edentulous *Amanocina-Nipponothracia-Elliptiolucina-Elongatolucina* group and the group consisting of *Beauvoisina*, *Cubatea*, *Ezolucina* and *Tehamatea*, whose members have one or two strong cardinal teeth in each valve. These groups likely represent two independent radiations within the Myrteinae. The West Atlantic *Jorgenia* and *Graecina* with their very flat shells, low umbo and small hinge teeth (Taylor & Glover, 2009) do not fit into either of these two groups and thus appear to represent a third group of seep-related myrteines. There are no fossils assignable to these two genera in the Eocene to Miocene fossil record of seep deposits in the Caribbean region (Gill *et al.*, 2005; Kiel & Peckmann, 2007; and herein) and they might thus represent a young, post-Miocene radiation.

The only other lucinid subfamily to include seep-inhabiting taxa is the Codakiinae, which are largely a shallow-water clade (Taylor *et al.*, 2011). The most widespread seep-inhabiting

genus of Codakiinae is *Lucinoma* (Salas & Woodside, 2002; Olu *et al.*, 2004), whose earliest occurrence at seeps and at local enrichments of organic matter is in the Oligocene (Goedert & Campbell, 1995; Goedert *et al.*, 1995; Kiel & Goedert, 2006). Taylor *et al.* (2011) suggested a Cretaceous origin of the extant Codakiinae, thus *Nymphalucina* might be one of its geologically oldest members. Whether *Nymphalucina* gave rise to the seep-inhabiting genus *Lucinoma*, however, remains unclear. Another potential member of the Codakiinae is *Epilucina* (cf. Taylor *et al.*, 2011), with *Epilucina washingtonia* reported from a late Eocene seep in California (Squires & Gring, 1996).

In summary, the majority of lucinids found in deep-water methane seep deposits of Jurassic and Cretaceous age belong to genera restricted to this type of environment. Furthermore, they belong to the subfamily Myrteinae, which today is largely a deep-water group, suggesting a deep-water ancestor for the seep-inhabiting genera. Several of these genera continued into the Cenozoic (Fig. 18). During the Cenozoic the Codakiinae also appeared at deep-water seeps, namely *Epilucina* and the widespread *Lucinoma*, but neither of these codakiine genera is restricted to seeps.

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