

# Mollusks and a crustacean from early Oligocene methane-seep deposits in the Talara Basin, northern Peru

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Kiel, S., Hybertsen, F., Hyžný, M., and Klompmaker, A.A. 2020. Mollusks and a crustacean from early Oligocene methane-seep deposits in the Talara Basin, northern Peru. *Acta Palaeontologica Polonica* 65 (1): 109–138.

A total of 25 species of mollusks and crustaceans are reported from Oligocene seep deposits in the Talara Basin in northern Peru. Among these, 12 are identified to the species-level, including one new genus, six new species, and three new combinations. *Pseudophopsis* is introduced for medium-sized, elongate-oval kalenterid bivalves with a strong hinge plate and largely reduced hinge teeth, rough surface sculpture and lacking a pallial sinus. The new species include two bivalves, three gastropods, and one decapod crustacean: the protobranch bivalve *Neilo altamirano* and the vesicomid bivalve *Pleurophopsis talarensis*; among the gastropods, the pyropeltid *Pyropelta seca*, the provannid *Provanna pelada*, and the hokkaidoconchid *Ascheria salina*; the new crustacean is the callianassid *Eucalliax capsulasetaea*. New combinations include the bivalves *Conchocele tessaria*, *Lucinoma zapotalensis*, and *Pseudophopsis peruviana*. Two species are shared with late Eocene to Oligocene seep faunas in Washington state, USA: *Provanna antiqua* and *Colus sekiuensis*; the Talara Basin fauna shares only genera, but no species with Oligocene seep fauna in other regions. Further noteworthy aspects of the molluscan fauna include the remarkable diversity of four limpet species, the oldest record of the cocculinid *Coccopigya*, and the youngest record of the largely seep-restricted genus *Ascheria*. *Eucalliax* is recorded for the first time from a seep and from the Oligocene.

**Key words:** Gastropoda, Bivalvia, Crustacea, Decapoda, biogeography, cold-seep, Paleogene, South America.

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Received 2 May 2019, accepted 20 September 2019, available online 6 December 2019.

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## Introduction

Our understanding of the fossil record of deep-water methane-seep communities, especially of the Cenozoic Era, has remarkably improved over the last decade. However, most systematic studies are restricted to a few regions in the northern Hemisphere, including western Washington state, USA (Kiel 2006, 2008; Kiel and Amano 2013; Hybertsen and Kiel 2018), Japan (Amano and Kiel 2010, 2011, 2012; Amano and Jenkins 2011a, b, 2013; Amano and Little 2014; Amano et al. 2014a; Miyajima et al. 2017), and Italy (Kiel and Taviani 2017, 2018; Kiel et al. 2018), and only a few studies have covered more than one region or had a world-wide scope (Amano and Kiel 2007; Kiel 2013; Gill and Little 2013; Kiel and Hansen 2015; Amano et al. 2015; Hryniewicz et al.

2017). For the southern Hemisphere, thorough taxonomic work has only been carried out for the Miocene seep deposits of New Zealand (Saether et al. 2010a, b, 2012, 2016; Amano et al. 2014b, 2015, 2018b), and a single Miocene site has been reported from central Chile (Contardo-Berríos et al. 2017).

Seep communities from Oligocene strata in northern Peru have long been known (Olsson 1931; Goedert and Squires 1993; Kiel and Peckmann 2007), but these species-rich faunas have never been systematically revised, except for a few lucinid bivalve specimens from Olsson's original collection (Kiel 2013). Here we report on newly collected mollusk and crustacean specimens from these seep deposits, and describe one new genus and six new species, provide taxonomic updates on several of the known species, and provide a comparison between Olsson's collection and the new fossils.

*Institutional abbreviations.*—NRM, Swedish Museum of Natural History, Stockholm, Sweden; PRI, Paleontological Research Institution, Ithaca, USA; USNM, Smithsonian Museum of Natural History, Washington, DC, USA.

*Other abbreviations.*—L, length; W, width; H, height; RV, right valve; LV, left valve.

*Nomenclatural acts.*—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:CA2D2F4A-AE41-441F-A205-B334CD055FBE

## Material and methods

Details on the sampling localities in the Talara Basin in northern Peru (Fig. 1) have been presented previously (Kiel et al. 2019). In short, the material reported here originates from three areas: (i) The Belén seep site, named after a long-vanished settlement from the initial oil boom in the early 1900s, situated about 10 km SE of Negritos. (ii) The Cerro La Salina hills along the southern side of Quebrada Seca north of Mancora, where nine individual limestone concretions were sampled; these are here referred to as La

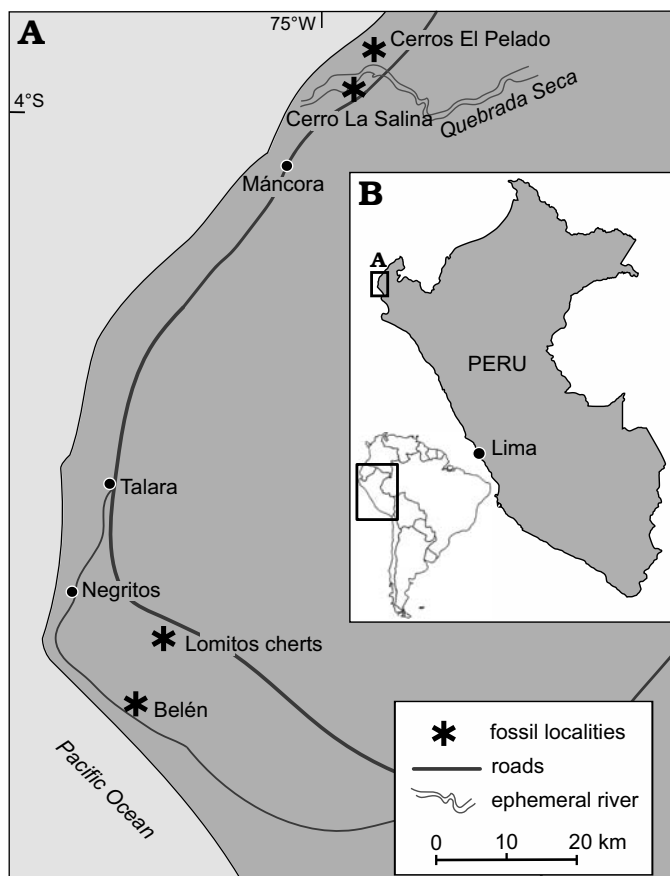


Fig. 1. Locality map of the seep deposits in the Talara Basin in northern Peru, where the here described mollusk and crustacean taxa were found (adopted from Kiel et al. 2019).

Salina blocks 1 to 9. (iii) The Cerros El Pelado hills along the northern side of Quebrada Seca north of Mancora; three individual limestone concretions were sampled here, but only one of them (block 2) yielded identifiable fossils (Kiel et al. 2019). The fossils from all three areas are of early Oligocene age, with a small chance that those from Cerros El Pelado may be of late Eocene age (Kiel et al. 2019).

All specimens are housed at NRM, except for material collected by Axel A. Olsson, including one neritid specimen from the Lomitos cherts about 6 km east of Negritos, which was mentioned but not illustrated by Olsson (1931), housed at PRI, and the holotypes of *Vesicomya tschudi* Olsson, 1931, and *V. ramondi* Olsson, 1931, both housed at PRI. Lastly, we illustrate several specimens of “*Pleurophopsis*” *peruviana* Olsson, 1931, housed at USNM. These specimens were collected by Wendell P. Woodring and Axel A. Olsson on January 15, 1958, at USGS locality 21219, which is located on the southeastern side of Cerro La Salina and has previously been characterized petrographically and isotopically (Kiel and Peckmann 2007).

The specimens were extracted and prepared from the rock matrix using a pneumatic hammer. Small specimens were photographed using a Cognisys Stackshot 3X stacking image system and the Zerene Stacker software, combining 15 to 25 pictures for each composite image. All specimens were coated with ammonium chloride for photography, except when noted otherwise.

## Systematic paleontology

Phylum Mollusca Linnaeus, 1758

Class Bivalvia Linnaeus, 1758

Subclass Protobranchia Pelseneer, 1889

Family Malletiidae Adams and Adams, 1858

Genus *Neilo* Adams, 1854

*Type species:* *Neilo cumingii* Adams, 1854 [= *Neilo australis* (Quoy and Gaimard, 1835)], by monotypy; Recent, New Zealand.

*Neilo altamirano* sp. nov.

Fig. 2A.

*Zoobank LCID:* urn:lsid:zoobank.org:act:4A36FC09-E842-43D3-9DFC-D55D9A246345

*Etymology:* In honour of Ali Altamirano (Lima, Peru), for his help collecting the fossils.

*Holotype:* NRM Mo187001, an internal and external mold of LV, with some shell material preserved.

*Type locality:* Cerro La Salina (block 1), northern Peru.

*Type horizon:* Presumably the early Oligocene part of the Heath shale.

*Material.*—Type material only.

*Diagnosis.*—Well-inflated, subrectangular shell, tallest at umbo, strongest inflation at posterior third; anterior margin truncate, straight; posterior margin straight; posterior

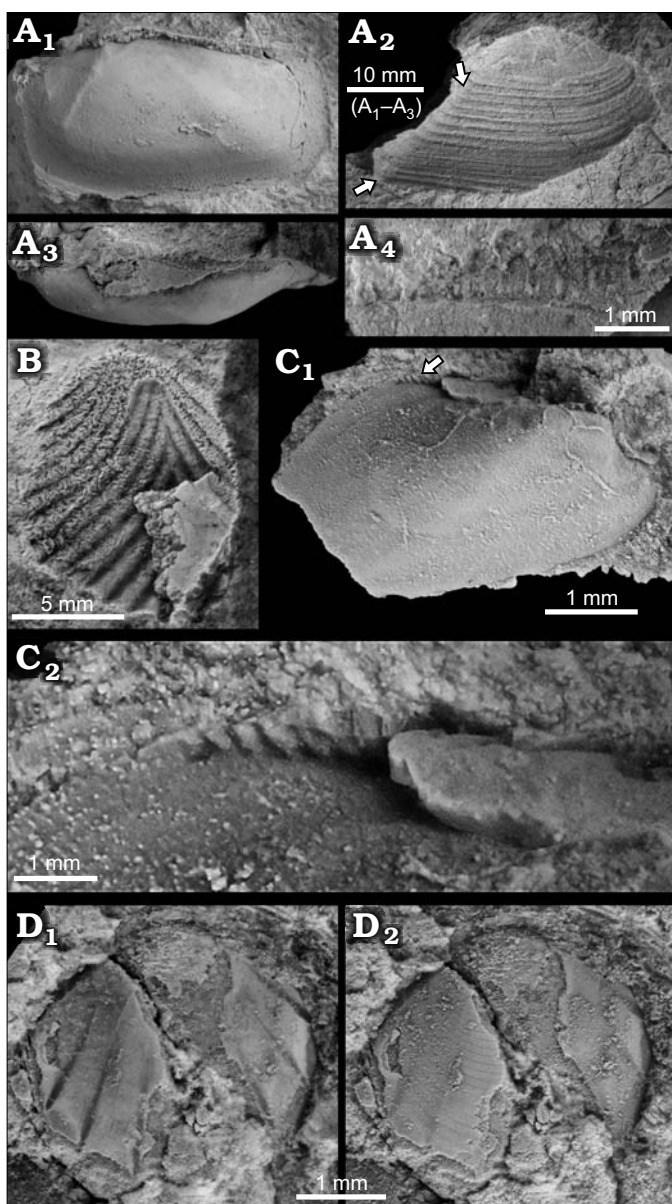


Fig. 2. Protobranch and pteriomorph bivalves from early Oligocene seep deposits from the Cerro La Salina (block 1, A; block 6, D; block 9, C) and Belén seep deposit (B), Talara Basin, northern Peru. **A.** Malletiid *Neilo altamirano* sp. nov. (NRM Mo187001, holotype), internal mold in lateral view (A<sub>1</sub>); external mold in lateral view (A<sub>2</sub>), arrows indicating the posterior ridge; view on the dorsal side (A<sub>3</sub>); close-up on the taxodont hinge dentition (A<sub>4</sub>). **B.** The possible nuculid *Acila?* sp. (NRM Mo187002), external mold of outer shell surface. **C.** The bathymodiolin *Idas* sp. (NRM Mo187003), internal mold of the entire specimen (C<sub>1</sub>), arrow indicating the taxodont teeth; close-up on taxodont teeth on posterodorsal shell margin (C<sub>2</sub>). **D.** Propeamussiidae indet. (NRM Mo187004), uncoated specimen showing internal radial ridges (D<sub>1</sub>); specimen coated with ammonium-chloride, highlighting external sculpture (D<sub>2</sub>).

ridge well defined; sculpture of irregularly spaced, blunt commarginal ribs, interspaces roughly twice the width of the ribs.

**Dimensions** (in mm).—The holotype NRM Mo187001, L = 20, H = 12, and the single valve ca. 4 mm thick.

**Description.**—Shell subrectangular, well-inflated, postumbonal part about 2/3 of shell length, maximum shell height at umbo; anterodorsal margin slightly convex, anterior margin truncate and straight, ventral margin slightly convex due to angulation opposite of umbo, posterior margin truncate, posterodorsal margin very slightly concave. Posterior area defined by ridge running from behind umbones to posteroventral corner; sculpture consists of irregularly spaced, blunt, commarginal ribs, with fine commarginal lines between; these ribs bent sharply upward at posterior ridge. Distinct groove internally from umbo to anteroventral margin; anterior adductor muscle scar oval and just anterior to this groove, posterior adductor muscle scar indistinct; hinge with row of taxodont teeth.

**Remarks.**—No *Neilo* species were reported from the Eocene to Miocene deposits in Peru and Ecuador so far. Quite similar in shell outline and sculpture are *Neilo ortmanni* Erdmann and Morra, 1985, from the late Eocene to early Oligocene San Julián Formation in eastern Patagonia (Argentina) and *Neilo ornata* (Sowerby, 1846) from late Oligocene–early Miocene sediments near Puerto Deseado in eastern Patagonia (Erdmann and Morra 1985; Del Río and Camacho 1998; Griffin and Nielsen 2008). Both species differ from *N. altamirano* by their rostrate posterior margin, whereas *N. altamirano* has a vertically truncated, almost straight posterior margin. The early Miocene *Neilo volckmanni* (Philippi, 1887) from the Navidad Formation in Chile is quite different by having a pentagonal outline and a distinctive change in sculpture from indistinct anterior of the diagonal posterior ridge to granular-commarginal on the posterodorsal side of the shell. *Neilo awamoana* Finlay, 1926, a species common in the offshore siltstone facies of the early Miocene of New Zealand, is similar in outline, but has more numerous, finer, and more closely spaced collabral ribs, and a fine ridge running along the angulation from the umbo to the posteroventral margin (Beu and Maxwell 1990: pl. 16a, c). The late Oligocene to early Miocene *Neilo sinangula* Finlay, 1926, from New Zealand lacks this fine ridge (Finlay 1926; Marshall 1978; Eagle and Hayward 1993), but also has finer and more numerous commarginal ribs compared to *N. altamirano*. The early Oligocene *Neilo funiculata* Hutton, 1887 from New Zealand has a much longer anterior part of the shell than *N. altamirano* sp. nov. (Beu et al. 2012).

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

## Family Nuculidae Gray, 1824

### Genus *Acila* Adams and Adams, 1858

**Type species:** *Nucula divaricata* Hinds, 1843, by subsequent designation; Recent, northern and tropical Pacific Ocean.

#### *Acila?* sp.

Fig. 2B.

**Material.**—One specimen (NRM Mo187002, W = 10.5 mm) from the Oligocene Belén seep site, northern Peru.

*Remarks.*—Judging from the divaricate ornament, this specimen appears to belong to *Acila*, but as other diagnostic features, such as the hinge, are missing, it is here hesitantly assigned to this genus. Olsson reported two species of *Acila* from Belén and Pajarabobo, *Acila paita* Olsson, 1931, and *Acila piura* Olsson, 1931. The specimen that we collected is too poorly preserved to be identified as either of these species.

#### Subclass Pteriomorpha Beurlen, 1944

#### Family Mytilidae Rafinesque, 1815

#### Subfamily Bathymodiolinae Kenk and Wilson, 1985

#### Genus *Idas* Jeffreys, 1876

*Type species:* *Idas argenteus* Jeffreys, 1876; Recent, North Atlantic Ocean.

#### *Idas* sp.

Fig. 2C.

*Material.*—One specimen (NRM Mo187003, L = 4 mm) from the Oligocene Cerro La Salina block 9, northern Peru.

*Remarks.*—The single specimen consists of RV mostly lacking shell material; it has straight dorsal and ventral margins, a pointed anterior margin, the umbo is positioned at about 10% of the total shell length from the anterior, and imprints of small, taxodont teeth can be seen at the posterior end of the posterodorsal margin. It is too poorly preserved to be identified, but seems to differ from the coeval *Idas olympicus* from Washington state, USA, by a less anteriorly positioned umbo (Kiel and Goedert 2007; Kiel and Amano 2013). Compared to geologically younger small bathymodiolins associated to whale falls in Japan, it differs by having a more modioliform shell and a more anteriorly positioned umbo (Amano and Little 2005; Amano et al. 2007; Jenkins et al. 2018a). *Idas* sp. reported from a whale fall at Orciano Pisano in Italy has parallel dorsal and ventral margin unlike the Peruvian specimen, and *Idas* reported from a Miocene seep deposit at Ca' Fornace in northern Italy has a more curved shell compared to the Peruvian specimen.

#### Family Propeamussiidae Abbott, 1954

#### Propeamussiidae indet.

Fig. 2D.

*Material.*—One specimen (NRM Mo187004) from the Oligocene Cerro La Salina block 6, northern Peru.

*Remarks.*—The single specimen lacks ears and cannot be determined to the genus-level. Propeamussiids, also known as “mud pecten”, are common dwellers of muddy sediments in deeper water and have been reported from several fossil seep deposits (Kelly et al. 2000; Kiel et al. 2008; Kiel 2010) and wood falls (Kiel and Goedert 2006a, b; Amano et al. 2018a).

#### Subclass Heterodonta Neumayr, 1884

#### Family Kalenteridae Marwick, 1953

#### Genus *Pseudophopsis* nov.

*Zoobank LCID:* urn:lsid:zoobank.org:act:9FF851DC-2A55-4CC0-888D-6E91D0042CB1

*Type species:* *Pleurophopsis peruviana* Olsson, 1931; Oligocene, Peru.

*Species included:* The type species and *Unio bitumen* Cooke, 1919.

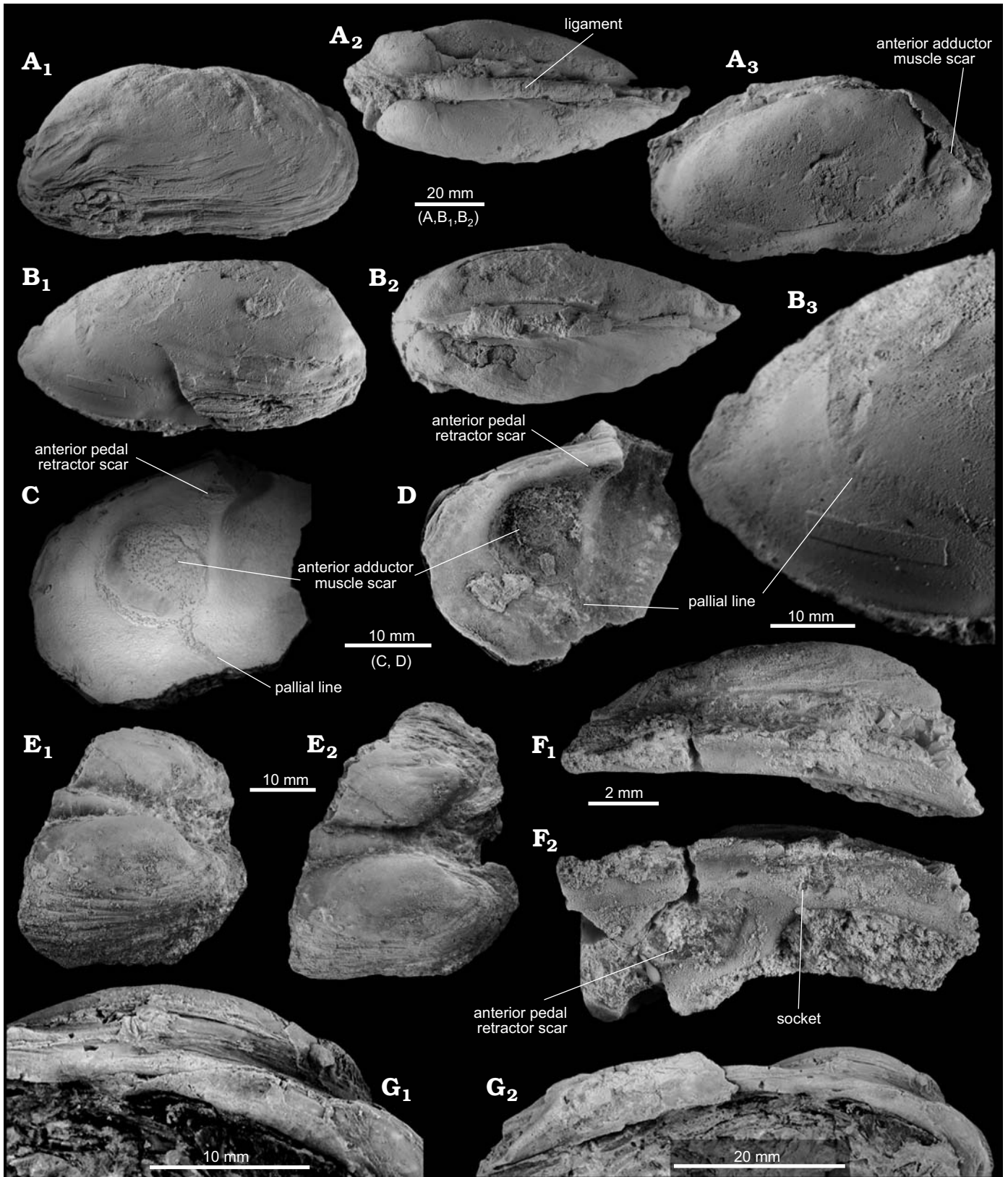
*Etymology:* For its superficial similarity to the vesicomid genus *Pleurophopsis*.

*Diagnosis.*—Medium-sized, well-inflated, elongate-oval kalenterid with blunt, somewhat elevated umbo in anterior third of shell; external sculpture rough, irregular; hinge plate strong, moderately narrow, with indistinct growth lines, hinge teeth weak, sub-parallel to shell margin, often reduced in adults; anterior adductor muscle scar deep, roundish, with peg in upper half of posterior margin; anterior retractor muscle scar large, roundish, above ridge bordering adductor muscle scar; onset of pallial line at posteroventral side of anterior adductor muscle scar, no pallial sinus; ligament external, long, strong.

*Remarks.*—Van Winkle (1919) derived the generic name *Pleurophopsis* from the Paleozoic “modiomorphid” genus *Pleurophorus* King, 1848 (a synonym of the beetle genus *Pleurophorus* Mulsant, 1842 and hence replaced by *Permorphorus* Chavan, 1954) because she considered *Pleurophopsis* to be a descendent of *Pleurophorus* based on the hinge structure and muscle scar pattern. Olsson (1931) adopted this classification when introducing *Pleurophopsis peruviana*, and placed *Pleurophopsis* in the Permorphoridae. It is now firmly established that the type species of *Pleurophopsis*, *P. unioides* (see below), belongs to the Vesicomidae (Kiel 2007; Krylova et al. 2010; Krylova and Sahling 2010). However, Olsson’s (1931) “*Pleurophopsis*” *peruviana* does indeed show “modiomorphid” hinge and muscle scar features and hence the new genus *Pseudophopsis*, with *P. peruviana* as the type species, is here placed among the Kalenteridae.

In contrast to vesicomids, *Pseudophopsis peruviana* has a relatively large anterior pedal retractor scar that is clearly separated from the adductor muscle scar. The entire anterior adductor muscle scar is sunken, whereas in vesicomids it is usually deepest on its posterior side and shallower impressed on the anterior side. Another distinguishing feature is the hinge plate, which is set distinctly inward from the umbones, whereas is situated directly underneath the umbones in vesicomids (or in other words, the umbones are more loosely coiled than in vesicomids). Such a distinctive hinge plate is for example seen in the kalenterid *Myoconcha neuquena* Leanza, 1940 from the Early Jurassic of Argentina (Leanza 1940; Griffin and Pastorino 2006). Similar fine growth lines on the hinge plate of *P. peruviana* (Fig. 3G<sub>1</sub>) can be seen in *Myoconcha neuquena*

Fig. 3. The kalenterid *Pseudophopsis peruviana* (Olsson, 1931) from early Oligocene seep deposits at Cerro La Salina (USGS loc. 21219, A–D; block 3, E, F), Talara Basin, northern Peru; **A.** Large articulated specimen (USNM PAL 728207) showing rough and very irregular growth increments; outer side of left valve (A<sub>1</sub>), the long and thick ligament (A<sub>2</sub>) and deep anterior adductor muscle scar (A<sub>3</sub>). **B.** Large articulated specimen (USNM PAL 728208) →



showing posterior half of pallial line (B<sub>1</sub>, B<sub>3</sub>) and thick ligament (B<sub>2</sub>). C, D. Inner sides of two fragmentary right valves preserving anterior margin (C, USNM PAL 728209; D, USNM PAL 530294), showing anterior adductor muscle scar and pedal retractor scar, and onset of pallial line. E. Fragment (NRM Mo187027) preserving anterior half of shell and thick calcified ligament; outer side of right valve (E<sub>1</sub>) and dorsal view (E<sub>2</sub>). F. Fragment (NRM Mo187028) preserving edentulous hinge area (F<sub>1</sub>) and large anterior pedal retractor scar (F<sub>2</sub>). G. Dorsal shell margin of large left valve (USNM PAL 530295), showing edentulous hinge (G<sub>1</sub>, close-up). D and G from Kiel and Peckmann (2007: fig. 6).

and also in the Miocene kalenterid *Madrynomys bruneti* Griffin and Pastorino, 2006. *Madrynomys* is clearly distinct from *Pseudophopsis* by its more coiled and more pointed umbones, and the much broader but shorter hinge plate. *Myoconcha* Sowerby, 1824, differs from *Pseudophopsis* by its bean-shaped posterior adductor muscle scar, and the anterior side of the pallial line, which is distinct from the anterior adductor muscle scar in *Myoconcha*, but starts at its posteroventral corner in *Pseudophopsis* (i.e., Leanza 1940; Newell 1957; Griffin and Pastorino 2006; Kaim and Schneider 2012). Lastly, *Pseudophopsis peruviana* has a coarser and much more irregular surface sculpture than any vesicomid, and also its ligament is longer relative to shell length as in vesicomids.

The late Mesozoic, seep-inhabiting kalenterid *Caspiconcha* Kelly in Kelly et al., 2000, typically has an elongated anterior adductor muscle scar with a posterodorsal projection, which is absent in *Pseudophopsis*, a more distinctive projection above the anterior adductor muscle scar (the so-called caspiconchid process) not seen in *Pseudophopsis*, and it lacks hinge dentition (Kelly et al. 2000; Kiel et al. 2010; Jenkins et al. 2013, 2018b). Further, several but not all species of *Caspiconcha* have an internal ridge running from the umbo to the posterior adductor scar, which is not seen in *P. peruviana*, and the pallial line tends to be closer to the ventral shell margin in *Pseudophopsis* than in *Caspiconcha* (see Jenkins et al. 2018b: fig. 2).

Another species included here in *Pseudophopsis* is the Eocene *Unio bitumen* Cooke, 1919, from the Elmira asphalt mine seep deposit in Cuba (Cooke 1919; Kiel and Peckmann 2007; Kiel and Hansen 2015). *Pseudophopsis bitumen* resembles *P. peruviana* by having a similar inward-set hinge plate with similarly reduced teeth, its thick ligament and very rough and irregular surface.

*Stratigraphic and geographic range.*—Early Oligocene of the Talara Basin, northern Peru and Eocene of Cuba.

### *Pseudophopsis peruviana* (Olsson, 1931)

Fig. 3.

1931 *Pleurophopsis peruviana* sp. nov.; Olsson 1931: 43–44, pl. 4: 1, 3.

*Material.*—One specimen (in two parts: NRM Mo187027 and NRM Mo187028) from Cerro La Salina block 1; two unnumbered specimens from Cerro La Salina block 3; several unnumbered fragments from Cerros El Pelado block 2, and several specimens (including USNM PAL 530294, 530294, 728207–728209) collected by Axel A. Olsson and Wendell P. Woodring at USGS loc. 21219. All upper Oligocene, Talara Basin, Peru. The shells reach 10 cm in length.

*Remarks.*—The Eocene Cuban *Pseudophopsis bitumen* (Cooke, 1919) has a hinge dentition that is quite similar that of small specimens of *Pseudophopsis peruviana* (see Kiel and Peckmann 2007: figs. 4A, B). *Pseudophopsis bitumen* differs from *P. peruviana* by having the maximum inflation in the middle, whereas it is located toward the anterior in *P. peruviana*.

*Stratigraphic and geographic range.*—Early Oligocene of the Talara Basin, northern Peru.

### Family Thyasiridae Dall, 1900

#### Genus *Conchocele* Gabb, 1866

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

#### *Conchocele tessaria* (Olsson, 1931)

Fig. 4.

1931 *Thyasira tessaria* sp. nov.; Olsson 1931: 53–54, pl. 6: 10, 14.

*Material.*—Six specimens (NRM Mo187005–187010, Fig. 4) and several further unnumbered specimens (often fragmentary) from Cerro La Salina blocks 1, 4, 6–9, upper Oligocene, Talara Basin, Peru.

*Description.*—Small to medium-sized for the genus (L max. = 35 mm), inflation moderate (L/W ratio ca. 1.9), rounded-pentagonal in outline; beak prosogyrate, elevated and pointed, umbonal angle 90–100°; posterior fold deep but not sharp, increasingly curved in larger specimens, with resulting in shallow posterior sinus; a weak, secondary sulcus also present in some specimens; anterior margin narrow, demarcated by blunt ridge; lunule symmetrical and well-demarcated; escutcheon lanceolate; external surface sculptured by irregular, commarginal growth lines only. Hinge plate narrow, edentulous, ligament nymph broad and elongate; internal surface with fine radial striations developing tubercles near ventral margin.

*Remarks.*—Olsson (1931) described three thyasirid species from northern Peru: *T. peruviana* and *T. staufti* from the Lomitos cherts, and *T. tessaria* from the Heath Formation at Pajarabobo, near Belén. Examination of Olsson's (1931) type material at PRI showed that the specimens of all three species are more inflated than the material we collected; strongly so in the cases of *T. peruviana* and *T. staufti*, and less so in the case of *T. tessaria*. Based on the overall similarity of our specimens to *T. tessaria*, especially their pentagonal outline, the broad posterodorsal area and the blunt posterior ridge, we considered the material reported here as belonging to *T. tessaria*. *Thyasira peruviana* differs from *T. tessaria* by its much more prominent umbo, the much broader anterior margin, and the much smaller posterodorsal area. *Thyasira staufti* differs from *T. tessaria* by its deeper and sharper posterior sulcus, its narrower posterodorsal area, and its more oval outline. *Thyasira montanita* (Olsson, 1931) from allegedly coeval strata in southern Ecuador has finer growth lines, a more rounded outline, a broader anterior margin, and a broader and shorter anterior adductor muscle scar (personal observations SK).

*Thyasira tessaria* is here transferred to *Conchocele* based on its anteriorly situated beaks, the steeply sloping anterior margin, the weakly impressed lunule, and the broadly rounded posterior margin bearing a deep sulcus, characteristics of *Conchocele* that are not present in this combination in *Thyasira*. *Conchocele tessaria* shows

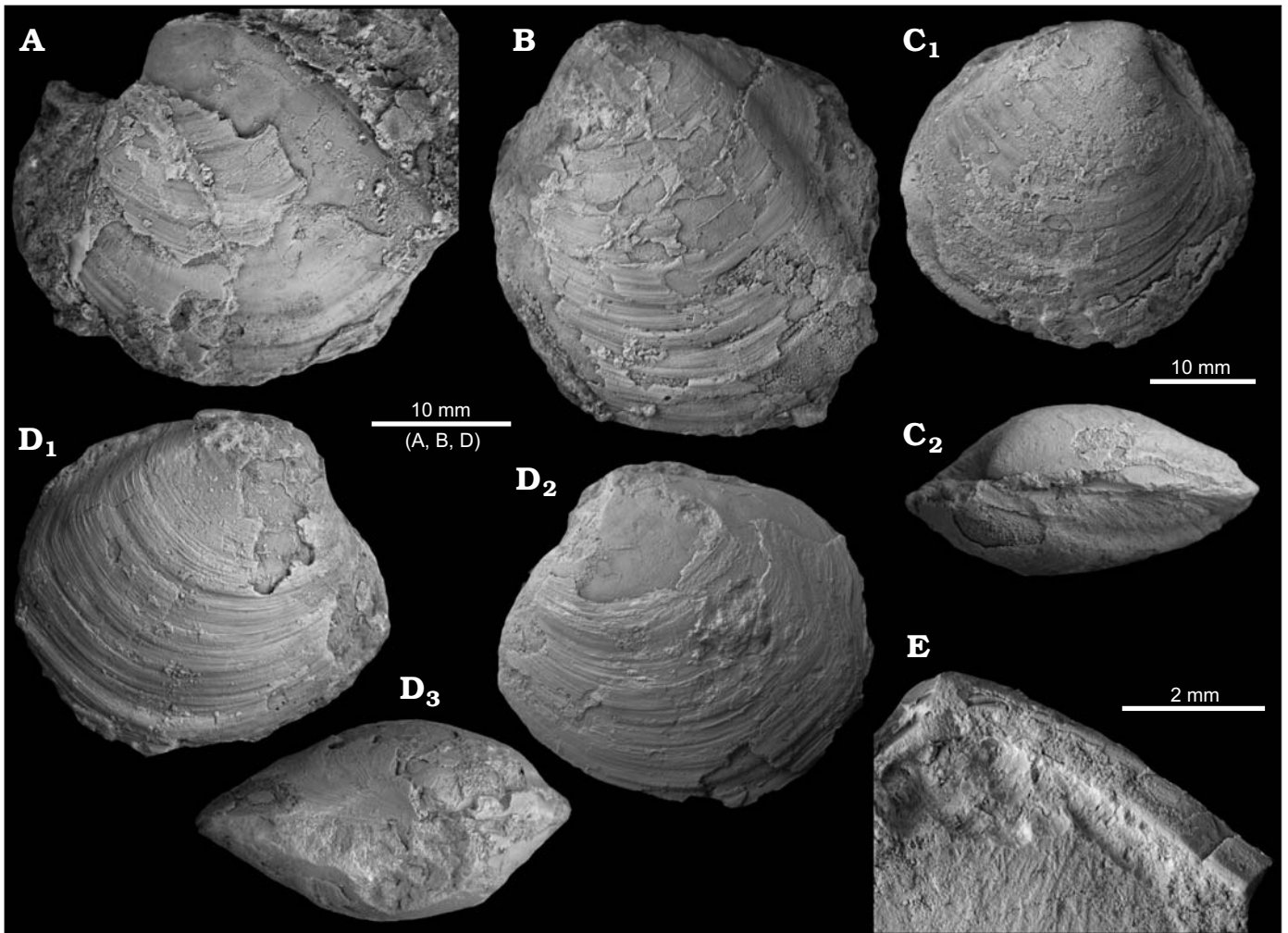


Fig. 4. The thyasirid *Conchocele tessaria* (Olsson, 1931) from early Oligocene seep deposits at Cerro La Salina (block 1, E; block 7, A–C; block 8, D), Talara Basin, northern Peru. **A**, **B**. Left valve of large specimen (**A**, NRM Mo187005; **B**, NRM Mo187006). **C**. Medium-sized specimen (NRM Mo187007), right valve showing fine growth increments (**C**<sub>1</sub>), dorsal view showing lunule (**C**<sub>2</sub>), left valve showing dorsal sulcus (**C**<sub>3</sub>). **D**. Small specimen (NRM Mo187008), left valve showing a healed shell injury (**D**<sub>1</sub>), right valve showing dorsal sulcus (**D**<sub>2</sub>) and dorsal view showing lunule posterior area (**D**<sub>3</sub>). **E**. Small specimen (NRM Mo187010) showing hinge of right valve.

the following differences to other *Conchocele* species: *C. townsendi* from Late Cretaceous strata on Seymour Island, Antarctica, has a similar pentagonal shape and narrow anterior margin, but has a deeper and sharper posterior fold (Hryniewicz et al. 2017). The Paleocene *C. conradii* from Svalbard is more inflated and has a longer anterior margin than *C. tessaria* (Hryniewicz et al. 2017). Also *C. taylori* Hickman, 2015, known from late Eocene to Oligocene strata of the North Pacific region, has a longer anterior margin, but its posterior fold is similar to that of *C. tessaria* (Hickman 2015; Hryniewicz et al. 2017). Another late Eocene to Oligocene species is *Conchocele bathyaulax* Hickman, 2015 from Oregon and Washington state, USA; compared to *C. tessaria*, it is much more inflated and has a more pointed, terminal umbo (Hickman 2015; Hryniewicz et al. 2017). The late Eocene *C. kiritachienensis* Hryniewicz, Amano, Jenkins, and Kiel, 2017, from a seep carbonate in Hokkaido, northern Japan, differs from *Conchocele tessaria* by its rhomboidal shape, very broad

anterior margin, and pointed, terminal umbo (Hryniewicz et al. 2017). Finally, *Conchocele adoccasa* (Van Winkle, 1919) from a Miocene seep deposit in Trinidad has a broader anterior margin and a more distinct (sharper) posterior fold. This applies also to the specimens assigned to *C. adoccasa* from presumably Oligocene seep deposits of Colombia (Kiel and Hansen 2015). Overall, most similar to *C. tessaria* is the late Eocene to Oligocene *C. taylori* that is widespread along the North Pacific margin (Hickman 2015; Hryniewicz et al. 2017).

One specimen (NRM Mo187008) shows two indentations on LV, which might represent a failed attack by a predator such as a durophagous crustacean. Damage to fossil seep mollusks attributed crustaceans has been noted previously (e.g., Kiel et al. 2016, and references therein, Klompaker et al. 2018).

*Stratigraphic and geographic range.*—Early Oligocene of the Talara Basin, northern Peru.

## Family Lucinidae Fleming, 1828

Genus *Lucinoma* Dall, 1901

*Type species: Lucinoma filosa* (Stimpson, 1851), by original designation; Recent, North Atlantic Ocean.

*Lucinoma zapotalensis* (Olsson, 1931)

Fig. 5.

1931 *Phacoides (Lucinoma) zapotalensis* sp. nov.; Olsson 1931: 49, pl. 5: 2, 5.

*Material*.—Three specimens (NRM Mo187011–187013) and several unnumbered, mostly fragmentary specimens from Cerro La Salina blocks 1, 3, 6–9, upper Oligocene, Talara Basin, Peru.

*Remarks*.—This species was reported by Olsson (1931) only from the Mambri shales near Zapotal in southern Ecuador, but not from any of the seep deposits in the Heath shale in northern Peru. According to Olsson (1931), the Mambri shales are the equivalent of the Heath shale and also of late Oligocene age. Similar is the “middle” Oligocene *Lucinoma playaensis* (Olsson, 1964) from the Playa Rica grits in northern Ecuador, though it differs from *L. zapotalensis* by having more numerous and more narrowly spaced ribs and a more rounded posterodorsal margin (Olsson 1964: pl. 6: 7). *Lucinoma acutilineatum* (Conrad, 1849) from the Miocene Astoria Formation in Oregon and Washington state, USA, is quite similar, but appears to differ from *L. zapotalensis* by being less inflated and having more widely spaced, and sharper, commarginal ribs; it also seems to have a more angular outline than *L. zapotalensis* (Conrad 1849; Moore 1963).

*Stratigraphic and geographic range*.—Early Oligocene of the Talara Basin, northern Peru.

## Family Vesicomidae Dall and Simpson, 1901

Genus *Pleurophopsis* Van Winkle, 1919

*Type species: Pleurophopsis unioides* Van Winkle, 1919, by monotypy; middle Miocene, Trinidad.

*Pleurophopsis lithophagoides* Olsson, 1931

Fig. 6.

1931 *Pleurophopsis lithophagoides* sp. nov.; Olsson 1931: 44, pl. 4: 2, 5, 7, 9.

*Material*.—Five specimens (NRM Mo187014–187018) and 63 unnumbered, often fragmentary specimens from the Belén seep site, upper Oligocene, Talara Basin, Peru.

*Description*.—Shell narrow (W/H ratio 0.58–0.66 of the six measured shells), elongate-oval shell (H/L ratio 0.52–0.45 of the five smallest [L = 22–27 mm] specimens, 0.33–0.40 of the five largest [L = 32–40 mm] specimens), umbones slightly elevated, prosogyrate, pointed, positioned anterior at c. 20% total shell length; anterior margin short, convex; posterodorsal margin gently sloping to acutely rounded posterior margin; ventral margin straight or slightly convex; sculpture of irregular growth increments only. Anterior ad-

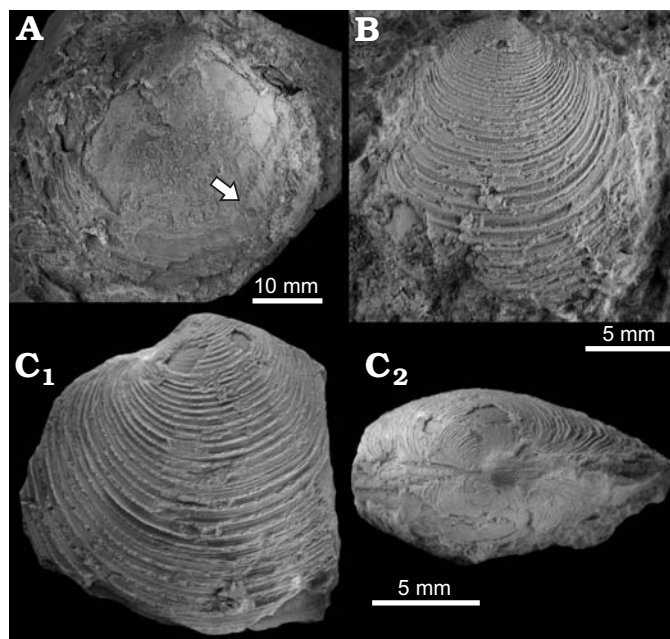


Fig. 5. The lucinid *Lucinoma zapotalensis* (Olsson, 1931) from early Oligocene seep deposit at Cerro La Salina (block 1, C; block 9, A) and Cerros El Pelado (block 2, B), Talara Basin, northern Peru. A. Internal mold of large left valve (NRM Mo187011), left valve showing anterior adductor muscle scar (arrow). B. NRM Mo187012, external sculpture on right valve. C. Articulated specimen (NRM Mo187013), showing external sculpture on left valve (C<sub>1</sub>) and lunule and ligament in dorsal view (C<sub>2</sub>).

ductor muscle scar kidney-shaped, somewhat impressed; anterior pedal retractor scars small, roundish and connected to adductor scar by fine groove. Narrow sinuous hinge plate; RV with two cardinals, 1 pointing anterior, 3b pointing slightly posterior; LV with three cardinals, 2a pointing antero-ventral, 2b pointing slightly posterior, 4b seen as elongated socket pointing posterior.

*Remarks*.—All specimens are fragmentary, and the full extent of the hinge plate is unknown. The details on the dentition given here are derived from silicon rubber casts of parts of the hinge and observations on internal molds (Fig. 6E). *Pleurophopsis lithophagoides* differs from the type species *P. unioides* by reaching a smaller maximum size (up to 40 mm in length compared to 77 mm for *P. unioides*) and by being more elongated. The Peruvian *Pleurophopsis talarensis* sp. nov. described below differs from *P. unioides* mainly by being much more elongated (H/L ratio 0.26 compared to 0.33–0.4 in large *P. lithophagoides*). Differences to other species of *Pleurophopsis* are summarized in Table 1.

*Stratigraphic and geographic range*.—Early Oligocene of the Talara Basin, northern Peru.

*Pleurophopsis talarensis* sp. nov.

Fig. 7.

Zoobank LCID: urn:lsid:zoobank.org:act:E668EC27-89CE-4B98-A2D0-B7A6FE856EA8

*Etymology*: For the Talara Basin.

*Type material*.—Holotype, NRM Mo187019 from block 6. Paratypes



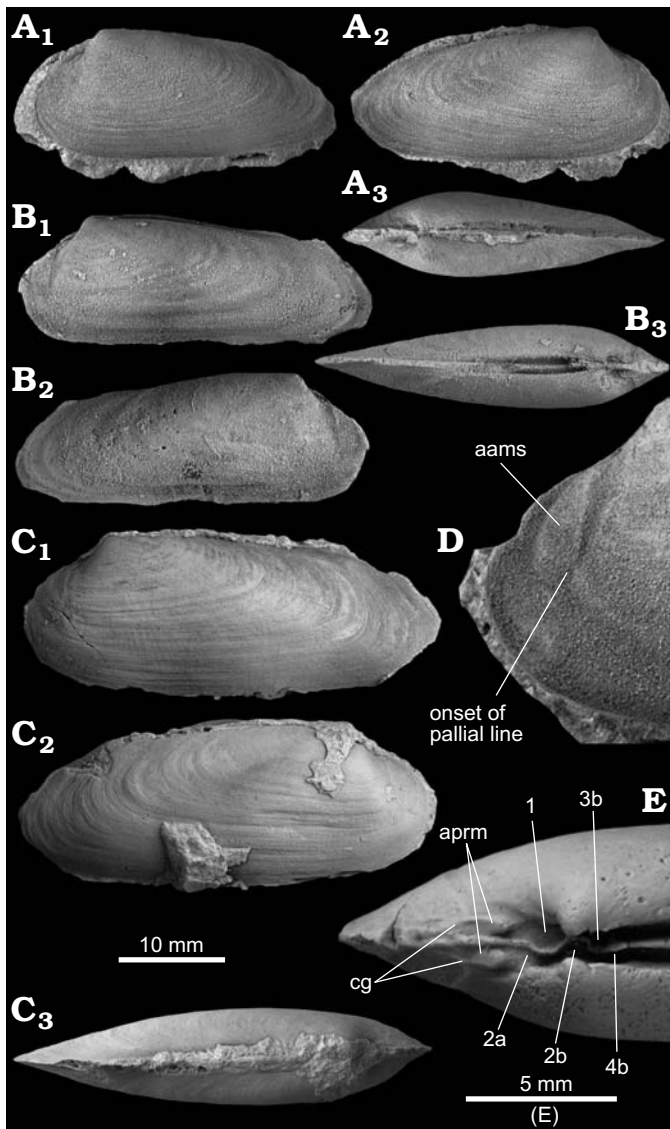


Fig. 6. The vesicomyid *Pleurophopsis lithophagoides* Olsson, 1931, from the early Oligocene Belén seep site, Talara Basin, northern Peru. **A.** Specimen with strongly sloping posterodorsal margin (NRM Mo187014), left valve (A<sub>1</sub>), right valve (A<sub>2</sub>), and dorsal view (A<sub>3</sub>). **B.** Specimen with rather straight posterodorsal margin (NRM Mo187015), left valve (B<sub>1</sub>), right valve (B<sub>2</sub>), and dorsal view (B<sub>3</sub>). **C.** Large specimen (NRM Mo187016), left valve (C<sub>1</sub>), right valve (C<sub>2</sub>), and dorsal view (C<sub>3</sub>). **D.** Close-up on anterior side of left valve (NRM Mo187018), showing anterior adductor muscle scar and onset of pallial line. **E.** Internal mold showing hinge and anterior muscle scars (NRM Mo187017). Abbreviations: aams, anterior adductor muscle scar; aprm, anterior pedal retractor scar; cg, connecting groove between aams and aprs.

NRM Mo187022, NRM Mo187024–26 from block 6, NRM Mo187023 from block 7, and NRM Mo187020 and NRM Mo187021 from block 9.

*Type locality:* The Cerro La Salina seep deposits, Talara Basin, Peru.

*Type horizon:* Presumably the early Oligocene part of the Heath shale.

*Material.*—The type material and further, unnumbered fragmentary specimens from type locality and horizon, blocks 1, 2, 6–9.

*Dimensions* (in mm).—NRM Mo187019, L = 37, H = 9.5, W (single valve) = 3; NRM Mo187020, L = 33 (incomplete),

H = 10.5, W = 6.5; NRM Mo187021, L = 36 (incomplete) and H = 10.

*Diagnosis.*—Small and very elongate *Pleurophopsis* (H/L ratio c. 0.26) with slightly curved shell with subparallel dorsal and ventral margins.

*Description.*—Shell small, very elongate (H/L ratio c. 0.26), and little inflated (W/H ratio c. 0.61–0.63), umbo anterior at c. 16% shell length, slightly elevated; dorsal and ventral margin subparallel, dorsal margin slightly convex, ventral margin slightly concave; no lunule or lunular incision; ligament external, about 1/3 of shell length; sculpture of irregular growth increments. Anterior adductor muscle scar subcircular, deeply impressed, pallial line starting at posteroventral corner; hinge plate narrow, hinge teeth radiating, RV with two strong cardinals, cardinal 1 short, pointing downward and somewhat anterior, cardinal 3b blunt, pointing posteroventrally; LV with three teeth, cardinal 2a very elongate, subparallel to anterodorsal margin, 2b blunt, broad, pointing downward, cardinal 4b short and thin; subumbonal pit large, elongate and deep in both valves.

*Remarks.*—The differences from *Pleurophopsis unioides* and *P. lithophagoides* have been outlined above. The early Miocene Japanese vesicomyid “*Adulomya*” *uchimuraensis* Kuroda, 1931, has a H/L ratio of c. 0.22 and is thus even more elongate than *P. talarensis*, and is also much larger (Kuroda 1931; Kanno et al. 1998; Amano and Kiel 2011). Differences to other species of *Pleurophopsis* are summarized in Table 1.

*Stratigraphic and geographic range.*—Early Oligocene of the Talara Basin, northern Peru.

### Genus *Vesicomya* Dall, 1886

*Type species:* *Callocardia atlantica* Smith, 1885, by original designation; Recent, North Atlantic Ocean.

### “*Vesicomya*” *tschudi* Olsson, 1931

Fig. 8.

1931 *Vesicomya tschudi* sp. nov.; Olsson 1931: 54, pl. 4: 6, 8.

*Material.*—One small, articulated specimen (NRM Mo 187029) from Cerro La Salina block 1; one medium-sized, articulated specimen (NRM Mo187030) from Cerro La Salina block 5; one large LV (NRM Mo187031) from Cerro La Salina block 5. All upper Oligocene, Talara Basin, Peru.

*Dimensions* (in mm).—NRM Mo187029, L = 20, H = 14, W = 10.5; NRM Mo187030, L = 41.5, H = 27, W = 19.5; NRM Mo187031, L = 59, H = 37.5, W (single valve) = 14.

*Description.*—Well-inflated, oval shell with large, prosogyrate and strongly protruding umbones; post-umbonal side of shell gently tapering into a slightly truncate posterior margin; lunular incision present, no escutcheon, but posterodorsal area marked by distinct ridge; external sculpture of indistinct, irregular, commarginal growth lines; anterior adductor muscle scar bean-shaped, small, and moderately impressed; posterior adductor scar indistinct, round, of moderate size; pallial line close to ventral margin, no pallial sinus.

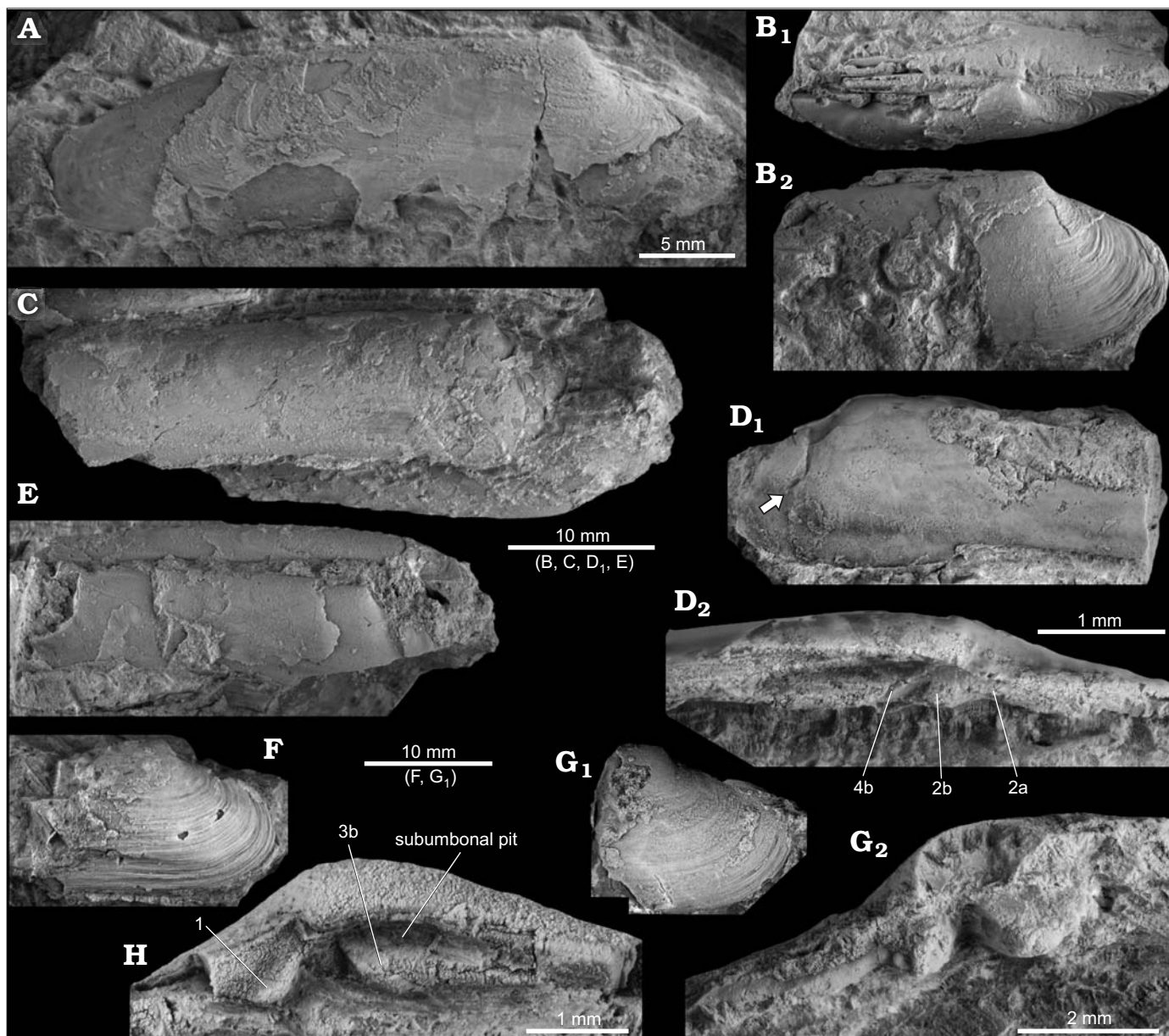


Fig. 7. The vesicomyid *Pleurophopsis talarensis* sp. nov., from early Oligocene seep deposits at Cerro La Salina (block 6, A, D, F–H; block 7, E; block 9, B, C), Talara Basin, northern Peru. **A.** Holotype (NRM Mo187019), right valve showing shell outline. **B.** Paratype (NRM Mo187022), posteriorly damaged, articulated specimen; view on dorsal side ( $B_1$ ) and on right valve ( $B_2$ ). **C.** Paratype (NRM Mo187020), right valve with posterior tip missing. **D.** Paratype (NRM Mo187023), internal mold of left valve showing anterior adductor muscle scar and pallial line ( $D_1$ ), arrow indicates onset of pallial; close-up on hinge area ( $D_2$ ). **E.** Paratype (NRM Mo187021), semi-articulated specimen, view on incomplete right valve). **F.** Paratype (NRM Mo187024), anterior part of right valve. **G.** Paratype (NRM Mo187026), anterior part of right valve ( $G_1$ ), view on hinge area ( $G_2$ ). **H.** Paratype (NRM Mo187025), hinge area of right valve.

**Remarks.**—Along with *Vesicomya tschudi*, Olsson (1931) also introduced *Vesicomya ramondi* Olsson, 1931, from the Heath shale around Belén and Pajarabobo, but he did not comment on the differences between the two species. Squires and Gring (1996) noted that *V. ramondi* has a more elongated shell, as can be seen when comparing the holotypes of the two species (see Fig. 8C, D). Squires and Gring (1996) assigned Eocene specimens from seep deposits of the Wagonwheel Formation in California, USA, to *V. tschudi*, based on their overall shape, although the specimens showed no hinge dentition, the lunule was imperfectly

preserved, and most specimens were smaller and had lower umbones than the Peruvian specimens.

Middle Eocene vesicomyid specimens from the Hump-tulips Formation in Washington state, USA, were identified as *Archivesica* cf. *tschudi* by Amano and Kiel (2007). Later, the same authors changed their assignment of these specimens from *Archivesica* to *Pliocardia* or a new genus (Amano and Kiel 2012). The middle Miocene *Pliocardia?* *tanakai* Miyajima, Nobuhara, and Koike, 2017, from central Japan (Miyajima et al. 2017) is similar to “*V.*” *ramondi* in terms of its outline, elongation, and absence of a pallial

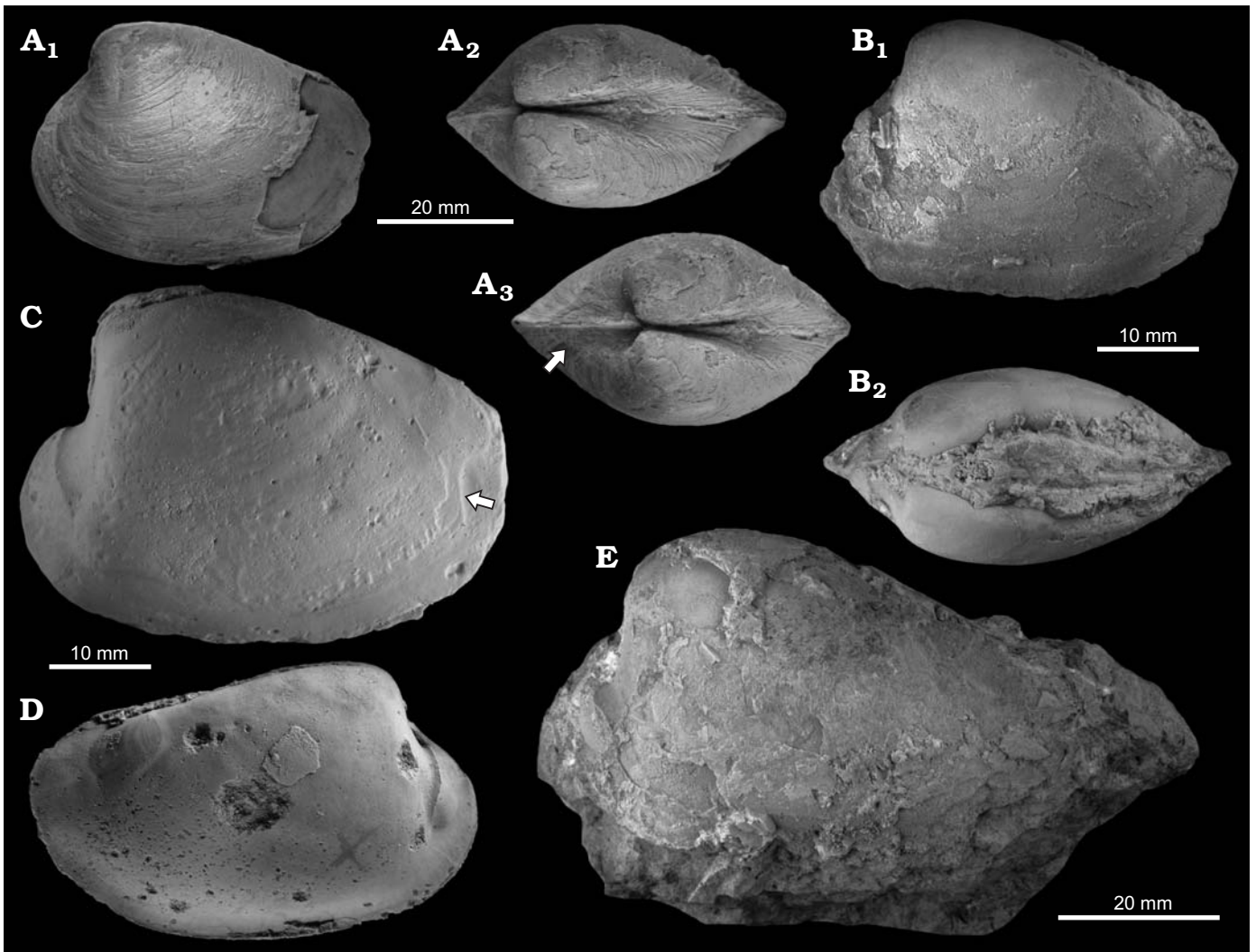


Fig. 8. The vesicomyids “*Vesicomya*” *tschudi* Olsson, 1931 (A–C, E) and “*Vesicomya*” *ramondi* Olsson, 1931 (D), from early Oligocene seep deposits in the Talara Basin, northern Peru. **A.** Small specimen (NRM Mo187029) from Cerro La Salina block 1, view on left valve (A<sub>1</sub>), dorsal view (A<sub>2</sub>), view on anterodorsal side showing lunular incision (A<sub>3</sub>, arrow). **B.** Medium-sized specimen (NRM Mo187030) from Cerro La Salina block 5, view on left valve (B<sub>1</sub>) and dorsal view (B<sub>2</sub>). **C.** Holotype (PRI 1965) from Pajarabobo, view on left valve showing posterior end of pallial line (arrow). **D.** Holotype (PRI 1962) from Pajarabobo, view on right valve. **E.** Large left valve (NRM Mo187031) from Cerro La Salina block 5, view of the outer side.

sinus, but is smaller, less inflated, and has smaller, more pointed, and less prosogyrate umbones than “*V.*” *ramondi*. *Pliocardia?* *tanakai* is much smaller and also more elongated than “*Vesicomya*” *tschudi*.

“*Vesicomya*” *tschudi* cannot be confidently placed in *Pliocardia* because it lacks a pallial sinus, a feature that is present in the type species of *Pliocardia*, *P. bowdeniana* Dall, 1903 (Krylova and Janssen 2006; personal observation SK). The presence or absence of a pallial sinus appears to be a character that distinguishes genera among the Vesicomylidae (Johnson et al. 2017). Furthermore, the genus *Pliocardia* Woodring, 1925 itself is in need of a taxonomic revision because the species presently assigned to it belong to at least two or three different clades (Decker et al. 2012; Valdés et al. 2013; Johnson et al. 2017). Hence the generic position of “*Vesicomya*” *tschudi* remains unresolved.

*Stratigraphic and geographic range.*—Early Oligocene of the Talara Basin, northern Peru.

## Class Gastropoda Cuvier, 1795

### Limpets of uncertain affinity

#### Limpet indet. 1

Fig. 9A.

*Material.*—One specimen (NRM Mo187032) from Cerro la Salina block 9, upper Oligocene, Talara Basin, Peru.

*Description.*—Tall, oval shell, broader anteriorly and more pointed posteriorly, and slightly wider than high; apex in central position; anterior slope straight, posterior slope slightly convex; shell sculptured by fine, broad, and flat concentric ribs; length 5.3 mm.

*Remarks.*—Tall, conical shells like this are found among limpet of very disparate taxonomic affinities, including the

Table 1. Characters of the species of *Pleurophopsis* Van Winkle, 1919; \* minimum values given only, because many *Pleurophopsis* species show allometric growth (i.e., they increase in length faster than in height). H, height; L, length; W, width.

Species	L (mm)	H (mm)	H/L*	W/H	Ventral margin	Pallial line posterior	Occurrence	Stratigraphic range	References
<i>P. akanudaensis</i>	71.1	32.9	0.39	0.24–0.4	concave	turns to anterior	Japan Sea	middle Miocene	Miyajima et al. 2017
<i>P. chinookensis</i>	90	27	0.3	0.73	straight to slightly convex	turns postero-dorsally	Washington state, USA	late Eocene–Oligocene	Squires and Goedert 1991
<i>P. chitanii</i>	70.4	21	0.3	0.7	straight to concave	turns to anterior	Japan	early to early middle Miocene	Amano and Kiel 2011
<i>P. hamuroi</i>	59.2	22.3	0.38	0.64	slightly concave	slight turn to anterior	Japan Sea	early to early middle Miocene	Amano and Kiel 2011
<i>P. hokkaidoensis</i>	66.2	22.6	0.34	weakly inflated	slightly concave	turns to anterior	Japan Sea	early middle Miocene	Amano and Kiel 2007
<i>P. kuroiwaensis</i>	66.7	24.6	0.34	0.6	slightly convex	turns to anterior	Japan Sea	latest middle Miocene	Amano and Kiel 2011
<i>P. lithophagoides</i>	40	15	0.33	0.58–0.66	straight to slightly convex	?	northern Peru	early Oligocene	Olsson 1931; and this paper
<i>P. matsumotoi</i>	112.5	39.3	0.35	0.67–0.73	concave	turns to anterior	Japanese Pacific coast	late Oligocene–early Miocene	Amano et al. 2019
<i>P. talarensis</i>	37	9.5	0.26	0.61–0.63	straight	?	northern Peru	early Oligocene	this paper
<i>P. uchimuraensis</i>	120.5	27.5	0.17	0.51–0.64	concave	turns to anterior	Japan	early to early middle Miocene	Kanno et al. 1998; Amano and Kiel 2011
<i>P. unioides</i>	77	33	0.43	0.55	straight to slightly convex	slight turn to anterior	Trinidad	middle Miocene	Van Winkle 1919; Kiel 2007

Recent lepetellid *Lepetella ionica* Nordsieck, 1973, as illustrated in Dantart and Luque (1994), and the fissurellid *Cornisepta antarctica* (Egorova, 1982), as illustrated in (McLean and Geiger 1998). The corroded protoconch and the lack of knowledge on the shell microstructure preclude a more precise taxonomic identification.

## Limpet indet. 2

Fig. 9B.

*Material*.—One specimen (NRM Mo187033) from Cerro la Salina block 6, upper Oligocene, Talara Basin, Peru.

*Description*.—Tall, narrow, elongate-oval limpet shell with pointed anterior and posterior ends and apex at about anterior third of shell; anterior slope straight, posterior margin gently convex; internal surface smooth except for faint growth increments.

*Remarks*.—Similar laterally compressed shells with anteriorly situated apex can be found among the pseudococculinid (Vetigastropoda) genera *Pseudococculina* Schepman, 1908, and *Tentaoculus* Moskalev, 1976 (Marshall 1986; McLean and Harasewych 1995), as well as among the pectinodontid (Patellogastropoda) genus *Serradonta* Dall, 1882 (Okutani et al. 1992; Jenkins et al. 2007).

Subclass Neomphaliones Bouchet, Rocroi, Hausdorf, Kaim, Kano, Nützel, Parkhaev, Schrödl, and Strong 2017

Order Cocculinida Haszprunar, 1987

Family Cocculinidae Dall, 1882

## Genus *Coccopigya* Marshall, 1986

*Type species*: *Cocculina spinigera* Jeffreys, 1883, by typification of replaced name; Recent, North Atlantic Ocean.

### *Coccopigya* sp.

Fig. 9C.

*Material*.—One specimen (NRM Mo187034) from Cerro la Salina block 6, upper Oligocene, Talara Basin, Peru.

*Description*.—Elongate-oval, moderately tall limpet shell with apex at about anterior third of shell; sculpture of indistinct but broad radial ribs, about 30 on each side of shell, more densely spaced at anterior end; fine radial growth increments visible.

*Remarks*.—With its narrow shell and anteriorly displaced apex, this specimen is remarkably similar to the early or middle Miocene *Coccopigya compunctum* (Marwick, 1931) from New Zealand (Marwick 1931; Marshall 1986).

Order Neomphalina McLean, 1981

Family Neomphalidae McLean, 1981

Genus *Retiskenea* Warén and Bouchet, 2001

*Type species*: *Retiskenea diploura* Warén and Bouchet, 2001, by original designation; Recent, North Pacific Ocean.

### *Retiskenea?* sp.

Fig. 10.

*Material*.—One specimen (PRI 80014) from the Lomitos cherts, numerous specimens (unnumbered specimens

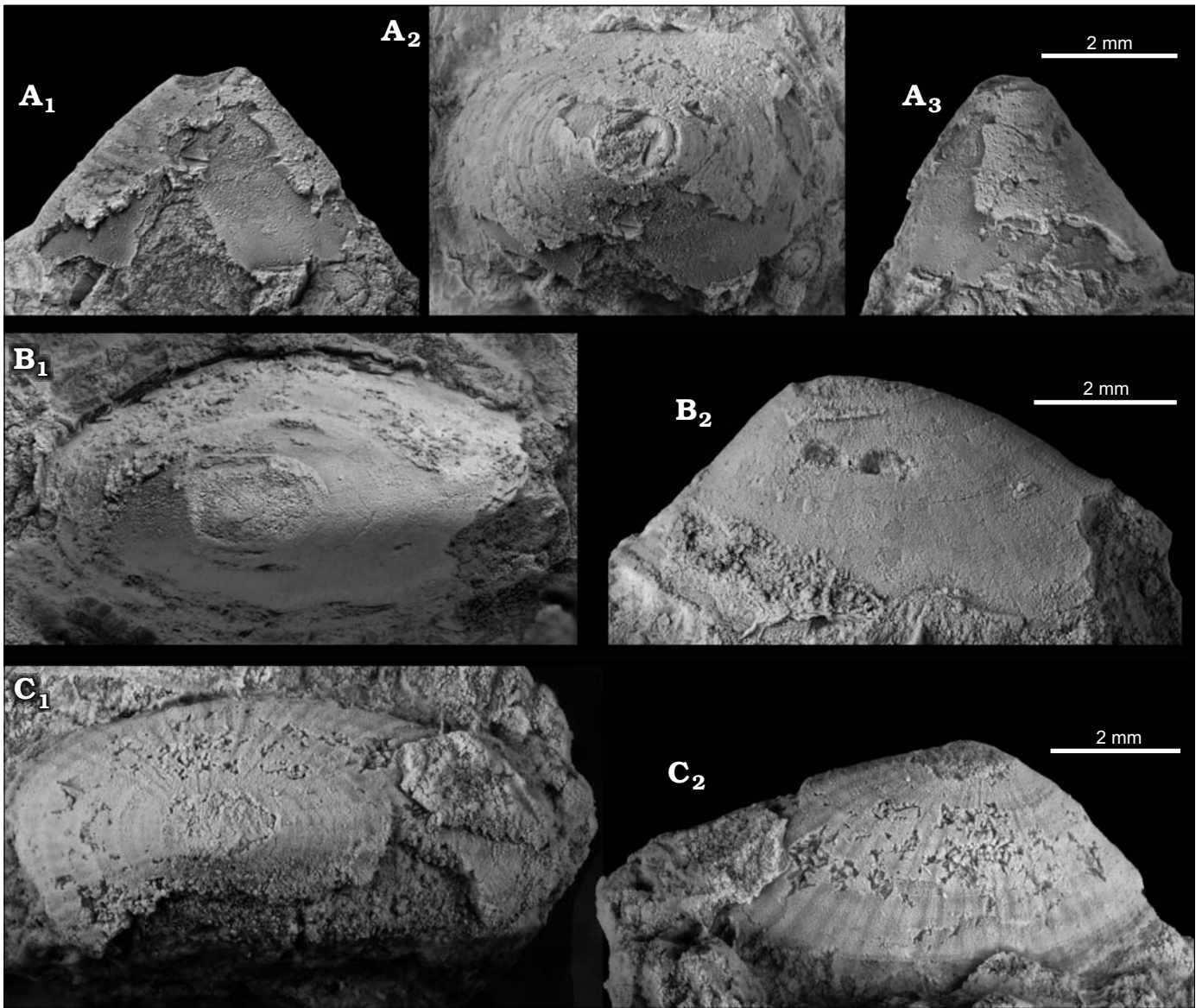


Fig. 9. Limpet gastropods from early Oligocene seep deposits at Cerro La Salina (block 6, B, C; block 9, A) Talara Basin, northern Peru. **A.** Limpet indet. 1 (NRM Mo187032) in lateral view ( $A_1$ ), apical view ( $A_2$ ) and seen from anterior view ( $A_3$ ). **B.** Limpet indet. 2 (NRM Mo187033) in apical ( $B_1$ ) and lateral ( $B_2$ ) views. **C.** The cocculinid *Coccopigya* sp. (NRM Mo187034) in apical ( $C_1$ ) and lateral ( $C_2$ ) views.

housed at NRM) from blocks of the Cerro La Salina seep deposits. All upper Oligocene, Talara Basin, Peru.

**Description.**—Shell globular, 2.5 evenly convex whorls with fine, dense prosocyrty growth lines; fine spiral lines present on early whorls; spire low, aperture large.

**Remarks.**—This species is represented by poorly preserved, small specimens only. The illustrated specimen from the Lomitos cherts shows a granular pattern on its protoconch, somewhat similar to that seen on other fossil *Retiskenea* species (Kiel 2006; Campbell et al. 2008; Kaim et al. 2014), but this feature might just be a preservational artifact. Hence, our assignment to *Retiskenea* remains tentative; they might as well belong to the Skeneidae or some other vetigastropod group.

The Eocene–Oligocene *Retiskenea statura* (Goedert and

Benham, 1999) from seep deposits in western Washington has a taller spire than the Peruvian *Retiskenea* sp.? (Goedert and Benham 1999; Kiel 2006) and the two species *R. kieli* Campbell, Peterson, and Alfaro, 2008, and *R. tuberculata* Campbell, Peterson, and Alfaro, 2008, from Cretaceous seep deposits in California, USA, have a more rapidly expanding whorl profile than the Peruvian *Retiskenea* sp.? (Campbell et al. 2008; Kaim et al. 2014).

Subclass Vetigastropoda Salwini-Plawen, 1980  
Family Pyropeltidae McLean and Haszprunar, 1987  
Genus *Pyropelta* McLean and Haszprunar, 1987

**Type species:** *Pyropelta musaica* McLean and Haszprunar, 1987, by original designation; Recent, Juan de Fuca Ridge, NE Pacific Ocean.

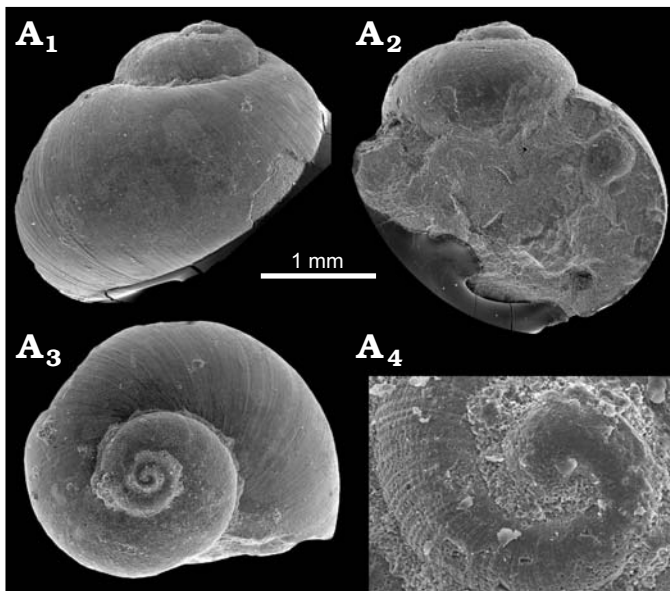


Fig. 10. The possible neomphalid *Retiskenea?* sp. (PRI 80014) from the early Cenozoic Lomitos cherts seep deposits near Negritos, Talara Basin, northern Peru.

*Pyropelta seca* sp. nov.

Fig. 11.

*Zoobank LCID:* urn:lsid:zoobank.org:act:005AF820-5BD6-42C1-9AE6-F1F03A3EC479

*Etymology:* For Quebrada Seca river valley.

*Type material:* Holotype: NRM Mo187036 from Cerro La Salina block 6. Paratypes: NRM Mo187035, 187037–187039 from block 6.

*Type locality:* Cerro La Salina block 6, Talara Basin, Peru.

*Type horizon:* Early Oligocene part of the Heath shale.

*Material.*—The type material and a few further unnumbered specimens from Cerro La Salina blocks 6 and 9, and one unnumbered specimen from Cerros El Pelado block 2. All upper Oligocene, Talara Basin, Peru.

*Dimensions* (in mm).—The largest specimen, L = 2.5, H = 1.4.

*Diagnosis.*—Tall, oval to elongate-oval shell; apex with a slight forward inclination; shell with cone-in-cone layering, surface smooth; base flat to concave.

*Description.*—Small limpet shell, tall, posterior slope gently and irregularly convex, anterior slope irregular, more-or-

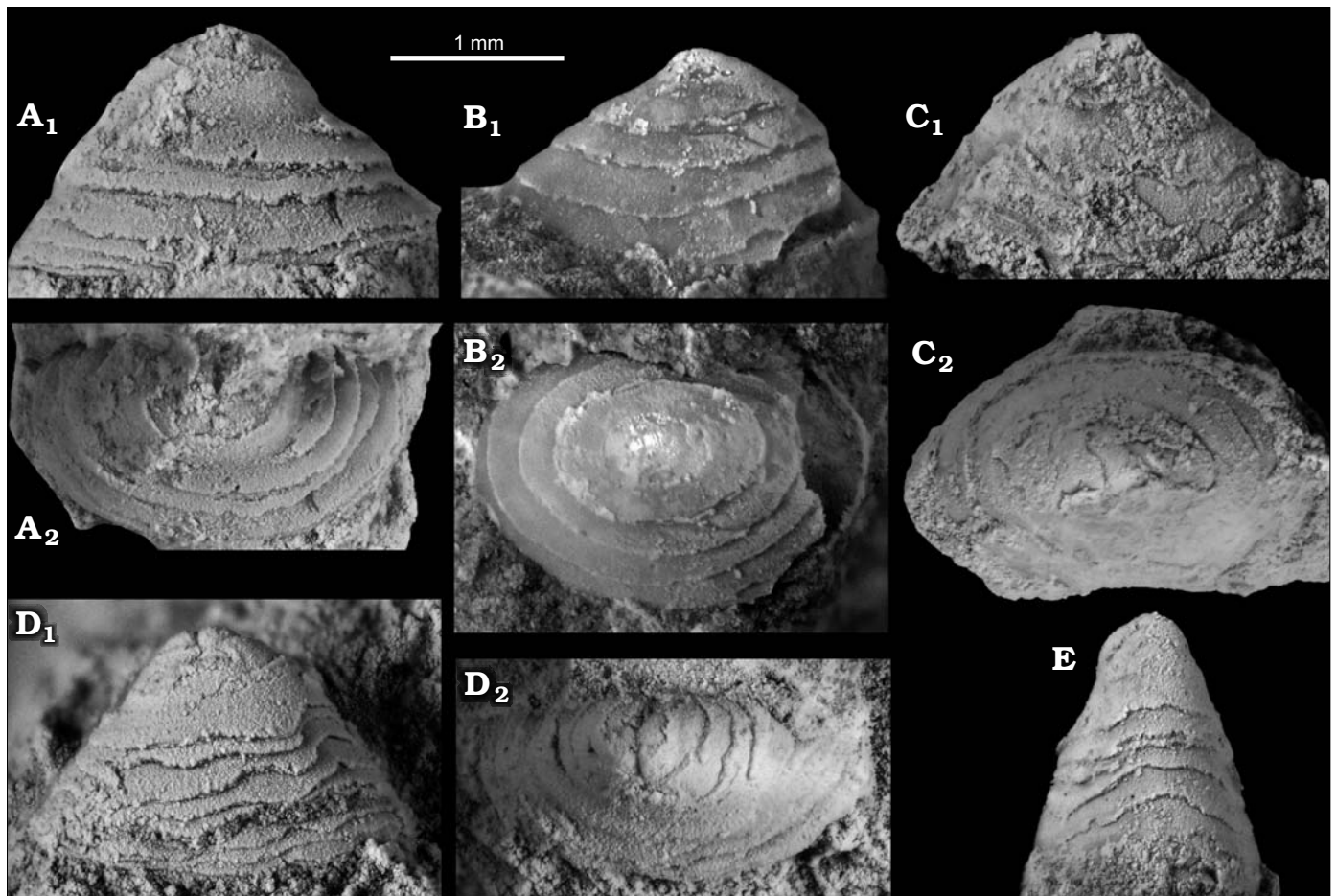


Fig. 11. The vetigastropod *Pyropelta seca* sp. nov. from early Oligocene seep deposits at Cerro La Salina block 6, Talara Basin, northern Peru. **A.** Paratype (NRM Mo187035) in lateral (A<sub>1</sub>) and apical (A<sub>2</sub>) views. **B.** Holotype (NRM Mo187036) in lateral (B<sub>1</sub>) and apical (B<sub>2</sub>) views. **C.** Paratype (NRM Mo187037) in lateral (C<sub>1</sub>) and apical (C<sub>2</sub>) views. **D.** Paratype (NRM Mo187038) in lateral (D<sub>1</sub>) and apical (D<sub>2</sub>) views. **E.** Paratype (NRM Mo187039) in anterior view.

less straight; base oval to elongate-oval, flat or convex with lateral margins lower than anterior and posterior margins; apex in central or very slightly anterior position, slightly inclined towards anterior; shell surface smooth, with cone-in-cone layering.

**Remarks.**—Although the shell microstructure and protoconch are unknown, this species is placed in *Pyropelta* based on its cone-in-cone type layered shell. This type of layering is regularly seen in *Pyropelta* (McLean and Haszprunar 1987; McLean 1992; Sasaki et al. 2003, 2008; Zhang and Zhang 2017) but not in other cocculiniform genera, and results from alternating layers with crossed lamellar or crossed acicular structure and prismatic structure (Kiel 2004).

Compared to *Pyropelta seca*, *Pyropelta elongata* Zhang and Zhang, 2017, from methane seeps in the South China Sea is similarly elongated, but not as tall (Zhang and Zhang 2017). *Pyropelta ryukyensis* Sasaki, Okutani, and Fujikura, 2008, from hydrothermal vents in the Okinawa Trough (Sasaki et al. 2008) is broader and less tall than *Pyropelta seca*. Even broader and lower are *Pyropelta musaica* and *Pyropelta craigsmiti* McLean, 1992; *Pyropelta corymba* McLean and Haszprunar, 1987, is also broader but can be as tall as *Pyropelta seca* (McLean and Haszprunar 1987; McLean 1992).

**Stratigraphic and geographic range.**—Early Oligocene of the Talara Basin, northern Peru.

#### Family Colloniidae Cossmann in Cossmann and Peyrot, 1917

#### Genus *Cantrainea* Jeffreys, 1883

**Type species:** *Turbo peloritana* Cantraine, 1835, by monotypy; Recent, Mediterranean Sea.

#### *Cantrainea* sp.

Fig. 12A, B.

**Material.**—One specimen (NRM Mo187040) from Cerro La Salina block 1; one (NRM Mo187041) from Cerro La Salina block 9; a single poorly preserved specimen possibly also belonging to *Cantrainea* sp. is present on the same sample as *Provanna pelada* (NRM Mo187054) from Cerros El Pelado block 2. All upper Oligocene, Talara Basin, Peru.

**Description.**—Small, trochiform shell with angular whorl profile and moderately wide umbilicus; subsutural ramp slightly convex and only slightly sloping, smooth except for strongly prosocline growth lines, margin to whorl's flank marked by fine groove and smooth keel; flank vertical, smooth except for fine axial growth lines; basal margin also marked by smooth keel; base smooth with inclination of about 45°; umbilicus occupying about 20 of base's width.

**Remarks.**—Most similar is *Cantrainea macleani* Warén and Bouchet, 1993 from Recent seeps in the Gulf of Mexico, which differs by its more conical shell, resulting from a steeper subsutural ramp that is concave rather than

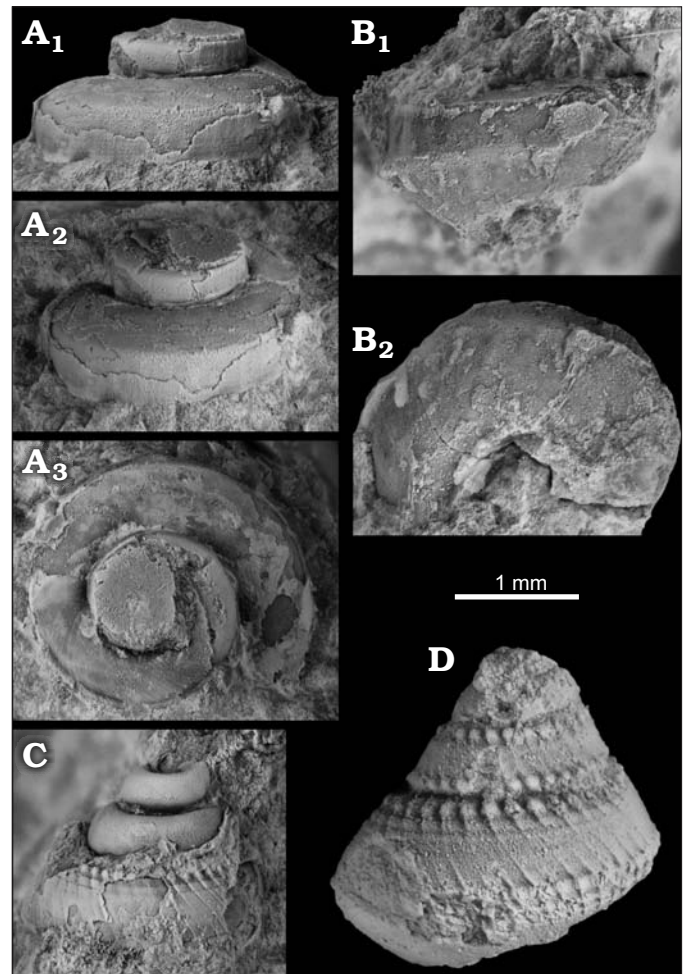


Fig. 12. Vetigastropoda from early Oligocene seep deposits at Cerro La Salina (block 1, A, D; block 2, C; block 9, B) Talara Basin, northern Peru. **A, B.** The colloniid *Cantrainea* sp. **A.** NRM Mo187040, specimen with base embedded in rock matrix in lateral (A<sub>1</sub>), oblique (A<sub>2</sub>) and apical (A<sub>3</sub>) views. **B.** NRM Mo187041, specimen with exposed base in lateral (B<sub>1</sub>) and basal (B<sub>2</sub>) views. **C, D.** The trochoid incertae sedis. **C.** NRM Mo187042. **D.** NRM Mo187043.

convex as in the specimen reported here. Indeed, most fossil and Recent species of *Cantrainea* have a steeper subsutural ramp than the Peruvian specimens illustrated here (Marshall 1979; Vilvens 2001; Okutani 2001; Kaim et al. 2009).

#### Family uncertain

#### Trochoid incertae sedis

Fig. 12C, D.

**Material.**—One specimen (NRM Mo187043) from Cerro La Salina block 1, one specimen (NRM Mo187042, H = 2.6 mm) from Cerro La Salina block 2. Both upper Oligocene, Talara Basin, Peru.

**Description.**—Fine, subsutural row of tubercles with fine, prosocline riblets underneath; apparently two keels on whorl's flank, and two (three) nodular spirals on base.

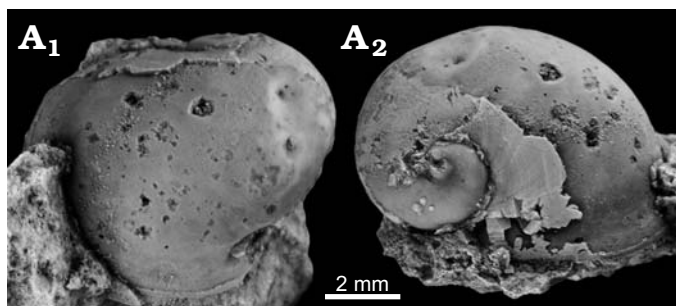


Fig. 13. *Neritimorpha* indet. (PRI 80015) from the early Cenozoic Lomitos cherts seep deposits near Negritos, Talara Basin, northern Peru.

*Remarks.*—These specimens are difficult to place among the Vetigastropoda. The sculpture is similar on both specimens, but specimen NRM Mo187042 has straight sides similar to some solariellids calliotropids, or calliostomatids (Hickman and McLean 1990), whereas specimen NRM Mo187042 with its more convex whorl profile resembles certain margaritids, and also the solariellid *Solariella (Pupillaria) columbiana* Squires and Goedert, 1991, from late Eocene seep deposits in Washington state, USA (Squires and Goedert 1991).

#### Subclass Neritimorpha Golikov and Starobogatov, 1975

##### *Neritimorpha* indet.

Fig. 13.

*Material.*—One specimen (PRI 80015) that is 8.5 mm across, from the Lomitos cherts, upper Oligocene, Talara Basin, Peru.

*Remarks.*—Olsson (1931) reported “*Nerita*” from the deposits near Belén and Pajarabobo and from the Lomitos cherts, but he never illustrated them. We did not find any neritids in the field, but a single specimen was found on the back side of the rock containing the holotype of *Solemya lomitensis*, from the Lomitos cherts. The specimen has a typical neritid shape but because neither the external surface nor the aperture is preserved, we cannot determine this specimen any further.

#### Subclass Caenogastropoda Cox, 1960

##### Family Provannidae Warén and Ponder, 1991

##### Genus *Provanna* Dall, 1918

*Type species:* *Trichotropis lomana* Dall, 1918, by monotypy; Recent, NE Pacific Ocean.

##### *Provanna antiqua* Squires, 1995

Fig. 14.

1995 *Provanna* n. sp.; Goedert and Campbell 1995: figs. 4–7.  
1995 *Provanna antiqua* sp. nov.; Squires 1995: 32, figs. 3–18.  
2006 *Provanna antiqua* Squires 1995; Kiel 2006: 125, figs. 5.1–5.8.  
2006 *Provanna antiqua* Squires 1995; Kiel and Goedert 2006a: fig. 2C.

*Material.*—Eight specimens (NRM Mo187044–187051) and numerous unnumbered specimens from Cerro La Salina

blocks 1, 4, 6, 8, 9; one unnumbered specimen from the Belén site. All upper Oligocene, Talara Basin, Peru.

*Remarks.*—We cannot see any differences between the Peruvian specimens from the La Salina sites and those described from late Eocene to Oligocene seep deposits in western Washington, USA (Goedert and Campbell 1995; Squires 1995; Peckmann et al. 2002). The extant West African *P. chevallieri* Warén and Bouchet, 2009, is also virtually indistinguishable.

*Stratigraphic and geographic range.*—Late Eocene to Oligocene of western Washington state, USA; early Oligocene of the Talara Basin, northern Peru.

##### *Provanna pelada* sp. nov.

Fig. 15.

*Zoobank LCID:* urn:lsid:zoobank.org:act:A2B18082-B13C-40BF-88DE-6C36E6AFC742

*Etymology:* For the type locality at Cerros El Pelado.

*Type material:* Holotype: NRM Mo187052. Paratypes: NRM Mo187053, NRM Mo187058.

*Type locality:* Cerros El Pelado block 2, Talara Basin, Peru.

*Type horizon:* The presumably early Oligocene part of the Heath shale.

*Material.*—The type material and several unnumbered specimens from the type locality.

*Dimensions.*—The largest specimen, H = c. 8 mm.

*Diagnosis.*—Slender provannid with at least two whorls and incised suture; whorls with basal constriction; shell surface nearly smooth, or with faint spiral threads or indistinct spiral cords, axial ornament consists either of fine or rough, prosocline, growth increments or indistinct prosocline ribs.

*Description.*—Shell small, slender, at least two whorls, suture deeply incised; whorl profile evenly convex or with slight subsutural constriction; base with constriction and bulge underneath; surface sculpture of fine, prosocline growth increments, sometimes also irregular, rough and irregular, low prosocline ribs, spiral sculpture ranging from absent to indistinct, low cords.

*Remarks.*—Compared to smooth (or nearly smooth) specimens of *P. antiqua*, *Provanna pelada* is slightly taller, its whorls are less convex, and the suture is less distinct. Also, its growth lines are prosocline, whereas those of *P. antiqua* are opisthocline or straight. The early Oligocene *P. urahoroensis* Amano and Jenkins, 2013, from a seep deposit in eastern Hokkaido, Japan, has a similar range of ornamentation, but differs from *P. pelada* by having lower whorls with a more convex profile, and by lacking the constriction and bulge at the base (Amano and Jenkins 2013). The two Miocene species *Provanna marshalli* Saether, Little, and Campbell, 2010a (from New Zealand) and *Provanna hirokoeae* Amano and Little, 2014 (from Japan) differ from *Provanna pelada* by having a broader apical angle and by having both spiral and axial sculpture (Saether et al. 2010a; Amano and Little 2014). There are three smooth Recent species; among them, *Provanna glabra* Okutani, Fujikura, and



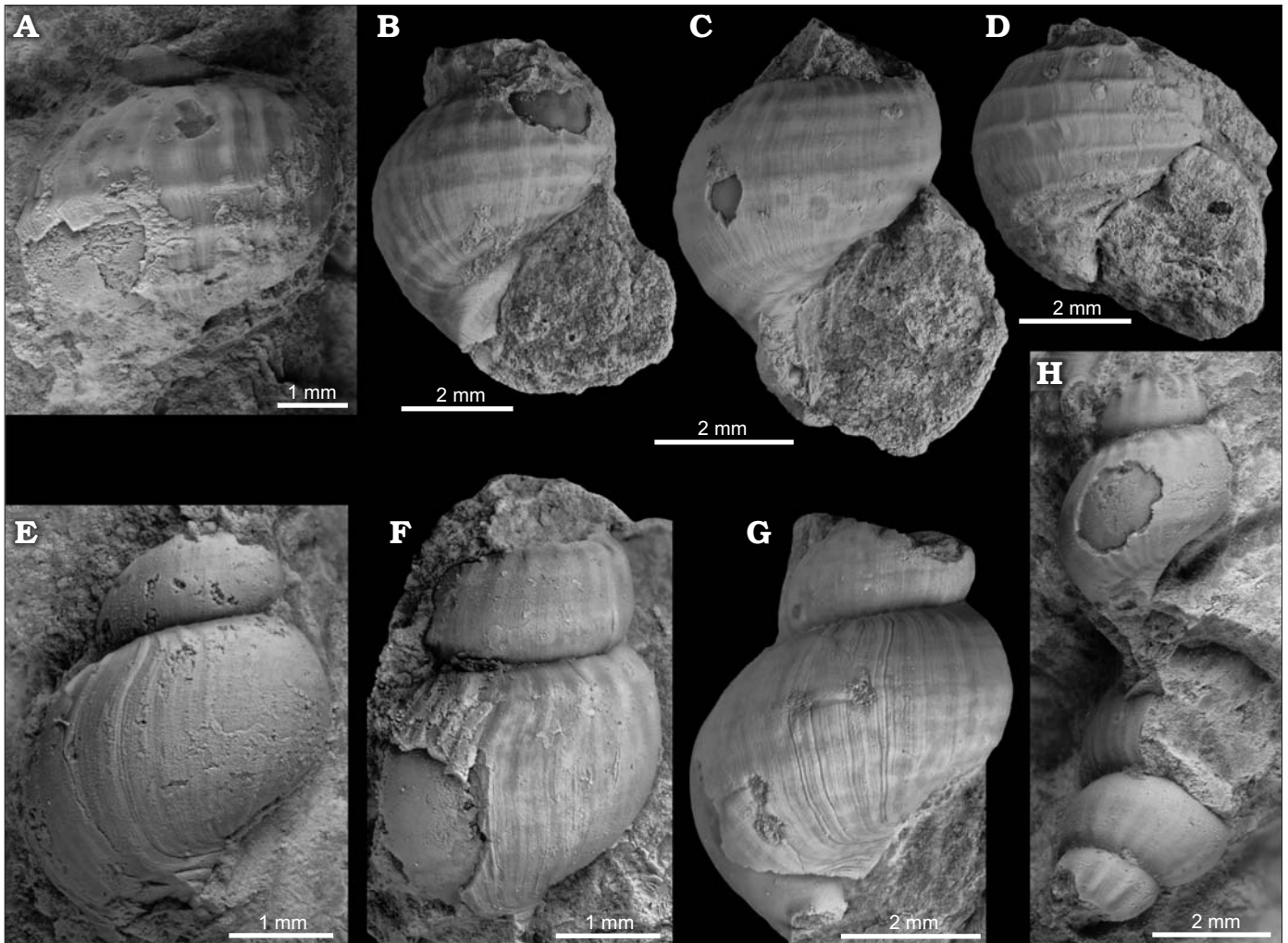


Fig. 14. The provannid gastropod *Provanna antiqua* Squires, 1995, from early Oligocene seep deposits at Cerro La Salina (block 1, A, F; block 4, H; block 6, B, C, D, G; block 8, E), Talara Basin, northern Peru. **A.** NRM Mo187044, specimen with distinctive axial and spiral sculpture, in abapertural view. **B.** NRM Mo187045, specimen with distinctive sculpture and showing the basal groove, in apertural view. **C.** NRM Mo187046, specimen with weak axial sculpture in the upper whorl, in apertural view. **D.** NRM Mo187047, fragmentary specimen with mainly spiral sculpture, in apertural view. **E.** NRM Mo187048, nearly smooth specimen showing slightly sinuous growth lines, in apertural view. **F.** NRM Mo187049, specimen with small shoulder and sculpture mainly in upper part of whorls, in apertural view. **G.** NRM Mo187050, specimen with faint axial and spiral sculpture, in apertural view. **H.** NRM Mo187051, two specimens with small shoulder and sculpture mainly in upper part of whorls.

Sasaki, 1993 is taller, *P. subglabra* Sasaki, Ogura, Watanabe, and Fujikura, 2016 has slightly less convex whorls, and *P. laevis* (Warén and Ponder 1991) has slightly more convex whorls. *Provanna fortis* Hybertsen and Kiel, 2018, from the middle Eocene Humptulips Formation in western Washington state, USA (Hybertsen and Kiel 2018), has stronger ornamentation and a much more angular whorl profile compared to that of *Provanna pelada*.

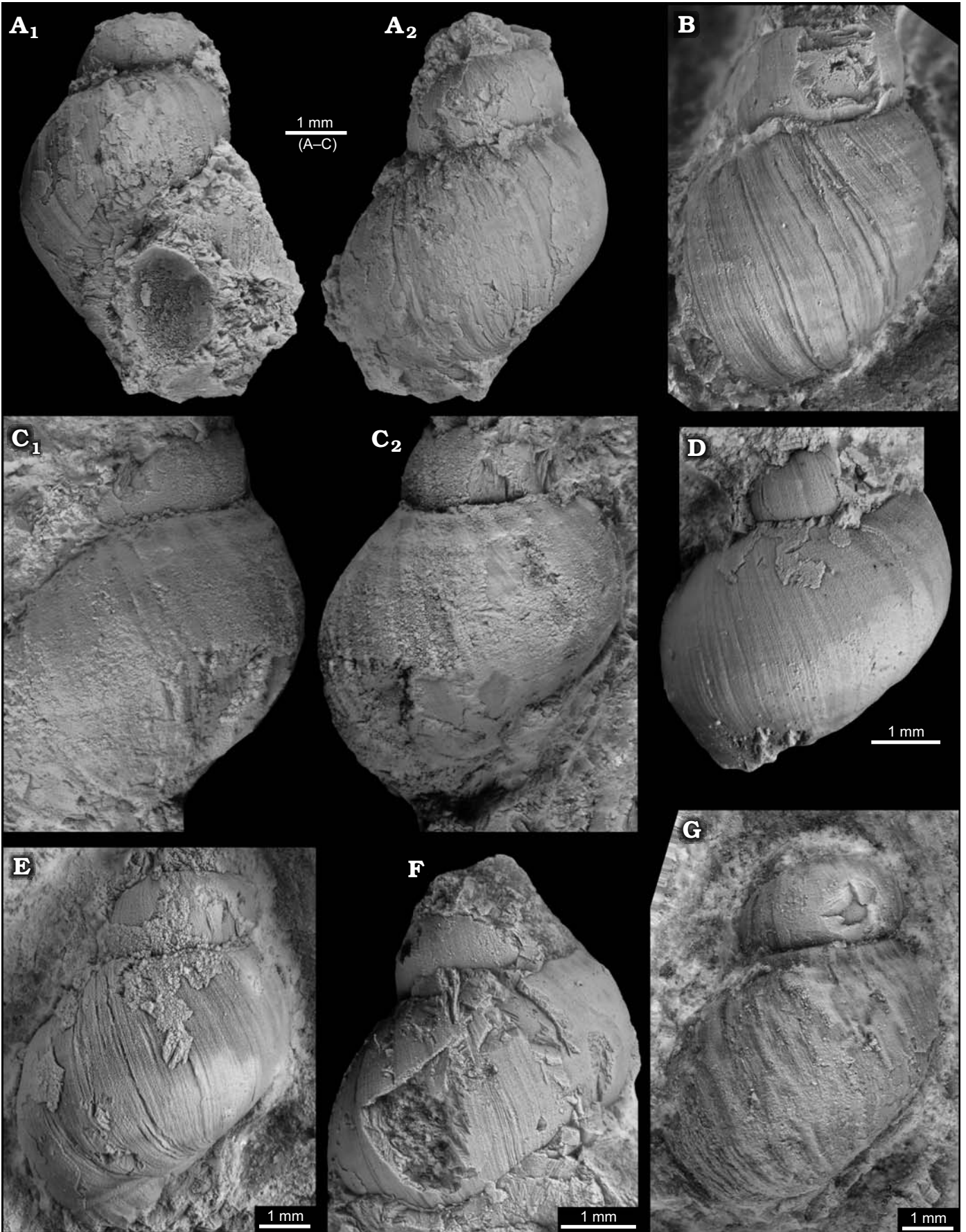
*Stratigraphic and geographic range.*—Type locality and horizon only.

Family Hokkaidoconchidae Kaim, Jenkins, and Warén, 2008

Genus *Ascheria* Kaim, Jenkins, Tanabe, and Kiel, 2014

*Type species:* *Abyssochrysos? giganteum* Kiel, Campbell, and Gaillard 2010, by original designation; Late Jurassic, California, USA.

*Remarks.*—Olsson (1931) introduced the genus *Anconia* for a large, high-spired gastropod from Punta Ancon (or Ancon Point) at Anconcito in southern Ecuador, *Anconia elenensis* Olsson, 1931. This species resembles members of *Ascheria* in every aspect (Kaim et al. 2014). Because *Anconia* Olsson, 1931, is a junior homonym of the grasshopper *Anconia* Scudder, 1876, we assign *Anconia elenensis* to *Ascheria*. Olsson (1931: 85) considered the strata at Punta Ancon as “equivalent of the Punta Bravo grits of Peru and therefore of middle Oligocene age”. Subsequent work on the radiolarians of these strata indicates a middle Eocene age instead (Ordóñez 1995). Hence, *Ascheria elenensis* is of roughly the same age as the large abyssochrysoid *Humptulipsia rauii* (Goedert and Kaler, 1996) from seep



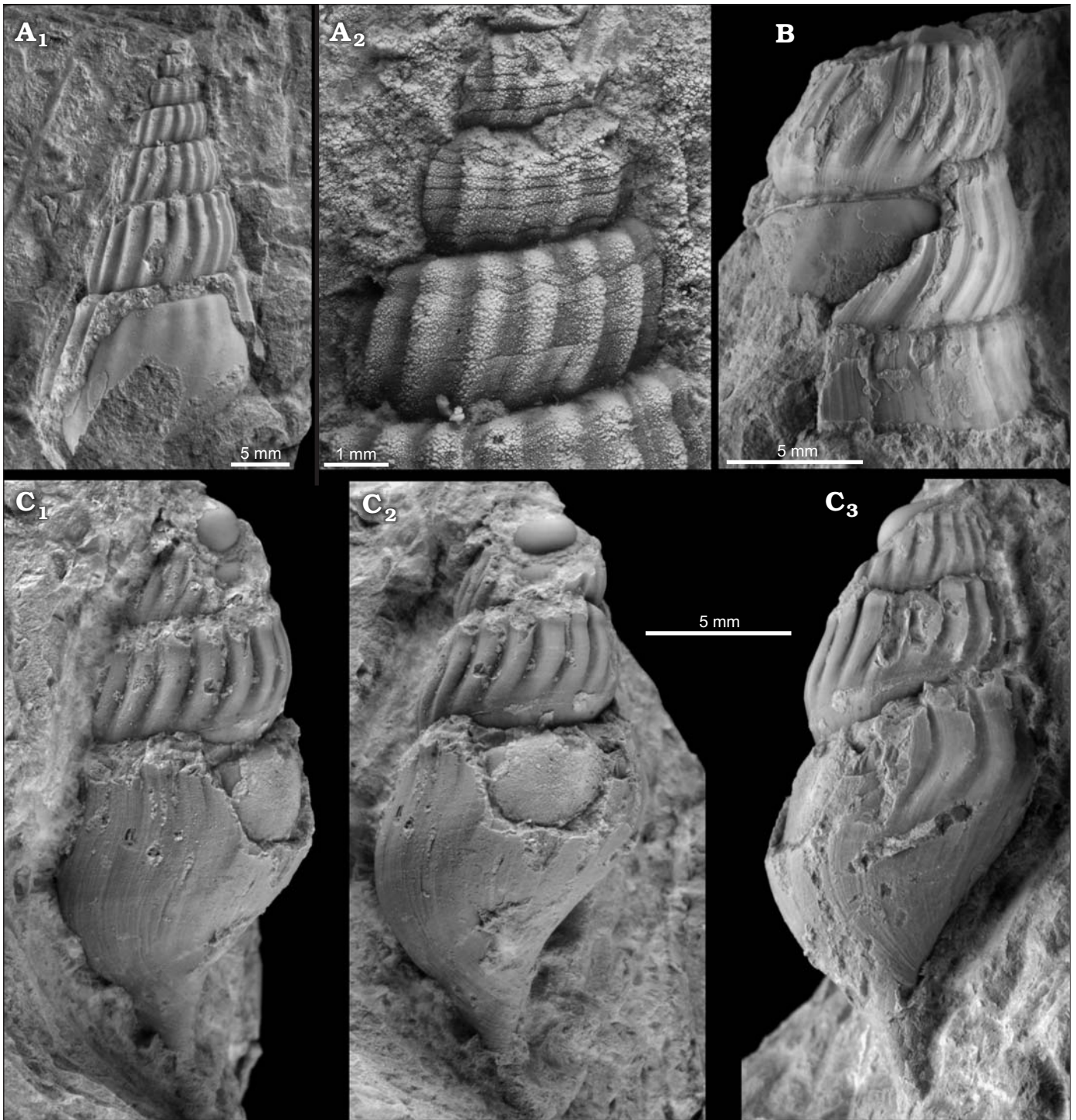


Fig. 16. The hokkaidoconchid gastropod *Ascheria salina* sp. nov. from early Oligocene seep deposits at Cerro La Salina (block 1, B, C; block 2, A) Talara Basin, northern Peru. **A**. Paratype (NRM Mo187059) showing fine spiral sculpture on early whorls (**A**<sub>2</sub>, close-up of the apical part). **B**. Paratype (NRM Mo187060) large fragmentary specimen. **C**. Holotype (NRM Mo187061) showing opisthocline axial ornament and faint spirals on last whorl (**C**<sub>1</sub>–**C**<sub>3</sub>, different lateral views). All in lateral view.

← Fig. 15. The provannid gastropod *Provanna pelada* sp. nov. from the early Oligocene seep deposit at Cerros El Pelado block 3, Talara Basin, northern Peru. **A**. Holotype (NRM Mo187052), smooth specimen in apertural (**A**<sub>1</sub>) and abapertural (**A**<sub>2</sub>) views. **B**. Paratype (NRM Mo187053), specimen with faint spiral ornament, in apertural view. **C**. Paratype (NRM Mo187054), specimen with axial and spiral sculpture, in two lateral views (**C**<sub>1</sub>, **C**<sub>2</sub>). **D**. Paratype (NRM Mo187055), nearly smooth specimen with faint spirals. **E**. Paratype (NRM Mo187056), showing distinctive prosocline growth increments and basal constriction. **F**. Paratype (NRM Mo187057), smooth specimen. **G**. Paratype (NRM Mo187058), specimen with rough, irregular prosocline ribs and fine spiral sculpture. All in lateral view, unless otherwise indicated.

deposits in the middle Eocene Humptulips Formation in Washington state, USA, and probably slightly older than the *Ascheria?* sp. specimens reported from seep deposits in Barbados (Kaim et al. 2014).

*Ascheria salina* sp. nov.

Fig. 16.

Zoobank LCID: urn:lsid:zoobank.org:act:6BDCBE13-9DA3-4AF0-9366-20014BEA1241

*Etymology*: For the type locality at Cerro La Salina.

*Type material*: Holotype: NRM Mo187061. Paratypes: NRM Mo 187059 from Cerro La Salina block 2 and NRM Mo187060 from Cerro La Salina block 1.

*Type locality*: Cerro La Salina block 1, Talara Basin, Peru.

*Type horizon*: Presumably the early Oligocene part of the Heath shale.

*Material*.—The type material and a few unnumbered fragments from Cerro La Salina block 1.

*Dimensions*.—Holotype (NRM Mo187061, H = 22 mm, W = 9 mm) with missing early whorls; fragmentary paratype (NRM Mo187060) W = 11.5 mm.

*Diagnosis*.—Small-sized *Ascheria* with blunt axial ribs that are opisthocline in lower part of whorls, a weak subsutural incision, and fine spiral incision in early whorls.

*Description*.—Medium-sized, high-spired cerithiform shell, at least seven slightly convex whorls. Sculpture consists of blunt axial ribs that are straight or slightly oblique in upper half of whorls and become increasingly opisthocline in lower half; ribs have subsutural constriction and blunt tubercles may develop above and below that constriction; early whorls have fine spiral incision but these disappear on whorls wider than 3 mm, later whorls with faint spiral threads; base is smooth except for opisthocyrt growth lines. Aperture appears to be elongate-oval.

*Remarks*.—*Ascheria salina* sp. nov. differs from *A. elenensis* by the shape of the axial ornament, which is strongly opisthocline just below the suture in *A. elenensis*, whereas the ribs become opisthocline only in the lower half of the whorl in *A. salina*. Furthermore, *A. elenensis* grows to a much larger size and appears to be higher spired (having a narrower apical angle) and *A. salina* has a higher whorl profile than *A. elenensis*. The Late Jurassic type species *A. gigantea* differs from *A. salina* by having spiral ornament also on large whorls, whereas in *A. salina* such spirals are only present on very early whorls (Kaim et al. 2014). *Ascheria?* sp. from Barbados (including the specimens reported as “cerithid sp.” by Kugler et al. (1984: pl. 7: 6–8), and as *Abyssochrysos* sp. by Gill et al. (2005: fig. 5D) has more oblique or sloping axial ribs and spiral ornament is also present on large specimens, in contrast to *A. salina*. As *Ascheria?* sp. from Barbados is most likely of Eocene age (Kiel and Hansen 2015), the early Oligocene Peruvian *Ascheria salina* is currently the youngest member of the genus; it is also the smallest species of *Ascheria*.

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

Family Buccinidae Rafinesque, 1815

Genus *Colus* Röding, 1798

*Type species*: *Murex islandicus* Mohr, 1786, by subsequent designation; Recent, North Atlantic Ocean.

*Colus sekiuensis* Kiel and Goedert, 2007

Fig. 17A, B.

2007 *Colus sekiuensis* sp. nov.; Kiel and Goedert 2007: 43, figs. 3D, E.

*Material*.—One specimen (NRM Mo187062; H = 21 mm) from Cerro La Salina block 2, one specimen (NRM Mo187063; H = 7 mm) from Cerro La Salina block 4. Both upper Oligocene, Talara Basin, Peru.

*Remarks*.—The specimens are rather imperfectly preserved; with their evenly convex whorl profile and spiral sculpture consisting of 11 low, nearly flat-topped, beaded spiral cords, the specimens are identical to those of *Colus sekiuensis* known from whale and wood falls from early Oligocene strata in Washington state, USA (Kiel and Goedert 2007). *Cyrtochetus? chiraensis* Olsson, 1931 from the Chira Formation in the Talara Basin, northern Peru, which is stratigraphically well below the Heath shale and now considered to be late Eocene in age (Higley 2004), is remarkably similar. That species differs from *Colus sekiuensis* by having finer and more numerous spiral cords with a more convex profile compared to the nearly flat-topped spiral of *Colus sekiuensis*. In general, the buccinid genus *Cyrtochetus* differs from *Colus* by having a varix at the aperture and denticles on the inner lip (Garvie 2013); however, those features cannot be recognized in the available material.

Olsson (1931) reported two species of *Siphonalia?* from Belén and Pajarabobo, *S.? belenensis* and *S.? tessaria*. Both differ from *Colus sekiuensis* by their more angular whorl profile. At least judging from the published drawing, *Siphonalia noachina* (Sowerby, 1846) as illustrated by Ortmann (1902: pl. 34: 5) from the late Oligocene to early Miocene of Patagonia, Argentina, has a similar overall sculpture, but a more convex whorl profile and fewer spirals per whorl.

In his faunal list for the limestone rocks near Belén and Pajarabobo, Olsson (1931: 22) lists “*Austrofusus? belenensis* n. sp.”, but a species of this name is neither described nor figured in his report. He also did not figure any neogastropods other than *S.? belenensis* and *S.? tessaria* from the Heath shale. Hence, *Austrofusus? belenensis* is a nomen dubium.

*Stratigraphic and geographic range*.—Oligocene to early Miocene of western Washington state, USA; early Oligocene of the Talara Basin, northern Peru.

Buccinidae indet.

Fig. 17C.

*Material*.—One specimen (NRM Mo187064, H = 7 mm) from the Belén seep site, upper Oligocene, Talara Basin, Peru.

*Remarks.*—The specimen differs from *Colus sekiuensis* by its distinctive opisthocline axial ribs and its seemingly more convex whorl profile. Among the buccinids reported by Olsson (1931) from northern Peru, *Cyrtochetus? chiraensis* Olsson, 1931, has an overall similar shape, but lacks distinctive axial ornament. Olsson's *Siphonalia* species discussed above in the context of *Colus sekiuensis* differ from this species by their more angular whorl profile.

Subclass Heterobranchia Burmeister, 1837

Family Acteonidae d'Orbigny, 1843

Genus *Acteon* Montfort, 1810

*Type species:* *Bulla tornatilis* Linnaeus, 1758, by original designation; Recent, North Atlantic Ocean.

“*Acteon*” sp.

Fig. 17D.

*Material.*—One specimen (NRM Mo187065, H = 3.3 mm) from Cerro La Salina block 7, upper Oligocene, Talara Basin, Peru.

*Remarks.*—The single available specimen is 3.3 mm high, has a distinct shoulder, and is sculptured by numerous fine, beaded spiral cords. A similar species is *Acteon annectens* Meyer, 1885, from the late Eocene Moodys Branch Formation in Mississippi, USA (Dockery 1977). Acteonids have also been reported from Late Cretaceous seep deposits in Japan (Kaim et al. 2009) and Oligocene seep deposits in Washington, USA (Kiel 2006). The generic name is given in inverted commas here because genera among the Acteonidae are mainly distinguished based on anatomy and radula rather than on conchological characters (Rudman 1971).

Family Cylichnidae Adams and Adams, 1854

Genus *Cylichna* Lovén, 1846

*Type species:* *Bulla cylindracea* Pennant, 1777, by subsequent designation; Recent, North Atlantic Ocean.

*Cylichna* sp.

Fig. 17E.

*Material.*—One specimen (NRM Mo187066, H = 5 mm) from Cerro La Salina block 1, one unnumbered specimen from Cerro La Salina block 6. Both upper Oligocene, Talara Basin, Peru.

*Remarks.*—The two available specimens are 5 mm high, have an evenly convex whorl profile, and show numerous fine spiral incisions. Olsson (1931) rarely reported specimens smaller than a centimeter and, hence, such small opisthobranchs are virtually unknown from the Peruvian fossil record. A similar species is *Cylichna atahualpa* (Dall, 1908) from the Pacific coast of Costa Rica (Valdés and Camacho-García 2004). *Cylichna*-like shells have occasionally been reported from fossil seep deposits, including an Early Cretaceous site in California (Kaim et al.

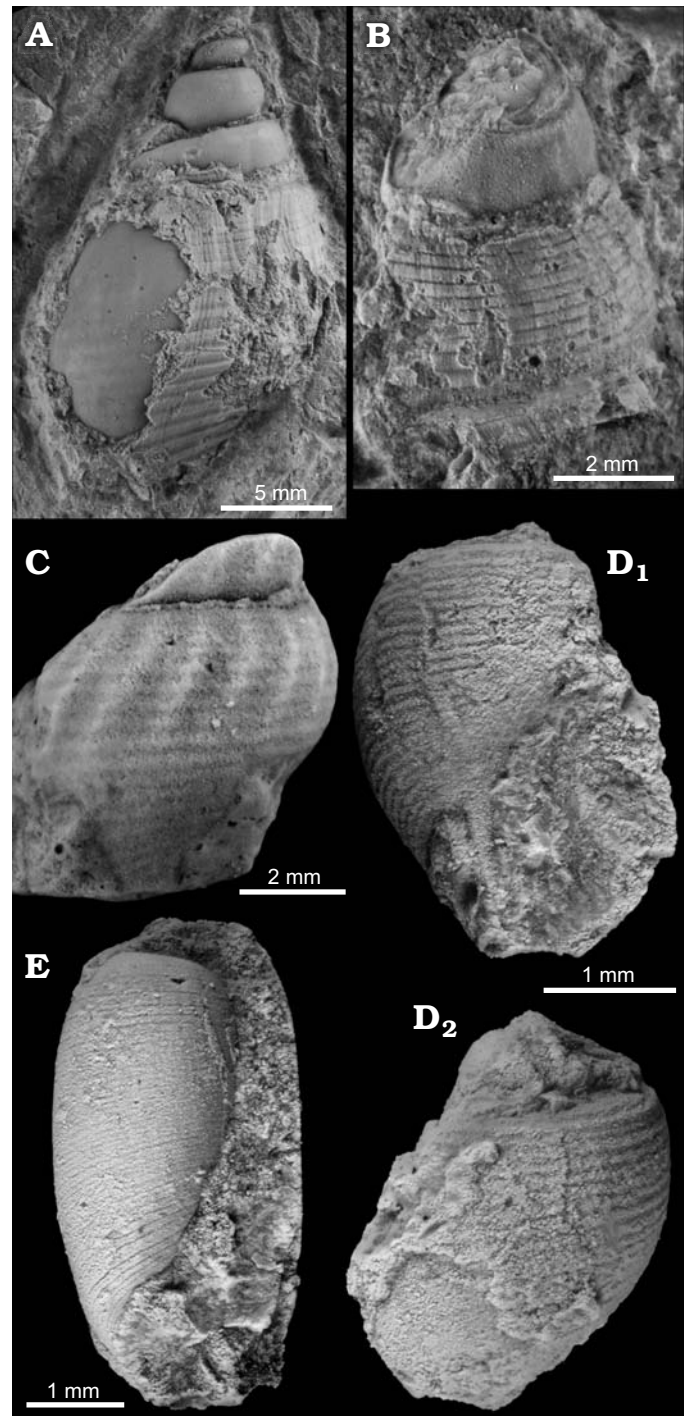


Fig. 17. Neogastropod and opisthobranch gastropods from early Oligocene seep deposits at Cerro La Salina (block 2, A; block 4, B; block 6, E; block 7, D) and Belén seep site (C), Talara Basin, northern Peru. **A, B.** The buccinid *Colus sekiuensis* Kiel and Goedert, 2007. **A.** Large specimen (NRM Mo187062), showing shape of last whorl. **B.** NRM Mo187063, fragment of an early whorl. **C.** Buccinidae indet. (NRM Mo187064), fragmentary specimen. **D.** NRM Mo187065, the opisthobranch “*Acteon*” sp. in apertural (D<sub>1</sub>) and lateral (D<sub>2</sub>) views. **E.** The opisthobranch *Cylichna* sp. (NRM Mo187066).

2014), a Paleocene site in Spitsbergen (Hryniewicz et al. 2019), and an Oligocene site in Washington, USA (Kiel 2006).

Phylum Arthropoda Von Siebold, 1848  
 Class Malacostraca Latreille, 1802  
 Order Decapoda Latreille, 1802  
 Suborder Pleocyemata Burkenroad, 1963  
 Infraorder Axiidea Saint Laurent, 1979  
 Family Callianassidae Dana, 1852  
 Subfamily Eucalliicinae Manning and Felder, 1991  
 Genus *Eucalliix* Manning and Felder, 1991

*Type species*.—*Callianassa quadracuta* Biffar, 1970, by original designation; Recent, western Atlantic Ocean.

*Eucalliix capsulasetaea* sp. nov.

Fig. 18.

*Zoobank LCID*: urn:lsid:zoobank.org:act:3742EC6D-CCAA-443D-A113-16EA7C8C30CD

*Etymology*: In reference to capsulated setae, one of diagnostic features of the species.

*Type material*: Holotype: right propodus (NRM Ar69394) from block 2. Paratypes: right propodus (NRM Ar69376) from block 6, left carpus (NRM Ar69377) from block 7, right propodus (NRM Ar69383) from block 4, and four specimens from block 2: left propodus (NRM Ar69393), right propodus (NRM Ar69397), right propodus (NRM Ar69398), left propodus (NRM Ar69401).

*Type locality*: Cerro La Salina seep deposits, Talara Basin, Peru.

*Type horizon*: Presumably the early Oligocene part of the Heath shale.

*Material*.—The type material and further fragmentary specimens from Cerro La Salina blocks 1, 2–4, 6–8. Complete left carpus (NRM Ar69377), block 7. Seven near-complete left propodi: NRM Ar69378, block 7; NRM Ar69380 (counterpart NRM Ar69379), block 7; NRM Ar69381, block 7; NRM Ar69389 (counterpart NRM Ar69390), block 8; NRM Ar69393, block 2; NRM Ar69401 (counterparts NRM Ar69395, NRM Ar69400) block 1; NRM Ar69402, block 2. Five near-complete right propodi: NRM Ar69376, block 6; NRM Ar69383 (counterparts Ar0069384, NRM Ar69385), block 4; NRM Ar69394, block 2; NRM Ar69397, block 2; NRM Ar69398, block 2. Three fragmentary propodi: NRM Ar69382, block 7; NRM Ar69387, block 1; NRM Ar69396, block 2. One broken right fixed finger: NRM Ar69399, block 2. One complete right dactylus: NRM Ar69388, block 1. One fragmentary dactylus: NRM Ar69386, block 1. All upper Oligocene, Talara Basin, Peru.

*Dimensions* (in mm).—Measurements are given only for sufficiently preserved propodi (maximum height and length of the manus). NRM Ar69376, H = 12.6, L = 11.5; NRM Ar69378, H = 11.9, L = 12.8; NRM Ar69383, H = 16.0, L = 16.2; NRM Ar69389, H = ~10.0, L = 11.4; NRM Ar69393, H = 18.3, L = 18.1; NRM Ar69394, H = 11.6, L = 10.5; NRM Ar69397, H = 8.6, L = 8.5; NRM Ar69398, H = 12.2, L = 11.4; NRM Ar69401, H = 15.2, L = 19.1.

*Diagnosis*.—Major manus subrectangular; outer and inner lateral surfaces of manus densely covered with round tuber-

cles, often with individual or serial setal pits; fixed finger with longitudinal keel.

*Description*.—Chelipeds (pereiopod 1) robust. Major carpus taller than long, not armed; upper margin keeled; lower and proximal margins forming continuous rounded margin with an indent at articulation with merus; distal margin with flange. Major propodus rectangular, robust; upper and lower margins keeled, parallel to each other or slightly converging distally; distal margin with or without blunt tooth below articulation with dactylus; area around articulation with dactylus forming bulge; inner and outer lateral surfaces strongly convex, densely covered with tubercles, tubercles closer to margins larger than those closer to longitudinal axis; larger tubercles occur closer to margins; tubercles usually with individual or serial setal pits. Outer lateral surface of fixed finger with longitudinal keel; occlusal margin of fixed finger with serrated keel forming blunt tooth distally. Dactylus robust, unarmed, tip slightly hooked; outer lateral surface with row of round setae positioned close to occlusal margin.

*Remarks*.—The species is placed within *Eucalliix* based on the subrectangular manus, the relatively short fixed finger with a triangular outline, and the presence of a longitudinal keel on the outer lateral surface of the fixed finger. This combination of features is characteristic for the genus as discussed in detail previously (Hyžný 2012; Hyžný and Hudáčková 2012).

*Eucalliix capsulasetaea* sp. nov. was presumably heterochelous, as are most representatives of Callianassidae (Dworschak et al. 2012; Hyžný and Klompmaker 2015). Consequently, all the studied, rather large and massively built cheliped elements are interpreted to represent remains of major claws of pereiopod 1. The remains are nearly equally distributed between right and left chelae (five versus six propodi, respectively). Callianassid ghost shrimps in general show random asymmetry (sensu Palmer 2009) in Recent (e.g., Sakai 1969; Labadie and Palmer 1996) and fossil examples (e.g., Hyžný 2012; Hyžný and Hudáčková 2012), and *Eucalliix capsulasetaea* sp. nov. supports this observation.

In *Eucalliix capsulasetaea* sp. nov., the manus is approximately as long as tall (H/L ratio = 0.93–1.10), but one relatively large specimen is distinctly longer (H/L ratio = 0.80; see Dimensions above). NRM Ar69401 is also less tuberculate than other specimens. Nevertheless, all specimens are considered conspecific for several reasons. In extant representatives of Eucalliicinae (i.e., the species of *Calliix* Saint Laurent, 1973, and *Eucalliix* Manning and Felder, 1991), considerable variation in the manus H/L ratio is observed and distinctly elongated forms are not uncommon, especially in larger individuals (Dworschak 2006; Hyžný and Gašparič 2014). Also, the presence of setal pores on top of the tubercles covering the lateral surfaces of the elongated manus supports the conspecificity of all callianassid specimens from Cerro La Salina.

The setal pits positioned at the top of tubercles represent

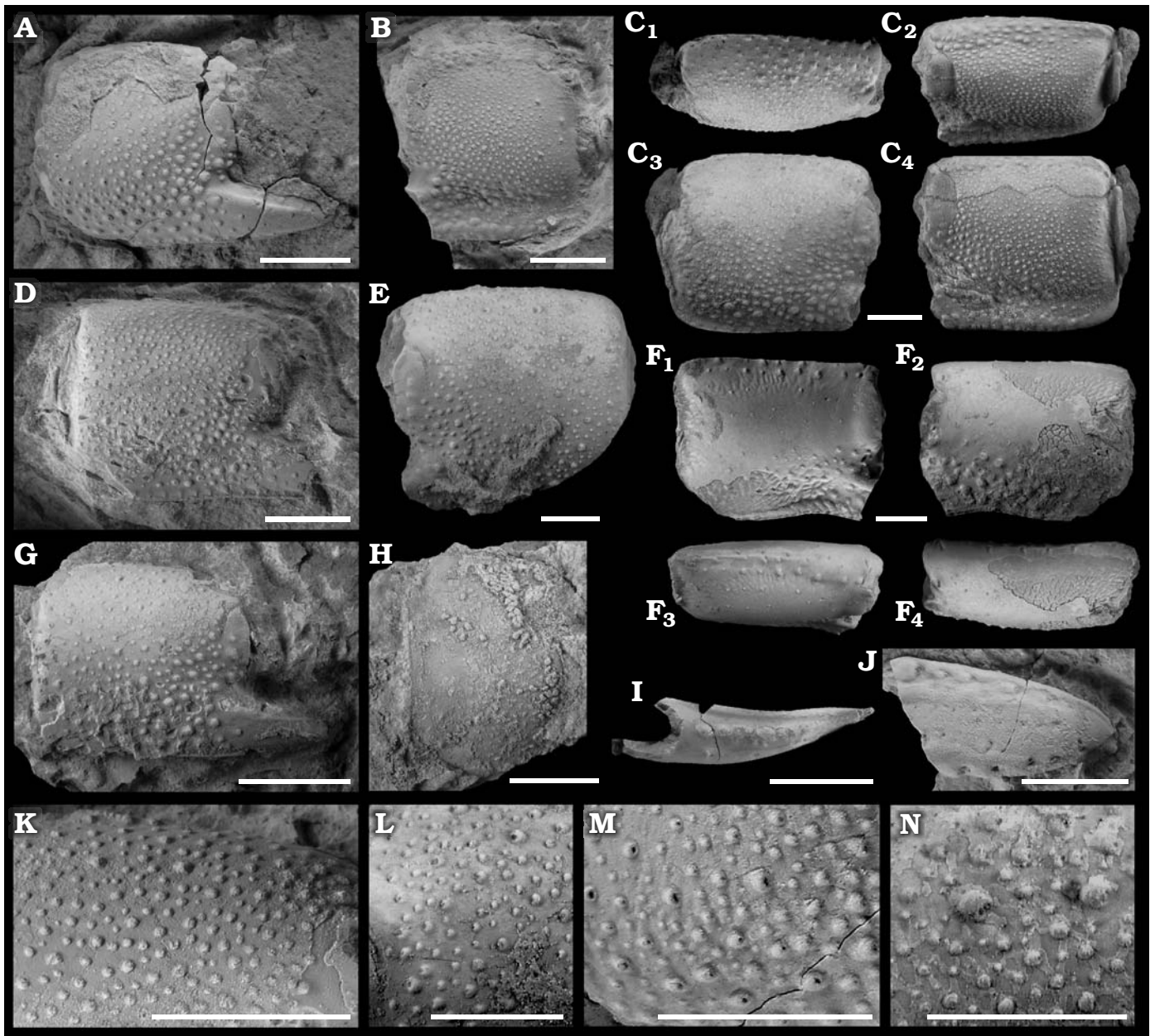


Fig. 18. The callianassid ghost shrimp *Eucalliax capsulasetaea* sp. nov. from early Oligocene seep deposits at Cerro La Salina, blocks 2, 4, 6, 7, in the Talara Basin, northern Peru. **A.** Holotype (NRM Ar69394), right propodus in outer lateral view. **B.** Paratype (NRM Ar69376), right propodus in inner lateral view. **C.** Paratype (NRM Ar69383), right propodus in dorsal (C<sub>1</sub>), dorso-lateral (C<sub>2</sub>), outer lateral (C<sub>3</sub>), and inner lateral (C<sub>4</sub>) views. **D.** Paratype (NRM Ar69398), right propodus in outer lateral view. **E.** Paratype (NRM Ar69393), left propodus in outer lateral view. **F.** Paratype (NRM Ar69401), left propodus in inner lateral (F<sub>1</sub>), outer lateral (F<sub>2</sub>) and dorso-lateral (F<sub>3</sub>, F<sub>4</sub>) views. **G.** Paratype (NRM Ar69397), right propodus in outer lateral view. **H.** Paratype (NRM Ar69377), left carpus in outer lateral view. **I.** NRM Ar69399, right fixed finger in occlusal view. **J.** NRM Ar69388, right dactylus in outer lateral view. **K–N.** Details of capsulated setae on outer lateral surfaces of major cheliped propodi. **K.** NRM Ar69398. **L.** NRM Ar69393. **M.** NRM Ar69394. **N.** NRM Ar69383. Scale bars 5 mm.

capsulated setae. They are not uncommon in hermit crabs (Paguroidea) and have been documented both in Recent (Komai 2003; Osawa 2012; Komai and Rahayu 2014) and fossil forms (Fraaije et al. 2011, 2015; Hyžný et al. 2016). Capsulated setae are rare in ghost shrimps. They have not been mentioned in taxonomic descriptions, but a quick survey of the published figures indicates their presence at least in fossil and extant species of *Callianopsis* Saint Laurent, 1973 (Karasawa 1997; Schweitzer Hopkins and Feldmann

1997; Lin et al. 2007), although they are limited to a more distal region (i.e., close to the articulation with the dactylus) and their number usually is not exceeding ten. In extant *Neocallichirus karumba* (Poore and Griffin, 1979) and its supposed fossil relatives, there are several (1–3) such tubercles present at the area of articulation with the dactylus (Dworschak 2008; Hyžný et al. 2016). Thus, *Eucalliax capsulasetaea* sp. nov. bearing numerous tubercles with capsulated setae is unique among both extant and fossil ghost

Table 2. List of species from the lower Oligocene seep carbonates in northern Peru; \* includes most likely also the “*Cytherea*” and “large *Cyprina*–*Isocardia*-like shells” listed by Olsson (see Kiel 2013).

Species	La Salina	El Pelado	Olsson's Quebrada Seca	Belén	Olsson's Belén and Pajarabobo	Lomitos	Comment
<b>Bivalvia</b>							
<i>Solemya lomitensis</i> Olsson, 1931						×	
<i>Solemya (Acharax) belenensis</i> Olsson, 1931					×		
<i>Nucula paboensis</i> Olsson, 1931					×		
<i>Acila paita</i> Olsson, 1931				?	×		possibly same as <i>Acila</i> sp. in this paper
<i>Acila piura</i> Olsson, 1931				?	×		possibly same as <i>Acila</i> sp. in this paper
<i>Neilo altamirano</i> sp. nov.	×						
<i>Idas</i> sp.	×						
Propeamussiidae indet.	×						
<i>Pseudophopsis peruviana</i> (Olsson, 1931)	×	×	×		×	×	
<i>Conchocele tessaria</i> (Olsson, 1931)	×				×		as <i>Thyasira</i> in Olsson (1931)
<i>Thyasira peruviana</i> Olsson, 1931						×	
<i>Thyasira staufti</i> Olsson, 1931						×	
<i>Myrtaea? cookei</i> Olsson, 1931			×				
<i>Myrtaea?</i> sp.						×	
<i>Lucinoma zapotalensis</i> (Olsson, 1931)	×	×					as “ <i>Phacoides (Lucinoma)</i> ” in Olsson (1931)
<i>Nipponothracia lomitensis</i> (Olsson, 1931)						×	as “ <i>Lucina? lomitensis</i> ” in Olsson (1931)*
<i>Pleurophopsis lithophagoides</i> Olsson, 1931				×	×		
<i>Pleurophopsis talarensis</i> sp. nov.	×		×		×		reported as <i>P. lithophagoides</i> by Olsson (1931)
“ <i>Vesicomya</i> ” <i>tchudi</i> Olsson, 1931	×				×	×	
“ <i>Vesicomya</i> ” <i>ramondi</i> Olsson, 1931					×		
<b>Gastropoda</b>							
Limpet 1	×						
Limpet 2	×						
<i>Coccoligya</i> sp.	×						
<i>Retiskenea?</i> sp.	×						
<i>Pyropelta seca</i> sp. nov.	×	×					
<i>Cantrainea</i> sp.	×	×					
Trochoid incertae sedis	×						
Neritimorpha indet.					×	×	listed as “ <i>Nerita</i> ” by Olsson (1931)
<i>Ampullina</i> or <i>Polinices</i>						×	internal casts
<i>Provanna antiqua</i> Squires, 1995	×			×			
<i>Provanna pelada</i> sp. nov.		×					
<i>Ascheria salina</i> sp. nov.	×						
<i>Colus sekiuensis</i> Kiel and Goedert, 2007	×						
Buccinidae indet.				×			
<i>Austrofusus? belenensis</i> Olsson, 1931					×		nomen dubium
<i>Siphonalia? belenensis</i> Olsson, 1931					×		
<i>Siphonalia? tessaria</i> Olsson, 1931					×		
<i>Acteon</i> sp.	×						
<i>Cylichna</i> sp.	×						
<b>Decapoda</b>							
<i>Eucalliax capsulasetaea</i> sp. nov.	×						

shrimp species described to date, to our knowledge. The new species is morphologically closest to *Eucalliax burckhardti* (Böhm, 1911) from the Maastrichtian and Danian of Argentina and Mexico (Hyžný et al. 2013). Both species share densely tuberculated propodi; *E. burckhardti*,

however, does not possess capsulated setae. Besides the presence of capsulated setae, the new species further differs from the type species *E. quadracuta* in the absence of diagnostic acute projections on the distodorsal and distoventral corners of the carpus and on the distodorsal corner of



the propodus (Biffar 1970). Cenozoic representatives, such as *E. vicetina* Beschin, Busulini, De Angeli, and Tessier, 2002, from the middle Eocene of Italy; *E. pseudorakosensis* (Lörenthey in Lörenthey and Beurlen 1929) from the middle Miocene of Europe; *E. yatsuoensis* (Karasawa 1993) from the middle Miocene of Japan; and *E. miyazakiensis* Karasawa, 1993, possess smooth lateral surfaces of the major cheliped propodi. In contrast to the new species, *E. yoshihiro* Karasawa, 1992, from the middle Eocene of Japan has sparse tubercles on the lateral surfaces of the major cheliped propodus, but it is not clear from the published figures alone whether setae are present at the top of the tubercles; no further details on this feature are mentioned in the description (Karasawa 1992). Newly presented material of *Eucalliax* reported from the late Eocene of Italy (Beschin et al. 2019) is too fragmentary and, based on the published figures, these specimens may not be congeneric with *Eucalliax*.

McLaughlin and Lane (1975) hypothesized that capsulated setae might act both to detect and repel predators, but more studies are needed to assess their function. The function of a limited number of capsulated setae in the ghost shrimps *Neocallichirus* and *Callianopsis* may be different than in hermit crabs and the here described new species of *Eucalliax* with numerous such setae. It is also worth noting that, whereas all *Callianopsis* species seem to possess capsulated setae, in *Neocallichirus* they are present only in the group of species morphologically close to *N. karumba*, a species differing profoundly from *N. horneri* Sakai, 1988, the type species of *Neocallichirus*. Consequently, the presence or absence of capsulated setae on ghost shrimps are not always a feature of generic importance, as currently understood.

Muscle scars are preserved in a number of specimens of *Eucalliax capsulasetaea* sp. nov. These are observed in specimens in which the cuticle is not fully preserved on the inner and outer sides of the manus (Fig. 18F), or, sometimes, on the cuticle. These scars represent closer (adductor) muscles (see Klompmaker et al. 2019), whereas the much smaller (abductor) opener is not seen here.

*Eucalliax* spp. have been found in the Late Cretaceous, Paleocene, Eocene, Miocene, Pliocene, and Recent (Hyžný and Klompmaker 2015: supplementary file 1). Thus, the new species is the first record from the Oligocene.

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

## Discussion

With Olsson's (1931) and our study combined, 39 species of mollusks have been reported from the seep deposits in the Talara Basin, but only five species are shared between Olsson's (1931) and our study (*Pseudophopsis peruviana*, *Conchocele tessaria*, *Pleurophopsis unioides*, *P. talarensis*, and "*Vesicomya*" *tschudi*; Table 2). The main reason for this

difference is that Olsson did not consider small specimens: many species reported here are smaller than ca. 10 mm. Another reason might be that the sediments from which Olsson (1931) extracted his most diverse fauna ("between Belén and Pajarabobo") appear to have been mostly eroded. This might explain why only five out of 13 of Olsson's (1931) larger bivalve species are shared with our study.

Notably among the taxa we found are *Coccopygia* sp., which represents the oldest record of this genus, and *Ascheria salina*, representing the youngest and smallest member of *Ascheria*. Fossils are rare in the deep-water deposits of the Heath shale (Olsson 1931; Palacios Moncayo 1994) and, hence, methane seeps with their rapid in situ carbonate precipitation are more likely to preserve specimens. Consequently, the deep-water genera *Neilo*, *Propeamusium*, *Coccopygia*, *Cantrainea*, and *Colus*, and also the seep-restricted taxa *Pyropelta*, *Provanna*, *Ascheria*, and perhaps *Retiskenea* are here reported for the first time from the fossil record of Peru.

Among decapods, callianassid ghost shrimps are common associates of ancient seep environments (Klompmaker et al. 2018: fig. 4). Klompmaker et al. (2018) argued that they may be more commonly reported from the fossil seeps compared to modern seeps because these burrowing shrimps are difficult to catch in today's ocean bottoms. The earliest records of callianassids from seeps thus far are mid-Cretaceous in age (Karasawa 2011; Kiel et al. 2013; Agirrezabala et al. 2013). *Eucalliax* had not been reported from a fossil seep thus far, unlike *Callianassa*, *Callianopsis*, *Calliax*, *Glypturus*, and *Neocallichirus* (see Klompmaker et al. 2018).

## Conclusions

Combined with Olsson's (1931) earlier work, our study revealed a remarkably diverse fauna of mollusks at the early Oligocene seeps in the Talara Basin in northern Peru, encompassing close to 40 species. The majority of them belong to genera known from both coeval and Recent seeps. The biogeographically closest ties are with late Eocene to Oligocene seep faunas in the northeastern Pacific region, with which they share two species and twelve genera. Notable is the absence of larger *Bathymodiolus* species from the seeps in the Talara basin, as these mussels are quite common in Oligocene seep deposits in the North Pacific region. A newly described ghost shrimp species of *Eucalliax* is the first occurrence of this genus reported from a seep.

## Acknowledgments

We thank Ali Altamirano (Museo de Historia Natural, Lima, Peru) for assistance in the field, Cris Little and Jordan Bestwick (both Leeds University, UK) for letting us use their images of *Pseudophopsis peruviana*, Andrzej Kaim (Institute of Paleobiology, Polish Academy of

Sciences, Warsaw, Poland) for comments on the gastropods, Jim Goedert (Wauna, USA) for comments on the provannids, Judith Nagel-Myers (St. Lawrence University, Canton, USA) and Leslie Skibinski (PRI) for loans of specimens, and the reviewers Kazutaka Amano (Joetsu University of Education, Japan) and Krzysztof Hryniewicz (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland) for their critical comments that greatly improved the manuscript. Financial support was provided by Vetenskapsrådet through grant 2016-03920 to SK, and by the Slovak Research and Development Agency through contract APVV-17-0555 to MH.

## References

- Abbott, R.T. 1954. *American Seashells*. xiv + 541 pp. Van Nostrand Reinhold, New York.
- Adams, H. and Adams, A. 1853–1858. *The Genera of Recent Mollusca Arranged According to Their Organization*. Vol. 1: vi–xl, 1–484; Vol. 2: 1–661. John Van Voorst, London.
- Agirrezabala, L.M., Kiel, S., Blumenberg, M., Schäfer, N., and Reitner, J. 2013. Outcrop analogues of pockmarks and associated methane-seep carbonates: a case study from Lower Cretaceous (Albian) of the Basque-Cantabrian Basin, western Pyrenees. *Palaeogeography, Palaeoclimatology, Palaeoecology* 390: 94–115.
- Amano, K. and Jenkins, R.G. 2011a. Fossil record of extant vesicomid species from Japan. *Venus* 69: 163–176.
- Amano, K. and Jenkins, R.G. 2011b. New fossil *Bathymodiolus* (s.l.) (Mytilidae, Bivalvia) from Oligocene seep-carbonates in eastern Hokkaido, Japan—with remarks on the evolution of *Bathymodiolus* (s.l.). *The Nautilus* 125: 29–35.
- Amano, K. and Jenkins, R.G. 2013. A new species of *Provanna* (Gastropoda: Provannidae) from an Oligocene seep deposit in eastern Hokkaido, Japan. *Paleontological Research* 17: 325–329.
- Amano, K. and Kiel, S. 2007. Fossil vesicomid bivalves from the North Pacific region. *The Veliger* 49: 270–293.
- Amano, K. and Kiel, S. 2010. Taxonomy and distribution of fossil *Archivesica* (Vesicomidae, Bivalvia) in Japan. *The Nautilus* 124: 155–165.
- Amano, K. and Kiel, S. 2011. Fossil *Adulomya* (Vesicomidae, Bivalvia) from Japan. *The Veliger* 51: 76–90.
- Amano, K. and Kiel, S. 2012. Two Neogene vesicomid species (Bivalvia) from Japan and their biogeographic implications. *The Nautilus* 126: 79–85.
- Amano, K. and Little, C.T.S. 2005. Miocene whale-fall community from Hokkaido, northern Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 215: 345–356.
- Amano, K. and Little, C.T.S. 2014. Miocene abyssochryoid gastropod *Provanna* from Japanese seep and whale-fall sites. *Acta Palaeontologica Polonica* 59: 163–172.
- Amano, K., Jenkins, R.G., and Kurita, H. 2018a. New and Mesozoic-relict mollusks from Paleocene wood-fall communities in Urahoro Town, eastern Hokkaido, northern Japan. *Journal of Paleontology* 92: 634–647.
- Amano, K., Jenkins, R.G., Ohara, M., and Kiel, S. 2014a. Miocene vesicomid species (Bivalvia) from Wakayama in southern Honshu, Japan. *The Nautilus* 128: 9–17.
- Amano, K., Little, C.T.S., and Campbell, K.A. 2018b. Lucinid bivalves from Miocene hydrocarbon seep sites of eastern North Island, New Zealand, with comments on Miocene New Zealand seep faunas. *Acta Palaeontologica Polonica* 63: 371–382.
- Amano, K., Little, C.T.S., and Inoue, K. 2007. A new Miocene whale-fall community from Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 247: 236–242.
- Amano, K., Little, C.T.S., Campbell, K.A., Jenkins, R.G., and Saether, K.P. 2015. Paleocene and Miocene *Thyasira* sensu stricto (Bivalvia: Thyasiridae) from chemosynthetic communities from Japan and New Zealand. *The Nautilus* 129: 43–53.
- Amano, K., Saether, K.P., Little, C.T.S., and Campbell, K.A. 2014b. Fossil vesicomid bivalves from Miocene hydrocarbon seep sites, North Island, New Zealand. *Acta Palaeontologica Polonica* 59: 421–428.
- Beschin, C., Busulini, A., De Angeli, A., and Tessier, G. 2002. Aggregamento ai crostacei eocenici di cava „Main“ di Arzignano (Vicenza, Italia settentrionale) (Crustacea, Decapoda). *Studi e Ricerche Associazione Amici Museo Zannato Museo Civico „G. Zannato“* 2002: 7–28.
- Beschin, C., Busulini, A., Fornacciari, F., Papazzoni, C.A., and Tessier, G. 2019. La fauna di crostacei associati a coralli dell'Eocene superiore di Campolongo di Val Liona (Monti Berici, Vicenza, Italia Nordorientale). *Bollettino del Museo di Storia Naturale di Venezia* 69: 129–215.
- Beu, A.G. and Maxwell, P.A. 1990. Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin* 58: 1–518.
- Beu, A.G., Nolden, S., and Darragh, T.A. 2012. Revision of New Zealand Cenozoic fossil Mollusca described by Zittel (1865) based on Hochstetter's collections from the *Novara Expedition*. *Memoirs of the Association of Australasian Palaeontologists* 43: 1–69.
- Beurlen, K. 1944. Beiträge zur Stammesgeschichte der Muscheln. *Bayrische Akademie der Wissenschaften, Sitzungsberichte* 1–2: 133–145.
- Biffar, T.A. 1970. Three new species of callianassid shrimp (Decapoda, Thalassinidea) from the western Atlantic. *Proceedings of the Biological Society of Washington* 83: 35–50.
- Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M., and Strong, E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61: 1–526.
- Burkenroad, M.D. 1963. The evolution of the Eucarida, (Crustacea, Eumalacostraca), in relation to the fossil record. *Tulane Studies in Geology and Paleontology* 2: 2–17.
- Burmeister, H. 1837. *Handbuch der Naturgeschichte, Vol. 2, Zoologie*. i–xii + 369–858 pp. Enslin, Berlin.
- Böhm, J. 1911. *Callianassa burckhardtii* n. sp. nebst einer Zusammenstellung der fossilen Arten der Gattung *Callianassa*. *Zeitschrift der deutschen geologischen Gesellschaft, Monatsberichte* 63: 37–46.
- Campbell, K.A., Peterson, D., and Alfaro, A.C. 2008. Two new species of *Retikenea*? (Gastropoda: Neomphalidae) from Lower Cretaceous hydrocarbon seep-carbonates of northern California. *Journal of Paleontology* 82: 140–153.
- Cantraine, F.J. 1835. Diagnoses ou descriptions succinctes de quelques espèces nouvelles de mollusques. *Bulletin de l'Académie Royale des Sciences et Belles-lettres de Bruxelles* 2: 380–401.
- Chavan, A. 1954. Les Pleurophorus et genres voisins. *Cahier Géologiques Seyssel* 22: 200.
- Conrad, R.A. 1849. Fossils from the northwestern America. In: J.D. Dana (ed.), *U.S. Exploration Expedition, 1838–1842, under Charles Wilkes. Geology, Volume 10*, 723–728 (appendix). C. Sherman, Philadelphia.
- Contardo-Berrios, X., Mena-Hodges, E., and Quirago, E. 2017. Hallazgo del primer seep fósil en la costa emergida de Chile central (33°56' S). Caracterización e implicancias. *Andean Geology* 44: 213–228.
- Cooke, C.W. 1919. Contributions to the geology and paleontology of the West Indies IV. Tertiary mollusks from the leeward islands and Cuba. *Carnegie Institution of Washington publications* 291: 103–156.
- Cossmann, M. and Peyrot, A. 1917. Conchologie néogénique de l'Aquitaine. Tome 3, Gastropodes, Scaphopodes et Amphineures. *Actes de la Société Linnéenne de Bordeaux* 69 (4), 285–365.
- Cox, L.R. 1960. Gastropoda. General characteristics of Gastropoda. In: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology. Pt I. Mollusca*, 1, 185–1169. Geological Society of America and University of Kansas Press, Lawrence.
- Cuvier, G.L.C.F.D. 1795. Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magasin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts* 2: 433–449.
- d'Orbigny, A. 1842–43. *Paléontologie Française, terrains crétacés. Vol. 2, Gastéropodes*. 645 pp. Privately published, Paris.
- Dall, W.H. 1882. On certain limpets and chitons from the deep waters off the eastern coast of the United States. *Proceedings of the U.S. National Museum of Natural History* 4: 400–414.
- Dall, W.H. 1886. Reports on the results of dredging, under the supervi-

- sion of Alexander Agassiz, in the Gulf of Mexico (1877–1878) and in the Caribbean Sea (1879–1880), by the U.S. Coast Survey steamer “Blake” XXIX. Report on the Mollusca. Part 1, Brachiopoda and Pelecypoda. *Bulletin of the Museum of Comparative Zoology, Harvard University* 12: 171–318.
- Dall, W.H. 1900. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Part 5, Teleodemeacea: *Solen* to *Diplodonta*. *Transactions of the Wagner free Institute of Science, Philadelphia* 3: 949–1218.
- Dall, W.H. 1901. Synopsis of the Lucinacea and of the American species. *Proceedings of the U.S. National Museum of Natural History* 23: 779–833.
- Dall, W.H. 1908. The Mollusca and the Brachiopoda. *Bulletin of the Museum of Comparative Zoology, Harvard University* 43 (6): 205–487.
- Dall, W.H. 1918. Description of new species of shells chiefly from Magdalena Bay, Lower California. *Proceedings of the Biological Society of Washington* 31: 5–8.
- Dall, W.H. and Simpson, C.T. 1901. The Mollusca of Porto Rico. *United States Fishery Commission, Bulletin* 20: 351–524.
- Dana, J.D. 1852. *Crustacea. Part I. United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N.13.* viii + 685 pp. C. Sherman, Philadelphia.
- Dantart, L. and Luque, Á.A. 1994. Cocculiniformia and Lepetidae (Gastropoda: Archaeogastropoda) from Iberian waters. *Journal of Molluscan Studies* 60: 277–313.
- Decker, C., Olu, K., Cunha, R.L., and Arnaud-Haond, S. 2012. Phylogeny and diversification patterns among vesicomid bivalves. *PLoS ONE* 7: e33359.
- Del Río, C.A. and Camacho, H.H. 1998. Tertiary nuculoids and arcoids of eastern Patagonia (Argentina). *Palaeontographica A* 250: 47–88.
- Dockery, D.T. 1977. Mollusca of the Moodys Branch Formation, Mississippi. *Mississippi Office of Geology Bulletin* 122: 1–212.
- Dworschak, P.C. 2006. A new species of *Eucalliax* Manning & Felder, 1991 (Decapoda: Callianassidae) from the Philippines. *The Raffles Bulletin of Zoology* 54: 349–359.
- Dworschak, P.C. 2008. *Neocallichirus kempii* Sakai, 1999, a junior synonym of *Callianassa karumba* Poore & Griffin, 1979 (Decapoda: Callianassidae). *The Raffles Bulletin of Zoology* 56: 75–84.
- Dworschak, P.C., Felder, D.L., and Tudge, C.C. 2012. Infraorders Axiidea de Saint Laurent, 1979 and Gebiidea de Saint Laurent, 1979 (formerly known collectively as Thalassinidea). In: F.R. Schram, J.C. von Vaupel Klein, M. Charmantier-Daures, and J. Forest (eds.), *Treatise on Zoology—Anatomy, Taxonomy, Biology—The Crustacea, Decapoda, Decapoda: Astacidea P.P. (Enoplometoidea, Nephropoidea), Glypheidea, Axiidea, Gebiidea, and Anomura, Vol. 9B*, 109–219. Brill, Leiden.
- Eagle, M.K. and Hayward, B.W. 1993. Oligocene paleontology and paleoecology of Waitete Bay, northern Coromandel Peninsula. *Records of the Auckland Institute and Museum* 30: 13–26.
- Egorova, E.N. 1982. Mollusca of the Davis Sea (the Eastern Antarctic region) [in Russian]. *Rezultaty biologičeskikh issledovanij sovetskikh antarkticeskikh ekspedicij 7, Issledovaniâ fauny morej* 26: 1–134.
- Erdmann, S. and Morra, G. 1985. Nuevos Moluscos de la Formación San Julián, Provincia de Santa Cruz. *Ameghiniana* 22: 289–295.
- Finlay, H.J. 1926. New shells from New Zealand Tertiary beds: Part 2. *Transactions of the New Zealand Institute* 56: 227–258.
- Fleming, J. 1828. *A History of British Animals, Exhibiting the Descriptive Characters and Systematical Arrangement of the Genera and Species of Quadrupeds, Birds, Reptiles, Fishes, Mollusca and Radiata of the United Kingdom; Including the Indigenous, Extirpated, and Extinct Kinds; Together with Periodical and Occasional Visitants.* xxiii + 554 pp. Bell & Bradfute, Edinburgh.
- Fraaije, R.H.B., van Bakel, B.W.M., Iserbyt, A., and Jagt, J.W.M. 2011. New extinct Paguroidea (Crustacea, Decapoda, Anomura), with the first example of capsulated setae from the fossil record. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 262: 247–255.
- Fraaije, R.H.B., van Bakel, B.W.M., and Jagt, J.W.M. 2015. A new Alban hermit crab (Anomura, Paguroidea) from France—another example of capsulated setae in an extinct form. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 277: 353–359.
- Gabb, W.M. 1866–1869. Cretaceous and Tertiary fossils. *California Geological Survey, Paleontology* 2: 1–299.
- Garvie, C.L. 2013. New Eocene Mollusca from the collections of the Texas Natural Science Center. *Bulletins of American Paleontology* 386: 163–183.
- Gill, F.L. and Little, C.T.S. 2013. A new genus of lucinid bivalve from hydrocarbon seeps. *Acta Palaeontologica Polonica* 58: 573–578.
- Gill, F.L., Harding, I.C., Little, C.T.S., and Todd, J.A. 2005. Palaeogene and Neogene cold seep communities in Barbados, Trinidad and Venezuela: An overview. *Palaeogeography, Palaeoclimatology, Palaeoecology* 227: 191–209.
- Goedert, J.L. and Benham, S.R. 1999. A new species of *Depressigyra?* (Gastropoda: Peltospiridae) from cold-seep carbonates in Eocene and Oligocene rocks of western Washington. *The Veliger* 42: 112–116.
- Goedert, J.L. and Campbell, K.A. 1995. An Early Oligocene chemosynthetic community from the Makah Formation, northwestern Olympic Peninsula, Washington. *The Veliger* 38: 22–29.
- Goedert, J.L. and Kaler, K.L. 1996. A new species of *Abyssochrysis* (Gastropoda: Loxonematoidea) from a Middle Eocene cold-seep carbonate in the Humptulips Formation, western Washington. *The Veliger* 39: 65–70.
- Goedert, J.L. and Squires, R.L. 1993. First Oligocene record of *Calyptogena* (Bivalvia: Vesicomidae). *The Veliger* 36: 72–77.
- Golikov, A.N. and Starobogatov, Y.I. 1975. Systematics of prosobranch gastropods. *Malacologia* 15: 185–232.
- Gray, J.E. 1824. *Shells. A Supplement to the Appendix of Captain Parry's Voyage for the Discovery of a North-west Passage, in the Years 1819–1820: Containing an Account of the Subjects of Natural History.* ccxl–ccxlvii pp. Murray, London.
- Griffin, M. and Nielsen, S.N. 2008. A revision of the type specimens of Tertiary molluscs from Chile and Argentina described by D’Orbigny (1842), Sowerby (1846) and Hupé (1854). *Journal of Systematic Palaeontology* 6: 251–316.
- Griffin, M. and Pastorino, G. 2006. *Madrynomys bruneti* n. gen. and sp. (Bivalvia: ?Modiomorphoidea): a Mesozoic survivor in the Tertiary of Patagonia? *Journal of Paleontology* 80: 272–282.
- Haszprunar, G. 1987. Anatomy and affinities of cocculinid limpets (Mollusca Archaeogastropoda). *Zoologica Scripta* 16: 305–324.
- Hickman, C.S. 2015. Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, part III: The heteroconchs. *PaleoBios* 32: 1–44.
- Hickman, C.S. and McLean, J.H. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Natural History Museum of Los Angeles County Science Series* 35: 1–169.
- Higley, D. 2004. The Talara basin province of northwestern Peru: Cretaceous–Tertiary total petroleum system. *U.S. Geological Survey, e-Bulletin* B-2206a: 52.
- Hinds, R.B. 1843. Descriptions of new species of *Nucula* from the collections of Sir Edward Belcher, C.B., and Hugh Cuming, Esq. *Proceedings of the Zoological Society of London* 1843: 97–101.
- Hryniewicz, K., Amano, K., Bitner, M.A., Hagström, J., Kiel, S., Klomp-maker, A.A., Mörs, T., Robins, C.M., and Kaim, A. 2019. A late Paleocene fauna from shallow-water chemosynthesis-based ecosystems in Spitsbergen, Svalbard. *Acta Palaeontologica Polonica* 64: 101–141.
- Hryniewicz, K., Amano, K., Jenkins, R.G., and Kiel, S. 2017. Thyasirid bivalves from Cretaceous and Paleogene cold seeps. *Acta Palaeontologica Polonica* 62: 705–728.
- Hutton, F.W. 1887. The Mollusca of the Pareora and Oamaru Systems of New Zealand. *Proceedings of the Linnean Society of New South Wales* 11: 205–237.
- Hybertsen, F. and Kiel, S. 2018. A middle Eocene seep deposit with silicified fauna from the Humptulips Formation in western Washington State, USA. *Acta Palaeontologica Polonica* 63: 751–768.
- Hyžný, M. 2012. *Calliaxina chalmasii* (Brocchi, 1883) comb. nov. (Decapoda: Axiidea: Callianassidae: Eucalliinae), a ghost shrimp from the Middle Miocene of Europe, with reappraisal of the fossil record of Eucalliinae. *Zootaxa* 3492: 49–64.
- Hyžný, M. and Gašparič, R. 2014. Ghost shrimp *Calliax* de Saint Laurent,

- 1973 (Decapoda: Axiidea: Callianassidae) in the fossil record: systematics, palaeoecology and palaeobiogeography. *Zootaxa* 3821: 37–57.
- Hyžný, M. and Hudáčková, N. 2012. Redescription of two ghost shrimps (Decapoda: Axiidea: Callianassidae) from the Middle Miocene of the Central Paratethys: systematics, intraspecific variation, and in situ preservation. *Zootaxa* 3210: 1–25.
- Hyžný, M. and Klompmaker, A.A. 2015. Systematics, phylogeny, and taxonomy of ghost shrimps (Decapoda): a perspective from the fossil record. *Arthropod Systematics & Phylogeny* 73: 401–437.
- Hyžný, M., Charbonnier, S., Merle, D., Ahmed Lashari, R., Bartolini, A., and Métais, G. 2016. New Early Cenozoic ghost shrimps (Decapoda, Axiidea, Callianassidae) from Pakistan and their palaeobiogeographic implications. *Geodiversitas* 38: 341–353.
- Hyžný, M., Fraaije, R.H.B., Martin, J.E., Perrier, V., and Sarr, R. 2016. *Paracapsulapagurus poponguinensis*, a new hermit crab (Decapoda: Anomura: Paguroidea) from the Maastrichtian of Senegal. *Journal of Paleontology* 90: 1133–1137.
- Hyžný, M., Vega, F.J., and Coutiño, M.A. 2013. Ghost shrimps (Decapoda: Axiidea: Callianassidae) of the Maastrichtian (Late Cretaceous) Ocozocoautla Formation, Chiapas (Mexico). *Boletín de la Sociedad Geológica Mexicana* 65: 255–264.
- Jeffreys, J.G. 1876. New and peculiar Mollusca of the *Pecten*, *Mytilus* and *Arca* families procured in the “Valorous” Expedition. *Annals and Magazine of Natural History* 4: 424–436.
- Jeffreys, J.G. 1883. On the Mollusca procured during the *Lightning* and *Porcupine* expeditions, 6. *Proceedings of the Zoological Society of London* 1883: 88–115.
- Jenkins, R.G., Kaim, A., Amano, K., Sakurai, K., and Matsubara, K. 2018a. A new Miocene whale-fall community dominated by bathymodiolin mussel *Adipicola* from Hobetsu area, Hokkaido, Japan. *Paleontological Research* 22: 105–111.
- Jenkins, R.G., Kaim, A., and Hikida, Y. 2007. Antiquity of the substrate choice among acmaeid limpets from the Late Cretaceous chemosynthesis-based communities. *Acta Palaeontologica Polonica* 52: 369–373.
- Jenkins, R.G., Kaim, A., Hikida, Y., and Kiel, S. 2018b. Four new species of the Jurassic to Cretaceous seep-restricted bivalve *Caspiconcha* and implications for the history of chemosynthetic communities. *Journal of Paleontology* 92: 596–610.
- Jenkins, R.G., Kaim, A., Little, C.T.S., Iba, Y., Tanabe, K., and Campbell, K.A. 2013. Worldwide distribution of modiomorphid bivalve genus *Caspiconcha* in late Mesozoic hydrocarbon seeps. *Acta Palaeontologica Polonica* 58: 357–382.
- Johnson, S.B., Krylova, E.M., Audzijonyte, A., Sahling, H., and Vrijenhoek, R.C. 2017. Phylogeny and origins of chemosynthetic vesicomid clams. *Systematics and Biodiversity* 15: 346–360.
- Kaim, A. and Schneider, S. 2012. A conch with a collar: Early ontogeny of the enigmatic fossil bivalve *Myoconcha*. *Journal of Paleontology* 86: 653–659.
- Kaim, A., Jenkins, R.G., and Hikida, Y. 2009. Gastropods from Late Cretaceous hydrocarbon seep deposits in Omagari and Yasukawa, Nakagawa area, Hokkaido, Japan. *Acta Palaeontologica Polonica* 54: 463–690.
- Kaim, A., Jenkins, R.G., and Warén, A. 2008. Provannid and provannid-like gastropods from Late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda: Abysochrysoidea). *Zoological Journal of the Linnean Society* 154: 421–436.
- Kaim, A., Jenkins, R.G., Tanabe, K., and Kiel, S. 2014. Mollusks from late Mesozoic seep deposits, chiefly in California. *Zootaxa* 3861: 401–440.
- Kanno, S., Tanaka, K., Koike, H., Narita, K., and Endo, T. 1998. *Adulomya uchimuraensis* Kuroda (Bivalvia) from the Miocene Bessho Formation in Shiga-mura, Nagano Prefecture, Japan. *Research Reports of the Shinshushinmachi Fossil Museum* 1: 17–28.
- Karasawa, H. 1992. Fossil decapod crustaceans from the Manda Group (middle Eocene), Kyushu, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series* 167: 1247–1258.
- Karasawa, H. 1993. Cenozoic decapod Crustacea from southwest Japan. *Bulletin of the Mizunami Fossil Museum* 20: 1–92.
- Karasawa, H. 1997. A monograph of Cenozoic stomatopod, decapod, isopod and amphipod Crustacea from west Japan. *Monograph of the Mizunami Fossil Museum* 8: 1–81.
- Karasawa, H. 2011. New axiidean Decapoda from the Albian (Lower Cretaceous) chemosynthetic community of Hokkaido, Japan. *Bulletin of the Mizunami Fossil Museum* 37: 27–29.
- Kelly, S.R.A., Blanc, E., Price, S.P., and Witham, A.G. 2000. Early Cretaceous giant bivalves from seep-related limestone mounds, Wollaston Forland, Northeast Greenland. In: E.M. Harper, J.D. Taylor, and J.A. Crame (eds.), *The Evolutionary Biology of the Bivalvia Geological Society of London, Special Publication*, 227–246. Geological Society of London, London.
- Kenk, V.C. and Wilson, B.R. 1985. A new mussel (Bivalvia: Mytilidae) from hydrothermal vents in the Galapagos Rift Zone. *Malacologia* 26: 253–271.
- Kiel, S. 2004. Shell structures of selected gastropods from hydrothermal vents and seeps. *Malacologia* 46: 169–183.
- Kiel, S. 2006. New records and species of mollusks from Tertiary cold-seep carbonates in Washington State, USA. *Journal of Paleontology* 80: 121–137.
- Kiel, S. 2007. Status of the enigmatic fossil vesicomid bivalve *Pleurophopsis*. *Acta Palaeontologica Polonica* 52: 639–642.
- Kiel, S. 2008. An unusual new gastropod genus from an Eocene hydrocarbon seep in Washington State, USA. *Journal of Paleontology* 82: 188–191.
- Kiel, S. 2010. On the potential generality of depth-related ecologic structure in cold-seep communities: Cenozoic and Mesozoic examples. *Palaeogeography, Palaeoclimatology, Palaeoecology* 295: 245–257.
- Kiel, S. 2013. Lucinid bivalves from ancient methane seeps. *Journal of Molluscan Studies* 79: 346–363.
- Kiel, S., Altamirano, A.J., Birgel, D., Coxall, H.K., Hybertsen, F., and Peckmann, J. 2019. Fossiliferous methane-seep deposits from the Cenozoic Talara Basin in northern Peru. *Lethaia* [published online, <https://doi.org/10.1111/let.12349>].
- Kiel, S., Amano, K., and Jenkins, R.G. 2008. Bivalves from Cretaceous cold-seep deposits on Hokkaido, Japan. *Acta Palaeontologica Polonica* 53: 525–537.
- Kiel, S., Amano, K., and Jenkins, R.G. 2016. Predation scar frequencies in chemosymbiotic bivalves at an Oligocene seep deposit and their potential relation to inferred sulfide tolerances. *Palaeogeography, Palaeoclimatology, Palaeoecology* 453: 139–145.
- Kiel, S. and Amano, K. 2013. The earliest bathymodiolin mussels: Evaluation of Eocene and Oligocene taxa from deep-sea methane seep deposits in western Washington State, USA. *Journal of Paleontology* 87: 589–602.
- Kiel, S. and Goedert, J.L. 2006a. A wood-fall association from Late Eocene deep-water sediments of Washington State, USA. *Palaaios* 21: 548–556.
- Kiel, S. and Goedert, J.L. 2006b. Deep-sea food bonanzas: Early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. *Proceedings of the Royal Society B* 273: 2625–2631.
- Kiel, S. and Goedert, J.L. 2007. Six new mollusk species associated with biogenic substrates in Cenozoic deep-water sediments in Washington State, USA. *Acta Palaeontologica Polonica* 52: 41–52.
- Kiel, S. and Hansen, B.T. 2015. Cenozoic methane-seep faunas of the Caribbean region. *PLoS ONE* 10: e0140788.
- Kiel, S. and Peckmann, J. 2007. Chemosymbiotic bivalves and stable carbon isotopes indicate hydrocarbon seepage at four unusual Cenozoic fossil localities. *Lethaia* 40: 345–357.
- Kiel, S. and Taviani, M. 2017. Chemosymbiotic bivalves from Miocene methane-seep carbonates in Italy. *Journal of Paleontology* 91: 444–466.
- Kiel, S. and Taviani, M. 2018. Chemosymbiotic bivalves from the late Pliocene Stirone River hydrocarbon seep complex in northern Italy. *Acta Palaeontologica Polonica* 63: 557–568.
- Kiel, S., Birgel, D., Campbell, K.A., Crampton, J.S., Schiøler, P., and Peckmann, J. 2013. Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 390: 17–34.
- Kiel, S., Campbell, K.A., and Gaillard, C. 2010. New and little known mollusks from ancient chemosynthetic environments. *Zootaxa* 2390: 26–48.
- Kiel, S., Sami, M., and Taviani, M. 2018. A serpulid-*Anodontia*-dominated methane-seep deposit from the Miocene of northern Italy. *Acta Palaeontologica Polonica* 63: 569–577.

- King, W. 1848. An account of some shells and other invertebrate forms found on the coast of Northumberland and of Durham. *Annals and Magazine of Natural History* 18: 233–251.
- Klompemaker, A.A., Hyžný, M., Portell, R.W., Jauvion, C., Charbonnier, S., Fussell, S.S., Klier, A.T., Tejera, R., and Jakobsen, S.L. 2019. Muscles and muscle scars in fossil malacostracan crustaceans. *Earth-Science Reviews* 194: 306–326.
- Klompemaker, A.A., Nyborg, T., Brezina, J., and Ando, Y. 2018. Crustaceans in cold seep ecosystems: fossil record, geographic distribution, taxonomic composition, and biology. *PaleorXiv* [preprint published online, <https://doi.org/10.31233/osf.io/tws6m>].
- Komai, T. 2003. Identities of *Pagurus japonicus* (Stimpson, 1858) and *P. similis* (Ortmann, 1892), with description of a new species of Pagurus. *Zoosystema* 25: 377–411.
- Komai, T. and Rahayu, D.L. 2014. New records and new species of the hermit crab genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from the Philippines. *The Raffles Bulletin of Zoology* 62: 620–646.
- Krylova, E.M. and Janssen, R. 2006. Vesicomidae from Edison Seamount (South West Pacific: Papua New Guinea: New Ireland fore-arc basin). *Archiv für Molluskenkunde* 135: 231–261.
- Krylova, E.M. and Sahling, H. 2010. Vesicomidae (Bivalvia): current taxonomy and distribution. *PLoS ONE* 5: e9957.
- Krylova, E.M., Sahling, H., and Janssen, R. 2010. *Abyssogena*: a new genus of the family Vesicomidae (Bivalvia) from deep water vents and seeps. *Journal of Molluscan Studies* 76: 107–132.
- Kugler, H.G., Jung, P., and Saunders, J.B. 1984. The Joes River Formation of Barbados and its fauna. *Eclogae Geologicae Helvetiae* 77: 675–705.
- Kuroda, T. 1931. Fossil Mollusca. In: F. Homma (ed.), *Geology of the Central Part of Shinano, Part 4*, 1–90. Kokon Shoin, Tokyo.
- Labadie, L.V. and Palmer, A.R. 1996. Pronounced heterochely in the ghost shrimp, *Neotrypaea californiensis* (Decapoda: Thalassinidea: Callinassidae): allometry, inferred function and development. *Journal of Zoology* 240: 659–675.
- Latreille, P.A. 1802–1803. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes*, 3. 468 pp. F. Dufart, Paris.
- Leanza, A.F. 1940. *Myoconcha neuquena* n. sp. del Lias de Piedra Pintada en el Neuquén. *Notas del Museo de La Plata, Paleontología* 5: 123–131.
- Lin, F.-J., Komai, T., and Chan, T.-Y. 2007. First record of the thalassinidean genus *Callianopsis* de Saint Laurent, 1973 (Decapoda, Ctenocheilidae) in the West Pacific, with the description of a new species from Taiwan. *Crustaceana* 80: 1193–1203.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. 824 pp. Salvius, Stockholm.
- Lovén, S.L. 1846. Molluscorum litora Scandinaviae occidentalis habitantium. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* 3: 134–160, 182–204.
- Lörentz, E. and Beurlen, K. 1929. Die fossilen Dekapoden der Länder der Ungarischen Krone. *Geologica Hungarica, Series Palaeontologica* 3: 1–421.
- Manning, R.B. and Felder, D.L. 1991. Revision of the American Callinassidae (Crustacea: Decapoda: Thalassinidea). *Proceedings of the Biological Society of Washington* 104: 764–792.
- Marshall, B.A. 1978. The genus *Neilo* in New Zealand (Mollusca: Bivalvia). *New Zealand Journal of Zoology* 5: 425–436.
- Marshall, B.A. 1979. The Trochidae and Turbinidae of the Kermadec Ridge (Mollusca: Gastropoda). *New Zealand Journal of Zoology* 6: 521–552.
- Marshall, B.A. 1986. Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12: 505–546.
- Marwick, J. 1931. The Tertiary Mollusca of the Gisborne District. *New Zealand Geological Survey Bulletin* 113: 1–177.
- Marwick, J. 1953. Divisions and faunas of the Hokonui System (Triassic and Jurassic). *New Zealand Geological Survey Palaeontological Bulletin* 21: 1–141.
- McLaughlin, P.A. and Lane, C.E. 1975. The morphology of unique structures on the spines of a deep-water Hawaiian hermit crab (Crustacea: Decapoda: Paguridae). *Journal of Zoology* 176: 519–526.
- McLean, J.H. 1981. The Galapagos Rift limpet *Neomphalus*: Relevance to understanding the evolution of a major Paleozoic–Mesozoic radiation. *Malacologia* 21: 291–336.
- McLean, J.H. 1992. Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. *Journal of Molluscan Studies* 58: 401–414.
- McLean, J.H. and Geiger, D.L. 1998. New genera and species having the *Fissurisepta* shell form, with a generic-level phylogenetic analysis (Gastropoda: Fissurellidae). *Contributions in Science, Natural History Museum of Los Angeles County* 475: 1–32.
- McLean, J.H. and Harasewych, M.G. 1995. Review of western Atlantic species of cocculinid and pseudococculinid limpets, with descriptions of new species (Gastropoda: Cocculiniformia). *Contributions in Science, Natural History Museum of Los Angeles County* 453: 1–33.
- McLean, J.H. and Haszprunar, G. 1987. Pyropeltidae, a new family of cocculiniform limpets from hydrothermal vents. *The Veliger* 30: 196–205.
- Miyajima, Y., Nobuhara, T., and Koike, H. 2017. Taxonomic reexamination of three vesicomid species (Bivalvia) from the middle Miocene Bessho Formation in Nagao Prefecture, central Japan, with notes on vesicomid diversity. *The Nautilus* 131: 51–66.
- Mohr, N. 1786. *Forsög til en islandsk naturhistorie*. 414 pp. C.F. Holm, Copenhagen.
- Montfort, D.P.d. 1810. *Conchyliologie systématique et classification méthodique des coquilles: Offrant leur figures, leur arrangement générale, leur description caractéristiques, leur noms; ainsi que leur synonymie en plusieurs langues*. 676 pp. F. Schoell, Paris.
- Moore, E.J. 1963. Miocene marine mollusks from the Astoria Formation in Oregon. *U.S. Geological Survey Professional Paper* 419: 1–109.
- Moskalev, L.I. 1976. On the generic classification in Cocculinidae (Gastropoda: Prosobranchia) [in Russian]. *Trudy Instituta Okeanologii Imeni P.P. Širšov* 99: 59–70.
- Mulsant, E. 1842. *Lamellicornes. Histoire naturelle des Coléoptères de France*. 304 pp. Maison, Paris.
- Neumayr, M. 1884. Zur Morphologie des Bivalvenschlosses. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften* 88: 385–419.
- Newell, N.D. 1957. Notes on certain primitive heterodont pelecypods. *American Museum Novitates* 1857: 1–14.
- Nordsieck, F. 1973. Molluschi abyssali dello Jonio. *La Conchiglia* 57–58: 4–7.
- Okutani, T. 2001. Six new bathyal and shelf trochoidean species in Japan. *Venus* 60: 121–127.
- Okutani, T., Fujikura, K., and Sasaki, T. 1993. New taxa and new distribution records of deepsea gastropods collected from or near the chemosynthetic communities in the Japanese waters. *Bulletin of the National Science Museum Series A (Zoology)* 19: 123–143.
- Okutani, T., Tsuchida, S., and Fujikura, K. 1992. Five bathyal gastropods living within or near the *Calyptogena*-community of the Hatsushima Islet, Sagami Bay. *Venus* 51: 137–148.
- Olsson, A.A. 1931. Contributions to the Tertiary paleontology of northern Peru: Part 4, The Peruvian Oligocene. *Bulletins of American Paleontology* 17: 97–264.
- Olsson, A.A. 1964. *Neogene Mollusks from Northwestern Ecuador*. 256 pp. Paleontological Research Institution, Ithaca.
- Ordóñez, M. 1995. Zonas de Radiolarios des Eoceno medio del grupo Ancon, peninsula de Santa Elena, Ecuador. *Asociación Paleontológica Argentina, Publicación Especial* 3: 107–117.
- Ortmann, A.E. 1902. *Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Vol. IV. Palaeontology. Part II. Tertiary Invertebrates*. 332 pp. E. Schweizerbart'sche Verlagsbuchhandlung (E. Nägele), Stuttgart.
- Osawa, M. 2012. A new species of the genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from the Ryukyu Islands, southwestern Japan. In: T. Naruse, T.Y. Chan, H.H. Tan, S.T. Ahyong, and J.D. Reimer (eds.), *Scientific Results of the Marine Biodiversity Expedition—KUMEJIMA 2009. Zootaxa* 3367: 155–164.
- Palacios Moncayo, O. 1994. Geología de los cuadrángulos de Paita, Piura, Taalra, Sullana, Lobitos, Quebrada Seca, Zorritos, Tombes y Zarumilla, Hojas 11-a, 11-b, 10-a, 10-b, 9-a, 9-b, 8-a, 8-b, 8-c y 7-c. *Boletín Ingemet. Serie A: Carta Geológica Nacional* 54: 1–190.

- Palmer, A.R. 2009. Animal asymmetry. *Current Biology* 19: R474–R477.
- Peckmann, J., Goedert, J.L., Thiel, V., Michaelis, W., and Reitner, J. 2002. A comprehensive approach to the study of methane-seep deposits from the Lincoln Creek Formation, western Washington State, USA. *Sedimentology* 49: 855–873.
- Pelseneer, P. 1889. Sur la classification phylogénétique des pélecypodes. *Bulletin scientifique de la France et de la Belgique* 20: 27–52.
- Pennant, T. 1777. *The British Zoology, 4th Edition*. 154 pp. Warrington, London.
- Philippi, R.A. 1887. *Die tertiären und quartären Versteinerungen Chiles*. 266 pp. F.A. Brockhaus, Leipzig.
- Poore, G.C.B. and Griffin, D.J.G. 1979. The Thalassinidea (Crustacea: Decapoda) of Australia. *Records of the Australian Museum* 32: 217–321.
- Quoy, J.R.C. and Gaimard, J.P. 1834–1835. *Voyage de découvertes de l'Astrolabe exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sur le commandement de M. J. Dumont d'Urville. J. Tastu, Paris. Zoologie, Mollusques*. 3. 1–366 (1834), 367–954 (1835), atlas 107 pls.
- Rafinesque, C.S. 1815. *Analyse de la nature, ou Tableau de l'univers et des corps organisés*. 224 pp. Barraveccia, Palermo.
- Rudman, W.B. 1971. The family Acteonidae (Opisthobranchia, Gastropoda) in New Zealand. *Journal of the Malacological Society of Australia* 2: 205–214.
- Röding, P.F. 1798. *Museum Boltenianum*. 199 pp. Johann Christian Trappi, Hamburg.
- Saether, K.P., Jingeng, S., Little, C.T.S., and Campbell, K.A. 2016. New records and a new species of bivalve (Mollusca: Bivalvia) from Miocene hydrocarbon seep deposits, North Island, New Zealand. *Zootaxa* 4154: 1–26.
- Saether, K.P., Little, C.T.S., and Campbell, K.A. 2010a. A new fossil provannid gastropod from Miocene hydrocarbon seep deposits, East Coast Basin, North Island, New Zealand. *Acta Palaeontologica Polonica* 55: 507–517.
- Saether, K.P., Little, C.T.S., Campbell, K.A., Marshall, B.A., Collins, M., and Alfaro, A.C. 2010b. New fossil mussels (Bivalvia: Mytilidae) from Miocene hydrocarbon seep deposits, North Island, New Zealand, with general remarks on vent and seep mussels. *Zootaxa* 2577: 1–45.
- Saether, K.P., Little, C.T.S., Marshall, B.A., and Campbell, K.A. 2012. Systematics and palaeoecology of a new fossil limpet (Patellogastropoda: Pectinodontidae) from Miocene hydrocarbon seep deposits, East Coast Basin, North Island, New Zealand with an overview of known fossil seep pectinodontids. *Molluscan Research* 32: 1–15.
- Saint Laurent, M. de 1973. Sur la systématique et la phylogénie des Thalassinidea: définition des familles des Callianassidae et des Upogebiidae et diagnose de cinq genres nouveaux (Crustacea Decapoda). *Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences, série D* 277: 513–516.
- Saint Laurent, M. de 1979. Sur la classification et la phylogénie des Thalassinides: définitions de la superfamille des Axioidea, de la sous-famille des Thomassiniinae et de deux genres nouveaux (Crustacea Decapoda). *Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences, Paris* 288: 1395–1397.
- Sakai, K. 1969. Revision of Japanese callianassids based on the variations of larger cheliped in *Callianassa petalura* Stimpson and *C. japonica* Ortmann (Decapoda: Anomura). *Publications of the Seto Marine Biological Laboratory* 17: 209–252.
- Sakai, K. 1988. A new genus and five new species of Callianassidae (Crustacea: Decapoda: Thalassinidea) from northern Australia. *The Beagle, Occasional Papers of the Northern Territory Museum of Arts and Sciences* 5: 51–69.
- Salvini-Plawen, L. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* 19: 249–278.
- Sasaki, T., Ogura, T., Watanabe, H., and Fujikura, K. 2016. Four new species of *Provanna* (Gastropoda: Provannidae) from vents and a seep off Nansei-shoto area, southwestern Japan. *Venus* 74: 1–17.
- Sasaki, T., Okutani, T., and Fujikura, K. 2003. New taxa and new records of patelliform gastropods associated with chemoautotrophic-based communities in Japanese waters. *The Veliger* 46: 189–210.
- Sasaki, T., Okutani, T., and Fujikura, K. 2008. A new species of *Pyropelta* (Gastropoda: Pyropeltidae) from hydrothermal vents in the Okinawa trough, southwestern Japan. *Journal of Molluscan Studies* 74: 309–316.
- Scudder, S.H. 1876. Appendix H9. Report on the Orthoptera collected under the direction of Lieut. G.M. Wheeler, during the season of 1875. *Annual Report of the Chief of Engineer's U.S. Geographical Surveys West of the 100th Meridian*. Appendix JJ: 498–515.
- Schepman, M.M. 1908–1913. *The Prosobranchia of the Siboga Expedition*. 352 pp. E.J. Brill, Leyden.
- Schweitzer Hopkins, C. and Feldmann, R.M. 1997. Sexual dimorphism in fossil and extant species of *Callianopsis* de Saint Laurent. *Journal of Crustacean Biology* 17: 236–252.
- Smith, E.A. 1885. Report on the Lamellibranchiata collected by H.M.S. *Challenger* during the years 1873–1876. *Reports of the Scientific Results of the Challenger Expedition, Zoology* 13: 1–341.
- Sowerby, J. de C. 1823–1825. *The Mineral Conchology of Great Britain or Coloured Figures and Descriptions of Those Remains of Testaceous Animals or Shells, Which Have Been Preserved at Various Times and Depths in the Earth. Vol. 5*. 168 pp. Sherwood, London.
- Sowerby, R. 1846. Descriptions of the Tertiary fossil shells from South America. In: C. Darwin (ed.), *Geological Observations on the Volcanic Islands and Parts of South America Visited During the Voyage of H.M.S. "Beagle"*. 548 pp. Appleton, London.
- Squires, R.L. 1995. First fossil species of the chemosynthetic-community gastropod *Provanna*: Localized cold-seep limestones in Upper Eocene and Oligocene rocks, Washington. *The Veliger* 38: 30–36.
- Squires, R.L. and Goedert, J.L. 1991. New Late Eocene mollusks from localized limestone deposits formed by subduction-related methane seeps, southwestern Washington. *Journal of Paleontology* 65: 412–416.
- Squires, R.L. and Gring, M.P. 1996. Late Eocene chemosynthetic? bivalves from suspect cold seeps, Wagonwheel Mountain, central California. *Journal of Paleontology* 70: 63–73.
- Stimpson, W. 1851. *A Revision of the Synonymy of the Testaceous Mollusks of New England, with Notes on Their Structure, and Their Geographical and Bathymetrical Distribution*. 58 pp. Phillips, Sampson, and company, Boston.
- Valdés, Á. and Camacho-García, Y.E. 2004. “Cephalaspidean” heterobranchs (Gastropoda) from the Pacific coast of Costa Rica. *Proceedings of the California Academy of Sciences* 55: 459–497.
- Valdés, F., Sellanes, J., and D'Elia, G. 2013. Phylogenetic position of vesicomid clams from a methane seep off central Chile (~36°S) with a molecular timescale for the diversification of the Vesicomidae. *Zoological Studies* 51: 1154–1164.
- Van Winkle, K. 1919. Remarks on some new species from Trinidad. *Bulletins of American Paleontology* 8: 19–27.
- Warén, A. and Bouchet, P. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta* 22: 1–90.
- Warén, A. and Bouchet, P. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. *The Veliger* 44: 116–231.
- Warén, A. and Bouchet, P. 2009. New gastropods from deep-sea hydrocarbon seeps off West Africa. *Deep-Sea Research I* 56: 2326–2349.
- Warén, A. and Ponder, W.F. 1991. New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam. n. (Caenogastropoda). *Zoologica Scripta* 20: 56–102.
- Woodring, W.P. 1925. Miocene Mollusca from Bowden Jamaica, pelecypods and scaphopods. *Carnegie Institution of Washington Publications* 336: 1–564.
- Vilvens, C. 2001. Description of a new species of *Cantrainea* (Gastropoda: Turbinidae: Colloniinae) from Guadeloupe. *Novapex* 2: 153–156.
- Von Siebold, C.T.E. 1848. Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere. Erster Theil. In: C.T.E. Von Siebold and H. Stannius (eds.), *Lehrbuch der vergleichenden Anatomie*, 679. Veit & Comp., Berlin.
- Zhang, S. and Zhang, S. 2017. Description of *Pyropelta elongata* sp. nov. (Gastropoda, Pyropeltidae) from a methane seep area in the South China Sea. *American Malacological Bulletin* 35: 51–54.