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

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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 vesicomyid 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 capsulatessa*. 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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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-Berrios 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.
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 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” peruiana 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 specimen 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._


_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...
Description.—Shell subrectangular, well-inflated, postuminal 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, posterior marginal very slightly concave. Posterior area defined by ridge running from behind umbo 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 Desendido in eastern Patagonia (Erdman 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.

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 Pteriomorphia Beurlen, 1944
Family Mytilidae Rafinesque, 1815
Subfamily Bathymodiolineae 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 posterior dorsal 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 bathymodioliines 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 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: Pseudophopsis peruviana Olsson, 1931; Oligocene, Peru.
Species included: The type species and Unio bitumen Cooke, 1919.
Etymology: For its superficial similarity to the vesicomyid 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 posteriorventral 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 Permophorus 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 Permophoridae. 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 vesicomyids, 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 vesicomyids 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 vesicomyids (or in other words, the umbones are more loosely coiled than in vesicomyids). 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) can be seen in Myoconcha neuquena.
showing posterior half of pallial line (B1, B3) and thick ligament (B2). 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 (E1) and dorsal view (E2). F. Fragment (NRM Mo187028) preserving edentulous hinge area (F1) and large anterior pedal retractor scar (F2). G. Dorsal shell margin of large left valve (USNM PAL 530295), showing edentulous hinge (G1, close-up). D and G from Kiel and Peckmann (2007: fig. 6).
and also in the Miocene kalenterid Madrynomya bruneti (Griffin and Pastorino, 2006. Madrynomya 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 posterolateral 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 vesicomyid, and also its ligament is longer relative to shell length as in vesicomyids.

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.

**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 narrower, 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...
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, Klompmaker et al. 2018).

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

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 (C1), dorsal view showing lunule (C2), left valve showing dorsal sulcus (C3). D. Small specimen (NRM Mo187008), left valve showing a healed shell injury (D1), right valve showing dorsal sulcus (D2) and dorsal view showing lunule posterior area (D3). E. Small specimen (NRM Mo187010) showing hinge of right valve.
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 Vesicomyidae 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 adductor 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 talaren- sis* 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 talaren- sis* sp. nov.

Fig. 7.


*Etymology.* For the Talara Basin.

*Type material.*—Holotype, NRM Mo187019 from block 6. Paratypes...
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 posterooral 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.
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...
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 *Vesicomyidae* (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
Recent lepetellid *Lepetella ionica* Nordsieck, 1973, as illustrated in Dantart and Luque (1994), and the fissurelid *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

**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

<table>
<thead>
<tr>
<th>Species</th>
<th>L (mm)</th>
<th>H (mm)</th>
<th>H/L*</th>
<th>W/H</th>
<th>Ventral margin</th>
<th>Pallial line posterior</th>
<th>Occurrence</th>
<th>Stratigraphic range</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. akamudaensis</em></td>
<td>71.1</td>
<td>32.9</td>
<td>0.39</td>
<td>0.24–0.4</td>
<td>concave</td>
<td>turns to anterior</td>
<td>Japan Sea</td>
<td>middle Miocene</td>
<td>Miyajima et al. 2017</td>
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<tr>
<td><em>P. chinoookensis</em></td>
<td>90</td>
<td>27</td>
<td>0.3</td>
<td>0.73</td>
<td>straight to slightly convex</td>
<td>turns posterior-dorsally</td>
<td>Washington state, USA</td>
<td>late Eocene–Oligocene</td>
<td>Squires and Goedert 1991</td>
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<td><em>P. chitanii</em></td>
<td>70.4</td>
<td>21</td>
<td>0.3</td>
<td>0.64</td>
<td>straight to concave</td>
<td>turns to anterior</td>
<td>Japan</td>
<td>early to early middle Miocene</td>
<td>Amano and Kiel 2011</td>
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<td><em>P. hamuroi</em></td>
<td>59.2</td>
<td>22.3</td>
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<td>0.74</td>
<td>slightly concave</td>
<td>slight turn to anterior</td>
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<td>latest middle Miocene</td>
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<td>15</td>
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<td>0.58–0.66</td>
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<td>early Oligocene</td>
<td>Olson 1931; and this paper</td>
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<td><em>P. matsumotoi</em></td>
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<td>0.67–0.73</td>
<td>concave</td>
<td>turns to anterior</td>
<td>Japanese Pacific coast</td>
<td>late Oligocene–early Miocene</td>
<td>Amano et al. 2019</td>
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<td>0.26</td>
<td>0.61–0.63</td>
<td>straight</td>
<td>?</td>
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<td><em>P. uchimuraensis</em></td>
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<td>early to early middle Miocene</td>
<td>Kanno et al. 1998; Amano and Kiel 2011</td>
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<td><em>P. unioides</em></td>
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<td>0.43</td>
<td>0.55</td>
<td>straight to slightly convex</td>
<td>slight turn to anterior</td>
<td>Trinidad</td>
<td>middle Miocene</td>
<td>Van Winkle 1919; Kiel 2007</td>
</tr>
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</table>

**References**

**Genus Coccopigya Marshall, 1986**

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

**Coccopigya sp.**

**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.**

**Material.**—One specimen (PRI 80014) from the Lomitos cherts, numerous specimens (unnumbered specimens...
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 prosocyrt 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 protococh, 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.
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 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-
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 ryukyuensis* 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 craigsmithi* 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 peloritanus* 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 *Provanana 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 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.
in Washington state, USA (Squires and Goedert 1991).

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


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. urahorenisi 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 whors 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 hirokoe 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
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 Humpulips 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 eilenensis* 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 grass-hopper *Anconia* Scudder, 1876, we assign *Anconia eilenensis* 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 eilenensis* is of roughly the same age as the large abyssochrysoid *Humpulipsia rau* (Goedert and Kaler, 1996) from seep
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 (A1) and abapertural (A2) views. B. Paratype (NRM Mo187060) large fragmentary specimen. C. Holotype (NRM Mo187061) showing opisthocline axial ornament and faint spirals on last whorl (C1–C3, different lateral views). All in lateral view.

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 (A2, 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 (C1–C3, different lateral views). All in lateral view.
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.


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 opisthochline in lower part of whorls, a weak subrotund 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 opisthochline in lower half; ribs have subrotund 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 opisthochline just below the suture in A. elenensis, whereas the ribs become opisthochline 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 Abyssochryos 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? chiaraensis 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 bucindus 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. 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 Axidea Saint Laurent, 1979
Family Callianassidae Dana, 1852
Subfamily Eucalliacinae Manning and Felder, 1991
Genus Eucalliax Manning and Felder, 1991

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

Eucalliax capsulasetaea sp. nov.

Fig. 18.


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 NRM Ar69384, 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, Perú.

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 tubercles, 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 Eucalliax 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).

Eucalliax 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 Eucalliax capsulasetaea sp. nov. supports this observation.

In Eucalliax 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 terebrulate than other specimens. Nevertheless, all specimens are considered conspecific for several reasons. In extant representatives of Eucalliacinae (i.e., the species of Calliax Saint Laurent, 1973, and Eucalliax 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...
Captulated 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). Captulated 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

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 (C1), dorso-lateral (C2), outer lateral (C3), and inner lateral (C4) 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 (F1), outer lateral (F2) and dorso-lateral (F3, F4) 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 Ar69383. L. NRM Ar69393. M. NRM Ar69394. N. NRM Ar69383. Scale bars 5 mm.
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 distoven-
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. yoshiiroï* 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 capsulataesae* 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 unioïdes*, *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 *Coccopigya* 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*, *Propeamussium*, *Coccopigya*, *Cantrainea*, and *Colus*, and also the seep-restricted taxa *Pyropelta*, *Povanna*, *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 (Karasa 2011; Kiel et al. 2013; Agirrezabala et al. 2013). *Eucalliax* had not been reported from a fossil seep thus far, unlike *Callianassa*, *Callianopsis*, *Callix*, *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.

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