Stockholm
University

Licentiate thesis

Marine Geology

Biogeography of methane-seep faunas through geologic time

Frida Hybertsen

Stockholm 2020

Department of Geological Sciences
Stockholm University
SE-106 91 Stockholm

Cover photo: Frida Hybertsen, November 2017

Abstract

The deep ocean has been stage for fascinating discoveries of new ecosystems and species for centuries, yet many evolutionary and biogeographic questions remain unanswered. In areas affected by past or ongoing tectonic activity, specialized systems are teeming with life. Hydrothermal vent and cold seep systems have been discovered to be home to chemosynthetic microorganisms and their associated invertebrate hosts. This fauna has a fossil record extending through the Cenozoic that provides direct evidence for the biogeography of the deep sea. In this PhD-project, ancient cold seep sites together with their fossilized fauna will be identified and described. This licentiate thesis reports of new cold seep deposits and species. Collected material will be analyzed using cladistics to assess the evolution of the bivalve family Vesicomyidae (cold seep specialists); Bayesian modeling to test dispersal and extinction rates between different geographic areas in the geological past; and network analysis to assess the fate of biogeographic provinces inhabited by chemosynthetic fauna through geological time. This can then, in the continuation of this PhD-project, reveal how the evolution of this fauna has been affected by past tectonic and climatic events. This licentiate thesis describes the first steps of the PhD-project and have so far included extensive fieldwork, two taxonomic papers including the description of several new species and one paper describing new cold seep deposits.

Sammanfattning

Djuphavet har länge varit en scen för fascinerande upptäckter av nya ekosystem och arter, men ännu är många frågor rörande de här arternas uppkomst och utbredning obesvarade. Områden där tektonisk aktivitet har pågått eller är pågående är hem till en blomstrande mängd organismer. Hydrotermala öppningar och fissurer där kolväten och andra reducerade kemiska komponenter sipprar ut har upptäckts vara hem för kemosyntetiska mikroorganismer och deras tillhörande ryggradslösa värdar. Den här faunan har ett fossilt arkiv som sträcker sig genom Kenozoikum fram till idag som direkta bevis på djuphavets biogeografiska utveckling. I det större doktorandprojektet identifieras och beskrivs fossila fissurer tillsammans med deras fossiliserade fauna. Den här licentiatavhandlingen rapporterar om nya platser för fissuravlagringar och arter. Insamlat material kommer att analyseras med hjälp av kladistik för att bedöma utvecklingen av bivalvfamiljen Vesicomyidae (specialister i dessa miljöer); Bayesisk modellering för att testa spridnings- och utrotningsgraden mellan olika geografiska områden under olika geologiska tidsspann; och nätverksanalys för att bedöma utvecklingen i biogeografiska provinser bebodda av kemosyntetisk fauna under olika geologiska tidsspann. Detta kan då, i fortsättningen av doktorandprojektet, avslöja hur utvecklingen av den här specialiserade faunan har påverkats av tidigare tektoniska och klimatiska händelser. Den här licentiatavhandlingen beskriver de första stegen och har hittills inkluderat omfattande fältarbete, två taxonomiska artiklar inklusive beskrivning av flera nya arter, och en artikel som beskriver nya fyndplatser.

Table of contents

x. List of papers and author contributions

This licentiate thesis reports two years of Frida Hybertsen's PhD work, including the following three papers, to which she has led or contributed in various ways, as described in the this section.

Paper I. 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 (4): 751-768.

Paper II. Kiel, S., Altamirano, A.J., Birgel, D., Coxall, H.K., Hybertsen, F., & Peckmann, J. 2019. Fossiliferous methane-seep deposits from the Cenozoic Talara Basin in northern Peru. *Lethaia*. Accepted, early access.

Paper III. 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 (X): xxx-xxx.

Frida Hybertsen, with the assistance of Steffen Kiel, wrote the main part of the initial draft for **Paper I**, etched specimens from carbonate blocks, photographed specimens and created several figures and tables. For **Paper II** and **Paper III**, fieldwork was carried out by Frida Hybertsen and Steffen Kiel with the assistance of Ali Altamirano for a period of one month. Frida Hybertsen described the geological setting of the Talara Basin and prepared a locality map for **Paper II**. All authors assisted in editing the manuscript. For **Paper III** Frida Hybertsen assisted in the photographing of specimens, preparing figure and writing the initial draft with focus on vesicomyid bivalves. The manuscript was edited by all co-authors.

1. Introduction

Much of the deep ocean floor is dark and lifeless, the few organisms that live there are largely dependent on food raining down from the surface ocean where photosynthesis occurs. Important exceptions to this are regions where fluids escape Earth's crust to the seafloor at hydrothermal vents and seeps. These regions are associated with unique communities of organisms that use chemical synthesis and geothermal heat as an energy source. These systems are important to understand as hydrothermal activity serves as a global heat transfer between the lithosphere and the ocean waters, chemical weathering of oceanic crust and the biogeochemistry of the deep-sea water and sediments. These systems play an important role in global geochemical cycling, they are restricted areas with unusual biodiversity and have been suggested to contain clues to the origin of life. Hydrothermal vents or hot vents, occurring at mid-ocean ridges, have been most studied in modern times as they do not fossilize well. In contrast, modern 'cold seeps', and their associated fauna have received less attention, however ancient fossil seeps have a high preservation potential. This PhD-project seeks to investigate the biogeographic evolution of deep-sea cold seep faunas through the last 50 million years of Earth's history on a global scale. The project will be carried out in different steps as listed:

1. Synthesize existing information on modern and Cenozoic fossilized cold seeps globally
2. Collect and study new fossilized cold seep material from underexploited regions
3. Perform phylogenetic analysis of typical cold seep organisms based on fossil morphology and modern molecular data to better understand the biodiversity and evolutionary relationships of cold seep organisms
4. Describe the turnover to the "modern seep fauna" with input from newly collected material and reassessment of the bivalve family Vesicomyidae, one of the most common and best preserved elements of cold seep faunas
5. Perform Bayesian modeling to detect dispersal patterns, potential extinction rates and biotic connectivity between geographical areas
6. Synthesize the newly described seep faunas with existing records to create an improved global data base of seep faunas. Using the expanded data base, assess the role of biogeography, local tectonism and climate change on seep fauna evolution through geological time using network analysis

This licentiate thesis includes descriptions of the work process on the first two steps along with the first phase of step 3.

1.1 Project overall focus and aim

This PhD-project aims to describe how key elements of cold seep faunas have been distributed across mid-ocean ridges and continental margins and how major tectonic and climatic events during the Cenozoic may have impacted the biota and their evolution with respect to local environmental changes and fluctuations in global oxygen concentrations.

2. Deep-sea environments

2.1 The ocean floor

At depths greater than 3000 m, the deep sea environment is an extensive, rather barren abyssal plain. It is covered by a thick layer of sediment, comprising combinations of carbonate and siliceous remnants of long-dead microorganisms such as foraminifera, diatoms and radiolarians coming from the water column (Van Dover 2000). At continental and ocean tectonic plate margins the landscape is influenced by steep slopes and canyons, volcanic seamounts and subduction zones, all shaping the relief of the otherwise flat abyssal plain. Barely any light penetrates the water in the deep sea and the organisms that live here mostly survive on organic matter produced in the photic zone, the topmost few hundred meters of the water column. Deep-water formation occurs in the North Atlantic, near Greenland and around Antarctica, where surface water cools, becomes dense and sinks. This results in generally cold ocean floor sea water temperatures. Salinity is relatively constant and oxygen concentration are close to saturation levels below 2 km depth. Life is sparse but specialized organisms can be found at low density. Among the organisms that have adapted to these circumstances are echinoderms, such as sea stars and brittle stars, sea cucumbers, sea urchins and sea lilies, and coelenterates, mainly sea anemones and solitary corals. On tops of seamounts or other topographic structures, suspension-feeding corals and seapens, sponges and brachiopods are found. A large number of infaunal organisms inhabit the seafloor sediments, mostly bivalve and gastropod mollusks, polychaete worms, crustaceans and microfauna such as foraminifera. These taxa have evolved within the deep sea environment or migrated from shallow water. They are also reliant on organic matter sinking as ‘marine snow’ through the water column at a rate of 100-150 meter per day (Gooday and Turley 1990) or the carcasses of large animals, mostly whale falls, and accumulation of wood debris.

In contrast to the sparsely populated, typical ocean floor, habitats surrounding hydrothermal vents are teeming with life. They are located along mid-ocean ridges, which make up the constructive boundaries between tectonic plates in the Earth’s crust. These are environments where seafloor spreading occurs; continental plates move apart by tectonic forces and hot, molten magma and lava emerges through underwater volcanic systems to form new basaltic crust.

2.2 Hydrothermal vents and cold seeps

Most organisms rely on solar energy to fuel their system, however below the photic zone, there is no sunlight to convert into chemical energy and thus photosynthesis cannot take place. However, at active mid-ocean ridges, large amounts of particle-laden fluids are flushed to the seafloor through vents and cracks in the newly forming oceanic crust. Huge quantities of organisms inhabit these areas and have developed their specific way of converting fluid-chemicals to fuel instead of sunlight (fig 1).

Discovered in 1977, hydrothermal vents and their associated faunas describe deep sea environments where food is still limited but animal communities are thriving. Major hydrothermal vent sites have, since their discovery, been extensively studied in areas where tectonic activities are ongoing today and inactive systems can be traced through geological time (fig 2). Examples of study areas include the East Pacific Rise and on the Juan Fuca, Gorda and Explorer Ridges in the Pacific, western Pacific back-arc basins, mid-ocean ridges in the Indian Ocean and around the northern Mid-Atlantic Ridge in the Atlantic (Van Dover 2000). Situated along the oceanic plate margins, these vent fields are part of hydrothermal systems in which heat is transferred from beneath the Earth’s crust into the sea water column.

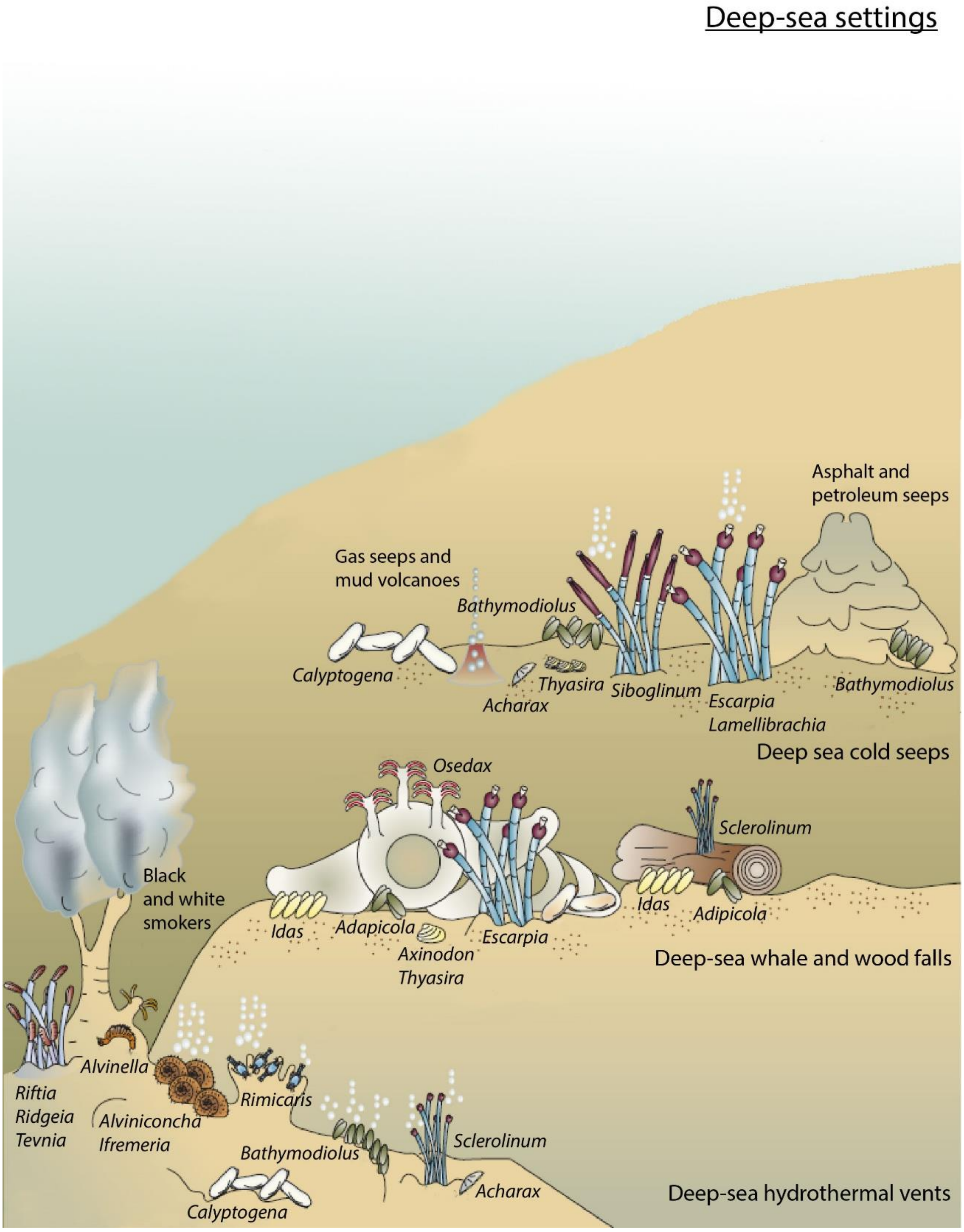


Figure 1. Deep-sea chemosynthetic environments illustrating examples of fauna at cold seeps, whale and wood falls, and hydrothermal vents. Modified from Dubilier et al 2008.

Hydrothermal vents form at mid-ocean spreading centers and subduction zones, where seawater percolates down through cracks in the ocean crust, resulting in a heat loss in the crust. At ~130°C, anhydrite ($CaSO_4$) precipitates from the water and as the seawater moves down through the rock, it is heated by underlying magma through convective cells that form underneath the crust. As the seawater reaches deep (~2 km) into the crust, it reaches temperatures above 350°C, reacts with the surrounding rock and may take on characteristics of a black-smoker-fluid. These fluids have low pH (3-5) and become enriched in hydrogen sulfide (H_2S), hydrogen (H_2), methane (CH_4) and manganese (Mn), as well as other metals (iron, aluminum, zinc, copper, lead, cobalt) in various concentrations (Van Dover 2000). The seawater can also undergo phase separation where pressure (P) and temperature (T) determines if the fluid exists as a liquid or coexisting liquid and vapor phases. This can for example happen if a submarine eruption takes places and magma intrudes the shallow crust (Von Damm 1995).

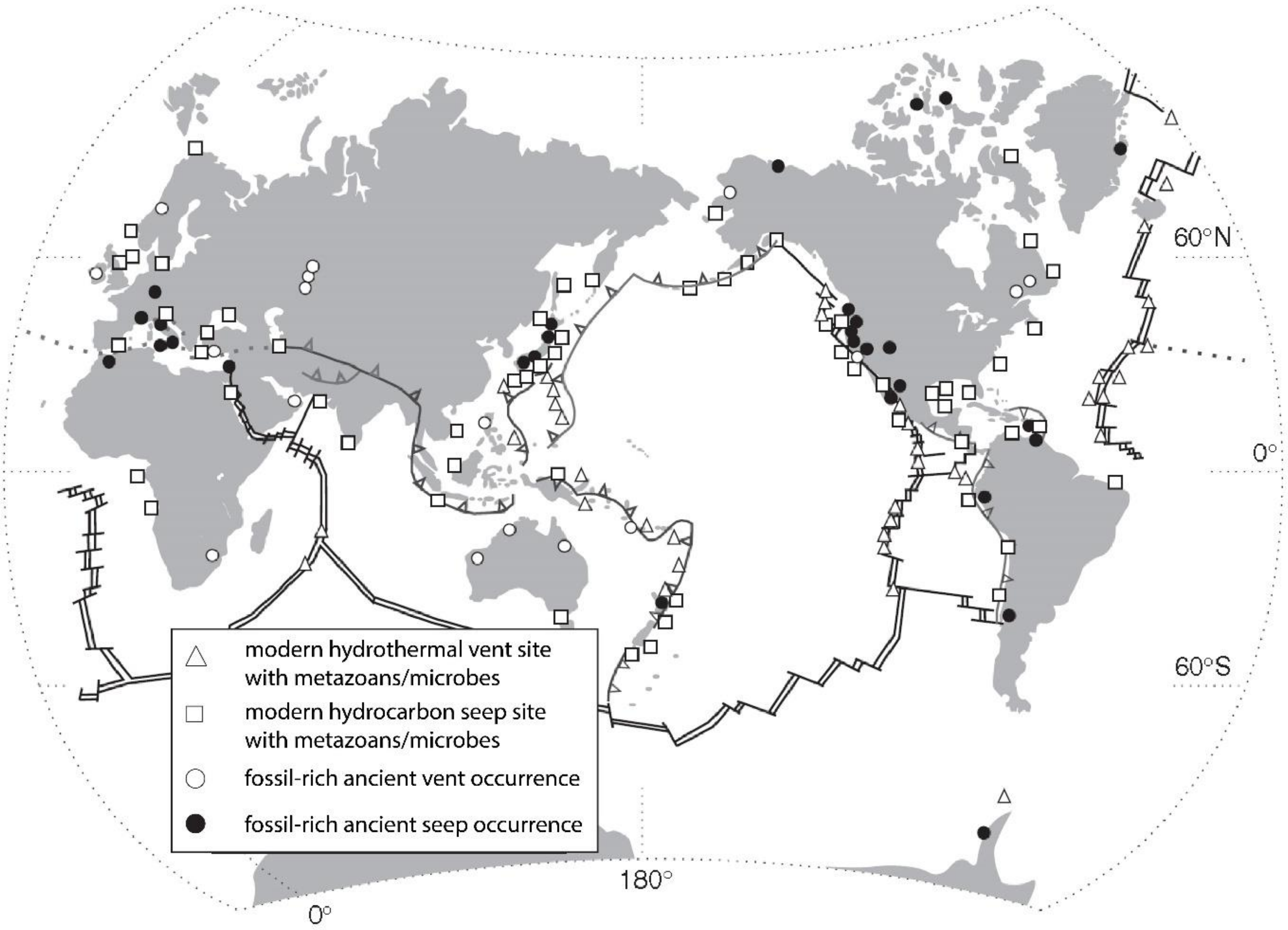


Figure 2. Map displaying global modern and ancient chemosynthesis-based settings. Legend symbols indicate modern hydrothermal vent and hydrocarbon seep occurrences, and fossil vent and seep occurrences with associated metazoan and/or microbial signatures. From Campbell 2006.

Eventually the subducted fluids become buoyant and rise back to the seafloor. When reemerging, the heated, chemical-rich fluids mix with the cold seawater and form deposits at the seafloor. Different structures and mineral products form depending on the temperature of the emerging fluids. At high temperatures, up to 400°C, the metal- and sulfide-rich, acidic fluids are vented into the colder, alkaline seawater and metal sulfides are precipitated. The precipitated minerals form a dark cloud over the vent that can be seen billowing above the vents called “black smokers”. Fluids with temperatures above 150°C, trigger anhydrite to precipitate from the surrounding seawater and rapidly forms anhydrite deposits that can isolate the hydrothermal fluids in tubular structures like tall chimneys. The chimneys vary in shape, grow as tall as 10-20 m and can be seen around mid-oceanic ridges. Chimneys with intermediate temperature fluids (100-300°C) are not hot enough to emit mineral particles as black smoke, instead silica, anhydrite and barite are precipitated as white smoke around these so-called “white smokers” (Hannington et al 1995).

Chimney column structures can mostly be observed in association with fast-spreading centers, and due to the constant tectonic movement these structures form rapidly and can be seen as fields of solitary chimneys. At intermediate-spreading centers, large (up to 200 m wide, ~50 m tall) complex sulfide mounds can form. These mounds are thought to have been individual structures that coalesced into one large mound with multiple orifices, venting high-temperature fluids into the ocean (Hannington et al 1995). Hydrothermal vent systems are ephemeral environments characterized by locally high temperatures which fluctuate strongly, pH, sulfide and oxygen concentrations. Depending on the geological setting, the systems last 50-100 years at fast-spreading centers and at slower-rate spreading centers they can last over ten thousands of years, with episodes of inactivity and reactivation (Lalou et al. 1993). These systems are heavily influenced by unpredictable conditions, such as new volcanic eruptions and the waxing and waning of the emitted fluids, which alters their lifespan. Even so, this mostly unstable and constantly altering environment has been discovered to be the home of a very specialized fauna that is thriving under these extreme conditions. At the discovery of hydrothermal vents, annelids, gastropods, crustaceans, bivalves and siboglinid worms were found in high abundance at the vent sites. These organisms are not reliant on organic material sinking through the water column, instead they sustain themselves through symbioses with chemosynthetic bacteria that exist in these environments. Many of these taxa can also be found at a second type of chemosynthetic ecosystem driven by hydrogen sulfide and involving much lower temperatures than at hydrothermal vents.

A further development in the study of vent biota occurred in 1984 in the Gulf of Mexico when hydrothermal vent-like organisms were dicovered densely packed and thriving around a fissure out of which fluid or gas was seeping (Paull et al 1984). Unlike mid-ocean ridge hot vents systems associated with new crust production, this type of vent is driven by pressure gradients created through tectonic compaction and diagenetic changes causing fluids to migrate through the sediment. With no elevation in the ambient water temperature, these environments became known as ‘cold seeps’ and have gained some interest since their discovery and seem to have quite diverse origins. Some cold seep systems occur as cracks or fissures resulting from tectonic activity, and have been found both on passive and active margins, at subduction zones, at depths ranging between 400-6000 m (e.g. Suess et al 1985; Sibuet et al 1988; Corselli & Basso 1996). At subduction zones, a mud volcano or mud mound typically form around the fissure. Mud volcanoes are not igneous, the name refers to the shape of the structure around the seep, and form when the build-up of pressure by gas in the sediment is released (e.g. Kioka & Ashi 2015). Other cold seeps are associated with seepage of oil above large petroleum reservoirs. A further sub set of seeps have been found in association with animal carcasses ending up on the seafloor. These provide a temporary source for organic carbon for opportunist taxa, but as microbial degradation of lipids leaching from the animal bones, sulfide is generated by sulfate-reducing bacteria (Deming et al 1997) and a chemosynthetic fauna can be supported in this seep system.

Whilst this diversity of cold seeps exists, most cold seeps occur at continental margins and shelf areas. Populations of thiotrophic bacteria can be found in bacterial mats on the sediment surface around seeps. They perform chemosynthesis in which the hydrogen sulfide and methane is metabolized for energy. Similar to the fauna at hydrothermal vents, some bacteria live in symbiotic relationships with other organisms. Cold seeps differ from vents though in that they are more stable, emitting seepage at slower rates and last longer than vents. They are not affected by strong fluctuations in temperature, pH or oxygen concentrations (Van Dover 2000). Ancient cold seep deposits can be found throughout the Phanerozoic (e.g. Goedert & Squires 1990; Conti et al 2004; Kiel 2006; Kaim et al 2008), the oldest are known from Late Silurian (Jakubowicz et al 2017). Marine sediments are large reservoirs of methane and at cold seeps, it is mostly methane that escapes from the deep reservoirs in the sediment into the water column. Methane is either produced by thermal cracking of organic material deeper down in the sediment or by methanogenesis, which is the most common in marine environments. In methanogenesis, methane is mostly generated by anaerobic archaea through acetate fermentation or CO_2-reduction from organic matter fermentation (Whiticar et al 1986). Produced this way, the methane is depleted in ^{13}C, with $\delta^{13}C$-values lower than -55‰ whereas the methane produced by thermal cracking has a $\delta^{13}C$-value corresponding to its original source, between -20‰ and -45‰ (Whiticar 1999). If methane concentrations exceeds its solubility, it diffuses upwards in the sediments through cracks and faults forming cold seeps at the seafloor. At the sediment surface, methane is oxidized under anaerobic conditions by sulfate, in a direct coupling between archaea (anaerobic methane oxidizer: ANME) and sulfate-reducing bacteria (Boetius et al 2000). Anaerobic oxidation of methane (AOM) forms bicarbonate that increases alkalinity locally and induces carbonate precipitation (Ritger et al 1987) forming extensive carbonate deposits around the seep.

$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + H_2O + HS^-$ (see also fig 3).

The methane formed by biological methanogenesis is depleted in ^{13}C, biomass and lipids of methanotrophic (methane-consuming) microorganisms are also depleted in ^{13}C, and the sediment including inorganically or biogenically precipitated carbonate by shell building organisms will inherit their stable carbon isotope composition. Negative ^{13}C-values therefore indicate a biogenic source of methane and can thus be used as a confirmation of seep origin for ancient seep sediments. The value is expressed in per mil as a ratio (R) between heavier and lighter carbon (^{13}C/^{12}C) and measured in relation to the standard VPDB:

$$\delta^{13}\mathrm{C} = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

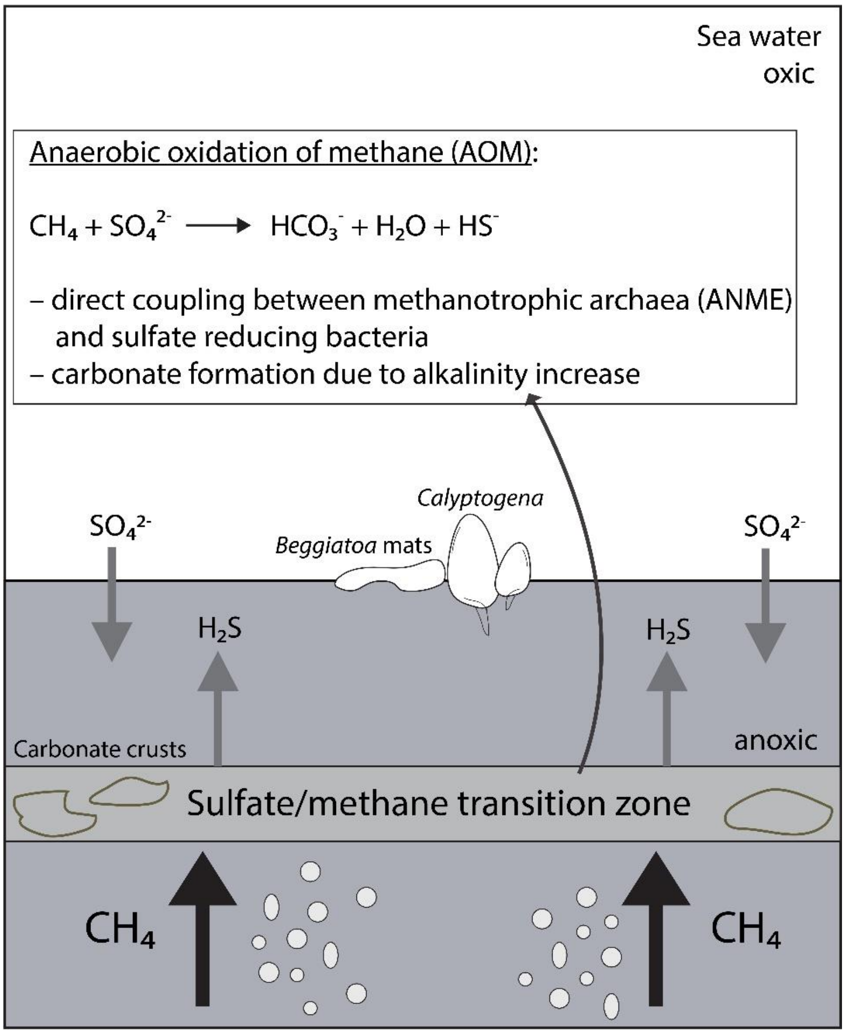


Figure 3. Biogeochemical principles of AOM in a methane-rich marine environment.

Oxygen isotope ratios in cold seep sediments do not deviate much from the sea water ratio in the surrounding sea, they are usually low for ancient seeps (Peckmann & Thiel 2004). Low δ^{18}O-values are indicative for a marine environment and analyzed together with carbon isotopes to further confirm seep origin of the sediments. It is also possible to analyze biomarkers of AOM-performing microbes to track ancient seep communities. ^{13}C-depletion is evident in the lipids of methane-utilizing taxa and show strongly negative carbon isotope signatures, δ^{13}C-values are often below -70‰ (Peckmann & Thiel 2004).

Cold seep carbonates (authigenic carbonates) occur as small nodules within the upper sediment layers, often underneath bacterial mats, as crusts, fractional slabs or sometimes as small dome-like structures (Bohrmann et al 2008). Seep carbonates typically consist of aragonite, Mg-calcite and dolomite and minor concentrations of sulfide minerals. Ancient cold seep carbonates are characterized by wavy laminations in yellow calcite, banded and botryoidal cements of calcite, clotted micrite and carbonate, incorporated mud clasts.

3. Chemosynthesis

Vents and seep environments are characterized by high concentrations of reduced energy sources such as sulfide and methane. These occur in close proximity to oxidants such as oxygen and sulfate. The process of oxidizing inorganic compounds instead of sunlight to produce biomass from carbon molecules is called chemosynthesis. The organisms that obtain this carbon via chemosynthesis are chemoautotrophs. Chemosynthesis is mostly used by organisms living in deep sea reduced environments at depths where light does not penetrate and photosynthesis cannot occur. In these environments sulfur compounds derived from hydrothermal vent fluids are primarily used by microbes to fix carbon dioxide and synthesize organic compounds by oxidation. Since vent fluids are highly toxic to most organisms, many microorganisms have a symbiotic relationship with an animal host and the synthesized organic compounds are passed on to the host. The process used by tubeworm *Riftia pachyptila*, housing chemosynthetic bacteria in their trophosome using hydrogen sulfide as energy source, can be described with the reaction:

$12\ H_2S + 6\ CO_2 \rightarrow C_6H_{12}O_6 + 6\ H_2O + 12\ S$

Generating organic compounds (CH_2O) from inorganic substrates like this uses chemical energy derived from the oxidation of sulfide. Similar to photosynthesis this reaction produces carbohydrates, but instead of releasing oxygen gas chemosynthesis yields solid sulfur. Chemosynthetic symbioses occur in a wide range of environments including hydrothermal vents, whale and wood falls, cold seeps, mud volcanoes, continental margins (Cavanaugh et al 2006; Smith and Baco 2003). On occasion chemosynthetic symbionts are reported from shallow-water communities but then only from some hosts, mainly bivalves (Tarasov et al 2005).

3.1 The chemosymbiotic fauna

The discovery of the giant gutless tubeworms *Riftia pachyptila* in deep-sea environments associated with hydrothermal vents first raised question regarding the nutrition of this annelid and the other elements of vent faunas (Corliss et al. 1979). Sampling and scanning of its trophosome (interior organ located in the coelomic cavity) tissue revealed lobes packed with prokaryotic cells (Cavanaugh et al 1981) and enzyme studies of this tissue showed evidence for sulfur metabolism and diagnostics for Calvin-Benson cycle carbon fixation (Felbeck 1981). Sulfur chemoautotrophy is a two-step process including production of ATP by oxidation of sulfide and fixation of carbon through biosynthesis (e.g. Calvin-Benson cycle). Stable isotope studies were also made on the tubeworm tissue revealing a $\delta^{13}C$ of -11‰ also pointing at a nonphotosynthetic diet in these worms (Rau 1981). These three studies confirmed that a diet mainly made up of photosynthetically derived carbon was not sufficient for these organisms but instead chemotrophic endosymbiotic bacteria were oxidizing sulfide and generating organic material from inorganic compounds delivered by their hosts, and thus in turn providing nutrition for their hosts. This was later confirmed and generalized by Southward (1982). With the discovery of vent tubeworm sulfide-oxidizing bacterial symbiosis other invertebrates were recognized having symbiotic bacterial relationships. Chemosynthetic bacteria especially depend on sources of inorganic carbon, sulfide and oxygen for sustainability. Extracting energy from narrow redox zones in marine environments require free-living microbes often occurring at seeps to sit in biofilms on sulfidic rocks or in mats like *Beggiatoa* spp. where they can absorb reduced gases from the substrate below and oxygen from the ambient water. Symbiotic microbes are more versatile and by exploiting the behavior, physiology and morphology of their animal hosts they can circumvent oxic-anoxic boundaries and extend their habitats (Stewart et al 2005).

The significance of chemoautotrophic primary production in these systems and the endosymbiotic relationships between sulfide-oxidizing bacteria and their invertebrate hosts were first described in 1979 and 1982. Since then, more vent communities have been discovered and are subjects for extensive research regarding biogeographic patterns in faunal distribution, ecological issues and habitat requirements, dispersal and population genetics. In 1984 new chemosynthetic faunas and arrange of different organisms were discovered to be supported by methane and bacterial oxidation of hydrogen sulfide at relatively low temperatures, and associated with diverse settings from hydrocarbon seeps to whale carcasses found on the sea floor.

Of the various organisms associated with deep sea reducing systems, bivalve mollusks are a common component. The giant clam *Calyptogena magnifica* and vent mussel *Bathymodiolus thermophilus* have especially developed host and symbiont strategies for nutrition in the energy-rich environments surrounding hydrothermal vents. *Calyptogena magnifica* mostly sits inside nestled cracks of basalt crust, with the foot extended into the crack where it is exposed to H_2S- and CO_2-rich vent fluids, and the siphon is extended into ambient CO_2- and O_2-rich water outside of the crack (Hessler et al. 1985). The blood in the foot stores and transports oxygen and sulfide, bound to haemoglobin, to the symbionts in the gill tissues (Zal et al 2000). Bathymodiolid mussels flush their gills with sea water and have bacteriocytes housed on the gill filaments taking up nutrients, mainly sulfide. Their haemoglobin concentrations are insignificant for uptake and transport of inorganic substrates and they lack sulfide-binding factors of their own (Fiala-Médioni and Le Pennec, 1987), but they are able to take up free amino acids from their environment (Fiala-Médioni et al. 1986) by flushing their gills with seawater. The bacteriocytes are provided with sulfide through diffusion of the incoming liquid to the gills. In the wake of studying vestimentiferan tubeworms, vesicomyid clams and bathymodiolid mussles, other chemoautotrophic endosymbioses have been recognized at vents. Other bivalve mollusk families Lucinidae, Thyasiridae and Solemyidae are among these. Lucinidae are the most diverse group of chemosymbiotic bivalves with around 400 species distributed at water depths from intertidal zones down to 2500 m, and the fossil record extends back into Lower Paleozoic. They host sulfur-oxidizing bacteria in their enlarged gills (Taylor and Glover 2000). Thyasiridae is also a very diverse group of bivalves distributed at all depths from intertidal to hadal zones (Payne and Allen 1991). The fossil record extends back to the early Cretaceous (Hryniewicz et al 2014). Not all thyasirids host endosymbiotic bacteria but in the species that do the bacteria lies beneath a thin cuticle and appears extracellular (Southward 1986). Solemyidae are known from early Ordovician (*Ovatoconcha*) (Cope 1996). They have a depth range from intertidal zones to 5350 m (Fujiwara 2003) and are very distinctive with their reduced or absent digestive tract. They host sulfur-oxidizing bacteria intracellularly within gill filaments (Stewart and Cavanaugh 2006).

Importantly, seep faunas have an excellent fossil record and can be identified back throughout geological time. The most common taxa found at modern cold seeps are vestimentiferan tube worms, mytilid mussels, vesicomyid clams and infaunal lucinid and thyasyrid clams (Van Dover 2000). With its high fossilization potential due to the rapid *in situ* carbonate precipitation at cold seeps, this characteristic fauna can be used to create models for the biogeographic evolution of deep-sea metazoans throughout periods of Earth's history on a global scale. Moreover, methane seeps and their ecosystems are part of the global methane cycle and thus connected to global climate. Climatic and oceanographic changes during the last 50 million years can be tracked through the fossil record of these organisms as they are likely to have affected their composition and distribution. The fossil record of vent and seep faunas have been growing since the discovery of vent and seep ecosystems, increasing the evidence for the evolution of these faunas.

3.2 Vesicomyid bivalves as temporal and spatial tracers of cold seep faunas

This project is focused around vesicomyid bivalves (fig 4). This group has been identified in fossil and modern seep communities worldwide, at different depths, since the middle Eocene (Amano & Kiel 2007). Bivalves, in general, are less common in Paleozoic to mid-Mesozoic seep deposits, leaving room for brachiopods to co-exist with them (Jakubowicz et al 2017). Previous work show that vesicomyid clams and bathymodiolin mussels start to populate the cold seep ecological niche again in the middle Eocene (Amano & Kiel 2007; Kiel & Amano 2013) and they have been dominating vent and seep environments ever since. This turnover to something that can be regarded as the modern seep fauna is not yet fully understood. Speculations suggest an extinction and origination event in parallel with the Paleocene-Eocene Thermal Maximum (Vrijenhoek 2013), with the proposal that fluctuations in marine sulfate concentrations was the main evolutionary driver (Kiel 2015). This idea is one of the key things to be tested in this PhD, while extending the fossil record of seep communities to estimate the origin of vesicomyid clams and potential extinction rates. Migration rates between different areas will also be analyzed in order to track area-specific changes and faunal dispersal, with the integration of molecular and fossil data of this group.

Vesicomyid bivalves are consistently the most abundant and diverse taxa in chemosynthetic systems. The family Vesicomyidae has a wide distribution, from shelf to hadal depths, and across different habitats including hydrothermal vents, cold seeps and whale carcasses. They are provided nutrients from chemautotrophic sulfur-oxidizing bacteria hosted in their gills (Fisher 1990). At sulfur-rich environments, they can grow large (over 30 cm in size) (Krylova & Sahling 2010). Other representatives of the family can be as small as a few millimeters, e.g. *Vesicomya atlantica* Smith, 1885 inhabiting deep-sea ocean basins and trenches. With its diversity and high level of specialization, broad geographical distribution and wide depth range, vesicomyid bivalves make good subjects for the study of biogeographical and ecological aspects of vent and seep communities. Vesicomyids have been well-studied since the discovery of hydrothermal vents and first described *Calyptogena magnifica* Boss and Turner 1980. However, their taxonomy has many uncertainties and inconsistencies. This has been assessed mainly by molecular data (e.g. Decker et al 2012; Johnson et al 2017), but also based on fossil shell morphologies (e.g. Cosel & Salas 2001; Amano & Kiel 2007). With this project, new sites will be sampled and the data will be incorporated with already existing data in new phylogenetic studies.

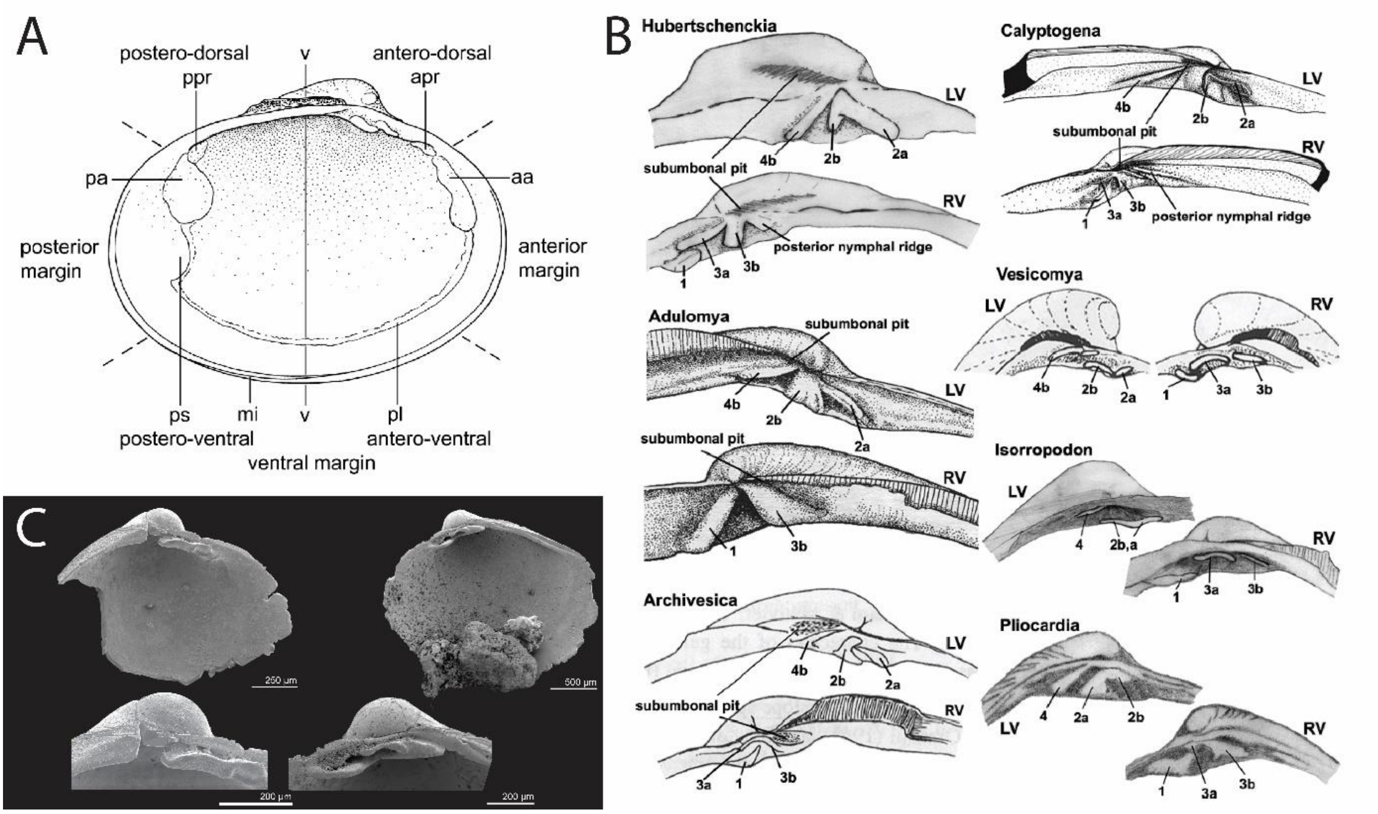


Figure 4. Illustrations of the morphological diagnostic features of vesicomyid bivalves. A: Left valve of a vesicomyid clam to show some descriptive terms. aa: anterior adductor muscle scar, apr: anterior pedal retractor scar, v: vertical midline, mi: marginal incision, pa: posterior adductor muscle scar, pl: pallial line, ppr: posterior pedal retractor scar, ps: pallial sinus. From Cosel and Salas, 2001. B: Examples of hinge line features and teeth terminology in different vesicomyid species. From Amano and Kiel 2007. C: Example of an unidentified fossil vesicomyid clam with hinge line dentition from western Washington State, USA. From Hybertsen & Kiel 2018.

4. Biogeographic patterns

This project will also assess the important question concerning distribution and dispersal of vent and seep ecosystems in geographic space and geological time. During the last 66 million years, Earth has been a stage for various tectonic and climatic events that have shaped and reformed ecological habitats and dispersal pathways, both on land and in the ocean (fig 5). Warming climate reached a peak with the Paleocene-Eocene Thermal Maximum and have showed a cooling trend in Mid-Late Cenozoic times (Zachos et al 2001; Raymo & Ruddiman 1992). Global shifts in ocean currents due to tectonic activity played a part in the cooling event. Separation of South America and Antarctica created the Antarctic Circumpolar Current around 41 Ma, an event that is connected to the onset of glaciation on Antarctica (Schackleton & Kennett 1975; Siegert et al 2008), although a threshold response to declining atmospheric CO_2 can more easily explain the abruptness of the glaciation (DeConto & Pollard 2003). The collision between Arabia and Eurasia around 35 Ma leading to the closure of the Tethys Ocean, a gateway that had been open since early Mesozoic, and could have contributed to reduced levels of atmospheric CO_2 due to increased chemical weathering (Allen & Armstrong 2008). Following the Messinian salinity crisis at around 5.9 Ma, the organisms in the Mediterranean Sea underwent huge environmental changes. Around 3 Ma South America and North America became attached through the Isthmus of Panama, creating a land bridge between the two continents and separating the Atlantic and Pacific Oceans (O'Dea et al 2016). These are major events that have affected diversity and dispersal of marine organisms on a global scale and evidence can be tracked through the fossil record.

Taxonomists have, since the discovery in 1977, described more than 400 species from vents and 200 from seeps (McArthur & Tunnicliffe 1998; Sibuet & Olu 1998). Some species derived from the surrounding deep sea environments and others originate from shallow waters. When studying the biogeography of past colonies of species, dispersability and the variance of ecology habitats is important. In the deep sea the movement of tectonic plates governs several processes that can create or remove physical barriers, affecting the distribution and abundance of vent and seep faunas. Hydrothermal vent and seep habitats are colonized by endemic species, of which the higher taxa are shared between the two different systems. Siboglinid tubeworms, bathymodiolin mussels and vesicomyid clams can be found in both settings, but on species level the faunas look different. This may be a result of different tectonic settings and physical properties. Vents are characterized by volcanic rocks and hot, metal-rich fluids and situated in open ocean settings, whereas cold seeps emit much colder fluids into soft sediment and carbonate rocks along continental margins (Van Dover 2000). In areas where both systems occur, for example around Japan and in the Gulf of California, the number of shared species is increased (Watanabe et al 2010; Van Dover et al 1990). Typical vent taxa have been discovered around whale carcasses

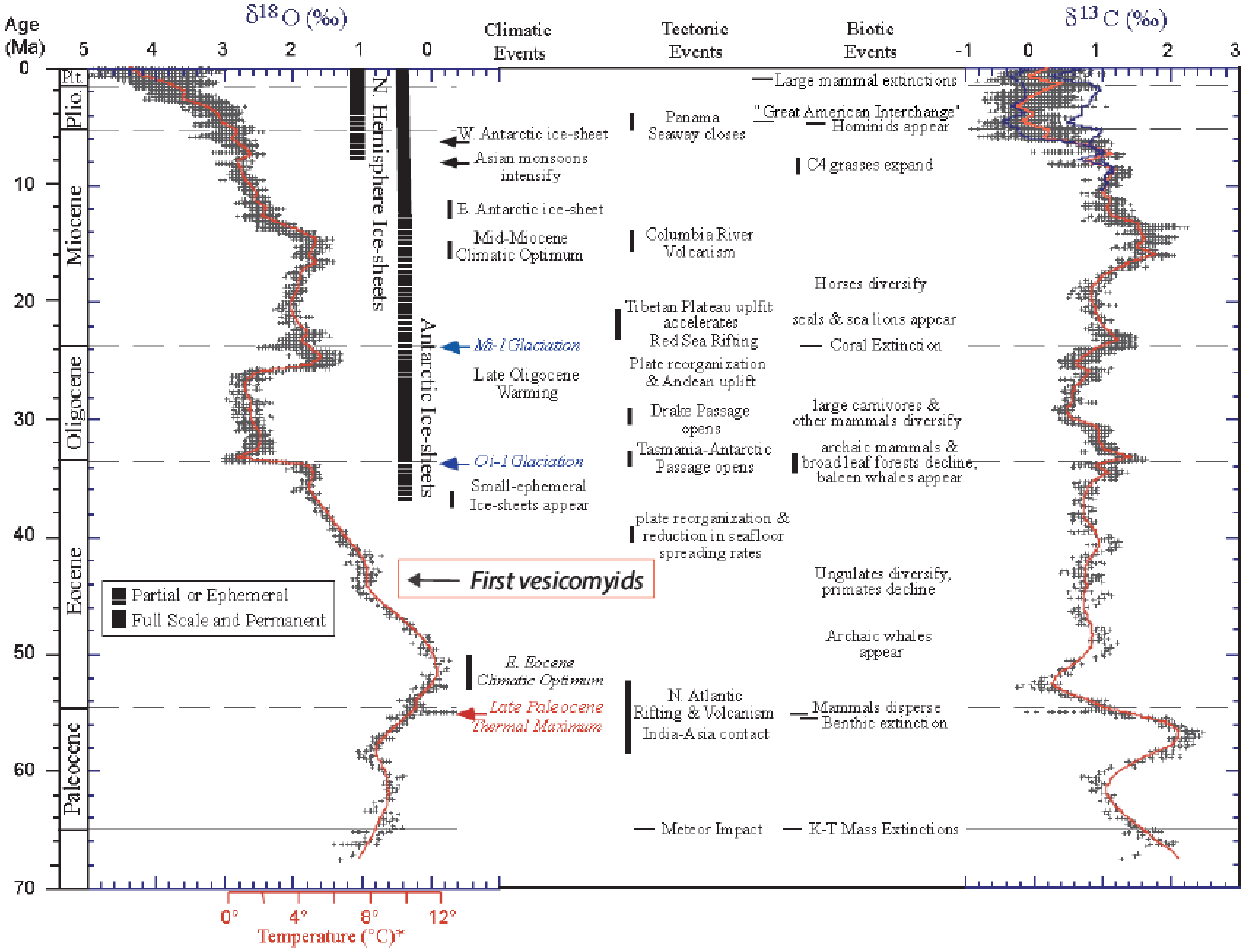


Figure 5. Global deep-sea oxygen and carbon isotope records showing past major biological and climatic events, including the first appearance of vesicomyids. The δ^{18}O-temperature scale (to the left) was computed for an ice-free ocean [~1.2‰ Standard Mean Ocean Water (SMOW)] From Zachos et al. 2001.

that have fallen to the ocean floor, suggesting that the vent and seep taxa may use ‘whale falls’ as stepping stones for dispersal (Smith & Baco 2003). Other discoveries of systems fueled by chemosynthetic primary production, such as a hydrothermal seeps, serpentinization vents and sedimented vents, have been regarded as conducive of the evolution of vent and seep biota (Levin et al 2012). The role of these intermediate habitats in the evolution of vent and seep faunas has been subject to network analysis with data including sites globally, where the biogeography of regular and intermediate sites were tested based on their connectivity. The result showed that sedimented vents, that are common at subduction zones and associated back-arc basins, were the main link between vents and seeps. The role of whale falls intermediate stepping stones is not entirely clear, but it is important to include them in network analyses for further assessment (Kiel 2016).

To assess the biogeography of vent and seep habitats through geological time, a network analysis taking fossil sites into account will provide the groundwork. This will be based on fossil sites that have been examined throughout this PhD-project as well as reports of fossil sites. This information will be used to assess the origin of the modern seep fauna and to test the role of major tectonic and climatic events during the Cenozoic and their impact on, mainly, the seep biota.

5. Materials and methods

This project started off with extensive fieldwork in different parts on the globe as well as synthesis of written material to yield an orienting overview of the projected study. The methodology of this initiating part of the project includes analytical steps undertaken in the order of collecting, preparing and analyzing material. For Paper I, material was already collected by James L. Goedert, Seattle (UW) and are available at the Swedish Museum of Natural History. Paper I was constructed as a first view of the PhD project and provided a general introduction to reducing systems (where energy from reduced inorganic chemical compounds is converted) systems, seep terminology, and geologic and taxonomic assessment of fossil material. This included acid etching of rock samples, microscopy to extract the phosphatic fossils, SEM and stacking imaging and manuscript writing. For Paper II and III, new material was collected specifically for this project. A list of all the collected fossils for this project is available as supplement in Table I.

5.1 Fieldwork

New fieldwork was undertaken as a part of this project, to expand the global archive of fossil seep faunas, especially in the relatively under sampled Southern Hemisphere. The fieldwork I took part in is summarized in the sections below and regions are marked in red in Figure 6 (fig 6).

5.1.1 Peru, November-December 2017

Fieldwork was first carried out in Peru and to investigate the potential of a western Pacific origin of the modern seep fauna. Field sites were chosen in the Talara Basin in northern Peru based on previous work by A. A. Olsson around the 1930’s (Olsson 1928; Olsson 1929; Olsson 1930; Olsson 1931; Olsson; 1932) and with the help of geological maps published by Instituto Geológico Minero y Metalúrgico (Ingemmet) and topographical maps by Instituto Geografico Nacional in Lima. Samples collected are described in Paper II and III.

5.1.2 Italy, June 2018

Fieldwork in Italy aimed to investigate old and new sites where the macrofauna associated with the Miocene “calcari a *Lucina*” has been found. The material will be analyzed to assess the faunal interchange between Atlantic and Indian Oceans when the ocean gateway connected the two oceans, and potential extinction and recolonization in the Mediterranean Sea following the Messinian salinity crisis at around 5.9 Ma. Seep deposits here are methane-seep carbonate blocks widespread throughout the Italian Apennines, named “calcari a *Lucina*”, after the large lucinid clams found within. In some places the carbonate blocks are *in situ*, and all of them contain a diverse chemosynthetic fauna, including mussels, lucinids, vesicomyids and gastropods (e.g. Taviani 1994; Kiel & Taviani

2017). Samples were collected from localites with mid-late Miocene deposits in the vicinities of Palazzuolo sul Senio, in the midst of Vespignano and Strabatenza. Some work was also done at a Pliocene locality on the southern beds of the Stirone River. 28 specimens were collected and included mainly bathymodiolin, vesicomyid and thyasyrid bivalves. These specimens have not been further analyzed yet.

5.1.3 Cuba, November-December 2018

Reports of lucinid and vesicomyid bivalves from the Elmira asphalt mine on Cuba (Kiel & Peckmann 2007; Kiel et al 2010) initiated an attempt at fieldwork in order to discover more potential seep sites and fossils. However, due to recent circumstances on Cuba, fieldwork could not take place. Reconnaissance visits to Museo Nacional de Historia Natural de Cuba, Cuba's geological society and smaller institutions, led to the conclusion that Cuba does not have an extensive record of fossil seep material.

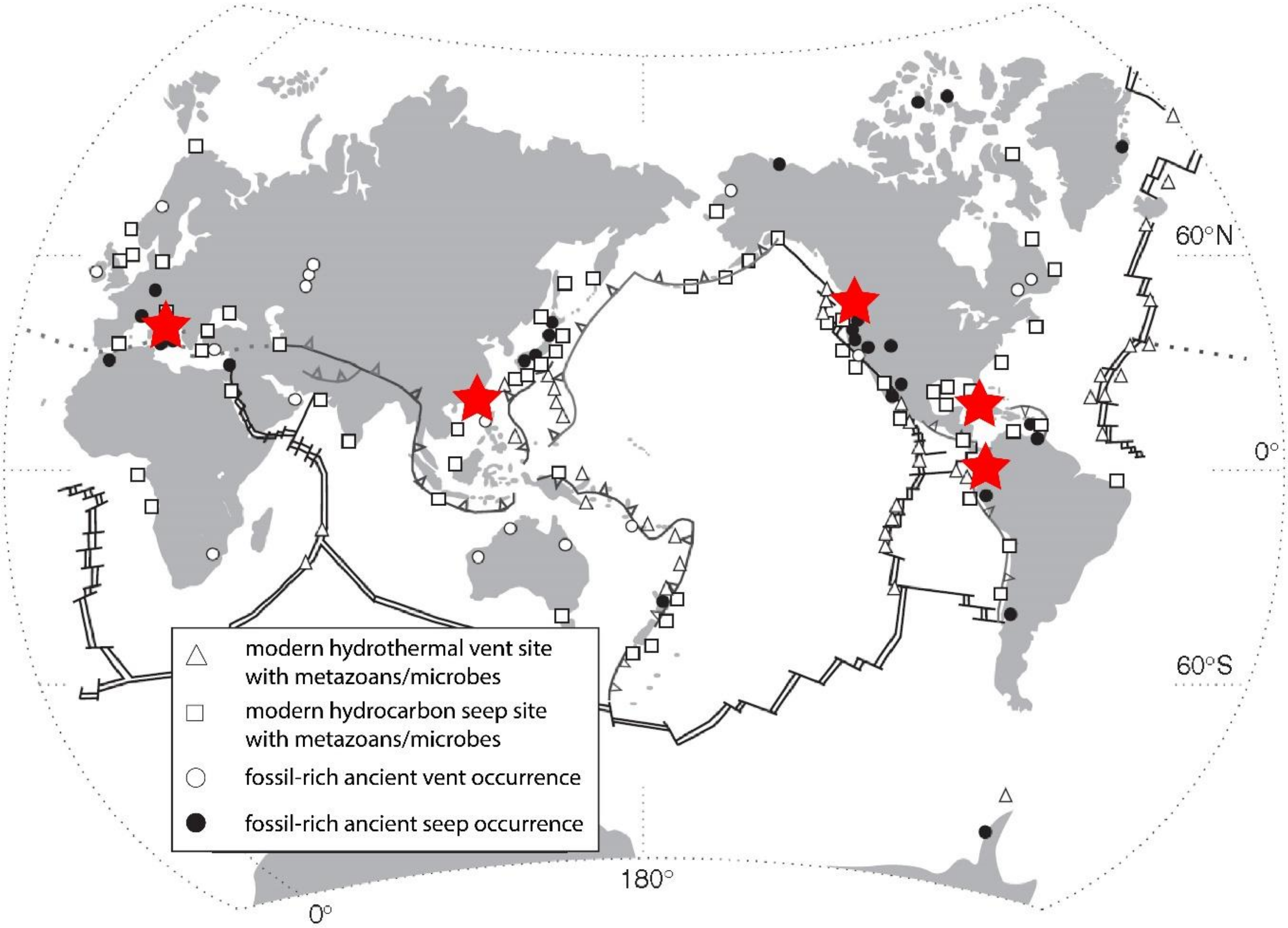


Figure 6. Map displaying global modern and ancient chemosynthesis-based settings. Legend symbols indicate modern hydrothermal vent and hydrocarbon seep occurrences, and fossil vent and seep occurrences with associated metazoan and/or microbial signatures. Red stars mark new occurrences described in this PhD-project. From Campbell 2006.

5.1.4 Taiwan, March 2019

Seep sites in Taiwan have been extensively described from Miocene and Pliocene (e.g. Wang et al. 2006; Chien 2012; Wang 2014). To address the potential origin of the modern seep fauna in a western Pacific setting, fieldwork was carried out in 2019. One Miocene locality was visited and the riverbeds there sampled for seep fossils. Seep deposits from Miocene, Pliocene and Pleistocene have been previously sampled by the National Museum in Taichung and a multitude of specimens was provided to us to analyze briefly and photograph for further assessment.

5.2 Preparation and analysis

At the sample sites, seep carbonates were mostly found as concretions or big nodules within sediment beds or as separate blocks sitting in dried up riverbeds. To extract fossils, bigger blocks were hammered to break loose smaller parts that can be packaged and transported to the lab.

5.2.1 Samples preparation and oxygen and carbon stable isotope analysis

In the lab, samples were hammered into ~10x10x10 cm pieces and gathered in plastic containers filled with 5-10% acetic acid solution. Over a period of > 4 weeks, dissolved rock fragments were picked out of the container, acidic residue was thoroughly rinsed with water and the rock fragments were dried at 60°C. Dry fossil specimens and fragments were picked out and examined using a stereo microscope. Some specimens were chosen for scanning electron microscopy (SEM); they were mounted and coated with gold before being photographed with the SEM. Other mollusk fossils were coated with ammonium chloride and photographed using a stacking image system that combine 15-25 images into one composite image.

A few samples of undissolved rock were made into thin sections. For the Humptulips and Peruvian seeps material, micrite, rim cement and calcite samples were extracted using a hand-held microdrill for oxygen and carbon isotope measurement. Carbonate powders were reacted with 100% phosphoric acid at 75°C using a mass spectrometer. Values were reported in per mil relative to VPDB standard by assigning a $\delta^{13}C$ value of +1.95‰ and a $\delta^{18}O$ value of −2.20‰ to NBS19. Reproducibility was checked by replicate analysis of laboratory standards and is better than ±0.05‰. For the Peruvian sites, one rock sample from each locality was chosen for lipid biomarker analyses to further assess the nature of the seep deposits (see details in Paper II).

5.2.2 Material dating methods

Dating of the material from Humptulips Formation and the Peruvian sites have been mainly been done by biostratigraphic comparisons to earlier described sites from the same area and geological maps of the investigated areas. Especially benthic and planktonic foraminifera have been used for providing biostratigraphic age constraint for the deposits.

5.2.3 Sample analysis and biogeographic modeling

Sorting through the gathered material, all vesicomyids have been set aside for extensive analysis. Morphological features are identified through microscopy and detailed photographing and will be further assessed as described in section 7. The best diagnosable features of, especially, vesicomyid clams are the hinge teeth and the hinge line. Most of the specimens found were non-articulated and the preservation poor. To get good images of the hinge line the specimens were prepared using a pneumatic rock hammer and silicone casts were made of the hinge line of two chosen specimens. The imprints on the casts were then analyzed under microscope. All of the newly collected material will be added to already existing fossil occurrence data found in the literature. From this, Bayesian modeling of dispersal, extinction and sampling rates can be investigated using probabilistic analyses (Silvestro et al 2019). Combining this method with network analysis, different evolutionary pathways for Vesicomyidae and the effects of tectonic and climatic changes on seep biota will be tested.

6. Paper summaries

6.1 Paper I

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.

Cold seep deposits within marine deep water sediments found in western Washington State, USA hold a wide diversity of seep fossils with good preservation, and have been used often to address taxonomic, geochemical and evolutionary inquiries regarding seep faunas. These deposits are carbonate blocks of Cenozoic age found in a section with early Eocene basalts at the bottom and middle Eocene to early Miocene marine sediments on top. The collected site is called the Satsop Weatherwax seep deposit. The purpose with this paper was to confirm the hypothetical seep origin of the deposit by assessing taxonomy and isotopic fingerprint of the fossil elements.

Carbon and oxygen stable isotope analyses were carried out to confirm seep origin of the collected samples. The rock samples were hammered into sizable pieces and dissolved in acetic acid to extract the fossils that were then analyzed through SEM and regular microscopy.

The Satsop Weatherwax seep deposit contains fossils of genera that are typically associated with deep sea methane seeps, including rare echinoderms and tube worms and gastropod and bivalve molluscs. The preservation is fairly poor due to dissolution of calcium carbonate and precipitation of silica occurring at seeps, silicifying the aragonitic shells of this fauna. Along with many fossil fragments material to describe five new species was found. The new species described are the bivalve *Tindariopsis acutilineata* (Nuculanoidea); gastropods *Desbruyeresia belliatus*, *Provanna fortis* (Provannidae) and *Orbitestella dioi* (Orbitestellidae); and the polyplachophoran *Leptochiton terryiverseni* (Leptochitonidae). The stable isotopes signatures correspond to those of similar deposits in western Washington and indicate a marine seep origin of the deposits.

Overall the fossil fauna found at Satsop Weatherwax seep deposit belong to recent genera, giving it a modern character and a rough estimate that it is 40 to 42.5 million years old. Well-known late Eocene to Oligocene seep faunas in Washington hold different species than the new reported site. *Orbitestella dioi* is the first record of and orbitestellid gastropod in an ancient cold seep deposit and no provannids have been recovered earlier from the Humptulips Formation. This is also the first record of *Desbruyeresia* from western North America.

6.2 Paper II

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]

In the 1930's Axel A. Olsson published a series of papers describing the paleontology of the Talara Basin. These reported of potentially oil-bearing sediments including their fossil fauna, the '*Pleurophopsis* fauna' for biostratigraphical correlations. Named after the most abundant bivalve *Pleurophopsis,* these fossils were mostly recovered from carbonate nodules within the late Oligocene "Heath shales". Two of the reported '*Pleurophopsis*'-sites have been confirmed to be seep deposits which spurred the interest for this study which aimed to reinvestigate the Cenozoic sediments in the Talara Basin to assess stratigraphy, ecology and fauna. This study also aimed to add to the sparse fossil record of seep faunas from the Southern Hemisphere.

The sediments of the Talara Basin have undergone frequent reformation during sea level transgressions and regressions as well as tectonics along the still active subduction zone outside the coast of South America. The sandstones of middle to upper Eocene Talara Group and the superjacent Oligocene Mancora formation have been sourced by the oil industry. The upper Oligocene Heath Formation, holding the *Pleurophopsis* zone, lies on top of the Mancora Formation.

With the aid of locally produced geological maps fieldwork was prepared and carried out for four weeks in late 2017, targeting mainly the marine deposits of the Heath shales described by Olsson in 1931. Rock samples were collected from three different locations called Belén seep site, Cerro La Salina sites and Cerros El Pelado sites. Phosphatic fossils were extracted from the rock sample by acidic etching and the residue was screened under a stereo microscope. Thin sections were prepared from samples of each site. Lipid biomarkers and carbon isotope compositions of hydrocarbons and carboxylic acids were measured and analyzed from each locality.

The Belén seep site was found after a notion from Olsson, that rock samples he collected from what he called, Belén fruit site showed lithological similarities to rocks containing the *Pleurophopsis* fauna. The collected material from the seep site is however, estimated to be of early-to-early late Oligocene age whereas the Belén fruit site is of early Oligocene age. The limestones here consisted of micrite with bioclasts, and oval peloids. The fauna shows low diversity consisting mainly of the bivalve *Pleurophopsis lithophagoides*, a few specimens of a provannid gastropod, and single specimens of a protobranch bivalve and a neogastropod. Olsson further described outcrops of the Heath shales along Quebrada Seca containing carbonate deposits with the *Pleurophopsis* fauna. Our fieldwork resulted in samples from nine fossiliferous seep carbonate blocks (Cerro La Salina block 1-9) from the Cerro La Salina sites found along the southern border of Quebrada Seca. The blocks were found as floats in the midst of the ravine, none were found *in situ*, but their lithologies are uniform. They consisted of micrite with nodules, and some voids filled with clasts lined by botryoidal rim cement. The age is somewhat uncertain, but they are considered to be of early Oligocene age, based on stratigraphic assessment along with identification of foraminifera for biostratigraphic assessment. The third investigated location was the northern border of the Quebrada Seca where three carbonate blocks (Cerros El Pelado block 1-3) were found as floats in creek beds. These carbonates consisted of shell fragments, abundant authigenic cement, detrital sediment, blocky calcite and minor amounts of micrite.

Stable carbon isotope analyses of the carbonates and lipid biomarkers showed ^{13}C-depleted carbonate phases and ^{13}C-depleted lipid biomarkers indicating that the limestones at Belén, Cerro La Salina and Cerro El Pelado are seep deposits. The fauna was found to be diverse with a high fossil abundance containing bivalves, gastropods, crustaceans, scaphopods and worm tubes. Planktonic foraminifera were identified in thin sections. Fish teeth, scales and bone fragments were revealed after acid dissolution of Cerro La Salina block 1. The fauna found at these different sites shows similarities to other Oligocene and late Eocene seep faunas in the world. Widespread genera such as bivalves *Conchocele* (Thyasiridae) and *Lucinoma* (Lucinidae) and gastropod *Provanna* are also known from seeps in Japan, USA and the Caribbean region. This study extends the Peruvian fossil record of seep faunas since fossil findings of all sizes were considered, everything < 1 cm was excluded in the work of Olsson. In addition, it shortens the stratigraphical gap in Southern Hemisphere seep faunas between Late Cretaceous and the Miocene.

6.3 Paper III

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 (X): xxx-xxx.

Most of our knowledge of fossil deep-water methane-seep communities from the Cenozoic Era comes from studies made in regions on the northern Hemisphere, e.g. USA, Japan, the Caribbean and Italy. The southern hemisphere has not been as thoroughly investigated, taxonomic work has been done on the Miocene seep deposits of New Zealand and a Miocene site from central Chile.

This paper holds the taxonomic descriptions of the fossils recovered from the Peruvian Oligocene methane-seep deposits reported of in **Paper II** and together with Olsson 1931 and this study, 39 species of mollusks have been reported from the seep deposits of the Talara Basin. Only five species are reported from both studies (*Pseudophopsis peruviana*, *Conchocele tessaria*, *Pleurophopsis unioides*, *Pleurophopsis talarensis*, and ‘*Vesicomya*’ *tschudi*) which probably was caused by differentiating sampling methods and erosion of the sediments that Olsson sampled.

Specimens were extracted using methods described in **Paper II** and photographed for further analysis. New taxa are bivalves; *Neilo altamirano* and *Pleurophopsis talarensis*, gastropods; *Pyropelta seca*, *Provanna pelada* and *Ascheria salina*, and a crustacean; *Eucalliax capsulasetaea*. This study comprise the first record of decapod *Eucalliax* from a seep and from the Oligocene, the youngest and smallest member of genus *Ascheria*, the oldest record of gastropod limpet *Coccopigya* sp. and the first reports from the Peruvian fossil record of deep-water genera *Neilo*, *Propeamussium*, *Coccopigya*, *Cantrainea* and *Colus*, and seep-restricted taxa *Pyropelta*, *Provanna*, *Ascheria* and uncertain *Retiskenea*.

7. Current and future work

7.1 Character coding and phylogenetic analyses of the family Vesicomyidae

To better depict the evolution of seep faunas, in time and space, the bivalve family Vesicomyidae is going to be studied in detail. In addition to modern species descriptions and records, the fossil record will be extensively mapped through collected samples and available literature and all known vesicomyid taxa will be analyzed together. With the help of fossils gathered through the new fieldwork efforts, along with published descriptions of fossil and recent species of the bivalve family Vesicomyidae from the wider literature, a character matrix is being prepared. This comprises all the specific morphological features of the different species and will be tested using phylogenetic analyses to reconstruct the phylogeny of Vesicomyidae. Using cladistics, phylogenetic trees will be constructed based both morphological and molecular data. The trees will be calibrated to their geological time-intervals and can then be compared to events in Earth’s history to investigate how these events may have affected the evolution of vesicomyids. The phylogenetic analyses of Vesicomyidae are more extensive on the molecular side and still lacking fossil data. The results of this project will hopefully yield a more extensive phylogeny for Vesicomyidae.

7.2 Network analysis of fossil and recent vent/seep fauna

The timing of appearance and characteristics of cold seep ecosystems have evolutionary connections to other seep systems as well as to hydrothermal vent systems. As mentioned, they host similar faunas, sharing the main taxa and in areas where vent and seeps are both included, the number of shared species increases (Watanabe et al 2010). Other intermediate systems such as hydrothermal seeps, serpentinization vents and sedimented vents work as links to the forming of new systems.

Network analysis (NA) is a method that uses a matrix dataset of relational data between, for example, different biogeographic provinces. The provinces are depicted as nodes that are bound together with several lines representing their relation and interactions with other provinces. With this method, the importance of individual sites connecting to other sites as well as the strength of these connections can be quantified. Faunal distribution can be divided into biogeographic provinces based on their characteristics and their connectivity and relations through geological time can be assessed. These provinces can for example be reducing systems, and with a dataset that compiled all vent, seep and intermediate systems, Kiel (2016) tested their biogeographic connectivity on a global scale. To address the methane-seep fauna, from the Cenozoic to recent, this project will use the occurrence of vesicomyid clams from their appearance in middle Eocene. With network analysis, it is possible to detect a center of origin for the genus and to track potential shifts in their habitat dispersal.

8. Acknowledgements

I would first like to thank my supervisors Steffen Kiel and Helen Coxall for their guidance, scientific support, availability and patience. I am also grateful for my colleagues at PAL who have been a great support when I have needed different input or a break from writing. I thank my extended family for their never-ending support.

9. References

Allen, M. B., & Armstrong, H. A. (2008). Arabia-Eurasia collision and the forcing of mid-Cenozoic global cooling. *Palaeogeography, Palaeoclimatology, Palaeoecology, 265*, 52-58.

Amano, K., & Kiel, S. (2007). Fossil vesicomyid bivalves from the North Pacific region. *The Veliger, 49*(4), 270-293.

Boetius, A., Ravenschlag, K., Schubert, C., Rickert, D., Widdel, F., Gieseke, A., Amann, R., Jørgensen, B., Witte, U., & Pfannkuche, O. (2000). A marine microbial consortium apparently mediating anaerobic oxidation of methane. *Nature, 407,* 623-626.

Bohrmann, G., and cruise participants. (2008). Report and preliminary results of R/V *Meteor* Cruise M74/3, Fujairah-Male. Cold seeps of the Makran subduction zone (continental margin of Pakistan). *Bereichte aus them Fachbereich Geowissenschaften der Universität Bremen, 266*, 161 pp.

Campbell, K. A., Nelson, C. S., Alfaro, A. C., Boyd, S., Greinert, J., Nyman, S., . . . Wallis, I. (2010). Geological imprint of methane seepage on the seabed and biota of the convergent Hikurangi Margin, New Zealand: Box core and grab carbonate results. *Marine Geology, 272*, 285-306.

Cavanaugh, C.M., Gardiner, C.L., Jones, M.L., Jannasch, H.W. & Waterbury, J.B. (1981). Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: Possible chemoautotrophic symbionts. *Science, 213*, 340-342.

Cavanaugh, C.M., McKiness, Z.P., Newton, I.L.G. & Stewart, F.J. (2006) *The Prokaryotes* (eds Dworkin, M., Falkow, S.I., Rosenberg, E., Schleifer, K-H. & Stackebrandt, E.) 475-507, Springer, New York, 2006.

Chien, C-W., Huang, C-Y., Chen, Z., Lee, H-C. & Harris, R. (2012). Miocene shallow-marine cold seep carbonate in fold-and-thrust Western Foothills, SW Taiwan. *Journal of Asian Earth Sciences, 56,* 200-211.

Contardo-Berríos, X., Mena-Hodges, E., & Quirago, E. (2017). Hallazgo del primer seep fósil en la costa emergida de Chile central (33°56’ S). Caracterización e implicancias. *Andean Geology, 44*(2), 213-228. doi: 10.5027/andgeoV44n2-a05

Conti, S., Fontana, D., Gubertini, A., Sighinolfi, G., Tateo, F., Fioroni, C., & Fregni, P. (2004). A multidisciplinary study of middle Miocene seep-carbonates from the northern Apennine foredeep (Italy). *Sedimentary Geology, 169*, 1-19.

Cope, J.C.W. (1996). Early Ordovician (Arenig) bivalves from the Llangynog Inlier, South Wales. *Palaeontology, 39,* 979-1025.

Corliss, J. B., Dymond, J., Gordon, L. I., Edmond, J. M., Von Herzen, R. P., Ballard, R. D., . . . Van Andel, T. H. (1979). Submarine thermal springs on the Galápagos Rift. *Science, 203*, 1073-1083.

Corselli, C., & Basso, D. (1996). First evidence of benthic communities based on chemosynthesis on the Napoli mud volcano (Eastern Mediterranean). *Marine Geology, 132,* 227-239.

Cosel, R. Von & Salas, C. (2001). Vesicomyidae (Mollusca: Bivalvia) of the genera *Vesicomya, Waisiuconcha, Isorropodon* and *Callogonia* in the eastern Atlantic and the Mediterranean. *Sarsia, 86,* 333-366.

DeConto, R.M., & Pollard, D. (2003). Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO_2. *Nature, 421*, 245-249.

Decker, C., Olu, K., Cunha, R.L., & Arnaud-Haond, S. (2012). Phylogeny and diversification patterns among vesicomyid bivalves. *PLoS One, 7,* e33359.

Deming, J. W., Reysenbach, A. L., Macko, S. A., & Smith, C. R. (1997). Evidence for the microbial basis of a chemoautotrophic invertebrate community at a whale fall on the deep seafloor: Bone-colonizing bacteria and invertebrate endosymbionts. *Microscopy Research and Technique, 37*(2), 162-170.

Felbeck, H. (1981). Chemoautotrophic potential of the hydrothermal vent tube worm, *Riftia pachyptila* Jones (Vestimentifera). *Science, 213*, 336-338.

Fiala-Médioni, A. & Le Pennec, M. (1987). Trophic structural adaption in relation to the bacterial association of bivalve molluscs from hydrothermal vents and subduction zones. *Symbiosis, 4*, 63-74.

Fiala-Médioni, A., Métivier, C., Herry, A., & Le Pennec, M. (1986). Ultrastructure of the gill of the hydrothermal-vent mytilid *Bathymodiolus* sp. *Marine Biology, 92,* 65-72.

Fisher, C. R. (1990). Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *Reviews in Aquatic Sciences, 2*(3, 4), 399-436.

Fujiwara, Y. (2003). Endosymbioses between invertebrates and chemosymbiotic bacteria. *Japanese Journal of Benthology, 58,* 26-33.

Goedert, J. L., & Squires, R. L. (1990). Eocene deep-sea communities in localized limestones formed by subduction-related methane seeps, southwestern Washington. *Geology, 18*, 1182-1185.

Gooday, A.J. & Turley, C.M. (1990). Responses by benthic organisms to inputs of organic material to the ocean floor: A review. *In*: H. Charnock, J.M. Edmond, I.N. McCave, A.L. Rice and Wilson, T.R.S. (eds). The Deep-Sea Bed: Its Physics, Chemistry and Biology. *Philos. Trans. R. Soc. Lond., A 331,* 119-138.

Hannington, M.D., Jonasson, I.R., Herzig, P.M. and Petersen, S. (1995). Physical and Chemical Processes of Seafloor Mineralization at Mid-Ocean Ridges. *In*: S.E. Humphris, R.A. Zierenberg, L.S. Mullineaux and R.E. Thomson (Eds.), Seafloor Hydrothermal Systems: Physical, Chemical, Biological, and Geological Interactions, *Geophysical Monograph*, *91,* American Geophysical Union, 115-157.

Hessler, R.R., Smithey, W.M. & Keller, C.H. (1985). Spatial and temporal variation of giant clams, tubeworms and mussels at deep-sea hydrothermal vents. *Bull. Biol. Soc. Wash*, *6,* 465-474.

Higley, D. (2004). The Talara basin province of northwestern Peru: Cretaceous–Tertiary total petroleum system. *U.S. Geological Survey, e-bulletin, B-2206a*, 52.

Hryniewicz, K., Little, C. T. S., & Nakrem, H. A. (2014). Bivalves from the latest Jurassic-earliest Cretaceous hydrocarbon seep carbonates from central Spitsbergen, Svalbard. *Zootaxa, 3859*, 1-66.

Jakubowicz, M., Hryniewicz, K., & Belka, Z. (2017). Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports, 7,* 14292. doi: 10.1038/s41598-017-14732-y

Johnson, S.B., Krylova, E.M., Audzijonyte, A., Sahling, H. & Vrijenhoek, R.C. (2017). Phylogeny and origins of chemosynthetic vesicomyid clams. *Systematics and Biodiversity, 15,* 346-360.

Kaim, A., Jenkins, R. G., & Warén, A. (2008). Provannid and provannid-like gastropods from Late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda: Abyssochrysoidea). *Zoological Journal of the Linnean Society, 154,* 421-436.

Kiel, S. (2006). New records and species of mollusks from Tertiary cold-seep carbonates in Washington State, USA. *Journal of Paleontology, 80*(1), 121-137.

Kiel, S. (2015). Did shifting seawater sulfate concentrations drive the evolution of deep-sea vent and seep ecosystems? *Proceedings of the Royal Society B, 282*, 20142908.

Kiel, S. (2016). A biogeographic network reveals evolutionary links between deep sea hydrothermal vent and methane seep faunas. *Proceedings of the Royal Society B, 283*, 20162337. doi: 10.1098/rspb.2016.2337

Kiel, S., & Peckmann, J. (2007). Chemosymbiotic bivalves and stable carbon isotopes indicate hydrocarbon seepage at four unusual Cenozoic fossil localities. *Lethaia, 40*(4), 345-357.

Kiel, S., & Amano, K. (2013). The earliest bathymodiolin mussels: Evaluation of Eocene and Oligocene taxa from deep-sea methane seep deposits in western Washington State, USA. *Journal of Paleontology, 87*(4), 589-602.

Kiel, S., & Taviani, M. (2017). Chemosymbiotic bivalves from Miocene methane-seep carbonates in Italy. *Journal of Paleontology, 91*(3), 444–466.

Kiel, S., Campbell, K. A., & Gaillard, C. (2010). New and little known mollusks from ancient chemosynthetic environments. *Zootaxa, 2390*, 26-48.

Kiel, S., Birgel, D., Campbell, K. A., Crampton, J. S., Schiøler, P., & Peckmann, J. (2013). Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology, 390*, 17-34.

Kioka, A. & Ashi, J. (2015). Episodic massive mud eruptions from submarine mud volcanoes examined through topographical signatures. *Geophys. Res. Lett., 42*, 8406-8414.

Krylova, E.M. & Sahling, H. (2010). Vesicomyidae (Bivalvia): Current taxonomy and distribution. *PLoS One, 5,* e9957.

Lalou, C., Reyss, J-L., Brichet, E., Rona, P.A. & Thompson, G. (1995). Hydrothermal activity on a 10^5-year scale at a slow-spreading ridge, TAG hydrothermal field, Mid-Atlantic Ridge 26°N. *Journal of Geophysical Research-Solid Earth, 100,* 17855-17862.

Levin, L. A., Orphan, V. J., Rouse, G. W., Rathburn, A. E., Ussler, W., Cook, G. S., . . . Strickrott, B. (2012). A hydrothermal seep on the Costa Rica margin: middle ground in a continuum of reducing ecosystems. *Proceedings of the Royal Society B, 279,* 20120205. doi: 10.1098/rspb.2012.0205

Manchester, S. R., Herrera, F., Fourtanier, E., Barron, J., & Martinez, J.-N. (2012). Oligocene age of the classic Belén fruit and seed assemblage of North coastal Peru based on diatom biostratigraphy. *Journal of Geology, 120*(4), 467–476.

McArthur, A.G & Tunnicliffe, V. (1998). Relics and antiquity revisited in the modern vent fauna. *In* Mills, R.A. & Harrison, K. (Eds.), Modern ocean floor processes and the geological record. *Geological Society Special Publications, London,* 271-291.

O'Dea, A. et al. (2016). Formation of the Isthmus of Panama. *Science advances, 2(8).*

Olsson, A.A. (1928). Contributions to the Tertiary paleontology of northern Peru: Part 1, Eocene Mollusca and Brachiopoda. *Bulletins of American Paleontology, 14,* 5-186.

Olsson, A.A. (1929). Contributions to the Tertiary paleontology of northern Peru: Part 2, Upper Eocene Mollusca and Brachiopoda. *Bulletins of American Paleontology, 15,* 1-120.

Olsson, A.A. (1930). Contributions to the Tertiary paleontology of northern Peru: Part 3, Eocene Mollusca and Brachiopoda. *Bulletins of American Paleontology, 17,* 1-96.

Olsson, A.A. (1931). Contributions to the Tertiary paleontology of northern Peru: Part 4, Eocene Mollusca and Brachiopoda. *Bulletins of American Paleontology, 17,* 97-264.

Olsson, A.A. (1932). Contributions to the Tertiary paleontology of northern Peru: Part 5, The Peruvian Miocene. *Bulletins of American Paleontology, 19,* 1-216.

Paull, C. K., Hecker, B., Commeau, R., Freeman-Lynde, R. P., Neumann, C., Corso, W. P., . . . Curray, J. (1984). Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science, 226*, 965-967.

Payne, C.M. & Allen, J.A. (1991). The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. *Philosophical transactions of the royal society of London Series B, 334,* 481-566.

Peckmann, J. & Thiel, V. (2004). Carbon cycling at ancient methane-seeps. *Chemical geology, 205,* 443-467.

Rau, G.H. (1981). Hydrothermal vent clam and vent tubeworm $^{13}C/^{12}C$: Further evidence of a nonphotosynthetic food source. *Science, 213,* 338-339.

Raymo, M.E. & Ruddiman, W.F. (1992). Tectonic forcing of late Cenozoic climate. *Nature, 359,* 117-122.

Ritger, S., Carson, B., & Suess, E. (1987). Methane-derived authigenic carbonates formed by subduction-induced pore-water expulsion along the Oregon/Washington margin. *Geological Society of America Bulletin, 98,* 147-156.

Schackleton, N.J. & Kennett, J.P. (1975). Palaeotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analysis in DSDP Sites 277, 279 and 281, *in* Kennett, J.P., Houtz, R.E., and al., e., eds., Initial Reports of the Deep Sea Drilling Project, *29*: Washington DC, U.S. Governments Printing Office, 881-884.

Sibuet, M., Juniper, S. K., & Pautot, G. (1988). Cold-seep benthic communities in the Japan subduction zones: Geological control of community development. *Journal of Marine Research, 46,* 333-348.

Sibuet, M. & Olu, K. (1998). Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Research II, 45,* 517-567.

Siegert, M., Barrett, P., Deconto, R., Dunbar, R., Ó Cofaigh, C., Passchier, S. & Naish, T. (2008). Recent advances in understanding Antarctic climate evolution. *Antarctic Science, 20,* 313-325.

Silvestro, D., Salamin, N., Antonelli, A., & Meyer, X. (2019). Improved estimation of macroevolutionary rates from fossil data using a Bayesian framework. *Palaeobiology, 45,* 546-570.

Smith, E.A. (1885). Report on the Lamellibranchiata collected by HMS Challenger during the years 1873-76. *Report on the scientific results of the voyager of H.M.S. Challenger during the years 1873-76, Zoology, 13,* 1-341.

Smith, C. R., & Baco, A. R. (2003). Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology: an Annual Review, 41*, 311-354.

Southward, E.C. (1982). Bacterial symbionts in Pognophora. *J. Mar. Biol. Assoc. U.K., 46,* 579-616.

Southward, E.C. (1986). Gill symbionts in thyasirids and other bivalve molluscs. *J. Mar. Biol. Assoc. U.K., 66*, 889-914.

Stainforth, R. M. (1948). Applied micropaleontology in coastal Ecuador. *Journal of Paleontology, 22*(2), 113-151.

Stewart, F. J., & Cavanaugh, C. M. (2006). Bacterial endosymbioses in Solemya (Mollusca: Bivalvia)-Model systems for studies of symbiont-host adaptation. *Antonie van Leeuwenhoek, 90,* 343-360.

Stewart, F.J., Newton, I., & Cavanaugh, C.M. (2005). Chemosynthetic endosymbiosis: adaptions to oxic-anoxic interfaces. *Trends in microbiology, 13,* 439-448.

Suess, E., Carson, B., Ritger, S. D., Moore, J. C., Jones, M. L., Kulm, L. D., & Cochrane, G. R. (1985). Biological communities at vent sites along the subduction zone off Oregon. *Bulletin of the Biological Society of Washington, 6*, 475-484.

Tarasov, V. G., Gebruk, A. V., Mironov, A. N., & Moskalev, L. I. (2005). Deep-sea and shallow-water hydrothermal vent communities: Two different phenomena? *Chemical Geology, 224*, 5-39.

Taviani, M. (1994). The “calcari a Lucina” macrofauna reconsidered: Deep-sea faunal oases from Miocene-age cold vents in the Romagna Apennine, Italy. *Geo-Marine Letters, 14,* 185-191.

Taylor, J.D., & Glover, E.A. (2000). Functional anatomy, chemosymbiosis and evolution of the Lucinidae. *In:* Harper, E.M., Taylor, J.D., Crame, J.A. (Eds.), *The evolutionary biology of the Bivalvia, Geological Society of London special publication, 177,* 207-225.

Van Dover, C. L., Grassle, J. F., & Boudrias, M. (1990). Hydrothermal vent fauna of Escanaba Trough (Gorda Ridge). In G. R. McMurray (Ed.), *Gorda Ridge* (pp. 285-287). New York: Springer.

Van Dover, C. L. (2000). *The ecology of deep-sea hydrothermal vents* (book ed.). Princeton: Princeton University Press.

Von Damm, K. L. (1995), Temporal and compositional diversity inseafloor hydrothermal fluids. *Rev. Geophys*., *33*, 1297–1305.

Vrijenhoek, R.C. (2013). On the instability and evolutionary age of deep-sea chemosynthetic communities. *Deep Sea Research II, 92,* 189-200.

Wang, S-W., Gong, S-Y., Mii, H-S., & Dai, C-F. Cold-seep carbonate hardgrounds as the initial substrata of coral reef development in a siliciclastic palaeoenvironment of southwesten Taiwan. *Terrestrial Atmospheric and Oceanic Sciences, 17,* 405-427.

Wang, S-W. & Mii, H-S. (2014). Stable isotope evidence for hydrocarbon seepages in the Kenting Mélange at Baoli, Hengchun Peninsula, Taiwan. *Collect. Res., 27,* 95-106.

Watanabe, H., Fujikura, K., Kojima, S., Miyazaki, J.-I., & Fujiwara, Y. (2010). Japan: Vents and seeps in close proximity. In S. Kiel (Ed.), *The Vent and Seep Biota* (Vol. 33, pp. 379-402). Heidelberg: Springer.

Whiticar, M. J., Faber, E., & Schoell, M. (1986). Biogenic methane formation in marine and freshwater environments: CO_2 reduction vs. acetate fermentation—Isotope evidence. *Geochimica et Cosmochimica Acta, 50*, 693–709.

Whiticar, M. J. (1999). Carbon and hydrogen isotope systematics of bacterial formation and oxidation of methane. *Chemical Geology, 161*, 291-314.

Zachos, J.C., Pagani, M., Sloan, L.C., Thomas, E., and Billups, K. (2001). Trends, rhythms, and aberration in global climate 65 Ma to present. *Sciene, 292,* 5513: 686-693.

Zal, F., Leize, E., Oros, D.R., Hourdez, S., Van Dorsselaer, A. & Childress, J.J. (2000). Haemoglobin structure and biochemical characteristics of the sulphide-binding component from the deep-sea clam *Calyptogena magnifica. Cah. Biol. Mar., 41,* 413-423.

10. Appendix

Table I. Compiled information of newly collected material for this PhD-project including location, sample sites, age and species.

Country	Location	Formation	Sample site	Coordinates	Age	Phylum	Species
USA	Washington State	Humptulips	Satsop Weatherwax site	47.317177°N, 123.565931°W	Middle Eocene	Annelida	Tube fragments
						Bivalvia	Vesicomyid
							Thyasira sp.
							Nuculana acutilineata
						Brachiopoda	*Discinisca* sp.
						Echinoidea	Echinoid spines
						Gastropoda	*Depressigyra* sp.
							Thalassonerita eocenica
							Limpets
							Desbruyeresia belliatus
							Provanna fortis
							Colus? Sp.
							Hyalogyrina sp.
							Orbitestella dioi
						Polyplacophora	*Leptochiton terryiverseni*
Peru	Talara Basin		Belén seep	4°44.239′S, 81°12.935´W	Early Oligocene	Bivalvia	*Pleurophopsis lithophagoides*
							Provanna antiqua
							Buccinidae indet.
			Cerro La Salina	4°3.302′S, 81°0.334′W	Early Oligocene	Bivalvia	*Neilo altamirano*
							Idas sp.
							Propeamussiidae indet.
							Pseudophopsis peruviana
							Conchocele tessaria
							Lucinoma zapotalensis

							Pleurophopsis talarensis
							”Vesicomya” tschudi
						Gastropoda	Limpets
							Coccopigya sp.
							Retiskenea? sp.
							Pyropelta seca
							Cantrainea sp.
							Trochoid
							Provanna antiqua
							Ascheria salina
							Colus sekiuensis
							Acteon sp.
							Cylichna sp.
						Decapoda	*Eucalliax capsulasetea*
			Cerros El Pelado	4°1.770′S, 80°58.601′W	Early Oligocene	Bivalvia	*Pseudophopsis peruviana*
							Lucinoma zapotalensis
						Gastropoda	*Pyropelta seca*
							Cantrainea sp.
							Provanna pelada
Italy					Mid-late Miocene	Bivalvia	Bathymodiolin
							Vesicomyid
							Thyasyrid
Taiwan			Cian-Feng Bridge		Miocene	Bivalvia	Lucinid
						Gastropoda	
			Nangtzuhsien River			Bivalvia	Lucinid
			East Takangshan Quarry		Pleistocene	Bivalvia	Bathymodiolin
							Lucinid
						Gastropoda	

A middle Eocene seep deposit with silicified fauna from the Humptulips Formation in western Washington State, USA

FRIDA HYBERTSEN and STEFFEN KIEL

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 (4): 751–768.

Carbonate blocks with silicified fossils were recovered from a newly recognized cold seep deposit, the Satsop Weatherwax site, in the basal Humptulips Formation, along the West Fork of Satsop River in Washington State, USA. The petrography and the stable carbon isotope signature of the carbonate, with values as low as -43.5‰, indicate that these carbonate blocks formed at an ancient methane seep. The fossils recovered from this block include five vesicomyid specimens, two fragments of a thyasirid, five specimens of the peltospirid *Depressigyra*, two specimens of the hyalogyrinid *Hyalogyrina*, 25 specimens of the neritimorph *Thalassonerita eocenica*, and three limpet specimens of two different species. Five species can be described as new: *Nuculana acutilineata* (Nuculanoidea), *Desbruyeresia belliatus* (Provannidae), *Provanna fortis* (Provannidae), *Orbitestella dioi* (Orbitestellidae), and *Leptochiton terryiverseni* (Polyplacophora). Other fossils recovered from this site are numerous serpulid tubes, echinoid spines, one brachiopod fragment and two neogastropods. Almost all species recovered belong to extant genera and the fauna has a modern character, but are different from species found in younger seeps in Washington State. This is the first record of an orbitestellid from an ancient cold seep deposit, the first fossil provannids from the Humptulips Formation, and the first fossil record of *Desbruyeresia* from North America.

Key words: Mollusca, Nuculoida, Caenogastropoda, deep sea, cold seeps, Eocene, Humptulips Formation, USA.

Frida Hybertsen [frida.hybertsen@nrm.se] and Steffen Kiel [steffen.kiel@nrm.se], Department of Palaeobiology, Swedish Museum of Natural History, Box 500 07, 104 05 Stockholm, Sweden.

Received 6 July 2018, accepted 11 October 2018, available online 29 November 2018.

Introduction

Cold-seep environments were first described in the 1980's from the Gulf of Mexico (Paull et al. 1984) and the associated fauna was found to be supported by methane and hydrogen sulfide, the oxidation of which is the main energy source in chemosynthesis-based ecosystems. These specific environments have been since found from all over the world at wide depth range along continental margins and host a diverse community of specialized biota. Methane and hydrogen sulfide present at cold-seeps provide energy to a chemosynthetically driven community of sulfur-reducing bacteria in symbiosis with other deep-sea organisms, for example tubeworms, mollusks, and crustaceans (e.g., Dubilier et al. 2008; Freytag et al. 2001; Schweitzer and Feldmann 2008). Increased pH values at seeps enhance carbonate precipitation and preservation of carbonaceous shells which gives seep communities a high abundance of fossils although their preservational condition varies. Seep carbonates are distinguishable from non-seep carbonates by their petrographical characteristics such as wavy laminations, clotted micrite and yellow calcite (cf. Peckmann et al. 2001) and to confirm seep origin stable carbon isotopes are analyzed. When microbial oxidation of methane occurs the carbonates become depleted in ^{13}C and thus seep carbonates yield negative δ^{13}C-values.

The fossil record of cold-seep communities has been growing ever since the discovery of these ecosystems, and although it is far from being complete, it provides a growing body of evidence for the evolution of these faunas. Modern and Cenozoic seep communities are dominated by chemosymbiotic bivalves, such as vesicomyids and bathymodiolins, but bivalves are less common in Palaeozoic to mid-Mesozoic seep deposits, which were thought to be mostly dominated by brachiopods (Campbell and Bottjer 1995; Little et al. 1997). This view was challenged in recent years by findings of the modiomorphid bivalve *Ataviaconcha* Hryniewicz, Jakubowicz, Belka, Dopieralska, and Kaim, 2016 in Silurian and Devonian seep deposits in Morocco (Hryniewicz et al. 2016; Jakubowicz et al. 2017), and by kalenterid and anomalodesmatan bivalves in Triassic seep deposits (Peckmann et al. 2011; Kiel et al. 2017; Kiel 2018), providing evidence that

https://doi.org/10.4202/app.00525.2018

bivalves and brachiopods co-existed in early seep-related ecosystems (Jakubowicz et al. 2017). Many of the bivalve and gastropod clades that are abundant and diverse at seeps today started appearing during the Jurassic and Cretaceous (Campbell and Bottjer 1995; Little and Vrijenhoek 2003; Kiel 2010), though most of the bivalves were infaunal. An exception to this is the large epifaunal to semi-infaunal kalenterid bivalve *Caspiconcha* Kelly in Kelly et al., 2000 that reached a world-wide distribution during the Early Cretaceous (Kiel and Peckmann 2008; Jenkins et al. 2013, 2018), but this genus declined in diversity and abundance towards the Late Cretaceous until its last occurrence in the Campanian (Jenkins et al. 2013, 2018). Its specific ecological niche was populated again by vesicomyid and bathymodiolin bivalves in middle Eocene (Amano and Kiel 2007; Kiel and Amano 2013) and these two clades have been dominating vent and seep sites until the present day. Cause and timing of this turnover and the rise of the modern fauna are the matter of debate. A hypothesis based on molecular age estimates suggests extinction and origination event around the Paleocene–Eocene Thermal Maximum (Vrijenhoek 2013), another hypothesis based on paleoecological pattern indicated marine sulfate concentrations as main driver (Kiel 2015). In any case, recently studied seep deposits from the Paleocene in the high Arctic revealed no vesicomyids or bathymodiolins, suggesting that the modern seep fauna did not originate before the Eocene (Hryniewicz et al. 2016).

The Cenozoic cold-seep deposits and associated faunas from deposits of western Washington State, USA have often been used to address taxonomic, geochemical and evolutionary inquiries due to their wide diversity and good preservation (e.g., Goedert and Squires 1990; Goedert et al. 2003; Kiel 2006; Kiel and Goedert 2006; Amano and Kiel 2007; Kiel and Goedert 2007; Schweitzer and Feldmann 2008). These deposits are most often found in the tectonic unit of the Coast Range terrane, which consists of early Eocene basalts at the base and middle Eocene to lower Miocene marine sediments on the top. The Humptulips Formation is the oldest seep-bearing rock formation in the Cenozoic accretionary prism of the Cascadia subduction zone, which forms the Olympic Mountains in Washington and is also exposed north and south of the Olympics, along the coast of British Columbia, Washington, and Oregon (Brandon and Vance 1992; Wells et al. 2014). Several of the oldest records of modern vent and seep-inhabiting clades have been reported from the Humptulips Formation, including the oldest record of the bathymodiolin mussel *Vulcanidas? goederti* Kiel and Amano, 2013 and the vesicomyid clam *"Archivesica"* cf. *tschudi* Olsson, 1931 (Amano and Kiel 2007; Kiel and Amano 2013), the thyasyrid *Maorithyas* (Hryniewicz et al. 2017), the neritid *Thalassonerita* (Squires and Goedert 1996a) and the galatheid crab *Shinkaia* (Schweitzer and Feldmann 2008). Many of these records have been used as calibration points in molecular phylogenetic studies of vent and seep clades (Kano et al. 2002; Lorion et al. 2013; Roterman et al. 2013; Vrijenhoek 2013; Valdés et al. 2013; Johnson et al. 2017), highlighting the importance of documenting the diversity of the seep fauna of the Humptulips Formation for understanding the origin and evolution of these unique ecosystems.

Institutional abbreviations.—LACIMP, Los Angeles County Museum, Invertebrate Paleontology, USA; NRM, Swedish Museum of Natural History, Stockholm, Sweden; UWBM, University of Washington, Burke Museum of Natural History and Culture, Seattle, USA.

Other abbreviations.—h, height; w, width.

Material and methods

The cold seep limestone boulder bearing the material reported here was found as float in the bed of the West Fork of the Satsop River (Fig. 1), approximately 240 m east and 200 m north of the southwest corner of Sec. 10, T. 21 N., R. 7 W., Grays Harbor County, Washington State, USA (map: Grisdale, Washington USGS quadrangle, 7.5 minute series, topo., 1990 provisional edition; coordinates: 47.317177°N, 123.565931°W). It is derived from the basal part of the

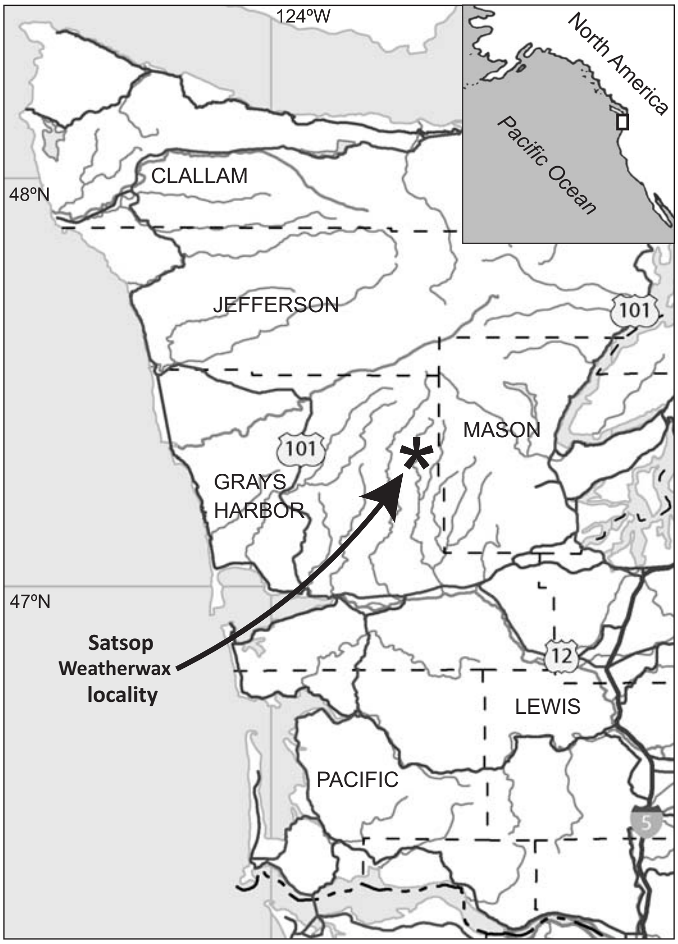


Fig. 1. Maps showing the location of the Satsop Weatherwax locality on the western coast of North America in the Grays Harbor County, Washington State, USA.

Humptulips Formation (possibly the basal boulder conglomerate) and is most likely of middle Eocene age (Prothero 2001), approximately 40–42.5 Ma, or late Lutetian to early Bartonian (Goedert et al. 2013). This seep deposit is here called the Satsop Weatherwax seep deposit, named for the Satsop River and Weatherwax Ridge, the nearest named topographical feature, about a mile to the northwest. This is UWBM locality number B8951.

The rock samples were hammered into ~10×10×10 cm blocks that were soaked in a 5–10% acetic acid solution. The dissolved rock fragments were washed, dried at 60°C and then examined using a binocular microscope. Some specimens were chosen for scanning electron microscopy; they were mounted and coated with gold and photographed using a Hitachi-4300 SEM at NRM. Macrofossils were coated with ammonium chloride and photographed using a Nikon D80 for capturing different angles and Cognisys Stackshot 3X stacking image system and the Zerene Stacker software, combining 20–25 pictures for each composite image.

Samples for carbon and oxygen stable isotope analyses were extracted from the counterparts of the thin sections using a hand-held microdrill, and carbonate powders were reacted with 100% phosphoric acid at 75°C using a Kiel III online carbonate preparation line connected to a ThermoFinnigan MAT 252 mass spectrometer. All values are reported in per mil relative to PDB by assigning a $\delta^{13}C$ value of +1.95‰ and a $\delta^{18}O$ value of -2.20‰ to NBS19. Reproducibility was checked by replicate analysis of laboratory standards and is better than ±0.05‰.

Results

Petrography and stable isotopes.—The carbonate is dominated by dark micrite, with occasional cavities lined by rim cement and sometimes filled with lighter micrite or calcite spar (Fig. 2). Silicified mollusks are abundant in patches and are also scattered throughout the deposit. The carbon isotope signature of the carbonates ranges from -43.5 to -38.0‰, with values of the micrite being slightly more negative than those of the rim cements; the corresponding oxygen isotope values range from -7.8 to -2.5‰ (Fig. 3).

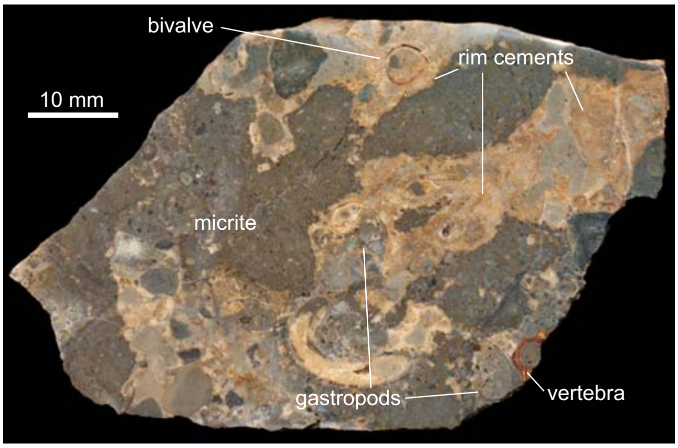


Fig. 2. Scanned polished slab of carbonate from the middle Eocene Satsop Weatherwax seep deposit showing its main petrographic features.

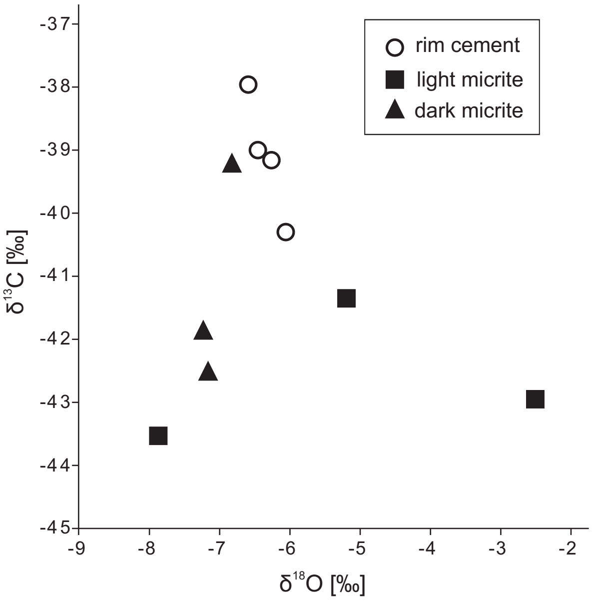


Fig. 3. Cross-plot of carbon and oxygen isotope data of the middle Eocene Satsop Weatherwax seep deposit; all values are given relative to the PDB standard.

Table 1. The fossils found at the Satsop Weatherwax seep deposit.

Phylum/Class	Species	Total number	Figure
Annelida	Serpulid tube fragments	5	11B, D
Bivalvia	Vesicomyid	5	5
	Thyasira sp.	8	4
	Nuculana acutilineata	>300	12
Brachiopoda	*Discinisca* sp.	1	11A
Echinoidea	Echinoid spines	2	11E
Gastropoda	*Depressigyra* sp.	5	7
	Thalassonerita eocenica	25	8
	Gastropod limpet 1	2	6A, B
	Gastropod limpet 2	1	6C
	Desbruyeresia belliatus	>230	13
	Provanna fortis	6	14
	Colus? sp.	2	9
	Hyalogyrina sp.	2	10
	Orbitestella dioi	2	15
Polyplacophora	*Leptochiton terryiverseni*	4	16

Fauna.—The Satsop Weatherwax seep deposit contains a variety of fossils including rare echinoderms and worm tubes, and abundant molluscs of the genera typically associated with deep-sea methane seeps. Their aragonitic shells have been silicified by the dissolution of calcium carbonate and precipitation of silica occurring at deep sea methane seeps and the preservation is mostly poor, however the great abundance makes this a lucrative site for seep fossils. Most taxa are briefly discussed below; new taxa are described in detail in the Systematic Paleontology section. The full list of speciesis shown in Table. 1.

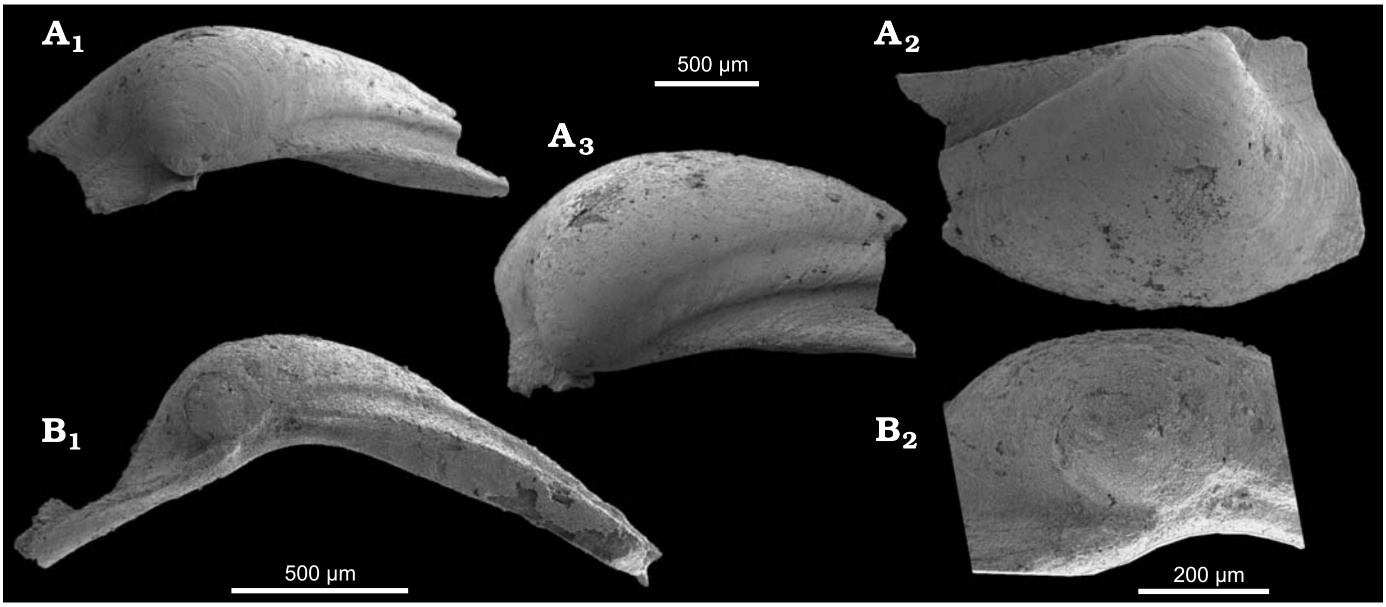


Fig. 4. Thyasirid bivalve *Thyasira* (*Thyasira*) sp. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185006; posterodorsal view of right valve hinge and umbo with two prominent ridges (A_1); lateral view (A_2); close-up on posterodorsal ridges (A_3). **B**. NRM Mo 185007 with edentulous hinge (B_1); close-up on prodissoconch (B_2).

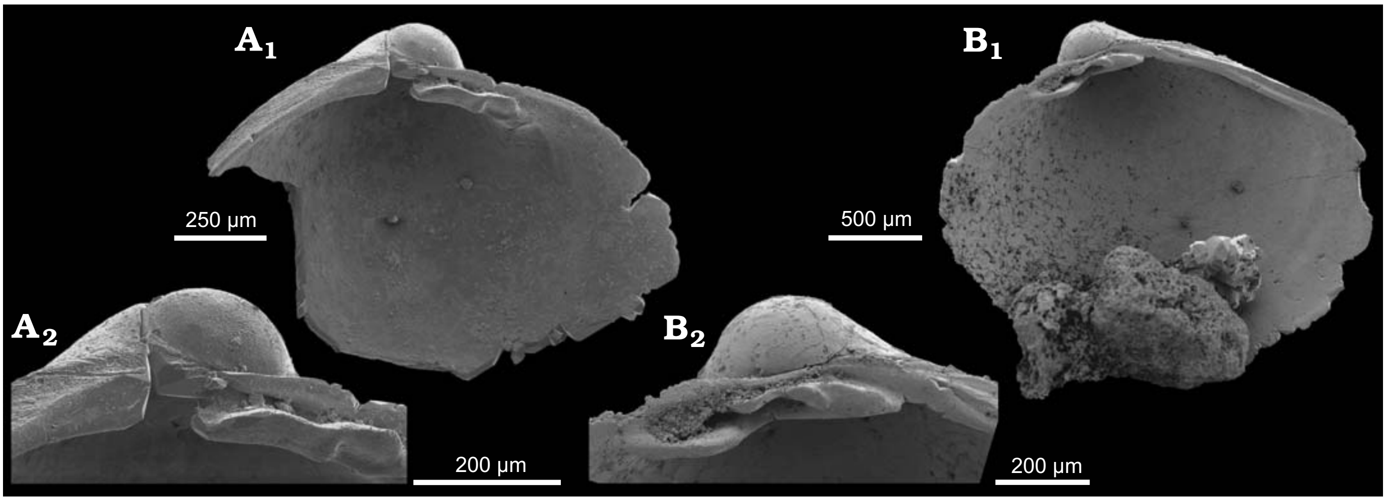


Fig. 5. Unidentified vesicomyid bivalve from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185002; left valve of young specimen showing hinge disrupted by a crack (A_1); close-up on hinge and dentition (A_2). **B**. NRM Mo 185005; right valve of young specimen showing hinge and ligament nymph (B_1); close-up on hinge and dentition (B_2).

Bivalves: These include a thyasirid, a vesicomyid, and a new species of *Nuculana* described below. The thyasirid is identified as *Thyasira* (*Thyasira*) sp. because the two available shell fragments show an edentulous hinge, a deep posterior sulcus and a deep submarginal sulcus separating a distinct auricle (Fig. 4). These features distinguish it also from *Maorithyas humptulipsensis* Hryniewicz, Amano, Jenkins, and Kiel, 2017, which is the only other thyasirid known from the Humptulips Formation (Hryniewicz et al. 2017). Five specimens of an unidentified vesicomyid (Fig. 5) were found, which show a typical vesicomyid hinge dentition but lack details of muscle scars and the pallial line. This makes them difficult to assign to any genus among the vesicomyids and also make their relation to the only other vesicomyid known from the Humptulips Formation—"*Archivesica*" cf. *tschudi* (Olsson, 1931) as shown in Amano and Kiel (2007) uncertain.

Gastropods: Among the gastropods recovered were two different limpet species, the peltospirid *Depressigyra* sp., *Thalassonerita eocenica,* buccinid neogastropods and the hyalogyrinid *Hyalogyrina* sp. Gastropod limpet 1 (Fig. 6A, B) is low, has a rounded-rectangular to oval outline, the apex is in a subcentral position and the sculpture appears to consist of indistinct concentric growth lines only. Most similar in outline and sculpture are *Cocculina rathbuni* and *C. ovata* illustrated by McLean (1987), and C. *messingi* McLean and Harasewych, 1995, and this species might hence belong to the Cocculiniformia. Gastropod limpet 2 (Fig. 6C) has a tall,

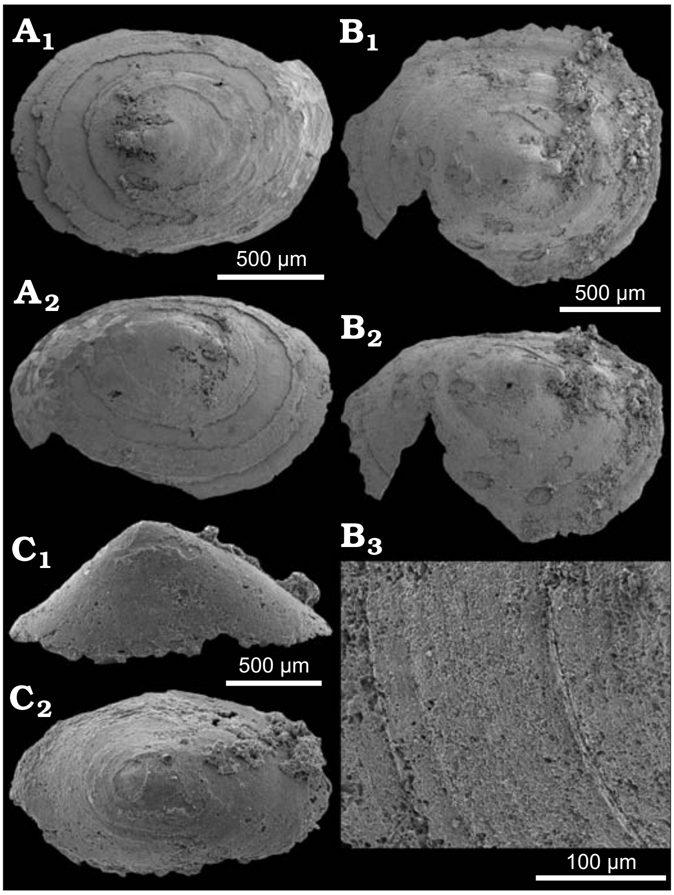


Fig. 6. Gastropod limpets from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**, **B**. Limpet 1, possibly belonging to the Cocculiniformia. **A**. NRM Mo 185019 slightly oval specimen in apical (A_1) and oblique (A_2) views. **B**. NRM Mo 185020 more rectangular specimen in apical (B_1) and oblique (B_2) views; close-up of sculpture (B_3). **C**. NRM Mo 185021, limpet 2 in lateral (C_1) and apical (C_2) views.

slender, elongate diamond-shaped shell with the apex displaced slightly to the anterior. The most similar extant species all belong to the pseudococculinid genus *Tentaoculus* (see McLean and Harasewych 1995 and Marshall 1986), but also *Pyropelta elongata* from the South China Sea (Zhang and Zhang 2017) is somewhat similar in shape. Both *Tentaoculus* and *Pyropelta* are members of the vetigastropod superfamily Lepetelloidea (see Kano et al. 2016), and therefore "Limpet 2" might belong here. Five poorly preserved specimens having a discoidal shell of two almost smooth whorls and a circular aperture are tentatively assigned to *Depressigyra* (Fig. 7). The Eocene to Oligocene *Depressigyra? statura* Goedert and Benham, 1999 from seep deposits in Washington State has been re-assigned to the genus *Retiskenea* Warén and Bouchet, 2001 based on protoconch morphology (Kiel 2006), and specimens reported as *Depressigyra*? sp. from Oligocene seep deposits in Washington State have a higher spire than the specimens reported here. The preservation of the 25 available specimens of *Thalassonerita eocenica* Squires and Goedert, 1996a (Neritimorpha; Fig. 8) is not ideal, but the specimens show several features characteristic for neritimorph gastropods, including the protoconch, an excavated shell interior, and also the shape of the aperture is typical for neritoids in general, and for *Thalassonerita* and the extant *Thalassonerita naticoidea* (Clarke, 1989) in particular. Unlike *Thalassonerita naticoidea*, *Thalassonerita eocenica* has spiral sculpture on the entire shell. Two specimens tentatively assigned to the buccinid neogastropod *Colus* (Fig. 9) are sculptured by blunt axial ribs that are strongest on the whorls' shoulder, crossed by broad and almost flat spiral cords with narrow interspaces. With this sculpture, the specimens resemble various species of the buccinid *Colus*, for example *C. kroeyeri* and *C. latericeus* from the deep North Atlantic Ocean have similar axial and spiral sculpture (Bouchet and Warén 1985). Its sculpture is also very similar to that of *Colus sekiuensis* Kiel and Goedert, 2007 from late Eocene to Oligocene from seeps and wood falls in western Washington State, USA (Kiel and Goedert 2007). The specimens are difficult to compare, though, because the known specimens of *Colus sekiuensis* are moderately sized adults

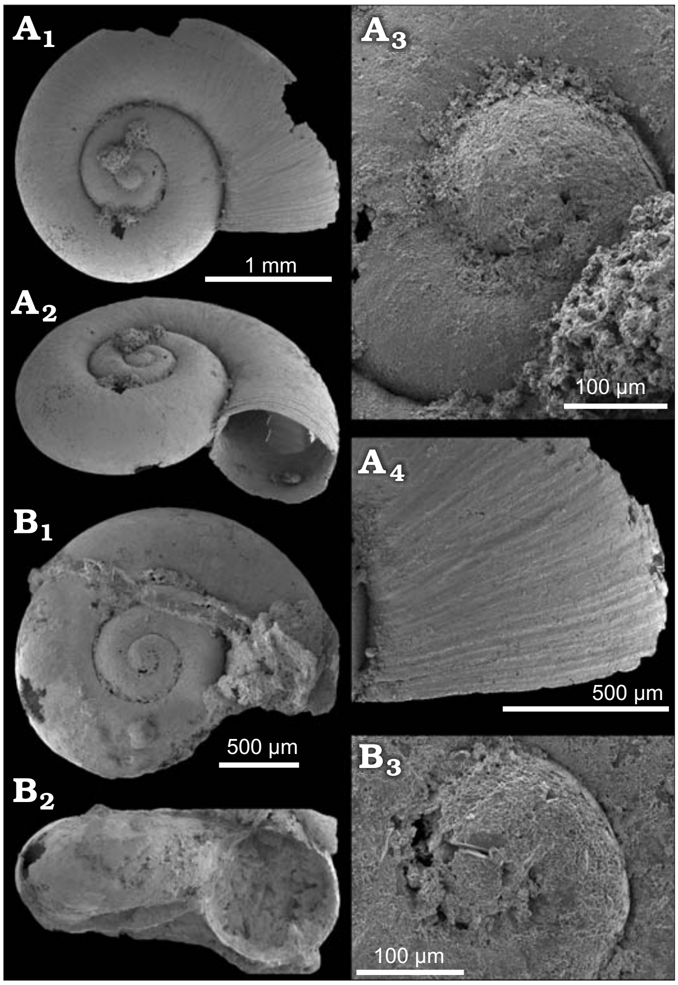


Fig. 7. The neomphalin gastropod *Depressigyra* sp. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185013; specimen with 2.5 whorls in apical (A_1) and oblique (A_2) views; close-up on protoconch (A_3); sculpture at the aperture (A_4). **B**. NRM Mo 185014, specimen with 2.25 whorls in apical view (B_1) and apertural view, showing its circular aperture (B_2), and close-up on protoconch (B_3).

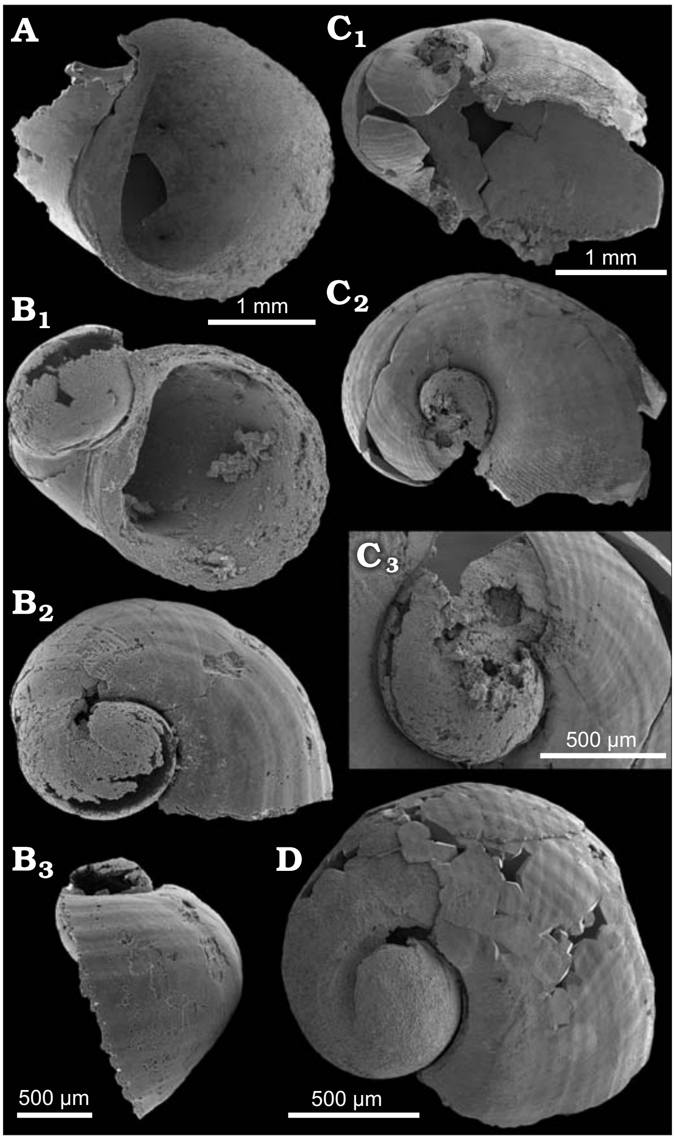


Fig. 8. The neritimorph gastropod *Thalassonerita eocenica* Squires and Goedert, 1996a from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185015, specimen with nicely preserved aperture. **B**. NRM Mo 185016, juvenile specimen; apertural view (B_1); apical view showing spiral sculpture and outline of protoconch (B_2); side view showing spiral sculpture (B_3). **C**. NRM Mo 185017, moderately sized specimen; oblique view showing dissolved interior of shell (C_1); apical view showing spiral and reticulate sculpture (C_2), note that the distinct, fine ribbing near the aperture is most likely the result of dissolution and not sculpture; close-up of protoconch (C_3). **D**. NRM Mo 185018, juvenile specimen in which the protoconch is preserved as internal mold, showing that its internal walls were dissolved; note also reticulate sculpture.

whereas we have only small juveniles available. Lastly, two specimens of the heterobranch *Hyalogyrina* sp. (Fig 10) are almost indistinguishable from shells of the extant *H. globularis* Warén and Bouchet, 2001 from vents of the Juan de Fuca Ridge, and from *H. amphorae* Warén, Carozza, and Rocchini 1996 from the Mediterranean Sea. The extant *H. umbellifera* Warén and Bouchet, 2001 from the Aleutian Trench is higher spired, and most other *Hyalogyrina* species, including the type species *H. glabra* Marshall, 1988 from sunken wood around New Zealand, are lower spired. A *Hyalogyrina* sp. previously reported from the Humptulips Formation (from LACMIP loc. 12385) has a higher whorl expansion rate than the present specimens (Kiel 2006: figs: 11-1, 11-2). In contrast to most *Hyalogyrina* species, the present one seems to lack the reticulate pattern on the initial part of the protoconch, but this might be a preservational issue.

Other taxa: These include the inarticulate brachiopod *Discinisca* sp. (Fig. 11A) showing concentric growth rings and a very fine reticulate pattern. The geographically and stratigraphically closest report is a "*Discinisca* sp. with fine radial sculpture" reported from the late middle Eocene Tejon Formation in southern California (Nilsen 1987: 90). Other similar Eocene species are *Discinisca insularis* from the Eocene London Clay (Muir-Wood 1939) and *Discinisca* sp. from the late Paleocene–early Eocene of New Zealand (Lee 1987). Numerous fragments of curved or coiled worm

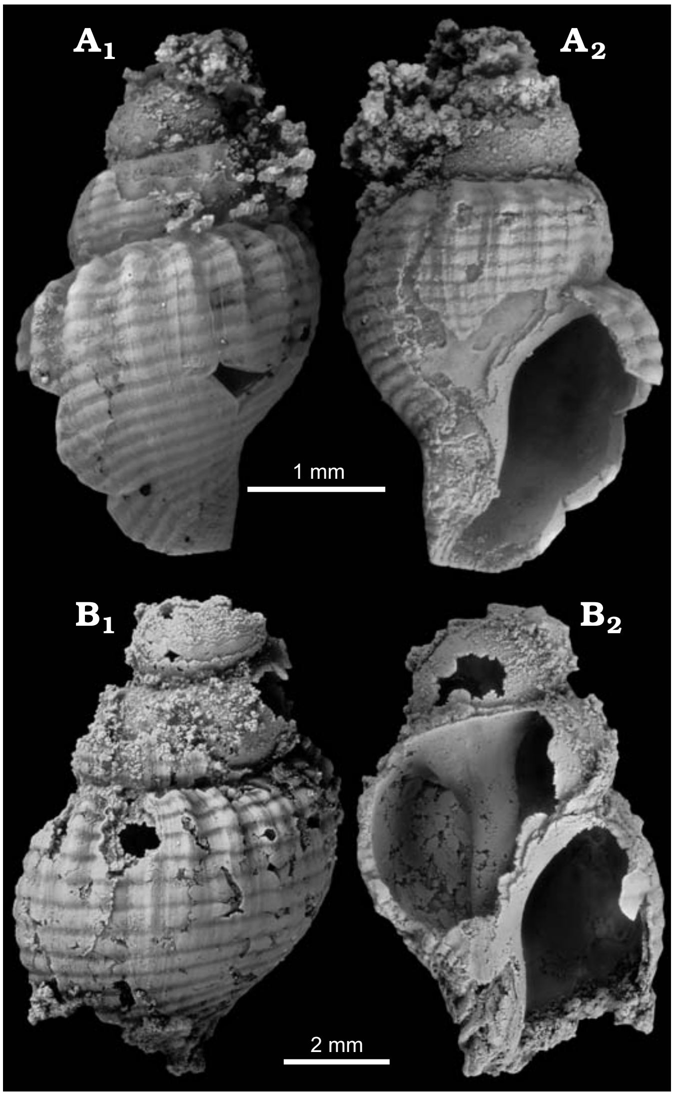


Fig. 9. The buccinid neogastropod *Colus*? sp. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185029, small specimen with well-preserved aperture and siphonal canal. **B**. NRM Mo 185030, larger specimen.

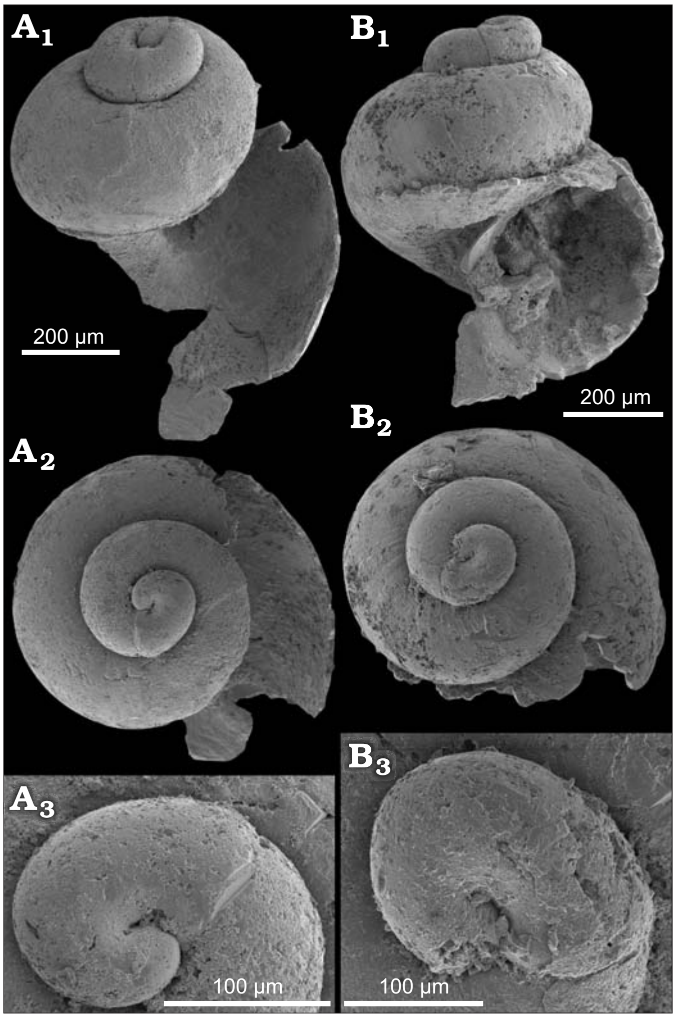


Fig. 10. The heterobranch gastropod *Hyalogyrina* sp. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185031; oblique (A_1) and apical (A_2) views; close-up of protoconch (A_3). **B**. NRM Mo 185032; apertural (B_1) and apical (B_2) views; close-up of protoconch (B_3).

tubes often bearing trumpet-like flanges and having a maximum diameter of 5 mm, most likely belong to the serpulids (Fig. 11D). Serpulid tubes are not uncommon at fossil seeps, where the worms were either free-living or attached to various hard substrates (Vinn et al. 2013). Two echinoid spines possibly belonging to the Atelostomata, one smooth, one with regular, low, blunt spines, were found (Fig. 11E), and a few fragmentary scaphopods (Fig. 11F).

Systematic palaeontology

Class Bivalvia Linneaus, 1758

Order Nuculoida Dall, 1889

Superfamily Nuculanoidea Adams and Adams, 1858

Genus *Nuculana* Link, 1807

Type species: *Nuculana pernula* (Müller, 1779); North Sea, Recent.

Nuculana acutilineata sp. nov.

Fig. 12.

Etymology: From Latin *acuti*, sharp and *lineae*, lines; in reference to the fine increments on the outer shell.

Type material: Holotype: NRM Mo 185009 consisting of a right valve with interior features. Paratypes: NRM Mo 185008, left valve; NRM Mo 185010, young articulated specimen; NRM Mo 185011, adult articulated specimen; NRM Mo 185012, right valve.

Type locality: The Satsop Weatherwax seep deposit, Washington State, USA.

Type horizon: Basal Humptulips Formation, middle Eocene.

Material.—More than 300 specimens at NRM, including type material, mostly single valves along with numerous shell fragments. Five specimens are deposited in the Burke Museum (UWBM 108856–60).

Diagnosis.—Elongated, oval and equivalve shell with slightly oval and wrinkled prodissoconch.

Description.—Prodissoconch slightly oval; sculptured by up to seven commarginal wrinkles; transition to dissoconch marked by thick prominent rib; single valve dimensions up to length 6 mm, height 2 mm and width 1.2 mm. Elongated oval dissoconch, equivalve; more than 25 fine commarginal growth lines; pointed beaks of fair size; umbo anterior (at 25% of total length); angular hinge line with taxodont teeth, at least 12 anterior and at least 18 posterior teeth found in three specimens (see Fig. 11B); anterior muscle scar pear-shaped, pallial line parallel to dorsal margin (see Fig. 11E).

Remarks.—*Nuculana acutilineata* does not have the elongated posterior end seen in the type taxon *Nuculana pernula* (Pliocene of North America and Japan to Recent). *Nuculana* sp. as described by Goedert and Campbell (1995) has thicker and fewer commarginal ribs on the shell than *N. acutilineata*. Both *Nuculana elenensis* (Sowerby, 1833) (Pleistocene of North America to Recent) and *Nuculana taphira* Dall, 1896 (Oligocene of northwestern North America to Recent) have fine and many commarginal growth lines similar to *N. acutilineata*, however, *N. acutilineata* has a more rounded posterior end and straighter anterodorsal margin than *N. elenensis*, and the posterior end on *N. taphira* is narrower than on *N. acutilineata*. The growth lines on *Nuculana minuta* Müller, 1776 (Pliocene of North America to Recent) are fine and about the same number as on *N. acutilineata*, but the prominent, pointy prodissoconch is different as well as the wide, marginal ridge defining the escutcheon on *N. minuta*. *N. acutilineata* does resemble the Recent *Nuculana grasslei* Allen 1993, possibly also associated with cold-seep carbonates of the Lincoln Creek Formation (Peckmann et al. 2002; Kiel 2006) which is characterized by a large, ornamented prodissoconch. *Nuculana grasslei* was re-assigned to "*Tindariopsis*" *grasslei* by Coan and Valentich-Scott (2012). The prodissoconch can be seen in our specimens with fairly strong wrinkles; however *N. acutilineata* has

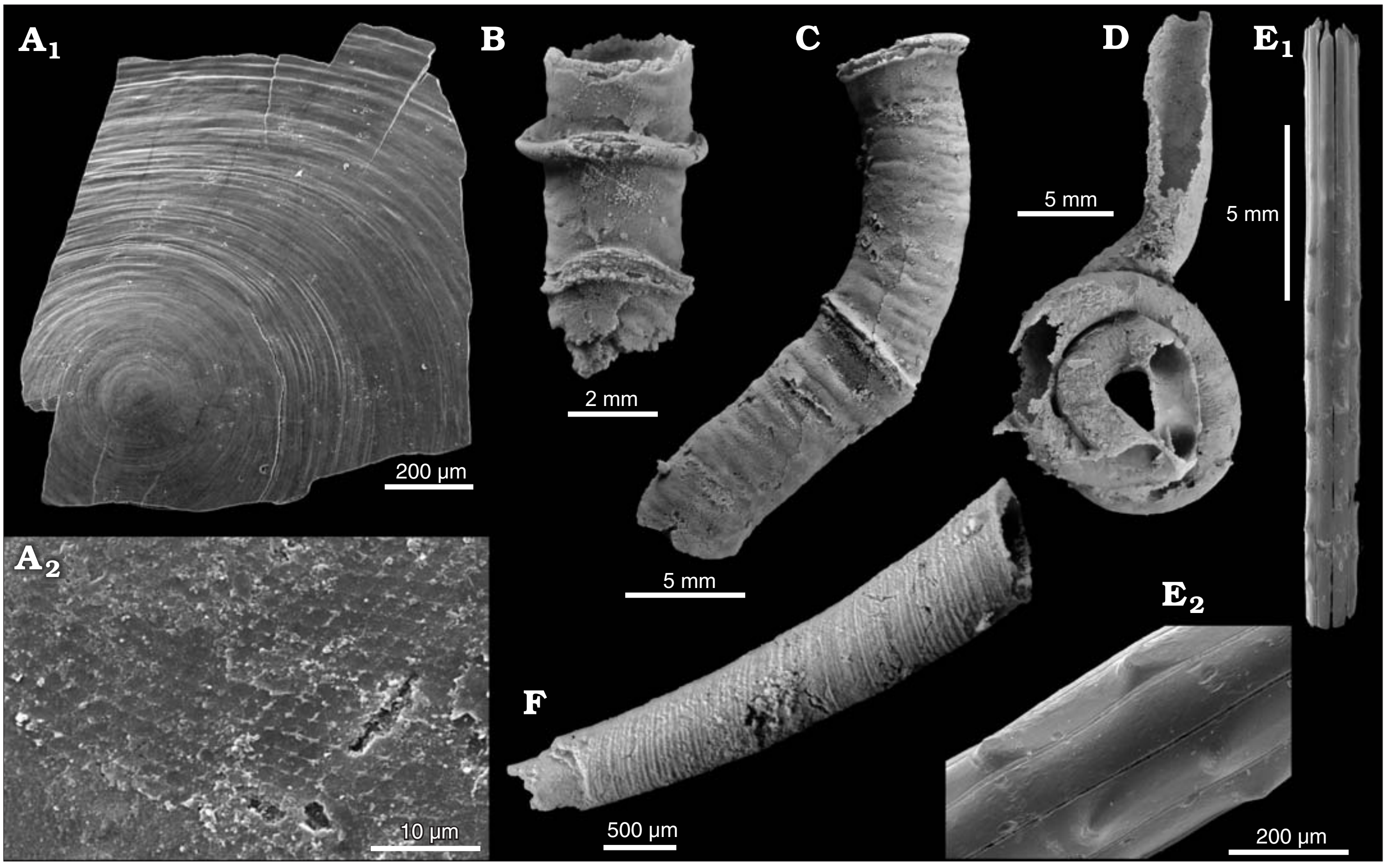


Fig. 11. Invertebrate fossils from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. The inarticulate brachiopod *Discinisca* sp. (NRM Br 149701); view on upper surface (A_1) and close-up of sculpture (A_2). **B**–**D**. Probable serpulid tubes; specimens with flanges (**B**, NRM An 3073; **C**, NRM An 3074); a partially coiled specimen lacking flanges (**D**, NRM An 3075). **E**. Spine possibly belonging to an atelostomatan echinoid (NRM Ec 34702), complete specimen (E_1) and detail of sculpture (E_2). **F**. Scaphopod with fine concentric ribs (NRM Mo 185038).

over 25 commarginal growth lines at a narrower distance than at least 20 growth lines on *T. grasslei*.

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

Class Gastropoda Cuvier, 1797

Subclass Caenogastropoda Cox, 1959

Superfamily Abyssochrysoidea, Tomlin 1927

Family Provannidae Warén and Ponder, 1991

Remarks.—Two new species described herein have regularly coiled shells with a high spire and rounded aperture, the shell structure is sculptured with axial ribs and spiral cords. Furthermore they have a tall protoconch with sharp axial ribs and fine spirals, which places them within the family Provannidae (Kaim et al. 2008).

Genus *Desbruyeresia* Warén and Bouchet, 1993

Type species: *Desbruyeresia spinosa* Warén and Bouchet, 1993; North Fiji Basin, Recent.

Desbruyeresia belliatus sp. nov.

Fig. 13.

Etymology: From Latin *belliatus*, plump; referring to the appearance of the shell.

Type material: Holotype: NRM Mo 185025 consisting of an almost fully intact shell with distinct sculpture. Paratypes: NRM Mo 185022–24; NRM Mo 185026, four specimens with distinct shell features.

Type locality: The Satsop Weatherwax seep deposit, Washington State, USA.

Type horizon: Basal Humptulips Formation, middle Eocene.

Material.—Type material and approximately 230 unnumbered specimens at NRM from the type locality. Three specimens are deposited in the Burke Museum (UWBM 108851–53).

Dimensions.—Holotype: 3.78 mm high and 1.54 mm wide.

Diagnosis.—Thick and sturdy high-spired shell with rounded whorls, strong axial sculpture forming nodes at axial-spiral intersections, apical angle approximately 45° reaching at least 5 mm in height and 3 mm in width.

Description.—Protoconch: up to 4 whorls; protoconch is decollated, silicified calcareous plug filling topmost whorl; maximum diameter 0.5 mm, minimum height 0.5 mm, sculptured by reticulate pattern, ~30 prominent, slightly ophistocline axial ribs, 14 weaker spiral ribs across whorl; aperture not thickened, teleoconch transition visible on fourth whorl.

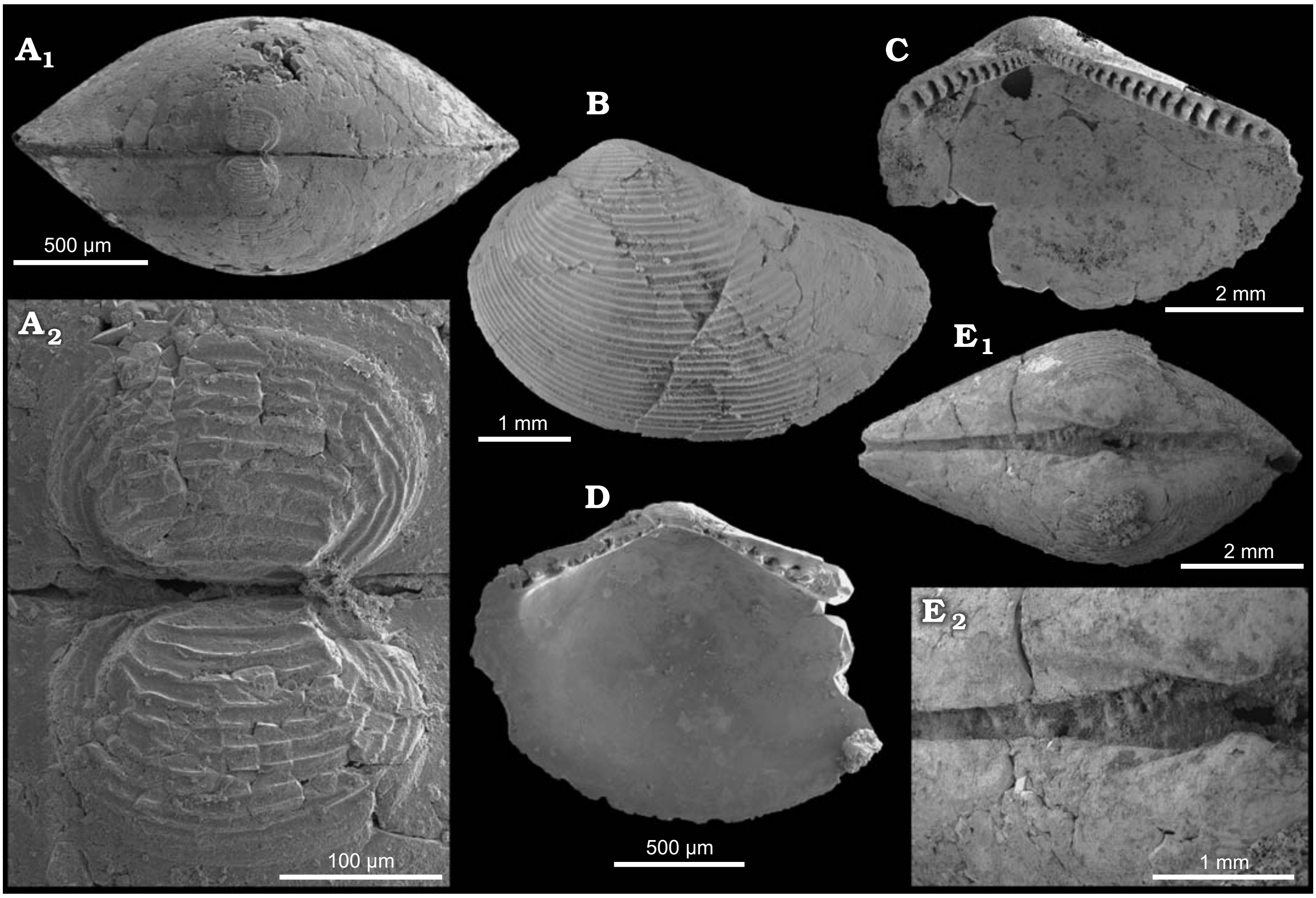


Fig. 12. The nuculanid bivalve *Nuculana acutilineata* sp. nov. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185010, almost complete young specimen with initial part intact (A_1); close-up on initial part (A_2). **B**. NRM Mo 185008, left valve in lateral view. **C**. NRM Mo 185009 (holotype), right valve in lateral view showing interior features. **D**. NRM Mo 185012, right valve specimen showing interior with hinge, faint muscle scar and pallial line. **E**. NRM Mo 185011; almost complete adult specimen (E_1); close-up of escutcheon and dentition (E_2).

Teleoconch: up to four whorls; sculptured by reticulate pattern, ~12 slightly opisthocline axial ribs, at least four spiral ribs, prominent nodes in oblique angle toward apex at intersections; adapical row of nodes on each whorl strong, successively weaker towards base of whorl; whorls slightly convex, incised sutures; basal margin marked by thick spiral cord; base has up to 5 spiral cords, downwards decreasing in strength; aperture oval with short, rounded siphonal notch; columella smooth; thin parietal callus.

Remarks.—Distinguishable from *Provanna* based on its more slender shell (Warén and Bouchet 1993) and the shell has “axial ribs, spiral cords, knobs and occasionally short spines” (Desbruyères et al. 2006), features that most of which are present in the species from Satsop Weatherwax, making it a likely member of *Desbruyeresia*. Type species *Desbruyeresia spinosa* Warén and Bouchet, 1993 is characterized by prominent spines forming at the crossings of the axial and spiral ribs on the whorls of the teleoconch, which can also be seen in *Desbruyeresia cancellata* Warén and Bouchet, 1993. No spines can be seen on *D. belliatus*, instead the shell structure more resembles that of *Desbruyeresia melanioides* Warén and Bouchet, 1993 with small nodes forming at the intersections of the ribs. *D. melanioides* have slightly curved axial ribs, but not as strongly ophistocline as seen on *D. belliatus*. The whorls of *Desbruyeresia marianaensis* have six or more spinal cords and there are no prominent nodes at the intersections of the apical and spinal cords as on *D. belliatus*. *Desbruyeresia antiqua* Bandel and Kiel, 2000 from a Late Cretaceous slump deposit in Spain is quite different from *Desbruyeresia belliatus* by having sharp axial ribs with a single, central row of spines. The species is based on a single specimen and its placement in *Desbruyeresia* has been questioned (Kaim et al. 2008), but without further material, these doubts can neither be confirmed nor rejected. The reticulate pattern on *Desbruyeresia chamorrensis* Chen, Ogura, and Okutani, 2016 is made up by three spiral cords whereas in *D. belliatus* there are at least four and *D. belliatus* is generally smaller. The reticulate pattern on the protoconch and the pointed nodes on the spire of *D. belliatus* closely resembles that of *Desbruyeresia kanajirisawensis* Kaim, Jenkins, and Warén, 2008 from the Cretaceous of Japan (Kaim et al. 2008) and the calcareous plug described in *D. kanajirisawensis* is also present in *D. belliatus*, however *D. kanajirisawensis* dis-

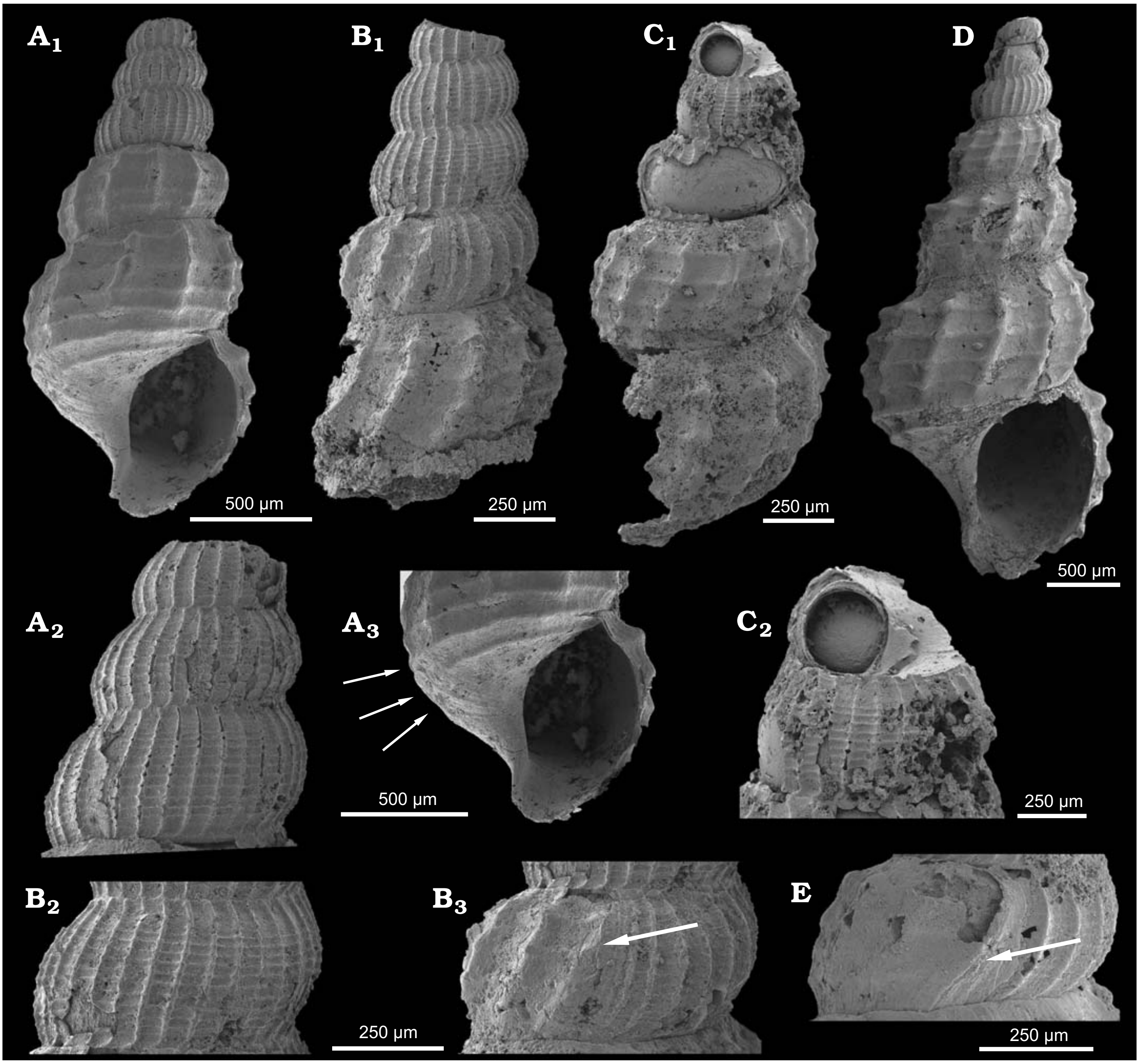


Fig. 13. The provannid gastropod *Desbruyeresia belliatus* sp. nov. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185022; almost complete specimen showing protoconch with 3 whorls (A_1); close-up on protoconch (A_2); spire with 2.5 whorls and the spire base with short siphonal notch, arrows pointing to spiral cords (A_3). **B**. NRM Mo 185023; protoconch with 3.5 whorls showing the protoconch-teleoconch transition (B_1); close-up of protoconch sculpture (B_2); close-up of protoconch-teleoconch transition (arrow) (B_3). **C**. NRM Mo 185024; decollated protoconch and calcareous plug (C_1); close-up on protoconch (C_2). **D**. NRM Mo 185025 (holotype) showing protoconch with 3 whorls and teleoconch with 3.5 whorls and an oval aperture. **E**. NRM Mo 185026, Close-up of specimen with protoconch-teleoconch transition (arrow).

plays six nodes making up a tight reticulate pattern whereas *D. belliatus* is of larger size and only has five nodes making up a wider pattern.

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

Genus *Provanna* Dall, 1918

Type species: *Trichotropis* (*Provanna*) *lomana* Dall, 1918; Magdalena Bay, USA, Recent.

Provanna fortis sp. nov.

Fig. 14.

Etymology: From Latin *fortis*, reinforced; referring to the appearance of the shell.

Type material: Holotype: NRM Mo 185028 with one intact whorl of protoconch and distinct nodes on the teleoconch. Paratype: NRM 185027 with distinct spiral cords on the base and aperture with siphonal notch.

Type locality: Satsop Weatherwax seep deposit, Washington State, USA.

Type horizon: Basal Humptulips Formation, middle Eocene.

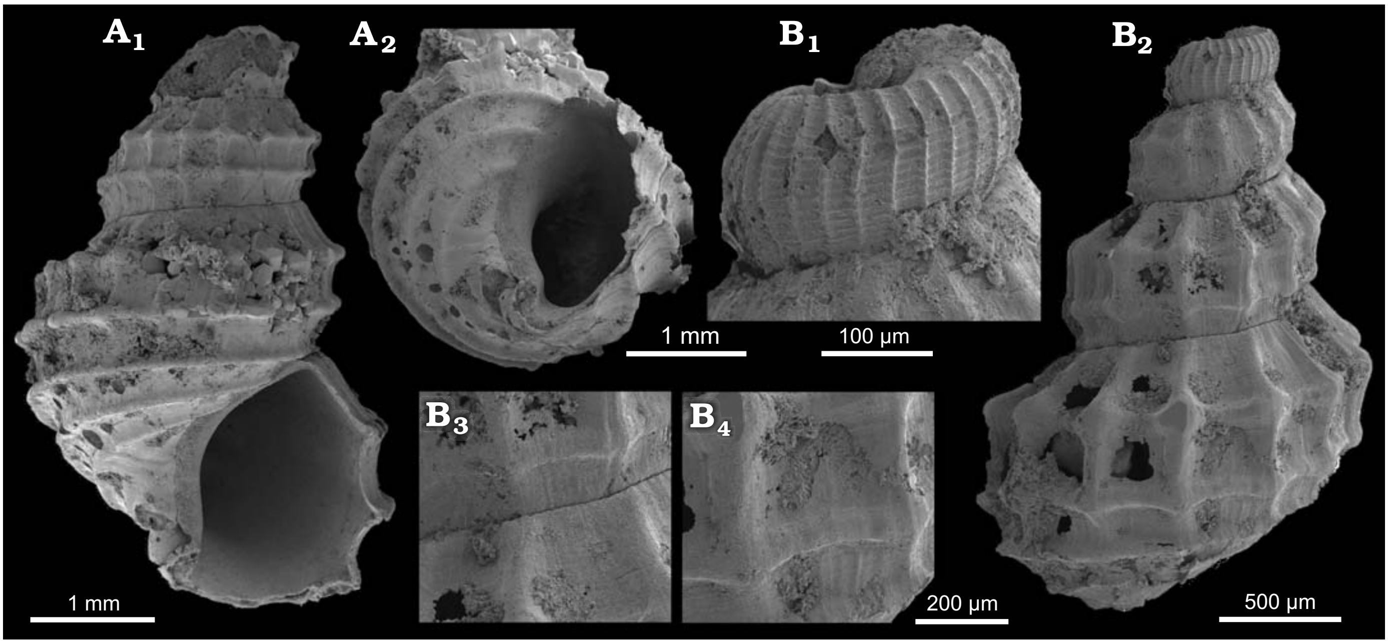


Fig. 14. The provannid gastropod *Provanna fortis* sp. nov. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185027, teleoconch with 2.5 whorls (A_1); basal view showing spiral cords and aperture with siphonal notch (A_2). **B**. NRM Mo 185028 (holotype); part of protoconch and teleoconch with 3 strongly angular whorls with spines (B_2); close-up on protoconch (B_1); spiral suture and fading axial rib (B_3); growth increments (B_4).

Material.—Type material and 5 other specimens. Two specimens deposited in the Burke Museum (UWBM 108854–55).

Dimensions.—Holotype is approximately 2.3 mm in height and 1.7 mm in width.

Diagnosis.—Sturdy, high-spired shell with prominent, angular whorls with spiny nodes at intersection of the axial and spiral ribs, apical angle of approximately 45° reaching at least 2.3 mm in height and 1.7 mm in width.

Description.—Protoconch: at least one whorl; maximum diameter 0.5 mm; sculptured by reticulate pattern, ~24 prominent, slightly sinuous axial ribs, ~16 fine spiral cords; transition to teleoconch unknown. Teleoconch: up to three whorls, sculptured by reticulate pattern, 14 orthocline axial ribs, two prominent and equally strong spiral ribs, blunt, short spines at intersections; spines more prominent on lower whorls; axial ribs start at the upper suture and fade below the lower spiral rib; irregularly spaced, fine spiral treads on whorl flank, fine axial growth increments; basal margin marked by distinct spiral rib, without spines; two spiral ribs of decreasing strength on base of the whorl; aperture broadly oval; short siphonal notch bordered by low ridge; columella smooth, thin callus on inner lip.

Remarks.—The strong angulation and spiny appearance of *Provanna fortis* can also be seen in other provannids such as for example *Provanna ios* Warén and Bouchet, 1986 and *Provanna muricata* Warén and Bouchet, 1986 from the East Pacific region (Warén and Bouchet 1986). Where the first one has one distinct spiral keel, *P. muricata* has developed two ribs on the spire which can also be seen in the *P. fortis* sp. nov. The protoconch of *P. muricata* was not recovered from the specimen described by Warén and Bouchet (1986) which aggravates a distinction between these two species. *Provanna antiqua* Squires, 1995 from Eocene and Oligocene seep deposits in western Washington shows a reticulate pattern but lacks spines and has rounded whorls instead of the prominent angulation seen on *P. fortis*. *Provanna alexi* Amano and Little, 2014 and *Provanna hirokoae* Amano and Little, 2014 from the middle Miocene of Japan (Amano and Little 2014) both lack the strong angulation seen on *P. fortis*. *Provanna marshalli* Saether, Little, and Campbell, 2010 from early to middle Miocene of New Zealand is similar to *P. antiqua*, also lacks strong angulation and has more spiral ribs on the whorls than *P. fortis*. *Provanna urahoroensis* Amano and Jenkins, 2013 reported from Oligocene deposits in Japan does not have the distinct reticulate pattern or anything resembling the spines on *P. fortis*. *Provanna nakagawensis* Kaim, Jenkins, and Hikida, 2009 from the Upper Cretaceous of Japan is sculptured by a distinct reticulate pattern, lacks the spines and does not have the shelf-structure made up by strong angulation as seen on the lowermost whorl of *P. fortis*. Kaim et al. (2008) also report *Provanna tappuensis* Kaim, Jenkins, and Warén, 2008 from the Cretaceous of Japan, which shows strong axial and spiral sculpture, although the spiral base has an increasing number of spiral ribs; up to five, beneath the spiral base where the *P. fortis* only has up to three spiral ribs in adult specimens and is therefore described as a new species.

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

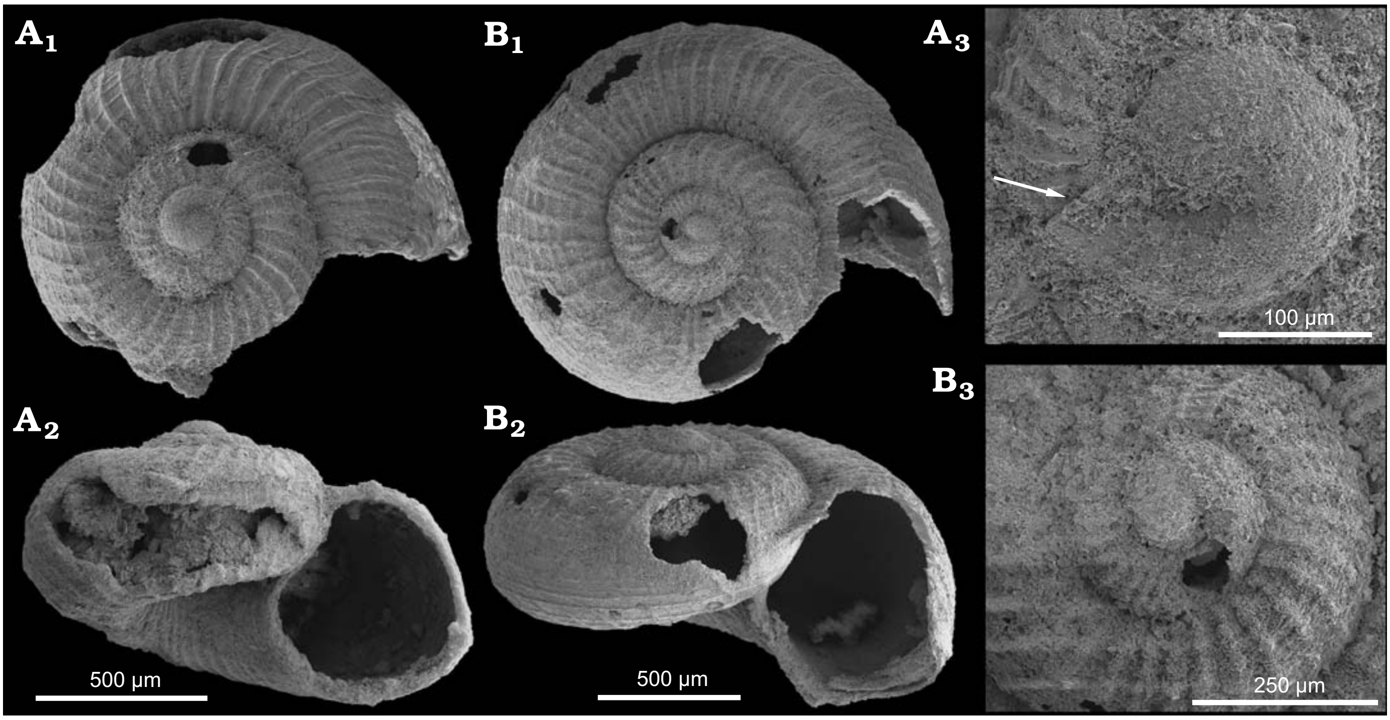


Fig. 15. The orbitestellid gastropod *Orbitestella dioi* sp. nov. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA. **A**. NRM Mo 185033; specimen with 2.25 whorls in apical view (A_1); apertural view showing a rounded aperture (A_2); close-up on .protoconch, arrow indicates protoconch-teleoconch transition (A_3). **B**. NRM Mo 185034 (holotype) with roughly 2 whorls in apical (B_1) and oblique (B_2) views; close-up on protoconch (B_3).

Subclass Heterobranchia Burmeister 1837

Superfamily Orbitestelloidea Iredale, 1917

Family Orbitestellidae Iredale, 1917

Genus *Orbitestella* Iredale, 1917

Type species: *Cyclostrema* (*Orbitestella*) *bastowi* Gatliff, 1906; Western Port Bay, Australia, Recent.

Orbitestella dioi sp. nov.

Fig. 15.

Etymology: Named after a musician Ronnie James Dio (1942–2010).

Type material: Holotype: NRM Mo 185034 with two mostly intact whorls with defined sculpture. Paratype: NRM Mo 185033 with elevated spire and intact protoconch.

Type locality: The Satsop Weatherwax seep deposit, Washington State, USA.

Type horizon: Basal Humptulips Formation, middle Eocene.

Material.—Type material only.

Dimensions.—Holotype: 0.75 mm in height and 1.5 mm in width.

Diagnosis.—Discoidal shell with wide umbilicus, a slightly elevated spire, a rounded-pentagonal whorl profile with an apical angle of 105°, with dimensions at least 0.75 mm in height and a diameter of 1.5 mm.

Description.—Protoconch diameter approximately 0.2 mm, terminates in thin varix, probably smooth. Teleoconch has three whorls with ~25 prominent, evenly spaced axial ribs, at least 12 weaker spiral ribs in reticulate pattern on spire; sinuous growth lines, ophistocline on shoulder, prosocyrt on periphery. Umbilicus deep, width around 1/3 of shell diameter, sculptured with strong axial ribs and finer spiral ribs; rounded aperture with sinuous peristome.

Remarks.—Shares the general shell sculpture and size dimensions with the Recent *Orbitestella patagonica* Simone and Zeyala, 2004 but has fewer axial ribs and less prominent spiral ribs. In *O. patagonica* the spiral ribs are more prominent than the axial ribs, which is the opposite from *O. dioi* sp. nov. A similar reticulate pattern on the outer surface of the shell is also found on the Recent *Orbitestella bermudezi* Aguayo and Borro, 1946 along with a sinuous peristome and rounded aperture, however in *O. bermudezi* the intersections between the axial ribs and spiral cords form pointed nodules and the aperture is subtriangular, which differs from *O. dioi* sp. nov. The prominent vertical ribs on the whorls of *Orbitestella granulata* Lozouet, 1998, from the Oligocene of France (Lozouet 1998) are coarser than on *O. dioi* and the former is also missing a reticulate ornamentation. *Orbitestella palaiopacifica* Squires and Goedert, 1996b from the Eocene of the Crescent Formation, North America lacks the spiral ribs on the whorls as well as an elevated spire. The organization of the growth lines on *O. dioi* follows the same pattern as the Recent *Lurifax goederti* (Kiel, 2006) but lacks the strong angulation and prominent spiral cords. *Lurifax* was placed within the family Orbitestellidae (Warén and Bouchet, 2001). Recently Lauridsen et al. (2014) reported an orbitestellid from the Faxe Formation, Denmark that is larger than our specimens and with a distinctively larger protoconch. *O. dioi* shares many features with the orbitestellids compared above, however, it does not fit to any already described species and therefore we describe this new species.

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

Class Polyplacophora Gray, 1821
Order Lepidopleurida Thiele, 1909
Family Leptochitonidae Dall, 1889
Genus *Leptochiton* Gray, 1847

Type species: *Leptochiton asellus* (Gmelin, 1791); Telemark, Norway, Recent.

Leptochiton terryiverseni sp. nov.

Fig. 16.

Etymology: For Terry Iversen, who helped in collecting this material.

Type material: Holotype: NRM Mo 185036 consisting of three articulated intermediate valves. Paratypes: NRM Mo 185035, NRM Mo 185037, UWBM 108862, three isolated intermediate valves.

Type locality: The Satsop Weatherwax seep deposit, Washington State, USA.

Type horizon: Basal Humptulips Formation, middle Eocene.

Material.—The type material only.

Dimensions.—The largest specimen is 6.7 mm wide and 3 mm long.

Diagnosis.—*Leptochiton* having moderately elevated, round-backed valves with angulation, lacking jugal area of the tegmentum; pleural area with fine, subparallel rows of granules; lateral areas with irregular but distinct commarginal ridges.

Description.—Elongate-oval outline, valves of moderate elevation (h/w ~0.33), round-backed with an angulation, side slopes slightly convex; jugal area of tegmentum absent, pleural area sculptured by fine granules arranged in subparallel, longitudinal rows; sculpture changes at abruptly at diagonal ridges, granules on lateral areas stronger, arranged somewhat irregularly near the middle, but forming distinct commarginal ridges toward the lateral margins. The apophyses are separated by a broad jugal sinus.

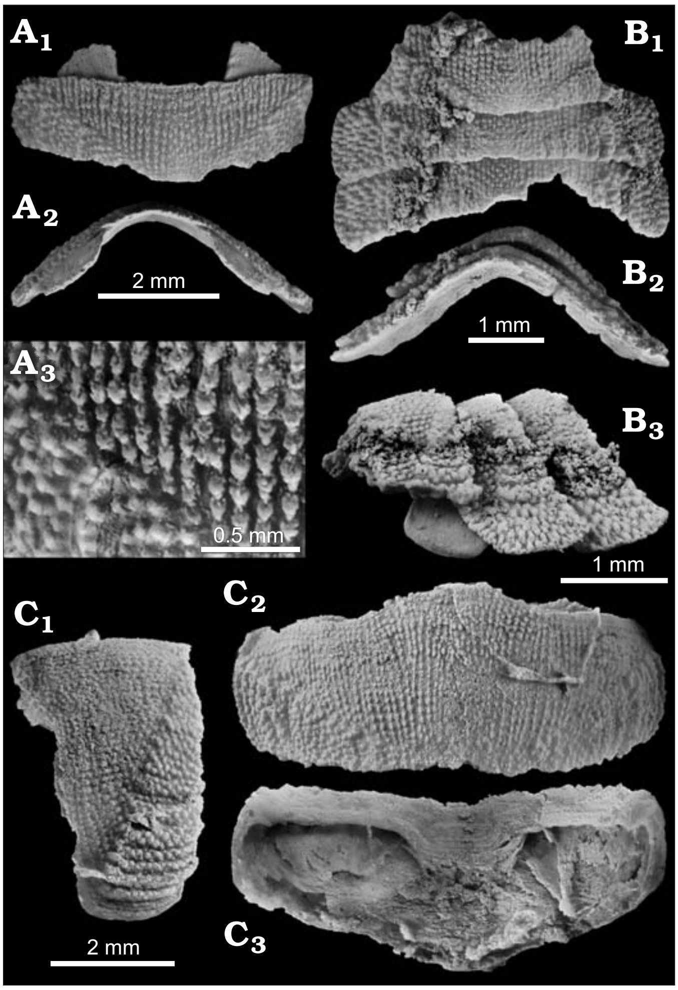


Fig. 16. The lepidopleurid polyplacophoran *Leptochiton terryiverseni* sp. nov. from the middle Eocene Satsop Weatherwax seep deposit, Washington State, USA; all specimens represented by intermediate valves. **A**. NRM Mo 185035 (paratype); isolated valve with preserved apophyses in dorsal (A_1) and anterior (A_2) views; close-up of sculpture (A_3). **B**. NRM Mo 185036 (holotype), three articulated valves in dorsal (B_1), posterior (B_2), and lateral (B_3) views. **C**. NRM Mo 185037 (paratype); isolated valve showing the broad jugal sinus in lateral (C_1), dorsal (C_2), and ventral (C_3) views.

Remarks.—Squires and Goedert (1995) reported the extant *Leptochiton alveolus* (Lovén, 1846) from Eocene–Oligocene seep deposits in western Washington. Their illustrated specimens are from the Oligocene Lincoln Creek Formation and show a quincunx arrangement of granules on the tegmentum, which is different from the longitudinal arrangement of granules in *L. terryiverseni* n. sp. Also mentioned by Squires and Goedert (1995) were two valves of *L. alveolus* from seep deposit LACMIP loc. 12385 in the Humptulips Formation, but they did not illustrate them. Hence it remains unclear whether they belong to the species from the Lincoln Creek Formation or to *L. terryiverseni*. Extant species similar to *L. terryiverseni* include *L. micropustulosus* Kaas, 1984 from ca. 1135 to 1236 m depth on the Barbados Prism (Kaas 1984) and *Leptochiton sarsi* Kaas, 1981 from Scandinavian waters (Kaas 1981; Dell'Angelo et al. 2009), both of which differ from *L. terryiverseni* by the granulae on the tegmentum gently curving around the diagonal ridges, in contrast to the sharp change in granulae arrangement in L. *terryiverseni*. *Leptochiton tenuidontus* Saito and Okutani, 1990 from a hydrothermal vent site in 1395 m depth in the Okinawa Trough (Saito and Okutani 1990) shows a similar arrangement of the granulae, but its valves are less elevated than those of L. *terryiverseni*.

Among fossil species of *Leptochiton*, an Eocene specimen from Seymour Island, Antarctic Peninsula (López Cabrera and Olivero 2011), has the longitudinally arranged granule distributed over a much broader area on the tegmentum than in *L. terryiverseni*, and laterally the granulae tend to radiate outward. In the late Eocene *Leptochiton* sp. reported from the Lincoln Creek Formation in western

Washington (Dell'Angelo et al. 2011), the granulae on the anterior-lateral sides tend to radiate outward rather than being longitudinally arranged, as in *L. terryiverseni*. Recently, that specimen was hesitantly assigned to the extant *L. cascadiensis* (Sigwart and Chen 2017). The wood-associated *Leptochiton lignatilis* Bertolaso, Garilli, Parrinello, Sosso, and Dell'Angelo, 2015 from the middle to late Miocene of northern Italy has irregularly arranged granulae (Bertolaso et al. 2015) in contrast to the longitudinal arrangement in *L. terryiverseni*. Early Oligocene specimens from France assigned to *Leptochiton* cf. *algesirensis* (Capellini, 1859) have outwardly directed beaded riblets rather than longitudinally arranged granules (Cherns and Schwabe 2017). Finally, the Paleocene *Leptochiton faxensis* Sigwart, Andersen, and Schnetler 2007 has a quincunx arrangement of granules.

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

Discussion

Petrography and stable isotopes.—The petrography and stable isotope signature of the Satsop River seep deposit is similar to that of other seep deposits in western Washington (Peckmann et al. 2002; Goedert et al. 2003; Kuechler et al. 2012). The negative carbon isotope signature (with values as low as -43.5‰) clearly indicate that carbonate was related to the oxidation of biogenic methane (Peckmann and Thiel 2004). Also the silicification of the fossils is most likely related to methane oxidation: the anaerobic oxidation (AOM) of methane causes an increase in alkalinity, thereby inducing the dissolution of silica skeletons; once AOM ceases the pH drops again, leading to dissolution of aragonite minerals (including shells) on the one hand, and to silica precipitation on the other (Kuechler et al. 2012; Smrzka et al. 2015; Miyajima et al. 2016). Virtually all silicified fossils reported here are mollusks that originally had an aragonitic shell (Carter 1990; Vinn et al. 2008); fossils of taxa with calcitic shells, such as ostracods, are notably absent.

Fauna.—Most mollusk species from the Satsop Weatherwax seep deposit belong to Recent genera, highlighting the modern character of this ca. 40–42.5 million year old seep fauna. Furthermore, although not assignable to any known genus, the Satsop Weatherwax seep deposit contains vesicomyid bivalves, a clade that is unknown from seeps of older age, including the two known Paleocene examples (Schwartz et al. 2003; Hryniewicz et al. 2016). There are nine described fossil species of Provannidae and they are mostly reported from hydrocarbon seep deposits, with a few exceptions of reports from other chemosynthetic environments such as wood falls or whale falls. Provannid gastropods have not been reported from the Humptulips Formation before. They precede *Provanna antiqua* Squires, 1995 from late Eocene Bear River deposit and are therefore the two geochronologically oldest provannid gastropods associated with deep-sea methane seeps in North America. Only six specimens of *P. fortis* were recovered, but all specimens show distinctive characters such as the prominent angulation of the spire and spiny whorls. In contrast, the more than 230 specimens of *D. belliatus* show rounded, spineless whorls and a protoconch with a calcareous plug as distinguishing features. This gives enough support to the notion that these fossils represent two new species and further extends the fossil record of the family Provannidae. *Orbitestella dioi* differs from the previously described *Orbitestella palaiopacifica* Squires and Goedert, 1996b from the Eocene of western Washington, because it has an elevated spire and spiral ribs crossing the axial ribs in a reticulate pattern. It is the first representative of the genus *Orbitestella* reported from the Humptulips Formation and Recent relatives have not been reported in association with present day vents and seeps. Our new material of *Thalassonerita eocenica* confirms that this species is a neritoid and does not belong to the vetigastropod genus *Sahlingia*, as suggested earlier (Warén and Bouchet 2001). This indicates that Phenacolepidae, the family which includes the extant *Thalassonerita naticoidea*, colonized deep-water habitats at latest in the middle Eocene (Kano et al. 2002). Their phylogenetic relationships to geologically older neritids from Cretaceous and Jurassic methane seeps (Kiel and Peckmann 2008; Kiel et al. 2010) remains unclear due to the poor preservation of those Mesozoic examples.

Whereas several gastropod and bivalve groups, including thyasirids, colloniids, and provannids, colonize both seeps and wood falls (Warén and Bouchet 2001; Gaudron et al. 2010) and are known to have been doing so since the Late Cretaceous (Kaim et al. 2008, 2014; Kiel et al. 2009), this seems to be different among polyplacophorans. Chitons have been reported from Middle Jurassic wood-fall sites (Kaim 2011; Sirenko 2013) and even a Carboniferous origin for the colonization of wood falls has been suggested (Sirenko 2004). But although Cretaceous seeps are increasingly well sampled (Campbell and Bottjer 1993, Campbell et al. 2002; Kaim et al. 2009, 2013; Kiel et al. 2013, 2017; Agirrezabala et al. 2013; Little et al. 2015; Hryniewicz et al. 2015; Meehan and Landman 2016), there is not a single report of seep-inhabiting chitons from this period. Whether this (still) reflects a sampling bias or if the adaptation of lepidopleuran chitons to seeps is a post-Paleocene affair, as in many other invertebrate groups (Vrijenhoek 2013; Kiel 2015), remains to be tested.

Conclusions

Overall the Satsop Weatherwax seep fauna has a modern character. But compared to the well-known late Eocene to Oligocene seep faunas in Washington, most taxa of the middle Eocene Satsop Weatherwax seep deposit, and the Humptulips Formation in general, are different species. Examples include the two new provannids *Desbruyeresia* *belliatus* and *Provanna fortis*, the new *Leptochiton terryiverseni*, and *Thalassonerita eocenica*, all of which are not known from the younger seeps. Previously published examples include the bathymodiolin *Vulcanidas goederti* Kiel and Amano, 2013 and *Maorithyas humptulipsensis* Hryniewicz, Amano, Jenkins, and Kiel, 2017, both from seep deposits in the Humptulips Formation. In these cases, not even the genera are known from the younger seep sites in western Washington, only members of their respective families and subfamilies (Kiel and Amano 2013; Hryniewicz et al. 2017).

Acknowledgments

First of all we sincerely thank James L. Goedert (Wauna, USA) and Terry Iversen (Bremerton, USA) for collecting this material and making it available to us. We greatly appreciate the continued cooperation of Green Diamond Resources Company and staff (Shelton, USA) for allowing access to the locality on their timberlands. We also thank Boris Sirenko (Russian Academy of Sciences, St. Petersburg, Russia) and Bruno Dell'Angelo (Genova, Italy) for advice on *Leptochiton*, Frank Wiese (University of Göttingen, Germany) for help with echinoid spine identification, and Anders Warén (Swedish Museum of Natural History, Stockholm, Sweden) for discussions on gastropods. We also thank the reviewers Kazutaka Amano (Joetsu University of Education, Japan) and Krzysztof Hryniewicz (Institute of Paleobiology PAS, Warsaw, Poland) for their constructive input to improve the manuscript. Financial support was provided by Vetenskapsrådet through grant 2016-03920 to SK.

References

Adams, H. and Adams, A. 1853–58. *The Genera of Recent Mollusca Arranged According to Their Organization*. 1: vi–xl + 484 pp.; 2: 661 pp. 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.

Aguayo, C.G. and Borro, P. 1946. Nuevos moluscos del terciario superior de Cuba. *Revista de la Sociedad Malacologica "Carlos de la Torre"* 4: 9–12.

Allen, J.A. 1993. A new deep-water hydrothermal species of *Nuculana* (Bivalvia: Protobranchia) from the Guaymas Basin. *Malacologica* 35: 141–151.

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 vesicomyid bivalves from the North Pacific region. *The Veliger* 49: 270–293.

Amano, K. and Little, C.T.S. 2014. Miocene abyssochrysoid gastropod *Provanna* from Japanese seep and whale–fall sites. *Acta Palaeontologica Polonica* 59: 163–172.

Bandel, K. and Kiel, S. 2000. Earliest known (Campanian) members of the Vermetidae, Provannidae and Litiopidae (Cerithioidea, Gastropoda), and a discussion of their possible relationships. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 84: 209–218.

Bertolaso, L., Garilli, V., Parrinello, D., Sosso, M., and dell'Angelo, B. 2015. A new Miocene deep-sea chiton and early evidence for Teredinidae-sustained wood-fall communities. *Palaeontologica Electronica* 18.2.41A: 1–15.

Bouchet, P. and Warén, A. 1985. Revision of the northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). *Bolletino Malacologico* Supplemento 1: 123–296.

Brandon, M.T. and Vance, J.A. 1992. Tectonic evolution of the Cenozoic Olympic subduction complex, Washington State, as deduced from fission track ages for detrital zircons. *American Journal of Science* 292: 565–636.

Burmeister, H. 1837. *Handbuch der Naturgeschichte, Vol. 2, Zoologie*. i–xii + 369–858 pp. Enslin, Berlin.

Campbell, K.A. and Bottjer, D.J. 1993. Fossil cold seeps. *National Geographic Research & Exploration* 9: 326–343.

Campbell, K.A. and Bottjer, D.J. 1995. Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold seep environments. *Geology* 23, 321–324.

Campbell, K.A., Farmer, J.D., and Des Marais, D. 2002. Ancient hydrocarbon seeps from the Mesozoic convergent margin of California: carbonate geochemistry, fluids and palaeoenvironments. *Geofluids* 2: 63–94.

Capellini, J. 1859. Catalogue des oscabrions se la Méditerranée. *Journal de Conchyliologie* 7: 320–328.

Carter, J.G. 1990. *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends Volume I*. 832 pp. Van Nostrand Reinhold, New York.

Chen, C., Ogura, T., Hirayama, H., Watanabe, H. K., Miyazaki, J., and Okutani, T. 2016. First seep-dwelling *Desbruyeresia* (Gastropoda: Abyssochrysoidea) species discovered from a serpentinite-hosted seep in the Southeastern Mariana Forearc. *Molluscan Research* 36: 277–284.

Cherns, L. and Schwabe, E. 2017. Eocene and Oligocene chitons (Polyplacophora) from the Paris and Hampshire Basins. *Historical Biology* [published online 10.1080/08912963.2017.1387545].

Clarke, A.H. 1989. New mollusks from undersea oil seep sites off Louisiana. *Malacology Data Net* 2: 122–134.

Coan, E.V. and Valentich-Scott, P. 2012. *Bivalve Seashells of Tropical West America. Marine Bivalve Mollusks from Baja California to Northern Peru*. 764 pp. Santa Barbara Museum of Natural History, Santa Barbara.

Cox, L.R. 1959. Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London* 33: 239–261.

Cuvier, G. 1797. 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 sociéte d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts, 1795* 2: 433–449.

Dall, W.H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer "Blake" XXIX. Report on the Mollusca. Part 2, Gastropoda and Scaphopoda. *Bulletin of the Museum of Comparative Zoology, Harvard University* 18: 1–492.

Dall, W.H. 1896. Note on *Leda caleata* Hinds. *The Nautilus* 10: 70.

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.

Dell'Angelo, B., Bonfitto, A., and Taviani, M. 2011. Chitons (Polyplacophora) from Paleogene strata in western Washington State, U.S.A. *Journal of Paleontology* 85: 936–954.

Dell'Angelo, B., Giusti, F., Paolini, P., Sosso, M., and Bonfitto, A. 2009. New data on Polyplacophora from Tuscan Archipelago. I. *Leptochiton sarsi* Kaas, 1981 and *Leptochiton pepezamorai* Carmona Zalvide, Urgorri & Garcia, 2004, two species new to the Mediterranean Sea. *Italian Journal of Zoology* 76: 76–82.

Desbruyères, D., Segonzac, M., and Bright, M. 2006. Handbook of deep-sea hydrothermal vent fauna. Second completely revised version. *Denisia* 18: 1–544.

Dubilier, N., Bergin, C., and Lott, C. 2008. Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nature Reviews Microbiology* 6: 725–740.

Freytag, J.K., Girguis, P.R., Bergquist, D.C., Andras, J.P., Childress, J.J., and Fisher, C.R. 2001. A paradox resolved: sulfide acquisition by roots of seep tubeworms sustains net chemoautotrophy. *Proceedings of the National Academy of Sciences* 98: 13408–13413.

Gatliff, J.H. 1906. On some Victorian marine Mollusca, new species and others little-known. *Proceedings of the Royal Society of Victoria, New Series* 19: 1–4.

Gaudron, S.M., Pradillon, F., Pailleret, M., Duperron, S., Le Bris, N., and Gaill, F. 2010. Colonization of organic substrates deployed in deep-sea reducing habitats by symbiotic species and associated fauna. *Marine Environmental Research* 70: 1–12.

Gmelin, J.F. 1791. Vermes. *In*: J.F. Gmelin (ed.), *Caroli a Linnaei Systema Naturae per Regna Tria Naturae, Ed. 13. Tome 1, Vol. 6*, 3021–3910. G.E. Beer, Lipsiae.

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 Squires, R.L. 1990. Eocene deep-sea communities in localized limestones formed by subduction-related methane seeps, southwestern Washington. *Geology* 18: 1182–1185.

Goedert, J.L., Peckmann, J., Benham, S.R., and Janssen, A.W. 2013. First record of the Eocene pteropod *Heliconoides nitens* (Gastropoda: Thecosomata: Limacinidae) from the Pacific Basin. *Proceedings of the Biological Society of Washington* 126: 72–82.

Goedert, J.L., Thiel, V., Schmale, O., Rau, W.W., Michaelis, W., and Peckmann, J. 2003. The late Eocene "Whiskey Creek" methane-seep deposit (western Washington State) Part I: Geology, palaeontology, and molecular geobiology. *Facies* 48: 223–240.

Gray, J.E. 1821. A natural arrangement of Mollusca, according to their internal structure. *The London Medical Repository* 15: 229–239.

Gray, J.E. 1847. A list of the genera of Recent Mollusca, their synonyma and types. *Proceedings of the Zoological Record of London* 15: 129–219.

Hryniewicz, K., Amano, K., Jenkins, R.G., and Kiel, S. 2017. Thyasyrid bivalves from Cretaceous and Paleogene cold seeps. *Acta Paleontologica Polonica* 62: 705–728.

Hryniewicz, K., Bitner, M.A., Durska, E., Hagström, J., Hjálmarsdóttir, H.R., Jenkins, R.G, Little, C.T.S., Miyajima, Y., Nakrem, H.A., and Kaim, A. 2016. Paleocene methane seep and wood-fall marine environments from Spitsbergen, Svalbard. *Palaeogeography, Palaeoclimatology, Palaeoecology* 462: 41–56.

Hryniewicz, K., Hagström, J., Hammer, Ø., Kaim, A., Little, C.T.S., and Nakrem, H.A. 2015. Late Jurassic–Early Cretaceous hydrocarbon seep boulders from Novaya Zemlya and their faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 436: 231–244.

Hryniewicz, K., Jakubowicz, M., Belka, Z., Dopieralska, J., and Kaim, A. 2016. New bivalves from a Middle Devonian methane seep in Morocco: the oldest record of repetitive shell morphologies among some seep bivalve molluscs. *Journal of Systematic Palaeontology* 15: 19–41.

Iredale, T. 1917. More molluscan name-changes, generic and specific. *Proceedings of the Malacological Society of London* 12: 322–330.

Jakubowicz, M., Hryniewicz, K., and Belka, Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports* 7: 14292.

Jenkins R.G., Kaim A., Hikida Y., and Kiel S. 2018. 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 vesicomyid clams. *Systematics and Biodiversity* 15: 346–360

Kaas, P. 1981. Scandinavian species of *Leptochiton* Gray, 1847 (Mollusca, Polyplacophora). *Sarsia* 66: 217–229.

Kaas, P. 1984. A new species of *Leptochiton* Gray, 1847 (Mollusca: Polyplacophora) from the South Barbados accretionary prism. *Zoologische Mededelingen Leiden* 68: 45–47.

Kaim, A. 2011. Non-actualistic wood-fall associations from Middle Jurassic of Poland. *Lethaia* 44: 109–124.

Kaim A., Hryniewicz K., Little C.T.S., and Nakrem H.A. 2017. Gastropods from the Late Jurassic–Early Cretaceous seep deposits in Spitsbergen, Svalbard. *Zootaxa* 4329: 351–374.

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: Abyssochrysoidea). *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.

Kaim, A., Skupien, P., and Jenkins, R.G. 2013. A new Lower Cretaceous hydrocarbon seep locality from Czech Carpathians and its fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 390: 42–51.

Kano, Y., Chiba, S., and Kase, T. 2002. Major adaptive radiation in neritopsine gastropods estimated from 28S rRNA sequences and fossil records. *Proceedings of the Royal Society B* 269: 2457–2465.

Kano, Y., Takano, T., Schwabe, E., and Warén, A. 2016. Phylogenetic position and systematics of the wood-associate limpet genus *Caymanabyssia* and implications for ecological radiation into deep-sea organic substrates by lepetelloid gastropods. *Marine Ecology* 37: 1116–1130.

Kelly, S.R.A., Blanc, E., Price, S.P., and Whitham, 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*, 227–246. Geological Society, London.

Kiel, S. 2006. New records and species of molluscs from Tertiary cold-Seep carbonates in Washington State, USA. *Journal of Paleontology* 80: 121–137.

Kiel, S. 2010. The fossil record of vent and seep mollusks. *In*: S. Kiel (ed.), *The Vent and Seep Biota. Aspects from Microbes to Ecosystems*, 255–277. Springer, Dordrecht.

Kiel, S. 2015. Did shifting seawater sulfate concentrations drive the evolution of deep-sea vent and seep ecosystems? *Proceedings of the Royal Society B* 282: 20142908.

Kiel, S. 2018. Three new bivalve genera from Triassic hydrocarbon seep deposits in southern Turkey. *Acta Palaeontologica Polonica* 63. 221–234.

Kiel, S., Amano, K., Hikida, Y., and Jenkins, R.G. 2009. Wood-fall associations from Late Cretaceous deep-water sediments of Hokkaido, Japan. *Lethaia* 42: 74–82.

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. 2006. 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 Peckmann, J. 2008. Paleoecology and evolutionary significance of an Early Cretaceous *Peregrinella*-dominated hydrocarbon-seep deposit on the Crimean Peninsula. *Palaios* 23: 751–759.

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., Krystyn, L., Demirtaş, F., Koşun, E., and Peckmann, J. 2017. Late Triassic mollusk-dominated hydrocarbon-seep deposits from Turkey. *Geology* 45: 751–754.

Kuechler, R.R., Birgel, D., Kiel, S., Freiwald, A., Goedert, J.L., Thiel, V., and Peckmann, J. 2012. Miocene methane-derived carbonates from southwestern Washington, USA, and a model for silicification at seeps. *Lethaia* 45: 259–273.

Lauridsen, B.W. and Schnetler, K.I. 2014. A catalogue of Danian gastropods from the Baunekule facies, Faxe Formation, Denmark. *Geological Survey of Denmark and Greenland Bulletin* 32: 1–117.

Lee, D.E. 1987. Cenozoic and recent inarticulate brachiopods of New Zealand: *Discinisca*, *Pelagodiscus* and *Neocrania*. *Journal of the Royal Society of New Zealand* 17: 49–72.

Link, D.H.F. 1807–1808. *Beschreibung der Naturalien-Sammlung der Universität zu Rostock*. Part 1: 160 pp., Part 2: 30 pp., Part 3: 38 pp. Adlers Erben, Rostock.

Linnaeus, C. 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. 824 pp. Salvius, Stockholm.

Little, C.T.S. and Vrijenhoek, R.C. 2003. Are hydrothermal vent animals living fossils? *Trends in Ecology and Evolution* 18: 582–588.

Little, C.T.S., Herrington, R.J., Maslennikov, V.V., Morris, N.J., and Zaykov, V.V. 1997. Silurian hydrothermal vent community from the southern Urals, Russia. *Nature* 385: 146–148.

Little, C.T.S., Birgel, D., Boyce, A.J., Crame, J.A., Francis, J.E., Kiel, S., Peckmann, J., Pirrie, D., Rollinson, G.K., and Witts, J.D. 2015. Late Cretaceous (Maastrichtian) shallow water hydrocarbon seeps from Snow Hill and Seymour Islands, James Ross Basin, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 418: 213–228.

López Cabrera, M.I. and Olivero, E.B. 2011. An Eocene articulated Polyplacophora (Mollusca) from the La Meseta Formation, Antarctica and the stratigraphy of the fossil-bearing strata. *Journal of Paleontology* 85: 970–976.

Lorion, J., Kiel, S., Faure, B.M., Masaru, K., Ho, S.Y.W., Marshall, B.A., Tsuchida, S., Miyazaki, J.-I., and Fujiwara, Y. 2013. Adaptive radiation of chemosymbiotic deep-sea mussels. *Proceedings of the Royal Society B* 280: 20131243.

Lovén, S.L. 1846. Molluscorum litora Scandinaviae occidentalia habitantium. *Öfversigt af Kongliga Vetenskaps Akademiens Förhandlingar* 3: 134–160, 182–204.

Lozouet, P. 1998. Nouvelles espèces de Gastéropodes (Mollusca: Gastropoda) de l'Oligocène et du Miocène inférieur de l'Aquitaine (sud-ouest de la France). *Cossmanniana* 5: 61–102.

Marshall, B.A. 1988. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History* 22: 949–1004.

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.

McLean, J.H. 1987. Taxonomic descriptions of cocculinid limpets (Mollusca, Archaeogastropoda): two new species and three rediscovered species. *Zoologica Scripta* 16: 325–333.

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.

Meehan, K.C. and Landman, N. 2016. Faunal associations in cold-methane seep deposits from the Upper Cretaceous Pierre Shale, South Dakota. *Palaios* 31: 291–301.

Miyajima, Y., Watanabe, Y., Yanagisawa, Y., Amano, K., Hasegawa, T., and Shimobayashi, N. 2016. A late Miocene methane seep deposit bearing methane-trapping silica minerals at Joetsu, central Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 455: 1–15.

Muir-Wood, H.M. 1939. Four species of *Discinisca* (Brachiopoda) from the Eocene of the Hampshire Basin. *Proceedings of the Geologists' Association* 50: 149–158.

Müller, O.F. 1776. *Zoologiae Danicae prodromus, seu animalium Daniae et Norvegiae indigenarum characters, nomina, et synonyma imprimis popularium.* xxxii + 274 pp. Hallageriis, Havniae.

Müller, O.F. 1779. Zwoen wenig bekannten Muscheln, der Schinkenarche und der gerunzelten Mahlermuschel. *Gesellschaft Naturforschender Freunde zu Berlin, Beschäftigengen* 4: 55–59.

Nilsen, T. 1987. Stratigraphy and sedimentology of the Eocene Tejon Formation western Tehachapi and San Emigdio Mountains, California. *United States Geological Survey Professional Paper* 1268: 1–110.

Olsson, A.A. 1931. Contributions to the Tertiary Paleontology of Northern Peru: Part 4, The Peruvian Oligocene. *Bulletins of American Paleontology* 17: 97–264.

Paull, C.K., Hecker, B., Commeau, R., Freeman-Lynde, R.P., Neumann, C., Corso, W.P., Golubic, S., Hook, J.E., Sikes, E., and Curray, J. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science* 226: 965–967.

Peckmann, J. and Thiel, V. 2004. Carbon cycling at ancient methane-seeps. *Chemical Geology* 205: 443–467.

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.

Peckmann, J., Kiel, S., Sandy, M. R., Taylor, D. G., and Goedert, J. L. 2011. Mass occurrences of the brachiopod *Halorella* in Late Triassic methane-seep deposits, Eastern Oregon. *Journal of Geology* 119: 207–220.

Peckmann, J., Reimer, A., Luth, U., Luth, C., Hansen, B.T., Heinicke, C., Hoefs, J., and Reitner, J. 2001. Methane-derived carbonates and authigenic pyrite from the northwestern Black Sea. *Marine Geology* 177: 129–150.

Prothero, D.R. 2001. Chronostratigraphic calibrations of the Pacific Coast Cenozoic: a summary. *The Pacific Section SEPM Special Publication* 91: 377–394.

Roterman, C.N., Copley, J.T., Linse, K., Tyler, P.A., and Rogers, A.D. 2013. The biogeography of the yeti crabs (Kiwaidae) with notes on the phylogeny of the Chirostyloidea (Decapoda: Anomura). *Proceedings of the Royal Society B* 280: 20130718.

Saether, K.P., Little, C.T.S., and Campbell, K.A. 2010. A new fossil provannid gastropod from Miocene hydrocarbon seep deposits, East Coast Basin, North Island, New Zealand. *Acta Palaeontologica Polonica* 55: 507–517.

Saito, H. and Okutani, T. 1990. Two new chitons (Mollusca: Polyplacophora) from a hydrothermal vent site of the Iheya Small Ridge, Okinawa Trough, east China Sea. *Venus* 49: 165–179.

Schwartz, H., Sample, J.C., Weberling, K.D., Minisini, D., and Moore, J.C. 2003. An ancient linked fluid migration system: cold-seep deposits and sandstone intrusions in the Panoche Hills, California, USA. *Geo-Marine Letters* 23: 340–350.

Schweitzer, C.E. and Feldmann, R.M. 2008. New Eocene hydrocarbon seep decapod crustacean (Anomura: Galatheidae: Shinkaiinae) and its paleobiology. *Journal of Paleontology* 82: 1021–1029.

Sigwart, J.D. and Chen, C. 2017. Life history, patchy distribution, and patchy taxonomy in a shallow-water invertebrate (Mollusca: Polyplacophora: Lepidopleurida). *Marine Biodiversity* [published online, 10.1007/s12526-017-0688-1].

Sigwart, J.D., Andersen, S.B., and Schnetler, K.I. 2007. First record of a chiton from the Palaeocene of Denmark (Polyplacophora: Leptochitonidae) and its phylogenetic affinities. *Journal of Systematic Palaeontology* 5: 123–132.

Sigwart, J.D., Schwabe, E., Saito, H., Samadi, S., and Giribet, G. 2010. Evolution in the deep sea: a combined analysis of the earliest diverging living chitons (Mollusca: Polyplacophora: Lepidopleurida). *Invertebrate Systematics* 24: 560–572.

Simone, L.R.L. and Zelaya, D.G. 2004. A new *Orbitestella* (Gastropoda:

Heterobranchia: Orbitestellidae) from Tierra del Fuego, Argentina. *The Nautilus* 118: 160–166.

Sirenko, B.I. 2004. The ancient origin and persistence of chitons (Mollusca, Polyplacophora) that live and feed on deep submerged land plant matter (xylophages). *Bolletino Malacologico* Supplemento 5: 105–110.

Sirenko, B.I. 2013. Four new species and one new genus of Jurassic chitons (Mollusca: Polyplacophora: Lepidopleurida) from the Middle Russian Sea. *Proceedings of the Zoological Institute RAS* 317: 30–44.

Smrzka, D., Kraemer, S.M., Zwicker, J., Birgel, D., Fischer, D., Kasten, S., Goedert, J.L., and Peckmann, J. 2015. Constraining silica diagenesis in methane-seep deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology* 420: 13–26.

Sowerby, G.B., I 1833. [… the collection of shells formed by Mr. Cuming on the western coast of South America][Archidae]. *Proceedings of the Zoological Society of London* 1 (for 1833): 16–22.

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. 1995. An extant species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene and Oligocene cold-seep limestones, Olympic Peninsula, Washington. *The Veliger* 38: 47–53.

Squires, R.L. and Goedert, J.L. 1996a. A new species of *Thalassonerita*? (Gastropoda: Neritidae?) from a Middle Eocene cold-seep carbonate in the Humptulips Formation, Western Washington. *The Veliger* 39: 270–272.

Squires, R.L. and Goedert, J. L. 1996b. New species of small to minute gastropods of Early Eocene Age from the Crescent Formation, Black Hills, Southwest Washington. *The Veliger 39*, 226–240.

Thiele, J. 1909. Revision des Systems der Chitonen. *Zoologica Stuttgart* 22: 1–132.

Tomlin, J.R.l.B. 1927. Reports on the marine Mollusca in the collections of the South African Museum II. Families Abyssochrysidae, Oocorythidae, Haliotidae, Tonnidae. *Annals of the South African Museum* 25: 77–83.

Valdés, F., Sellanes, J., and D'Elía, G. 2013. Phylogenetic position of vesicomyid clams from a methane seep off central Chile (~36°S) with a molecular timescale for the diversification of the Vesicomyidae. *Zoological Studies* 51: 1154–1164.

Vinn, O., Kupriyanova, E.K., and Kiel, S. 2013. Serpulids (Annelida, Polychaeta) at Cretaceous to modern hydrocarbon seeps: ecologic and evolutionary patterns. *Palaeogeography, Palaeoclimatology, Palaeoecology* 390: 35–41.

Vinn, O., Mutvei, H., Ten Hove, H.A., and Kirsimäe, K. 2008. Ultrastructure and mineral composition of serpulid tubes (Polychaeta, Annelida). *Zoological Journal of the Linnean Society* 154: 633–650.

Vrijenhoek, R.C. 2013. On the instability and evolutionary age of deep-sea chemosynthetic communities. *Deep-Sea Research II* 92: 189–200.

Warén, A., and Bouchet, P. 1986. Four new species of *Provanna* Dall (Prosobranchia, Cerithiacea?) form East Pacific hydrothermal sites. *Zoologica Scripta* 15: 157–164.

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 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.

Warén, A., Carozza, F., and Rocchini, R. 1996. Description of two new species of Hyalogyrinidae (Gastropoda, Heterobranchia) from the Mediterranean. *Bolletino Malacologico* 32: 57–66.

Wells, R.E., Bukry, D., Friedman, R.M., Pyle, D., Duncan, R., Haeussler, P., and Wooden, J.L. 2014. Geologic history of Siletzia, a large igneous province in the Oregon and Washington Coast Range: Correlation to the geomagnetic polarity time scale and implications for a long-lived Yellowstone hotspot. *Geosphere* 10: 692–719.

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.

Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

Fossiliferous methane-seep deposits from the Cenozoic Talara Basin in northern Peru

STEFFEN KIEL, ALI J. ALTAMIRANO, DANIEL BIRGEL, HELEN K. COXALL, FRIDA HYBERTSEN AND JÖRN PECKMANN

LETHAIA

Kiel, S., Altamirano, A. J., Birgel, D., Coxall, H. K., Hybertsen, F., & Peckmann, J. 2019: Fossiliferous methane-seep deposits from the Cenozoic Talara Basin in northern Peru. *Lethaia*, https://doi.org/10.1111/let.12349.

Thirteen fossiliferous limestone deposits from Cenozoic strata in the Talara Basin in northern Peru are identified as ancient methane-seep deposits. Planktonic foraminifera and the existing stratigraphical framework of the Talara Basin indicate an early Oligocene, or possibly late Eocene, age of these deposits. They are found in three distinct areas – Belén, Cerro La Salina and Cerros El Pelado – and differ in their petrography, stable isotope signatures, and lipid biomarker and macrofaunal contents. At Belén, the carbon stable isotope signature of the carbonate and the abundance of *n*-alkanes indicates the possibility of oil seepage in addition to methane seepage; for Belén and Cerro La Salina the high abundance of the biomarker crocetane indicates a dominance of anaerobic methane-oxidizing archaea of the ANME-2 group, whereas the rather small combined crocetane/phytane peak of a Cerros El Pelado limestone agrees with mixed ANME-1/ANME-2 input. The macrofauna consists mainly of molluscs; the Cerro La Salina sites include mostly infaunal thyasirid and lucinid bivalves and only few vesicomyid bivalves; gastropods include *Provanna antiqua*, the limpet *Pyropelta* and several vetigastropods. The Belén site is dominated by the elongate vesicomyid bivalve *Pleurophopsis lithophagoides*. The most common bivalve at the Cerros El Pelado sites is an undetermined, possible vesicomyid, and a smooth provannid gastropod. Biogeographically the faunas are most similar to those of the northwestern United States, as indicated by two joint species; similarities on the genus level (*Conchocele*, *Lucinoma*, *Pleurophopsis*, *Provanna*, *Colus*) exist also with Japan and the Caribbean region. □ *Deep sea, Oligocene, seep fauna, South America, Thyasiridae, Vesicomyidae.*

Steffen Kiel✉ [steffen.kiel@nrm.se], and Frida Hybertsen [frida.hybertsen@nrm.se], Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, 10405 Stockholm, Sweden; Ali J. Altamirano [eraexcusa@yahoo.es], Departamento de Paleontología de Vertebrados, Museo de Historia Natural e, Universidad Nacional Mayor San Marcos (MUSM), Av. Arenales 1256, Lima, Peru ; Daniel Birgel [daniel.birgel@uni-hamburg.de], Jörn Peckmann [joern.peckmann@uni-hamburg.de], Institute for Geology, Center for Earth System Research and Sustainability, Universität Hamburg, 20146 Hamburg, Germany; Helen K. Coxall [helen.coxall@geo.su.se], Department of Geological Sciences, Stockholm University, SE-106 91 Stockholm, Sweden; *manuscript received on 7/03/2019; manuscript accepted on 17/05/2019.*

Geological and palaeontological investigations in the Talara Basin in northern Peru have a long history due to the oil potential of these sediments (Grzybowski 1899; Bosworth 1922; Higley 2004). In the 1930s, Axel A. Olsson published a series of papers on the palaeontology of the Talara Basin (Olsson 1928, 1929, 1930, 1931, 1932), and especially the molluscs were used for biostratigraphical correlations. In this context, he reported some curious occurrences of the '*Pleurophopsis* fauna', often found within carbonate nodules within the late Oligocene Heath shales (Olsson 1931). This fauna is named after its most common bivalve, *Pleurophopsis*, which was first reported from Cenozoic deposits in Trinidad (Van Winkle 1919) and Cuba (Cooke 1919), and later found by Olsson also in Ecuador (Olsson 1931) and Colombia (Olsson 1942). The subsequent discovery of faunal communities around deep-sea hydrothermal vents and methane seeps in the modern oceans (Corliss *et al.* 1979; Paull *et al.* 1984) led to the reinterpretation of various 'unusual' fossil faunas as ancient methane-seep faunas (Gaillard *et al.* 1985; Goedert & Squires 1990; Taviani 1994), including the *Pleurophopsis* faunas at the type locality in Trinidad and those in Peru (Goedert & Squires 1993). Using material from Olsson's collection deposited in the Smithsonian Natural History Museum, at least two of the Peruvian *Pleurophopsis* localities were confirmed as fossil seep deposits (Kiel & Peckmann 2007) based on the carbon stable isotope fingerprint of carbonates that precipitated as a consequence of anaerobic oxidation of methane (Peckmann & Thiel 2004).

The faunas around vents and seeps show a high degree of adaptation to these habitats. The dominant taxa, such as vesicomyid clams, bathymodiolin mussels and vestimentiferan tube worms, live in symbiosis with

DOI 10.1111/let.12349

chemotrophic bacteria from which they derive most, if not all, their nutrients (Fisher 1995). Many of these species are endemic to vent and seep habitats, but show a wide geographical distribution along mid-ocean ridges and continental margins (Tunnicliffe & Fowler 1996; Van Dover *et al.* 2002; Moalic *et al.* 2012; Kiel 2016). Their reliance on an *in situ* source of nutrition also suggests that the evolutionary history of these faunas is likely buffered from mass-extinction events and other perturbations affecting shallow-marine ecosystems, and instead seem to be driven by changes in seawater sulphate concentrations (Kiel 2015). Understanding the evolutionary and biogeographical history of vent and seep faunas requires a well-documented fossil record. The Cenozoic record of seep communities and especially their mollusc fauna is already quite well known, but sampling is heavily biased towards the Northern Hemisphere (Campbell 2006; Kiel 2010a,b,c). Here, we report new insights into the stratigraphy, ecology and fauna of the *Pleurophopsis*-bearing limestones in the Talara Basin.

Geology of the Talara Basin province

The active continental margin lining the western South American coast has a long history of tectonic activity resulting from the formation and break-up of the supercontinents Gondwana and Pangea. These formation and break-up stages can be divided into shorter periods of tectonic activity, which have affected sedimentation in the coastal regions of South America (Charrier *et al.* 2007).

The province of the Talara Basin is situated on the northern continental shelf lining the coast of Peru. It is delineated to the east by the La Brea-Amotape Mountains of the Coastal Range, to the south by the Trujillo Basin and to the west by the Nazca Plate subduction zone under the South American Plate. The northern boundary of the Talara Basin province is composed of the Pillar of Zorritos; a basement uplift and associated fault zone, right at the southern border of the Dolores-Guayaquil megashear zone (Zúñiga-Rivero *et al.* 1999).

The Talara Basin province lies on top of a larger basin affected by Cretaceous tectonic events, which also underlies part of the Neogene structures of the adjacent Progreso and Secura-Salaverry Basin provinces. These systems are separated from the Talara Basin province by faults containing intrusive rocks. These three basins stretch out seaward west of the Coastal Range and were initially characterized as forearc basins (Lonsdale 1978), but since there is no associated volcanic arc in the area, they have been considered as linear downwarps filled with clastic terrigenous sediments and shallow to deep marine limestones (Zúñiga-Rivero *et al.* 1998).

During the Early Devonian, clastic shallow-marine material was deposited into the Talara Basin province, and during Middle Devonian times, sedimentation increased. The uppermost Devonian and the Lower Carboniferous are marked by glaciomarine and fan-deltaic sediments with clasts derived from the underlying sediments. In the middle Carboniferous, there is a hiatus in sedimentation, the age and duration of which varies across the region. The hiatus is followed by continuous sedimentation, but during the Late Carboniferous and Early Permian, the area experienced regional sea-level fluctuations, possibly influenced by tectonics, resulting in unconformities between Devonian and Carboniferous strata of Peru (Isaacson & Diaz Martinez 1995). During the Early Cretaceous, oceanic crust was forming (Jaillard *et al.* 1995), resulting in Cretaceous mid-oceanic ridge basalt (MORB) unconformably overlying the Late Carboniferous Amotape Formation basement rocks (Higley 2004). The Late Cretaceous is marked by low volumes of terrigenous sediments restricted by slow Andean uplift in combination with wind-driven oceanic upwelling along the coast (Ziegler *et al.* 1981), creating a nutrient-rich palaeoenvironment and organic-rich sediments (Macellari & DeVries 1987). Between the Late Cretaceous and late Eocene the oceanic floor and southern coastal regions of Ecuador underwent plate and intra-plate collisions, basin subsidence and several phases of uplift (Jaillard *et al.* 1995), slowing sedimentation and rearranging the sediments in the Talara Basin province. The thickness of the stratigraphical sequences from the Cretaceous until the Holocene varies between 8,500 and 18,000 m (Zúñiga-Rivero & Hay-Roe 1998).

During the Palaeocene and Eocene, the Talara Basin province was affected by subduction of the Nazca Plate under the South American Plate, creating transtensional and extensional deposition resulting in high-angle faults delineating horst–graben structures (Raez Lurquin 1999). At the Palaeocene–Eocene boundary is an unconformity that underlies the Chacra-Salinas Group of clastic shelf deposits containing sandstones and conglomerates from the lower Eocene (Seranne 1987). This group is unconformably overlain by coarse-grained sandstones belonging to the Talara Group (Terebratula, Lobitos, Helico, Monte and Talara formations in succeeding order) of middle to late Eocene age, formed during an Andean orogenic phase connected to collision between coastal Ecuador and the Andean margin (Jaillard *et al.* 1995). Late Eocene through early Oligocene times are marked by the Inaic orogeny of the

Andes, which can be seen as a regionally continuous erosional unconformity overlying the Talara Group in the Talara Basin province and at the base of the Oligocene Mancora Formation in the southern Progreso Basin province (Higley 2004). Above the unconformity follows the upper Eocene Lagunitos Group (Verdun, Chira, Mirador and Carpitas formations in succeeding order), which includes poorly fossiliferous, thick sandstones and sandy shales. This group is overlain by the Oligocene Mancora and Heath formations, which consist of clastic rocks deposited as a result of rapid erosion. The base of the Mancora Formation is marked by an unconformity, resulting from the Chira transgression during the early Oligocene, followed by rapid erosion under a short-timed uplift in middle Oligocene. The Heath Formation consists of fine material deposited in a marine setting (Olsson 1931). The rocks of the Talara and Lagunitos groups are heavily eroded in most of the Talara Basin province and a period of block faulting has affected the northern part of the basin. The Miocene Zorritos Formation follows the Heath Formation. Reservoirs in the upper Eocene Verdun Formation have been mostly targeted by the oil industry (Montagna *et al.* 1999), but oil fields are extended throughout the whole basin sourced from mostly sandstones of other formations such as the Oligocene Mancora Formation and the middle and upper Eocene Talara Group (Higley 2004).

Materials and methods

To locate and record the sampling sites during our fieldwork in 2017, we used geological maps published by the Instituto Geológico Minero y Metalúrgico (Ingemmet), specifically the 1:100,000 maps of the Lobitos quadrangle (0662) 9-a, digital version 1999, the Quebrada Seca quadrangle (0762) 9-b, 1989, digital version 1999, and the Talara quadrangle (0661) 10-a, digital version 1999, and topographical maps of the same quadrangles published by the Instituto Geografico Nacional, Lima, Peru.

Thin sections of 50–60 μm thickness were prepared for each site and imaged under an Olympus SZX10 stereomicroscope. Samples for carbon and oxygen stable isotope analyses were extracted from the counterparts of the thin sections using a handheld microdrill; sampled were micrite, rim cement and blocky calcite. Carbonate powders were reacted with 100% phosphoric acid at 75°C using a Kiel III online carbonate preparation line connected to a Thermo Finnigan MAT 252 mass spectrometer. All values are reported in per mil relative to V-PDB by assigning a δ^{13}C value of +1.95‰ and a δ^{18}O value of −2.20‰ to NBS19. Reproducibility was checked by replicate analysis of laboratory standards and is better than ±0.05‰.

Phosphatic fossils were extracted from the rock by dissolving the carbonate using a 5–10% acetic acid solution and screening the residue under a stereo microscope. The mollusc fossils were coated with ammonium chloride prior to photography. All specimens are housed in the Swedish Museum of Natural History, Department of Palaeobiology (NRM).

One sample from each locality (Belén, Cerro La Salina block 1, Cerros El Pelado block 2) was chosen for lipid biomarker studies. The sample weight was between 60 and 80 g. Prior to biomarker extraction, the samples were cleaned and surfaces were cut off. Carbonates were crushed to pea-sized pieces and dissolved with 10% HCl (see Gischler *et al.* 2017 for details). Afterwards the samples were saponified with 6% KOH in methanol to release fatty acids bound to the carbonate matrix. The samples were extracted with dichloromethane:methanol (3:1) in an ultrasonic bath until the extract became colourless. The total lipid extract was further separated into (1) an *n*-hexane soluble fraction and (2) a dichloromethane soluble fraction. The *n*-hexane soluble fraction was further separated by solid-phase chromatography using an aminopropyl-modified silica gel column (see Birgel *et al.* 2008a,b). The total lipid extract was separated into hydrocarbons, ketones, alcohols and carboxylic acids. Only the hydrocarbons and carboxylic acid fractions were found to contain indigenous compounds. Consequently, the alcohol and ketone fractions are not further discussed below. Carboxylic acids were derivatized to methyl esters by reacting the free fatty acids with 20% boron trifluoride in methanol at 70°C for one hour. Hydrocarbon and carboxylic acid fractions of all three sites were measured for identification on a gas chromatograph coupled to a mass spectrometer (GC-MS), a Thermo Scientific Trace GC Ultra coupled to a Thermo Scientific DSQ II mass spectrometer. Quantification was done by gas chromatography–flame ionization detection (GC-FID) using a Fisons Instruments GC 8000. Internal standards used were 5α-cholestane for hydrocarbons and 2-methylated C_{18}-fatty acid for carboxylic acids. Both gas chromatographs were equipped with an Agilent HP-5 MS UI fused silica column (30 m × 0.25 mm inner diameter, 0.25 μm film thickness). The carrier gas was helium for GC-MS and hydrogen for GC-FID measurements. The GC temperature program for both fractions was 50°C (3 min); from 50°C to 230°C (held for 3 min) at 25°/min; from 230°C to 325°C (held for 20 min) at 6°C/min.

Compound-specific carbon isotope compositions of hydrocarbons and carboxylic acids were measured on an Agilent 6890 gas chromatograph coupled with a Thermo Finnigan Combustion III interface to a Thermo Finnigan Delta Plus XL isotope ratio mass spectrometer. The GC conditions were as described above. The carboxylic acids were corrected for the addition of carbon from derivatization (methylation). Stable carbon isotope values are given as $\delta^{13}C$ values in per mil relative to Vienna Peedee Belemnite (V-PDB). The analytical error was below 0.7‰.

Planktonic foraminifera were identified in thin sections. Taxonomy follows morphological concepts described in Wade *et al.* (2018). Molluscs were identified after Olsson (1931) and other studies on Eocene–Oligocene seep molluscs (Kiel 2006, 2013; Amano & Kiel 2007; Kiel & Goedert 2007; Amano *et al.* 2013; Kiel & Amano 2013; Kiel & Hansen 2015; Hryniewicz *et al.* 2017).

The deposits

Belén seep site

Olsson (1931, p. 21) reported this locality as being situated 'Near Belen and Pajarabobo, a few miles south of Lagunitas'. All three places were settlements related to the initial oil boom in the early 1900s and remnants of Lagunitas can apparently still be found (Manchester *et al.* 2012), but Belén and Pajarabobo have completely vanished. We found a single hill with both fossiliferous and non-fossiliferous carbonate crusts embedded in greyish marls at 4°44.239′S, 81°12.935′W (Fig. 1), about 2.5 km NE of the Belén fruit site (Manchester *et al.* 2012).

According to Olsson (1931) the rocks in this area ('the central part of the Lagunitas syncline') belong to the Heath shales, which he considered as late Oligocene in age based on their mollusc associations. When discussing the nearby Belén fruit site, Olsson (1931, p. 16) pointed out the lithological similarities between the rocks of the Belén fruit site and those containing the *Pleurophopsis* fauna and indicated that the fruit site belongs to the 'middle' Oligocene Mancora Formation, which underlies the Heath shales. Recent work on the diatoms from the Belén fruit site provided an early Oligocene age (Manchester *et al.* 2012). Thus, we infer that the Belén seep site is just slightly younger than the fruit site and is most likely of late early-to-early late Oligocene age.

Cerro La Salina sites

According to Olsson (1931), outcrops of the Heath shales occur between Mancora and Punta Bravo, and along Quebrada Seca they contain large carbonate deposits with the *Pleurophopsis* fauna. Quebrada Seca is a large valley with an ephemeral river just north of Mancora. We found fossiliferous and unfossiliferous seep deposits, about 30–60 cm in diameter, in the coastal hills on both the northern and southern side of the mouth of Quebrada Seca (Fig. 1). The hills on the southern side are called Cerro La Salina, and those on the northern side are called Cerros El Pelado.

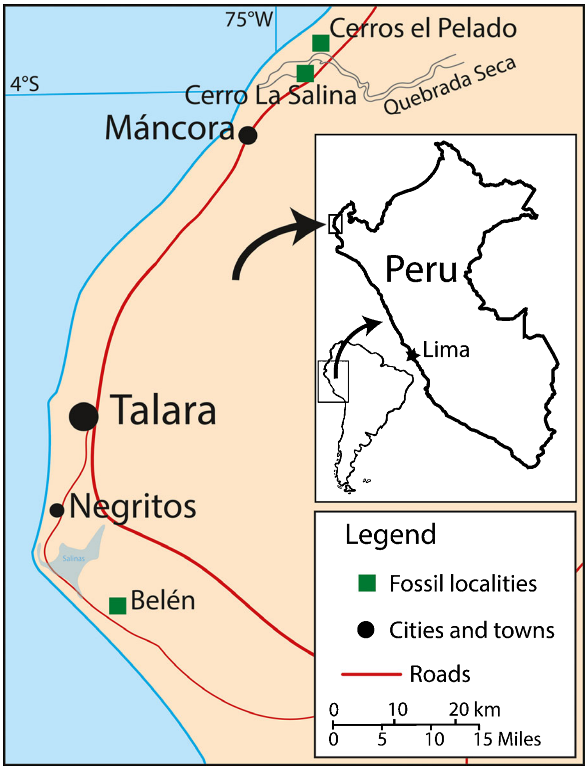


Fig. 1. Map showing the fossil localities.

Nine blocks of fossiliferous seep carbonate were found at the northwestern side of Cerro La Salina; these are here referred to as Cerro La Salina blocks 1–9. All deposits were found as floats in the beds or at the mouths of two gullies of Cerro La Salina; blocks 1–8 were found in a gully that empties into Quebrada Seca at 4°3.302′S, 81°0.334′W, block 9 was found about 400 m further NE at the northern end of Cerro La Salina at 4°3.1607′S, 81°0.1103′W.

The lithostratigraphical origin of these rocks remains questionable for several reasons. Although we have thoroughly explored this part of Cerro La Salina, we have never seen such carbonate deposits *in situ*, only as floats in the gully beds. The rocks composing Cerro La Salina were considered as 'Heath shales' by Olsson (1931), but are mapped as the late Eocene Carpitas Formation on the Ingemmet geological map. However, the lithology of the sediments observed in the field matches that of the Heath

Formation as described in the explanations to the geological maps (Palacios Moncayo 1994), but not that of the Carpitas Formation. To confuse matters even more, in the description of the Heath Formation, Palacios Moncayo (1994) reported *Pleurophopsis* as being typical for the Oligocene, but reported *Pleurophopsis* also from the Carpitas Formation, which he considered as late Eocene in age.

Thin sections of sample Cerro La Salina block 1 reveal occasional planktonic and benthic foraminifera. Identification of species in thin section is challenging. However, among the planktonic foraminifera, morphologies fall into two broad classes that are suggestive of several taxa that provide some degree of biostratigraphical constraint. The first diagnostic form is the small biserial test suggestive of the genus *Chiloguembelina* (Fig. 2A–D). Benthic species can also have biserial-chambered tests, including some other specimens seen in thin sections from Cerro La Salina block 1, but those considered as *Chiloguembelina* can be distinguished by having a porous and thinner wall. *Chiloguembelina* can be common in high productivity setting, consistent with the Peru margin setting. Its stratigraphical range extends from the early Palaeocene to middle Oligocene (highest common occurrence at the top of Biozone O4), but it can be especially common in the late Eocene to early Oligocene (Pearson *et al.* 2006; Wade *et al.* 2018).

The second diagnostic morphology is a globular-quadrate form typical of the late Eocene to Oligocene genus *Dentoglobigerina* (Fig. 2E–J). Several specimens with such a form have 3–4 chambers in the final whorl, suggestive of *D. galavisi*. Two have a more compressed and cap-like final chamber reminiscent of *D. eotripartita* or *D. pseudovenezuelana*. These species range from the late Eocene Biozone E13 to the early Oligocene Biozone O1. The occurrence of these taxa together is consistent with a late Eocene to early Oligocene age of Cerro La Salina block 1. The specimens with rather continuous peripheral outlines (Fig. 2F, H) could be a species of *Dentoglobigerina* or possibly *Catapsydrax unicavus*. *Catapsydrax unicavus* is a long-ranging genus (early Eocene–upper Oligocene) that is biostratigraphically not very useful, although its occurrence would certainly be consistent with a late Eocene or early Oligocene assignment.

Cerros El Pelado sites

In the Cerros El Pelado on the northern side of Quebrada Seca we found three seep carbonate boulders in the bed of a dry creek running in a northwesterly

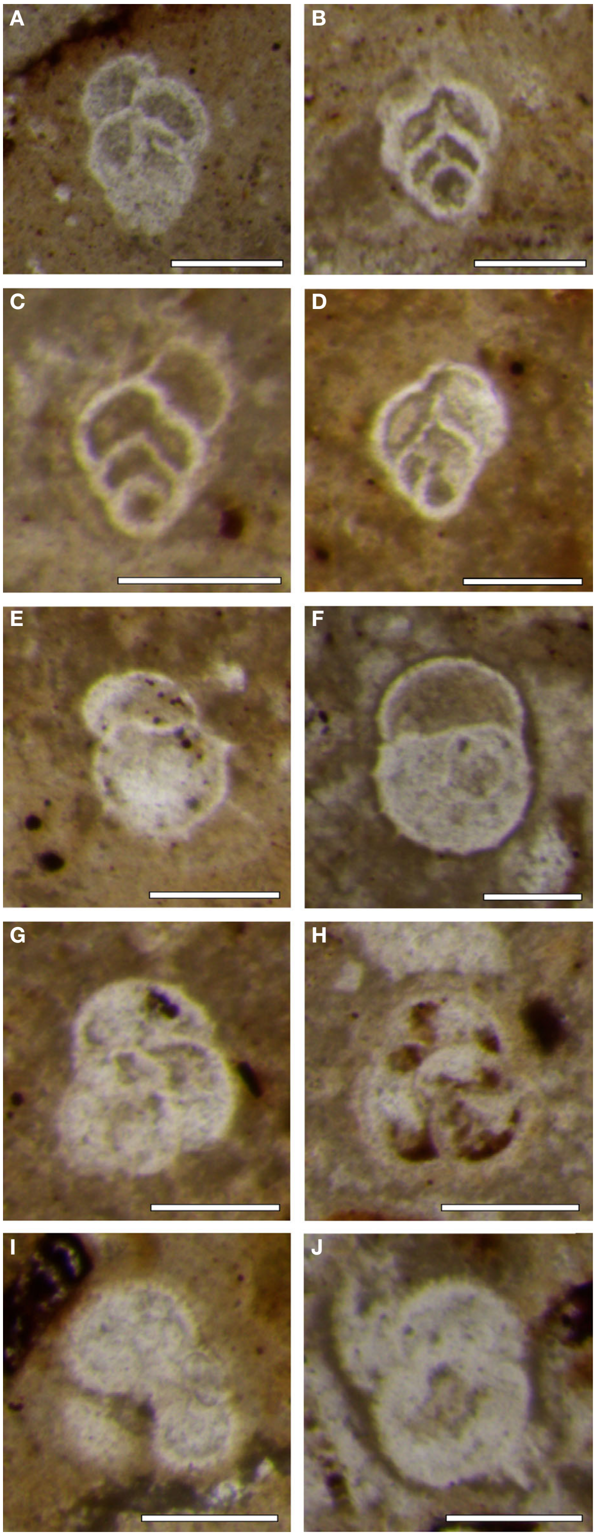


Fig. 2. Thin-section images of Cerro La Salina block 1 showing stratigraphically important planktonic foraminifera. A-D, biserial tests suggestive of the genus *Chiloguembelina*. E-J, globular-quadrate morphologies typical of *Dentoglobigerina* (E, G, I and J) or *Catapsydrax* (F, H). The occurrence of these taxa is consistent with a late Eocene to early Oligocene age. All scale bars are 0.2 mm.

direction at about 4°1.770′S, 80°58.601′W; this is the only creek in the Cerros El Pelado marked on the Ingemmet Quebrada Seca quadrangle geological map. Analogous to the Cerro La Salina, the rocks composing the southern part of the Cerros El Pelado were considered as Heath shales by Olsson (1931), but were mapped as the late Eocene Carpitas Formation on the Ingemmet Quebrada Seca quadrangle geological map. Also analogous to the Cerro La Salina, we have not found any carbonate deposit *in situ*, just as floats in the creek beds. The lack of foraminiferans in the thin sections hampers a reliable age determination of these limestones, but in analogy to the Cerro La Salina sites, we consider them as early Oligocene, despite their lithological differences.

Petrography and stable isotopes

Belén seep site

The limestone of the Belén seep deposit consists dominantly of brownish to ochre-coloured micrite with mm- to cm-sized bioclasts, and common oval peloids (Figs 3A, 4A). Pyrite is finely dispersed throughout the carbonate and geopetals occur. The common voids are lined by banded and botryoidal rim cement, blocky calcite and authigenic quartz. Bivalve shells are either articulated or fragmented, and many are recrystallized and consist of an outer layer of scalenohedral calcite crystals apparently lined by iron oxyhydroxides, and blocky calcite within (Fig. 4B). The stable carbon isotope ($\delta^{13}C$) signatures of the Belén carbonate are very heterogeneous, even within the same carbonate phase. The rim cements show values of −24.5 to +4.2‰, micrite with shell debris shows values from −8.2 to +3.7‰, and the most negative sample is a sparry calcite at −25.9‰. The corresponding oxygen stable isotope ($\delta^{18}O$) values are much more homogeneous with values from −2.3 to +2.3‰ (Fig. 5, Table 1).

Cerro La Salina sites

The nine blocks from Cerro La Salina are petrographically similar to each other and distinct from both the Belén site and the Cerros El Pelado sites. The bioturbated limestones consist of varying amounts of ochre-coloured micrite that often forms nodules with corroded margins (Figs 3B, 4C). Voids are rare to common and are filled by clasts, clotted micrite and shell debris, and are often lined by banded and botryoidal rim cement (Fig. 4D). Pyrite commonly occurs in clumps or as linings along shell surfaces, cracks and the margin of nodules. The main differences to the Belén site are the nodular appearance and the lack of authigenic quartz. Samples for carbon and oxygen stable isotope analyses were taken from blocks 1, 4 and 9. The $\delta^{13}C$ values for rim cements range from −41.3 to −25.0‰ and those for micrites range from −46.0 to −25.9‰. The least negative $\delta^{13}C$ value of −19.8‰ was measured in a bivalve shell. The corresponding $\delta^{18}O$ values range from −8.4 to −1.8‰, with one outlier at +1.7‰, which is associated with the most negative $\delta^{13}C$ value (Fig. 5, Table 1).

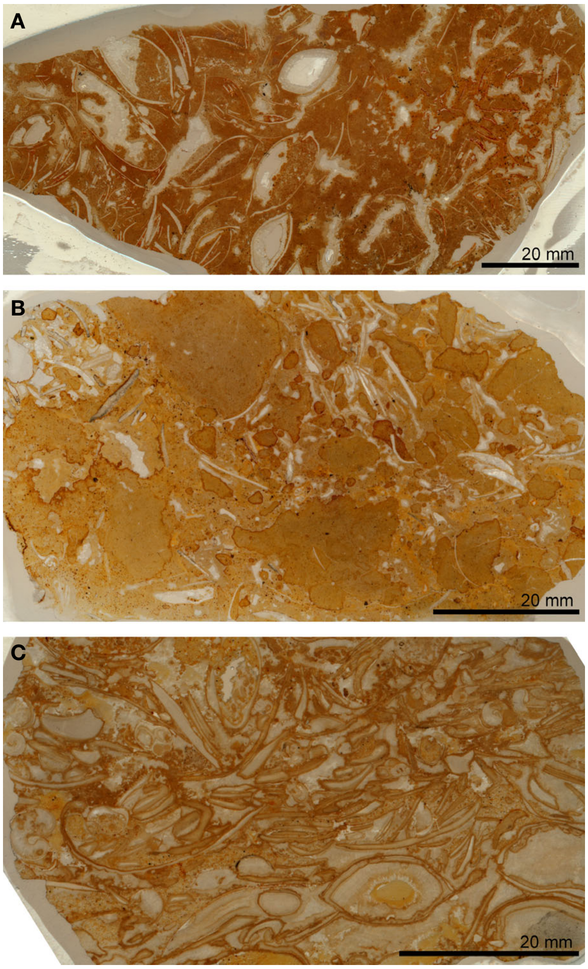


Fig. 3. Scanned thin sections. A, Belén. B, Cerro La Salina block 8. C, Cerros El Pelado block 2.

Cerros El Pelado sites

Only from blocks Cerros El Pelado 2 and 3 thin sections were prepared; whereas block 2 contains abundant, sorted shell fragments and detrital sediment cemented by fibrous rim cement and some blocky calcite (Figs 3C, 4E), block 3 consists essentially of large shell fragments floating in a matrix of fibrous

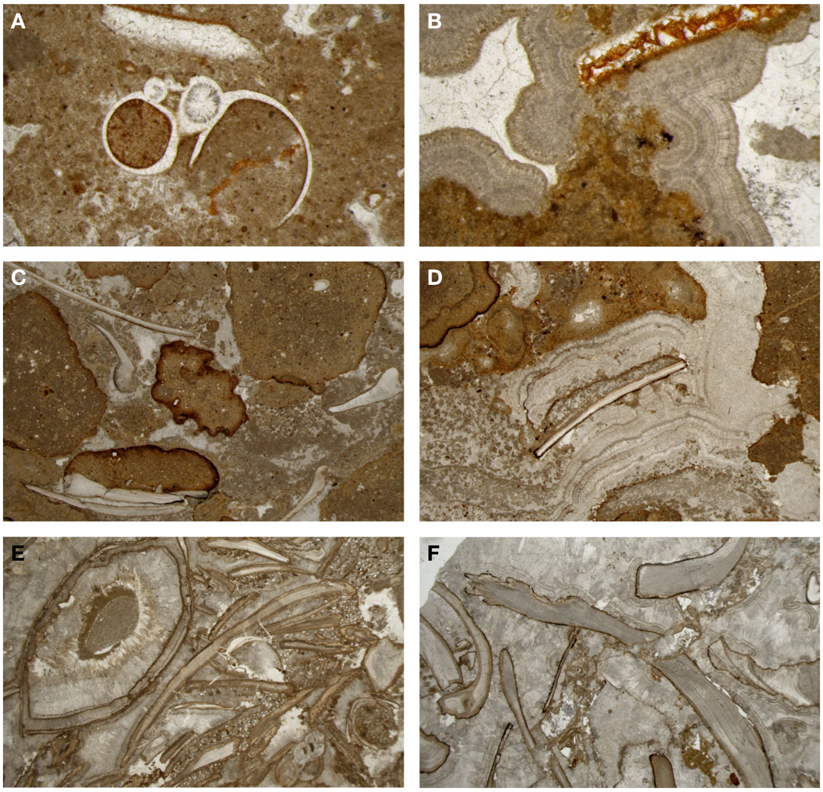


Fig. 4. Thin-section micrographs illustrating petrographical details. (A, B) Belén site; A, skeneiform gastropod in micrite. B, voids lined by banded and botryoidal rim cement and a recrystallized shell fragment (upper right). C, D, Cerro La Salina block 1; C, micrite nodules with corroded margins and shell debris; D, voids lined by banded and botryoidal rim cement; note clotted micrite (lower left). E, F, Cerros El Pelado; E, block 2, shell debris cemented by fibrous cement; note interspersed detrital sediment (right); F, block 3, partially corroded shells cemented by fibrous cement.

cements and only very minor amounts of peloidal micrite (Fig. 4F). They differ from the Cerro La Salina limestones by the lack of a nodular fabric and the lack of evidence of bioturbation, and from both the Cerro La Salina and Belén limestones by the lack of abundant micrite. Samples for stable isotope analyses were taken from block 2. The carbon isotope signature of the fibrous rim cements ranges from −42.0 to −34.0‰, samples with detrital material show values from −36.5 to −34.8‰, and a single sample of sparry calcite yielded a value of −35.8‰. The corresponding δ^{18}O values range from −6.6 to −2.6‰ and show a negative correlation with the δ^{13}C values (Fig. 5, Table 1).

Lipid biomarkers

The lipid biomarker contents varied significantly from site to site. The highest lipid biomarker content was observed for the Cerro La Salina sample with 3770 ng/g rock (Table 2); Cerros El Pelado and Belén had lower contents with 827 ng/g rock and 227 ng/g rock, respectively. Only the samples Cerro La Salina and Cerros El Pelado contained carboxylic acids, whereas hydrocarbons were preserved in the rocks from all sites. Carboxylic acids predominated with 82.2 weight% of all lipids measured for Cerro La Salina and 78.1% of all lipids for Cerros El Pelado (Table 2).

The Belén hydrocarbon fraction was dominated by *n*-alkanes, representing 60% of all hydrocarbons. In contrast, the rocks from the other locations yielded only 20–30% *n*-alkanes (Table 2). All *n*-alkanes ranged from *n*-C_{17} to *n*-C_{33}; short- to mid-chain *n*-alkanes were more abundant than long-chain *n*-alkanes (data not shown). The most prominent compounds in Cerro La Salina and Cerros El Pelado samples were isoprenoids, comprising 51% and 56% of all hydrocarbons, respectively. In the Belén sample, isoprenoids were less abundant (32% of all hydrocarbons). In Cerros El Pelado and Belén limestones, 2,6,10,15,19-pentamethylicosane (PMI) was the most abundant isoprenoid (Table 2); in the Cerro La Salina sample, PMI was as abundant as the combined phytane/crocetane peak. The irregular isoprenoid crocetane

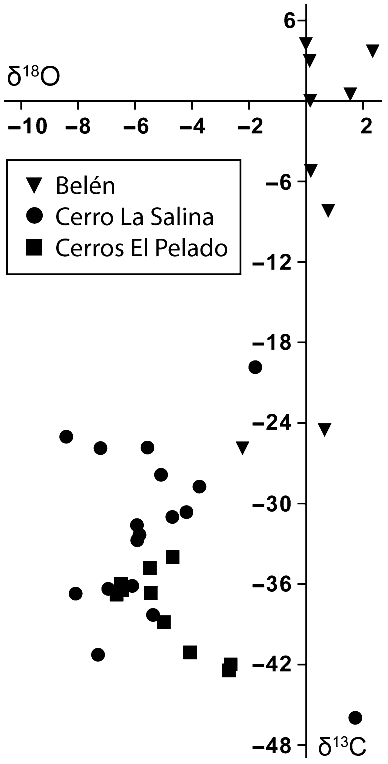


Fig. 5. Isotope plot. All values are given in per mil against the V-PDB standard.

Table 1. Carbon and oxygen stable isotope data; all values in per mil relative to the V-PDB standard

Sample	$\delta^{13}C$	$\delta^{18}O$
Belén site		
Rim cement	4.2	0.0
Rim cement	3.0	0.1
Blocky calcite	−25.9	−2.2
Dark micrite	3.7	2.3
Dark micrite	0.5	1.6
Ochre micrite	−5.2	0.2
Ochre micrite	0.0	0.1
Rim cement	−24.5	0.7
Ochre micrite	−8.2	0.8
Cerro La Salina block 1		
Micrite	−38.3	−5.4
Rim cement	−36.4	−6.9
Rim cement	−41.3	−7.3
Rim cement	−36.7	−8.1
Micrite	−32.7	−5.9
Micrite	−36.1	−6.1
Cerro La Salina block 4		
Micrite	−27.9	−5.1
Micrite	−32.3	−5.8
Rim cement	−25.8	−5.6
Rim cement	−25.0	−8.4
Micrite	−25.9	−7.2
Micrite	−31.6	−5.9
Cerro La Salina block 9		
Micrite	−31.0	−4.7
Micrite	−30.6	−4.2
Micrite	−46.0	1.7
Micrite	−28.7	−3.7
Shell	−19.8	−1.8
Cerros El Pelado block 2		
Rim cement	−42.4	−2.7
Rim cement	−42.0	−2.6
Micrite	−36.5	−6.5
Blocky calcite	−36.8	−6.7
Rim cement	−36.7	−5.4
Rim cement	−41.1	−4.1
Rim cement	−34.0	−4.7
Micrite	−34.8	−5.5
Rim cement	−38.8	−5.0
Micrite	−36.0	−6.5

(2,6,11,15-tetramethylhexadecane) comprised about 60% of the combined peak in all samples. Other isoprenoid hydrocarbons were acyclic and monocyclic biphytanes; the latter was only found in the Cerro La Salina sample (Table 3). In the Cerros El Pelado limestone, acyclic biphytane was more abundant than combined phytane and crocetane. Other, minor isoprenoid hydrocarbons detected are pristane and squalane. Especially the tail-to-tail linked isoprenoids crocetane and PMI are common biomarkers of methanotrophic archaea involved in the anaerobic oxidation of methane (AOM) and are stable on geological time-scales (Peckmann & Thiel 2004; Birgel *et al.* 2008b). Apart from alkanes and isoprenoids, steranes contributed with 5–10% to the hydrocarbon fractions (Table 2). Hopanes were found only in small amounts. Gammacerane was found in the Cerro La Salina sample with 2% of all hydrocarbons. Various 4-(di)methylated steranes (lanostanes) were identified in the Cerros El Pelado limestone (4% of all hydrocarbons; Table 2), which have been previously described from a few other ancient seep limestones (Peckmann *et al.* 2004; Birgel & Peckmann 2008; Natalicchio *et al.* 2015).

The carboxylic acid fractions from the Cerro La Salina and Cerros El Pelado sites were dominated by *n*-fatty acids ranging from *n*-C_{14} to *n*-C_{33} (Cerro La Salina) and *n*-C_{14} to *n*-C_{26} (Cerros El Pelado; data not shown). Branched fatty acids were less abundant (11% of all lipids) and comprised *iso*- and *anteiso*-C_{15} and C_{17} fatty acids and minor amounts of 10-methylated C_{16} fatty acid. Minor compounds were isoprenoic acids, such as phytanic acid in Cerro La Salina and Cerros El Pelado samples and biphytanic diacids in the Cerro La Salina sample. The most abundant biphytanic diacid was monocyclic biphytanic diacid, acyclic and monocyclic biphytanic diacids were only found in traces (Table 2).

Compound-specific isotopes

All fractions from all sites were measured for their compound-specific carbon stable isotope

Table 2. Overview of major lipid groups in the hydrocarbon and carboxylic acid fractions

	Cerro La Salina			Cerros El Pelado			Belén	
	Contents (ng/g rock)	% of all lipids	% of hydrocarbons	Contents (ng/g rock)	% of all lipids	% of hydrocarbons	Contents (ng/g rock)	% of hydrocarbons
Hydrocarbons								
n-Alkanes	204	5.4	30.5	32	3.9	18.0	135	59.6
Isoprenoids	341	9.0	50.9	101	12.2	55.9	73	32.3
Steranes	70	1.8	10.6	10	1.2	5.5	13	5.6
Lanostanes	n.d.	n.d.	n.d.	9	1.0	4.4	n.d.	n.d.
Hopanes	42	1.1	6.4	29	3.6	16.3	6	2.5
Gammacerane	10	<1	1.6	n.d.	n.d.	n.d.	n.d.	n.d.
Sum hydrocarbons	667	17.8		172	21.9		227	100
Carboxylic acids								
n-Fatty acids	2526	66.9		516	62.5		n.d.	n.d.
Branched fatty acids	421	11.2		98	11.8		n.d.	n.d.
Isoprenoic acids	156	4.1		32	3.8		n.d.	n.d.
Sum carboxylic acids	3103	82.2		646	78.1		n.d.	n.d.
Sum all lipids	3770			827			227	

n.d., not detected. Please note that no pristine compounds were preserved in the carboxylic acid fraction of Belén.

Table 3. Detailed lipid biomarker composition (in relative % of all lipids) and compound-specific $\delta^{13}C$ in ‰

	Cerro La Salina		Cerros El Pelado		Belén	
Location	Rel % of all lipids	$\delta^{13}C$ (‰)	Rel % of all lipids	$\delta^{13}C$ (‰)	Rel % of all lipids	$\delta^{13}C$ (‰)
Isoprenoids						
Pristane	<1	n.m.	tr		1.1	n.m.
Phytane/crocetane*	3.8	−89	<1	n.m.	12.2	n.m.
PMI	3.1	−124	7.2	−122	13.8	n.m.
Squalane	<1	n.m.	1.3	−96	2.7	n.m.
Acyclic biphytane	1.2	−53	2.8	−122	5.1	n.m.
Monocyclic biphytane	<1	n.m.	n.d.		n.d.	
Phytanic acid	1.3	−98	3.8	−115	n.d.	
Acyclic biphytanic diacid	<1	n.m.	n.d.		n.d.	
Monocyclic biphytanic diacid	2.8	−116	n.d.		n.d.	
Bicyclic biphytanic diacid	tr		n.d.		n.d.	
n-Alkyl lipids						
n-C_{18} alkane	<1	n.m.	<1	n.m.	2.0	n.m.
n-C_{23} alkane	<1	n.m.	<1	n.m.	4.2	n.m.
n-C_{29} alkane	<1	n.m.	tr		7.4	n.m.
n-C_{14} fatty acid	3.5	−64	5.2	−69	n.d.	
n-C_{15} fatty acid	3.8	−60	5.3	−74	n.d.	
n-C_{16} fatty acid	17	−55	23.5	−63	n.d.	
n-C_{17} fatty acid	8.6	−51	3.7	−84	n.d.	
n-C_{18} fatty acid	6.6	−46	13.6	−53	n.d.	
Branched alkyl lipids						
iso-C_{15} fatty acid	2.3	−81	3.0	−79	n.d.	
anteiso-C_{15} fatty acid	2.8	−87	2.8	−84	n.d.	
iso-C_{17} fatty acid	2.1	−78	2.3	−85	n.d.	
anteiso-C_{17} fatty acid	2.0	−86	2.4	−85	n.d.	
Cyclic terpenoids						
Ergostane (C_{28}-sterane)	<1	n.m.	<1	n.m.	2.8	n.m.
T_s	n.d.		<1	n.m.	n.d.	
T_m	n.d.		<1	n.m.	n.d.	
Hopane (17α(H), 21β(H)-C_{30} hopane)	<1	n.m.	2.6	−82	2.5	n.m.
Gammacerane	<1	n.m.	<1	n.m.	n.d.	
Lanostane	n.d.		<1	n.m.	n.d.	
nor-Lanostane	n.d.		<1	n.m.	n.d.	
*(% crocetane of mixture)	56%		58%		58%	

Please note that in this table, not all compounds identified are displayed (see text for more details). PMI: 2,6,10,15,19-pentamethylicosane; T_s: 18α(H)-22,29,30-trisnorhopane; T_m: 17α(H)-22,29,30-trisnorhopane. n.d., compound was not detected in the sample; n.m.: contents were too low for compound-specific isotope measurements.

compositions. Unfortunately, lipid contents in the Belén sample were not sufficient for analysis.

For the Cerro La Salina sample $\delta^{13}C$ values of *n*-fatty acids ranged from −64‰ (*n*-C_{14} fatty acid) to −46‰ (*n*-C_{18} fatty acid; Table 3); *n*-alkane contents were too low for analysis. Terminally branched fatty acids with 15 and 17 carbons varied from −87 to −78‰. The *anteiso* fatty acids were 6 to 8‰ more ^{13}C-depleted than the corresponding *iso* fatty acids. Most negative values were measured for isoprenoids, ranging from −124‰ for PMI to −53‰ for cyclic biphytane (Table 3). Contents of all cyclic terpenoids (hopanes, steranes and gammacerane) were too low for isotope analysis.

For the Cerros El Pelado sample $\delta^{13}C$ values of *n*-fatty acids ranged from −84‰ (*n*-C_{17} fatty acid) to −53‰ (*n*-C_{18} fatty acid); *n*-alkane contents were too low for analysis. Terminally branched fatty acids with 15 and 17 carbons yielded values ranging from −85 to −79‰. The *anteiso*-C_{15} fatty acid was more ^{13}C-depleted than the *iso*-C_{15} fatty acid, and the other two terminally branched fatty acids yielded the same value (Table 3). Like for the Cerro La Salina sample, most negative values were obtained for the isoprenoids, varying from −122‰ for PMI and acyclic biphytane to −96‰ for squalane. Contents of cyclic terpenoids (hopanes, steranes, lanostane and gammacerane) were too low for isotope measurements except for $17\alpha(H),21\beta(H)$-C_{30}-hopane (−82‰).

Fauna

The limestones contain a diverse invertebrate fauna consisting of, in decreasing order of abundance, bivalves, gastropods, crustaceans, scaphopods and worm tubes. In addition, rock fragments from Cerro La Salina block 1 revealed a diverse fish microfauna after carbonate dissolution, consisting of teeth, scales and bone fragments. Both the mollusc and the fish faunas are the subjects of forthcoming, more detailed taxonomic studies.

The fauna at Belén is of low diversity, containing only the small, elongate vesicomyid bivalve *Pleurophopsis lithophagoides* (Fig. 6D), a few specimens of a provannid gastropod, and single specimens of a protobranch bivalve and a neogastropod. Most diverse is the fauna of the limestones from Cerro La Salina, with the thyasirid *Conchocele tessaria* (Fig. 6 E) being the most common element. Less common are vesicomyid bivalves (including a very elongate *Pleurophopsis* and further species), lucinid bivalves with *Lucinoma zapotalensis*; in contrast to Olsson (1931), we have not found any solemyid bivalves. Remarkable are a single, small specimen of a mytilid (Fig. 6B) resembling the bathymodiolin *Idas*, from Cerro La Salina block 9, and a specimen of the deep-water genus *Neilo* (Fig. 6A). Notable among the gastropods are a small and abundant provannid virtually identical to *Provanna antiqua* Squires 1995 (Fig. 6H) from the Oligocene of Washington State, USA, a moderately sized abyssochrysoid belonging to *Ascheria* (Fig. 6G), several limpets including *Pyropelta* (Fig. 6F), and a buccinid resembling *Colus sekiuensis* Kiel & Goedert 2007 (Fig. 6J). In addition, we found several skeneiform and trochiform gastropods. Scaphopods are rare and include a smooth and a ribbed species. Crustaceans are represented by callianassid claws (Fig. 6C). The fish remains include vertebrae of the Engraulidae among the bony fishes, and the teeth of the shark families Centrolophidae, Mitsukurinidae and Etmopteridae. The fauna of the Cerros El Pelado sites is dominated by poorly preserved and difficult to determine vesicomyid bivalves and a few specimens of the lucinid *Lucinoma*. The most common gastropod is a mostly smooth *Provanna* (Fig. 6I) that differs from *Provanna antiqua* from the Cerro La Salina sites; there are also rare limpets and trochiform gastropods.

Discussion

Nature of the seep deposits

The presence of ^{13}C-depleted carbonate phases (cf. Ritger *et al.* 1987) and ^{13}C-depleted lipid biomarkers of the AOM consortium (cf. Peckmann & Thiel 2004) identifies the limestones at Belén, Cerro La Salina and Cerros El Pelado as seep deposits. The occurrence of pyritiferous micrite, clotted micrite, micrite nodules, banded and botryoidal cement, and authigenic quartz (cf. Peckmann & Thiel 2004; Campbell 2006; Kuechler *et al.* 2012) agrees with this interpretation. Unlike for Cerro La Salina and Cerros El Pelado, it is more difficult to reconstruct the composition of seepage fluids in the case of the Belén site, where the lowest $\delta^{13}C$ value is only −25.9‰, suggesting that other hydrocarbon sources in addition to methane, such as crude oil, could have been present (cf. Smrzka *et al.* in press). The greater abundance of *n*-alkanes in the Belén limestone agrees with oil seepage, but only represents circumstantial evidence since the timing of *n*-alkane ingress is unknown. The highest $\delta^{13}C$ values of +4.2‰ for rim cement and +3.7‰ for micrite of the Belén limestone may be taken as evidence for the episodic occurrence of autotrophic methanogenesis in the ancient seep environment. Such high $\delta^{13}C$ values and values even higher have been reported for authigenic minerals of

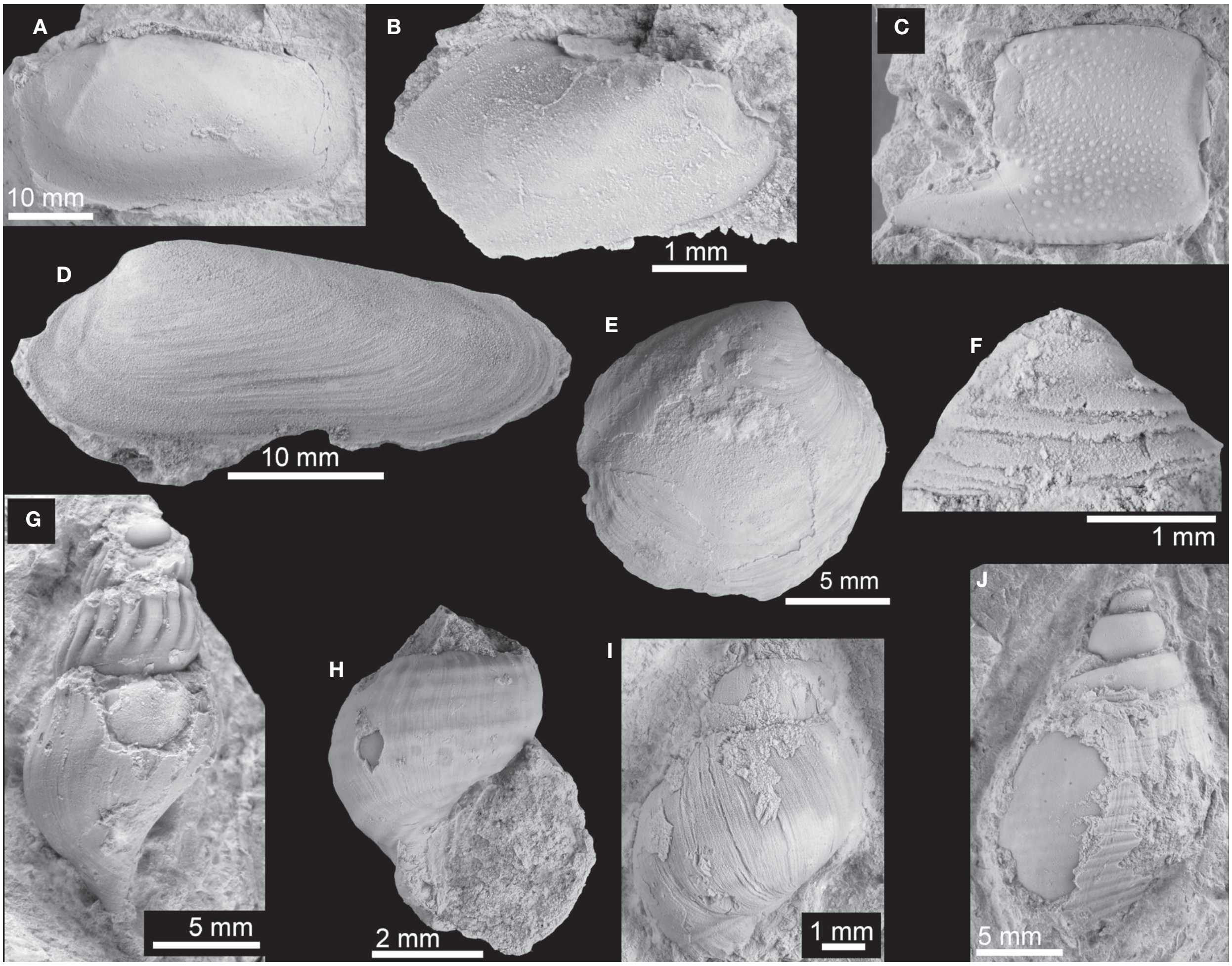


Fig. 6. Invertebrate macrofauna of the Talara Basin seep deposits. All specimens are from the La Salina sites except where noted. A, *Neilo* sp., Mo187001. B, *Idas* sp., Mo187003. C, callianassid claw. D, *Pleurophopsis lithophagoides* Olsson 1931 from the Belen site. E, *Conchocele tessaria* (Olsson 1931), Mo187008. F, *Pyropelta* sp., Mo187035. G, *Ascheria* sp., Mo187061. H, *Provanna antiqua* Squires 1995, Mo187046. I, *Provanna* sp. from Cerros El Pelado, Mo187056. J, *Colus sekiuensis* Kiel & Goedert 2007, Mo187062.

a number of seep deposits, reflecting a pool of pore-water dissolved inorganic carbon that has been imprinted by the preferential removal of $^{12}CO_2$ by autotrophic methanogens (Peckmann *et al.* 1999; Orphan *et al.* 2004; Naehr *et al.* 2007). Interestingly, group 1 anaerobic methanotrophic archaea (ANME-1) have been found to be capable of performing methanogenesis in addition to methane oxidation (Lloyd *et al.* 2011; Bertram *et al.* 2013) and geochemical evidence suggests that methanogenesis can be an at least episodically prominent process at seeps (Feng *et al.* 2014). Since the contents of archaeal biomarkers in the Belén limestone were too low to allow for compound-specific isotope analysis, it cannot be evaluated if some of the isoprenoids may have been partly derived from methanogenic archaea in addition to methanotrophic archaea.

Rocks of the three sites contain characteristic lipid biomarkers of the AOM consortium with low $\delta^{13}C$ values, including molecular fossils of ANMEs like PMI, crocetane, squalane, biphytanes and biphytanic diacids, as well as molecular fossils of sulphate-reducing bacteria (terminally branched fatty acids). For the Cerro La Salina and Cerros El Pelado limestones, lowest values were found for PMI, as well as biphytane and phytanic acid in the case of Cerros El Pelado and monocyclic biphytanic diacid in the case of Cerro La Salina. Lipid biomarkers of ANMEs have been previously used to decide whether archaea of the ANME-1 or the ANME-2 group were predominating. Such differentiation is based on the presence or absence of crocetane (Blumenberg *et al.* 2004; Niemann & Elvert 2008) and the ratio of archaeol to hydroxyarchaeol. The latter ratio cannot be used in this study, because ether-bond isoprenoid alcohols are not preserved. In the case of Cerro La Salina and Belén, combined crocetane and phytane are as abundant as PMI, and crocetane is contributing with 60%

to the combined peak. This pattern suggests that ANME-2 may have dominated at the ancient seep. However, in the case of Cerros El Pelado the combined crocetane/phytane peak is rather small, a pattern that is typical for seeps dominated by ANME-1. Taking into account only this limited information, Cerros El Pelado probably represents a mixed ANME-1/ANME-2 signal, whereas the others seeps were rather dominated by ANME-2. Interestingly, the Cerros El Pelado limestone contains isoprenoids with a very similar carbon isotopic composition except for squalane; this even applies to acyclic biphytane which is commonly less ^{13}C-depleted than other biphytanes in seep limestones (Feng *et al.* 2014). In the Cerro La Salina limestone, however, the isotopic composition of acyclic biphytane was affected by input of lipids from other, non-ANME sources, possibly representing marine thaumarchaeal sources. The combined crocetane/phytane peak also represents mixed input since phytane derives from different sources, including phototrophic organisms producing chlorophyll. In contrast to biphytane, monocyclic biphytanic diacid in the Cerro La Salina sample is only slightly less ^{13}C-depleted than PMI. This confirms the earlier finding that biphytanic diacids are commonly good recorders of past seepage (Birgel *et al.* 2008a) and are apparently not affected by input from other sources than ANMEs, even though some exceptions have been reported (Smrzka *et al.* 2017).

The Peruvian seep deposits not only contain biomarkers of ANME, but also yielded molecular fossils of sulphate-reducing bacteria involved in AOM. These are ^{13}C-depleted terminally branched fatty acids including *iso*- and *anteiso*-C_{15} and C_{17} fatty acids. The ratio of *anteiso*-C_{15} to *iso*-C_{15} fatty acid, which is used to discern ANME-1-dominated from ANME-2-dominated syntrophic consortia, is at around 1. Values above 2 indicate the dominance of the sulphate-reducing bacteria of ANME-1 consortia, whereas smaller ratios point to ANME-2 consortia (cf. Niemann & Elvert 2008). However, given the lower preservation potential of fatty acids compared to apolar isoprenoids, this proxy should only be used with caution for ancient deposits. One peculiarity of the Cerros El Pelado limestone is the presence of minute amounts of three lanostanes, which have been described from other seep deposits before (Peckmann *et al.* 2004; Birgel & Peckmann 2008; Natalicchio *et al.* 2015). The only known source of these 4-methylated steranes is aerobic methanotrophic bacteria, testifying to the occurrence of aerobic oxidation of methane at the Cerros El Pelado seep. The C_{30} hopane and gammacerane cannot be assigned with certainty to a specific group of bacteria, but gammacerane may also have derived from aerobic methanotrophic bacteria (Banta *et al.* 2015) based on its occurrence in a seep limestone.

The water depth at which these carbonates and their faunas were deposited is difficult to constrain. The faunal communities are dominated by chemosymbiotic bivalves and other taxa that are restricted to vent and seep sites (i.e., *Ascheria, Provanna, Pyropelta*; cf. (Kiel 2006; Amano & Jenkins 2013; Kaim *et al.* 2014). Observations on modern seep faunas indicate that such a high degree of endemism develops only below water depth of about 200–400 m (Sahling *et al.* 2003; Tarasov *et al.* 2005; Dando 2010). Also fossil seep communities ranging back at least to the Jurassic (and probably longer) are known to show this restriction to deeper water (Amano *et al.* 2010; Kiel 2010c). Hence, it is reasonable to assume a depositional depth at the outer shelf to slope below 200 m for the seep deposits in the Talara Basin.

Age of the seep deposits

The reliability of the stratigraphical dating of the studied seep deposits varies and is not entirely satisfactory. According to Olsson (1931) the *Pleurophopsis* fauna – the fauna found in the seep deposits reported here – occurs in the lower part of the Heath Shales (or Heath Formation; Olsson used these two terms interchangeably). The Belén seep deposit occurs *in situ* and is stratigraphically slightly above the Belén fruit site, which is part of the Mancora Formation and is well dated as early Oligocene by diatoms, and hence, the seep deposit is also of early Oligocene age or slightly younger. This age is consistent with the stratigraphical scheme of Higley (2004), which considers the Heath Formation to have its base in the early Oligocene (Fig. 7).

The seep deposits of Cerro La Salina are lithologically rather uniform, and we assume them to be derived from the same stratigraphical level. Although all limestone deposits were found as float, the surrounding sediments match the descriptions of the Heath Formation of both Olsson and of the accompanying notes to the Ingemmet geological maps (Palacios Moncayo 1994), and thus, we consider the limestone deposits to be derived from the Heath Formation. In Olsson's (1931) mollusc-based stratigraphy, the Heath Formation was regarded as late Oligocene. A subsequent study of planktonic foraminifera from similar strata in Ecuador ‘demonstrated that the Middle Oligocene of the molluscan timescale based on Ecuadorean-Peruvian faunas is equivalent to the Upper Eocene of the foraminiferal timescale as generally accepted in the Caribbean region’

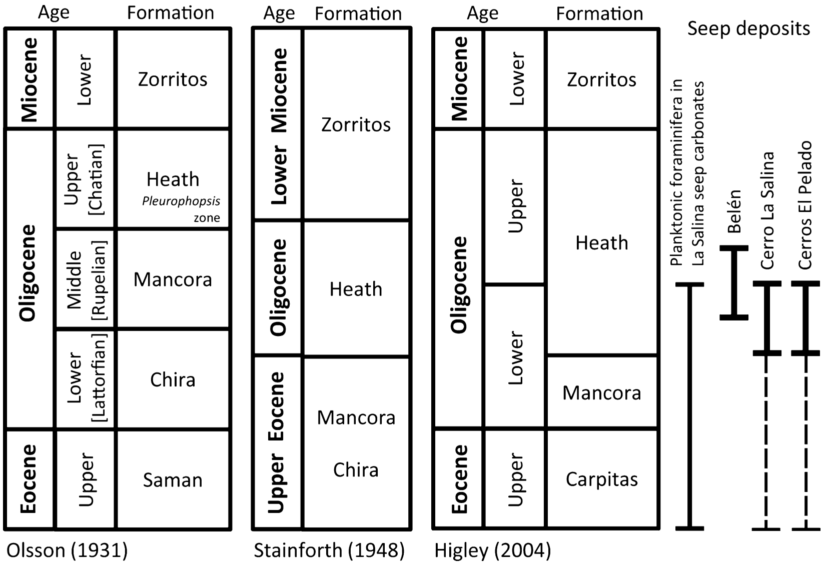


Fig. 7. Stratigraphical schemes of the northern Talara Basin and age assignments for the Belén, Cerro La Salina and Cerros El Pelado seep deposits. Solid lines in the age assignments are our interpretation of the available data, and dashed lines indicate the uncertainties discussed in the text.

(Stainforth 1948, p. 113). Thus, the overlying Heath Formation should be of early Oligocene age, and it is indeed considered as having its base in the early Oligocene in more recent stratigraphical schemes (Palacios Moncayo 1994; Higley 2004). We therefore assume an early Oligocene age for the Cerro La Salina seep deposits. It should be said, though, that all limestones were found float and that the area is mapped as Carpitas Formation in the Ingemmet geological map, although the sediments seen at Cerro La Salina do not match the description in the accompanying notes (Palacios Moncayo 1994). Obviously, a small uncertainty regarding the age of the Cerro La Salina seep deposits remains.

Most difficult to constrain is the age of the Cerros El Pelado seep deposits because no foraminifera were observed in the thin sections. Otherwise, the situation is identical to Cerro La Salina: the area was mapped as Carpitas Formation but sediments look like Heath Formation, and all limestones were found as floats. In summary, the most likely age for the seep deposits from all three areas is early Oligocene, though in the cases of Cerro La Salina and Cerros El Pelado remains the possibility of a late Eocene age.

Taphonomy and faunal diversity

Although taxonomic work is still ongoing, it is apparent that the seep deposits in the Talara Basin show a remarkable heterogeneity in faunal diversity. For example, from Belén and Pajarabobo, Olsson (1931) reported as many as 15 different species, making it the most diverse of his '*Pleurophopsis* faunas'. In contrast, we found only four species at the Belén seep site. Furthermore, Olsson reported skeletons of toothed whales from the area around Belén and Pajarabobo, which we have not seen at all. Northern Peru is subject to frequent El Nino events with heavy rainfall in an otherwise arid region, resulting in strong erosion of any soft sediment. Our impression is that a substantial portion of the Heath shales that covered the area around Belén and Pajarabobo at Olsson's time has since been eroded away, including the fossils. We would not be surprised if also the hill that we sampled would be levelled after a few more El Nino events. Adding to this view is the fact that Olsson's material from Belén and Pajarabobo seen in the PRI collection was lithologically different from our material: it seemed to lack silicification and had a softer texture compared to the material that we collected. Thus, we probably have not found the same spots that Olsson sampled, but new sites that have since weathered out of those shales.

In contrast, from the 'limestone concretion along Quebrada Seca' Olsson reported only three species, whereas we found five species at Cerros El Pelado and about 20 species at Cerro La Salina. This difference might in part result from the fact that Olsson rarely considered species smaller than about 1 cm in size and hence did not report the provannids, limpets and small trochoid and skeneid gastropods that we found. Among the more conspicuous species, we found mostly taxa that had already been reported by

Olsson from the various seep deposits of the heath Shales, including *Pleurophopsis lithophagoides*, *Conchocele tessaria* and *Lucinoma zapotalensis*. In summary, the seep faunas from the Belén and Pajarabobo area and the Cerro La Salina area do not show large overall differences and are likely to be of similar diversity. Increased sampling will likely result in the discovery of new species, especially among the small-sized ones.

The seep sites show an interesting relationship between the life habits of the fauna and sedimentological features. The Cerro La Salina seep carbonates show clear signs of bioturbation, such as nodules with corroded margins and burrows with shell fragments. This agrees well with their sediment-dwelling fauna of predominantly infaunal bivalves (thyasirids, lucinids) and common callianassid claws. These deposits were thus cemented well within the sediment and preserved mainly infaunal (sediment-dwelling) invertebrates *in situ*. In contrast, the Belén and especially the Cerros El Pelado deposits preserve mainly epifaunal and semi-infaunal mollusc associations consisting of chemosymbiotic vesicomyid bivalves and provannid gastropods that are typically confined to sites of advective seepage. These shells show evidence for reworking on the sediment surface, such as being fragmentary and layered. Furthermore, they are cemented by banded and botryoidal cement. Interestingly, banded and botryoidal cement tends to form close to the seafloor during advective seepage (Peckmann *et al.* 2009; Haas *et al.* 2010; Feng *et al.* 2016). Cementation of shells should have consequently taken place at or close to the sediment surface, and shortly after the reworking of the shells. This suggests the following taphonomic scenario: the molluscs lived at, and depended on, an active seep site; after death their shells were reworked – possibly due to expulsive seepage activity that physically rearranged shells on the sediment surface – and then were cemented by carbonate precipitation resulting from renewed or continued methane seepage and oxidation. When applied with caution, such petrographical features might hint to an epifaunal or infaunal life style of extinct taxa at fossil seep deposits from the distant geological past.

Biogeographical relationships

The studied fauna shows similarities to other Oligocene and late Eocene seep faunas worldwide. It includes some widespread genera such as the bivalves *Conchocele* (Thyasiridae) and *Lucinoma* (Lucinidae), and the gastropod *Provanna*, that are known from seeps in Japan, Washington State (USA) and the Caribbean region (Goedert & Squires 1990; Gill *et al.* 2005; Majima *et al.* 2005; Kiel 2010a,b; Kiel & Hansen 2015). Also shared among these regions is probably the vesicomyid genus *Pleurophopsis*, which most likely is a senior synonym of the North Pacific vesicomyid genus *Adulomya* (cf. Kiel 2007).

Remarkable is the presence of *Provanna antiqua* and *Colus sekiuensis*, two species known from Oligocene seep deposits in western Washington State, USA (Squires 1995; Peckmann *et al.* 2002; Kiel 2006). On the genus level, the Talara Basin seeps and the seeps in Washington share the gastropod *Pyropelta* (Kiel 2006; Kiel & Goedert 2007). With Cenozoic seeps in the Caribbean region, the Talara Basin seeps share *Pleurophopsis* (Gill *et al.* 2005; Kiel & Hansen 2015) and the abyssochrysoid gastropod *Ascheria* (Kaim *et al.* 2014). In addition to the widespread genera *Conchocele* and *Provanna*, the Japanese Oligocene seep faunas share the deep-water buccinid *Colus* with the Talara basin seep fauna (Amano *et al.* 2013).

Conclusions

Consistent with a previous assessment based on museum material (Kiel & Peckmann 2007), our new carbon stable isotope and biomarker data confirm that the carbonate deposits with the *Pleurophopsis* fauna from the Talara Basin in northern Peru are methane-seep deposits with a typical seep fauna. Regarding the stratigraphical age of the deposits, the simplest and perhaps least conflicting stratigraphical scheme we can offer is that Olsson was correct in that the *Pleurophopsis*-bearing carbonate rocks occur in the lower part of the Heath Formation and that the Heath Formation is not entirely of late Oligocene age (as stated by Olsson) but instead has its base in the early Oligocene. Thus, we consider the seep deposits to be of early Oligocene age, though in the case of the sites around Quebrada Seca (the Cerro La Salina and Cerros El Pelado sites), we cannot entirely exclude a late Eocene age.

Biogeographically the fauna shares genera with late Eocene to Oligocene seep faunas from all other regions worldwide, including Japan, the northwestern United States and the Caribbean region. Fossil seep faunas are rare in the Southern Hemisphere, and our study shortens the stratigraphical gap in Southern Hemisphere seep faunas between the Late Cretaceous (New Zealand; Kiel *et al.* 2013) and the Miocene (New Zealand; Campbell *et al.* 2010; Chile; Contardo-Berríos *et al.* 2017). Typical present-day seep-inhabiting taxa such as bathymodiolins, vesicomyids, *Provanna* and *Pyropelta* were present in the Southern Hemisphere by the early Oligocene at latest. The record of *Idas* represents the earliest bathymodiolin from the Southern Hemisphere and contradicts claims that bathymodiolins radiated globally only in the Miocene (Miyazaki *et al.* 2010).

The Peruvian seep deposits show a notable agreement between petrographical and faunal observations. The Cerro La Salina sites show petrographical evidence for bioturbation, such as burrows and a nodular fabric, which agrees with the observed predominance of infaunal bivalves and the common callianassid claws. In contrast, the Belén and Cerros El Pelado deposits show petrographical evidence for reworking of shells on the sediment surface and their subsequent cementation in the very shallow subsurface. This agrees with the predominance of semi-infaunal vesicomyid bivalves and epifaunal provannid gastropods. When applied with caution, such petrographical features might be used to infer the mode of life (i.e., epifaunal *versus* infaunal) of extinct taxa at fossil seeps from the more distant geological past.

Acknowledgements. – We thank Tom DeVries (Burton, WA) and Rodolfo Salas-Gismondi (Lima) for help with fieldwork, Nicola Krake (Hamburg) for extraction and preparation of lipid biomarkers, and Jim Goedert (Wauna) for discussion of fossil molluscs. Andrzej Kaim (Warsaw) and an anonymous reviewer are thanked for their constructive criticism of the manuscript. Financial support was provided by Vetenskapsrådet through Grant 2016-03920 to SK.

References

Amano, K. & 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. & Kiel, S. 2007: Fossil vesicomyid bivalves from the North Pacific region. *The Veliger 49*, 270–293.

Amano, K., Jenkins, R.G., Aikawa, M. & Nobuhara, T. 2010: A Miocene chemosynthetic community from the Ogaya Formation in Joetsu: evidence for depth-related ecologic control among fossil seep communities in the Japan Sea back-arc basin. *Palaeogeography, Palaeoclimatology, Palaeoecology 286*, 164–170.

Amano, K., Jenkins, R.G., Sako, Y., Ohara, M. & Kiel, S. 2013: A Paleogene deep-sea methane-seep community from Honshu, Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology 387*, 126–133.

Banta, A.B., Wei, J.H. & Welander, P.V. 2015: A distinct pathway for tetrahymanol synthesis in bacteria. *Proceedings of the National Academy of Sciences of the USA 112*, 13478–13483.

Bertram, S., Blumenberg, M., Michaelis, W., Siegert, M., Krüger, M. & Seifert, R. 2013: Methanogenic capabilities of ANME-archaea deduced from ^{13}C-labelling approaches. *Environmental Microbiology 15*, 2384–2393.

Birgel, D. & Peckmann, J. 2008: Aerobic methanotrophy at ancient marine methane seeps: A synthesis. *Organic Geochemistry 39*, 1659–1667.

Birgel, D., Elvert, M., Han, X. & Peckmann, J. 2008a: ^{13}C-depleted biphytanic diacids as tracers of past anaerobic oxidation of methane. *Organic Geochemistry 39*, 152–156.

Birgel, D., Himmler, T., Freiwald, A. & Peckmann, J. 2008b: A new constraint on the antiquity of anaerobic oxidation of methane: Late Pennsylvanian seep limestones from southern Namibia. *Geology 36*, 543–546.

Blumenberg, M., Seifert, R., Reitner, J., Pape, T. & Michaelis, W. 2004: Membrane lipid patterns typify distinct anaerobic methanotrophic consortia. *Proceedings of the National Academy of Sciences of the USA 101*, 11111–11116.

Bosworth, T.O. 1922: *Geology of the Tertiary and Quaternary Periods in the North-West Part of Peru, with an Account of the Paleontology by H. Woods*, 434 pp. Macmillan and Co, London.

Campbell, K.A. 2006: Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: Past developments and future research directions. *Palaeogeography, Palaeoclimatology, Palaeoecology 232*, 362–407.

Campbell, K.A., Nelson, C.S., Alfaro, A.C., Boyd, S., Greinert, J., Nyman, S., Grosjean, E., Logan, G.A., Gregory, M.R., Cooke, S., Linke, P., Milloy, S. & Wallis, I. 2010: Geological imprint of methane seepage on the seabed and biota of the convergent Hikurangi Margin, New Zealand: Box core and grab carbonate results. *Marine Geology 272*, 285–306.

Charrier, R., Pinto, L. & Rodríguez, M. 2007: Tectonostratigraphic evolution of the Andean Orogen in Chile. In Moreno, T. & Gibbons, W. (eds): *The Geology of Chile*, 21–114. The Geological Society of London, Special Publication, London.

Contardo-Berríos, X., Mena-Hodges, E. & 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.

Corliss, J.B., Dymond, J., Gordon, L.I., Edmond, J.M., Von Herzen, R.P., Ballard, R.D., Green, K., Williams, D., Bainbridge, A., Crane, K. & Van Andel, T.H. 1979: Submarine thermal springs on the Galápagos Rift. *Science 203*, 1073–1083.

Dando, P.R. 2010: Biological communities at marine shallow-water seep and vent sites. In Kiel, S. (ed): *The Vent and Seep Biota*, volume *33*, 333–378. Springer, Heidelberg.

Feng, D., Birgel, D., Peckmann, J., Roberts, H.H., Joye, S.B., Sassen, R., Liu, X.-L., Hinrichs, K.-U. & Chen, D. 2014: Time integrated variation of sources of fluids and seepage dynamics archived in authigenic carbonates from Gulf of Mexico Gas Hydrate Seafloor Observatory. *Chemical Geology 385*, 129–139.

Feng, D., Peng, Y., Bao, H., Peckmann, J., Roberts, H.H. & Chen, D. 2016: A carbonate-based proxy for sulfate-driven anaerobic oxidation of methane. *Geology 44*, 999–1002.

Fisher, C.R. 1995: Toward an appreciation of hydrothermal-vent animals: Their environment, physiological ecology, and tissue stable isotope values. *In* Humphris, S.E., Zierenberg, R.A., Mullineaux, L.S. & Thomson, R.E. (eds): *Seafloor Hydrothermal Systems: Physical, Chemical, Biological, and Geochemical Interactions*, 297–316. Geophysical Monograph Series, Blackwell, Washington, DC.

Gaillard, C., Bourseau, J.-P., Boudeulle, M., Pailleret, P., Rio, M. & Roux, M. 1985: Les pseudo-biohermes de Beauvoisin (Drôme): un site hydrothermal sur lar marge téthysienne a l'Oxfordien? *Bulletin de la Société Géologique de France 8*, 69–78.

Gill, F.L., Harding, I.C., Little, C.T.S. & Todd, J.A. 2005: Palaeogene and Neogene cold seep communities in Barbados, Trinidad and Venezuela: An overview. *Palaeogeography, Palaeoclimatology, Palaeoecology 227*, 191–209.

Gischler, E., Birgel, D., Brunner, B., Eisenhauer, A., Meyer, G., Buhre, S. & Peckmann, J. 2017: A giant underwater, encrusted stalactite from the Blue Hole, Lighthouse Reef, Belize, revisited: A complex history of biologically induced carbonate accretion under changing meteoric and marine conditions. *Journal of Sedimentary Research 87*, 1260–1284.

Goedert, J.L. & Squires, R.L. 1990: Eocene deep-sea communities in localized limestones formed by subduction-related methane seeps, southwestern Washington. *Geology 18*, 1182–1185.

Goedert, J.L. & Squires, R.L. 1993: First Oligocene record of *Calyptogena* (Bivalvia: Vesicomyidae). *The Veliger 36*, 72–77.

Grzybowski, J.. 1899: Die Tertiärablagerungen des nördlichen Peru und ihre Molluskenfauna. Beiträge zur Geologie und Paläontologie von Südamerika. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band 12*, 610–644.

Haas, A., Peckmann, J., Elvert, M., Sahling, H. & Bohrmann, G. 2010: Patterns of carbonate authigenesis at the Kouilou pockmarks on the Congo deep-sea fan. *Marine Geology 268*, 129–136.

Higley, D. 2004: The Talara basin province of northwestern Peru: Cretaceous-Tertiary total petroleum system. *U.S. Geological Survey e-bulletin B-2206a*, 52.

Hryniewicz, K., Amano, K., Jenkins, R.G. & Kiel, S. 2017: Thyasirid bivalves from Cretaceous and Paleogene cold seeps. *Acta Palaeontologica Polonica 62*, 705–728.

Isaacson, P.E. & Diaz Martinez, E. 1995: Evidence for a middle-late Paleozoic foreland basin and significant paleolatitudinal shift, Central Andes. *American Association of Petroleum Geologists Memoir 62*, 231–249.

Jaillard, E., Ordonez, M., Benitez, S., Berrones, G., Jimenez, N., Montenegro, G. & Zombrano, I. 1995: Basin development in an accretionary, oceanic-floored forearc setting: southern coastal Ecuador during Late Cretaceous–late Eocene time. *American Association of Petroleum Geologists Memoir 62*, 615–631.

Kaim, A., Jenkins, R.G., Tanabe, K. & Kiel, S. 2014: Mollusks from late Mesozoic seep deposits, chiefly in California. *Zootaxa 3861*, 401–440.

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 vesicomyid bivalve *Pleurophopsis*. *Acta Palaeontologica Polonica 52*, 639–642.

Kiel, S. 2010a: An Eldorado for paleontologists: the Cenozoic seep deposits of western Washington State, USA. In Kiel, S. (ed): *The Vent and Seep Biota*, volume *33*, 433–448. Springer, Heidelberg.

Kiel, S. 2010b: The fossil record of vent and seep mollusks. In Kiel, S. (ed): *The Vent and Seep Biota*, volume *33*, 255–278. Springer, Heidelberg.

Kiel, S. 2010c: 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. 2015: Did shifting seawater sulfate concentrations drive the evolution of deep-sea vent and seep ecosystems? *Proceedings of the Royal Society B 282*, 20142908.

Kiel, S. 2016: A biogeographic network reveals evolutionary links between deep sea hydrothermal vent and methane seep faunas. *Proceedings of the Royal Society B 283*, 20162337.

Kiel, S. & Amano, K. 2013: The earliest bathymodiolin mussels: Evaluation of Eocene and Oligocene taxa from deep-sea methane seep deposits in western Washington State, USA. *Journal of Paleontology 87*, 589–602.

Kiel, S. & 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. & Hansen, B.T. 2015: Cenozoic methane-seep faunas of the Caribbean region. *PLoS ONE 10*, e0140788.

Kiel, S. & Peckmann, J. 2007: Chemosymbiotic bivalves and stable carbon isotopes indicate hydrocarbon seepage at four unusual Cenozoic fossil localities. *Lethaia 40*, 345–357.

Kiel, S., Birgel, D., Campbell, K.A., Crampton, J.S., Schiøler, P. & Peckmann, J. 2013: Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology 390*, 17–34.

Kuechler, R.R., Birgel, D., Kiel, S., Freiwald, A., Goedert, J.L., Thiel, V. & Peckmann, J. 2012: Miocene methane-derived carbonates from southwestern Washington, USA, and a model for silicification at seeps. *Lethaia 45*, 259–273.

Lloyd, K.G., Alperin, M.J. & Teske, A. 2011: Environmental evidence for net methane production and oxidation in putative anaerobic methanotrophic (ANME) archaea. *Environmental Microbiology 13*, 2548–2564.

Lonsdale, P. 1978: Ecuadorian subduction system. *American Association of Petroleum Geologists Bulletin 62*, 2454–2477.

Macellari, C.E. & DeVries, T.J. 1987: Late Cretaceous upwelling and anoxic sedimentation in northwestern South America. *Palaeogeography, Palaeoclimatology, Palaeoecology 59*, 279–292.

Majima, R., Nobuhara, T. & Kitazaki, T. 2005: Review of fossil chemosynthetic assemblages in Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology 227*, 86–123.

Manchester, S.R., Herrera, F., Fourtanier, E., Barron, J. & Martinez, J.-N. 2012: Oligocene age of the classic Belén fruit and seed assemblage of North coastal Peru based on diatom biostratigraphy. *Journal of Geology 120*, 467–476.

Miyazaki, J.-I., Martins, L.D.O., Fujita, Y., Matsumoto, H. & Fujiwara, Y. 2010: Evolutionary process of deep-sea *Bathymodiolus* mussels. *PLoS ONE 5*, e10363.

Moalic, Y., Desbruyères, D., Duarte, C.M., Rozenfeld, A.F., Bachraty, C. & Arnaud-Haond, S. 2012: Biogeography revisited with network theory: Retracing the history of hydrothermal vent communities. *Systematic Biology 61*, 127–137.

Montagna, A., Leyva, J., Ortega, J., Rodrequez, J., Palomino, D. & Yesquen, S. 1999: Caracterizacion de reservorios maduros en el noroeste Peruano. 16. Exploration and exploitation of petroleum and gas, Ingepet ‘99 seminar, Oct. 26-29, EXPL-SY-04.pdf, Lima, Peru.

Naehr, T.H., Eichhubl, P., Orphan, V.J., Hovland, M., Paull, C.K., Ussler, W., Lorenson, T.D. & Green, H.G. 2007: Authigenic carbonate formation at hydrocarbon seeps in continental margin sediments: A comparative study. *Deep-Sea Research II 54*, 1268–1291.

Natalicchio, M., Peckmann, J., Birgel, D. & Kiel, S. 2015: Seep deposits from northern Istria, Croatia: a first glimpse into the Eocene seep fauna of the Tethys region. *Geological Magazine 152*, 444–459.

Niemann, H. & Elvert, M. 2008: Diagnostic lipid biomarker and stable carbon isotope signatures of microbial communities mediating the anaerobic oxidation of methane with sulphate. *Organic Geochemistry 39*, 1668–1677.

Olsson, A.A. 1928: Contributions to the Tertiary paleontology of northern Peru: Part 1, Eocene Mollusca and Brachiopoda. *Bulletins of American Paleontology 14*, 5–186.

Olsson, A.A. 1929: Contributions to the Tertiary paleontology of northern Peru: Part 2, Upper Eocene Mollusca and Brachiopoda. *Bulletins of American Paleontology 15*, 1–120.

Olsson, A.A. 1930: Contributions to the Tertiary paleontology of northern Peru: Part 3, Eocene Mollusca. *Bulletins of American Paleontology 17*, 1–96.

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. 1932: Contributions to the Tertiary paleontology of northern Peru: Part 5, The Peruvian Miocene. *Bulletins of American Paleontology 19*, 1–216.

Olsson, A.A. 1942: Tertiary deposits of northwestern South America and Panama. *In* Oehser, P.H. (ed.): *Proceedings of the 8th American Science Congress held in Washington, 1940, volume 4*, 231–287.

Orphan, V.J., Ussler, W.I., Naehr, T., House, C.H., Hinrichs, K.-U. & Paull, C.K. 2004: Geological, geochemical, and microbiological heterogeneity of the seafloor around methane vents in the Eel River Basin, offshore California. *Chemical Geology 205*, 265–289.

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 Ingemmet. Boletín Ingemmet. Serie A: Carta Geológica Nacional 54*, 1–190.

Paull, C.K., Hecker, B., Commeau, R., Freeman-Lynde, R.P., Neumann, C., Corso, W.P., Golubic, S., Hook, J.E., Sikes, E. & Curray, J. 1984: Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science 226*, 965–967.

Pearson, P.N., Olsson, R.K., Hemleben, C., Huber, B.T. & Berggren, W.A. 2006: *Atlas of Eocene Planktonic Foraminifera Cushman Foundation of Foraminiferal Research*, *Special Publication, Volume 41*, 513 pp. Allen Press, Lawrence, Kansas.

Peckmann, J. & Thiel, V. 2004: Carbon cycling at ancient methane-seeps. *Chemical Geology 205*, 443–467.

Peckmann, J., Thiel, V., Michaelis, W., Clari, P., Gaillard, C., Martire, L. & Reitner, J. 1999: Cold seep deposits of Beauvoisin (Oxfordian; southeastern France) and Marmorito (Miocene; northern Italy): microbially induced authigenic carbonates. *International Journal of Earth Sciences 88*, 60–75.

Peckmann, J., Goedert, J.L., Thiel, V., Michaelis, W. & 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.

Peckmann, J., Thiel, V., Reitner, J., Taviani, M., Aharon, P. & Michaelis, W. 2004: A microbial mat of a large sulfur bacterium preserved in a Miocene methane-seep limestone. *Geomicrobiology Journal 21*, 247–255.

Peckmann, J., Birgel, D. & Kiel, S. 2009: Molecular fossils reveal fluid composition and flow intensity at a Cretaceous seep. *Geology 37*, 847–850.

Raez Lurquin, M.A. 1999: *Tectonica en la cuenca Talara costaafuera, nor-oeste Peru. 19*. Exploration and exploitation of petroleum and gas, Ingepet ‘99 seminar, Oct. 26-29, 1 CD-ROM, EXPR-1-MR-12.pdf, Lima, Peru.

Ritger, S.D., Carson, B. & Suess, E. 1987: Methane-derived authigenic carbonates formed by subduction-induced pore-water expulsion along the Oregon/Washington margin. *Geological Society of America Bulletin 98*, 147–156.

Sahling, H., Galkin, S.V., Salyuk, A., Greinert, J., Foerstel, H., Piepenburg, D. & Suess, E. 2003: Depth-related structure and ecological significance of cold-seep communities - a case study from the Sea of Okhotsk. *Deep-Sea Research I 50*, 1391–1409.

Seranne, M. 1987: Evolution tectono-sedimentaire du Bassin de Talara (nord-ouest du Perou). *Bulletin de l'Institut Français des Etudes Andines 14*, 103–125.

Smrzka, D., Zwicker, J., Kolonic, S., Birgel, D., Little, C.T.S., Marzouk, A.M., Chellai, E.H., Wagner, T. & Peckmann, J. 2017: Methane seepage in a Cretaceous greenhouse world recorded by an unusual carbonate deposit from the Tarfaya Basin, Morocco. *The Depositional Record 3*, 4–37.

Smrzka, D., Zwicker, J., Misch, D., Walkner, C., Gier, S., Monien, P., Bohrmann, G. & Peckmann, J. in press: Oil seepage and carbonate formation: a case study from the southern Gulf of Mexico. *Sedimentology*. https://doi.org/10.1111/sed.12593.

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.

Stainforth, R.M. 1948: Applied micropaleontology in coastal Ecuador. *Journal of Paleontology 22*, 113–151.

Tarasov, V.G., Gebruk, A.V., Mironov, A.N. & Moskalev, L.I. 2005: Deep-sea and shallow-water hydrothermal vent communities: Two different phenomena? *Chemical Geology 224*, 5–39.

Taviani, M. 1994: The ‘calcari a *Lucina*’ macrofauna reconsidered: Deep-sea faunal oases from Miocene-age cold vents in the Romagna Apennine, Italy. *Geo-Marine Letters 14*, 185–191.

Tunnicliffe, V. & Fowler, M.R. 1996: Influence of sea-floor spreading on the global hydrothermal vent fauna. *Nature 379*, 531–533.

Van Dover, C.L., German, C.R., Speer, K.G., Parson, L.M. & Vrijenhoek, R.C. 2002: Evolution and biogeography of deep-sea vent and seep invertebrates. *Science 295*, 1253–1257.

Van Winkle, K. 1919: Remarks on some new species from Trinidad. *Bulletins of American Paleontology 8*, 19–27.

Wade, B.S., Olsson, R.K., Pearson, P.N., Huber, B.T. & Berggren, W.A. 2018: Atlas of Oligocene Planktonic Foraminifera. *Cushman Foundation Special Publication 46*, 1–528.

Ziegler, A.M., Barrett, S.F. & Scotese, C.R. 1981: Paleoclimate, sedimentation, and continental accretion. *Philosophical Transactions of the Royal Society of London A301*, 253–264.

Zúñiga-Rivero, F. & Hay-Roe, H. 1998: Oil, gas potential in shallow water: Peru's continental shelf basins. *Oil and Gas Journal 16*, 92–96.

Zúñiga-Rivero, F., Keeling, J.A. & Hay-Roe, H. 1998: Attractive potential seen in 10 sub-basins off Peru. *Oil and Gas Journal 7*, 117–122.

Zúñiga-Rivero, F., Hay-Roe, H. & Vargas, T. 1999: Talara: A new look at an old petroleum basin. p. Exploration and exploitation of petroleum and gas, Ingepet ‘99 seminar, Oct. 26-29, EXPR-1-FZ-15.pdf, Lima, Peru.

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

STEFFEN KIEL, FRIDA HYBERTSEN, MATÚŠ HYŽNÝ, and ADIËL A. KLOMPMAKER

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 (X): xxx–xxx.

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 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.

Steffen Kiel [steffen.kiel@nrm.se] and Frida Hybertsen [frida.hybertsen@nrm.se], Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, 10405 Stockholm, Sweden.
Matúš Hyžný [matus.hyzny@uniba.sk], Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia.
Adiël A. Klompmaker [adielklompmaker@gmail.com], Department of Integrative Biology & Museum of Paleontology, University of California, Berkeley, 1005 Valley Life Sciences Building #3140, Berkeley, CA 94720, USA; The University of Alabama Museums & Alabama Museum of Natural History, The University of Alabama, Box 870340, Tuscaloosa, AL 35487, USA.

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

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 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).

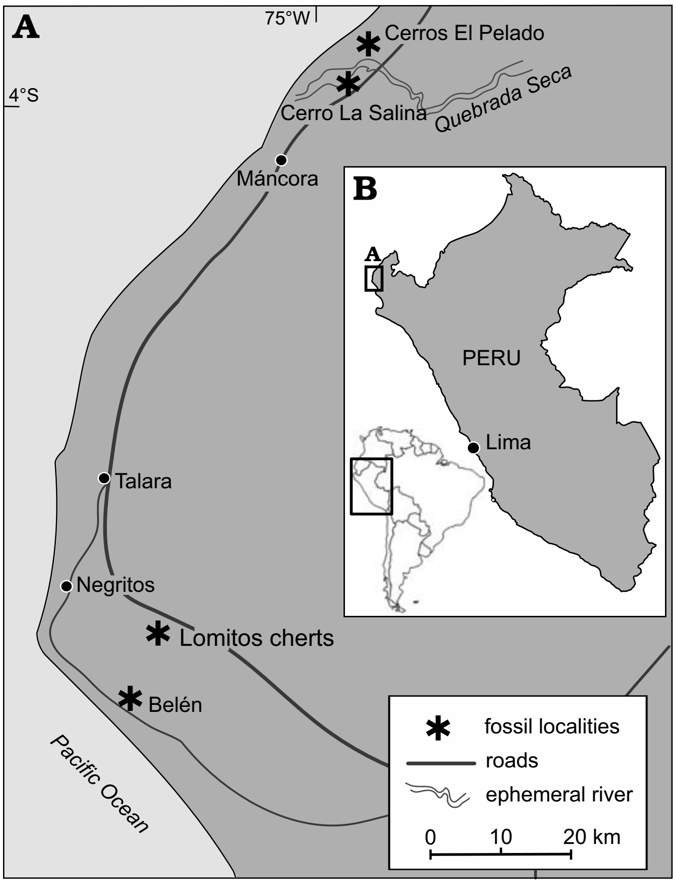


Fig. 1. Locality map of the seep deposits in the Talara Basin in northern Peru, where the here described mollusk and crustacean taxa were found (adopted from Kiel et al. 2019).

We also illustrate 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 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.

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 a left valve, 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

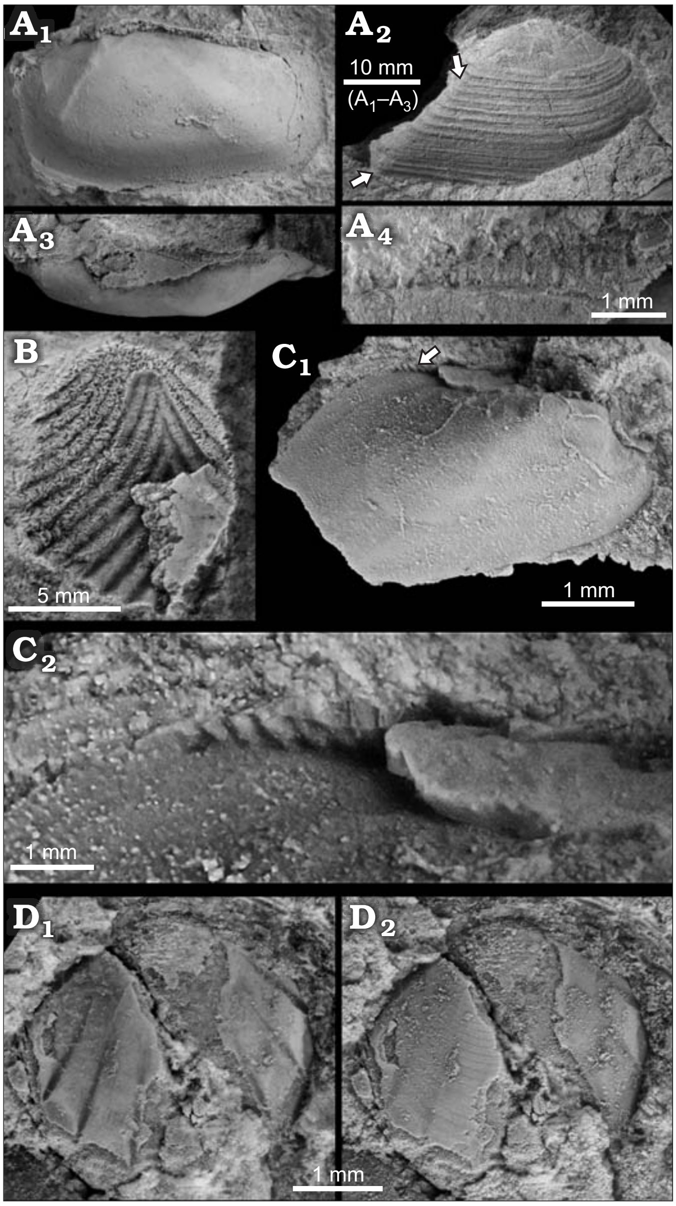


Fig. 2. Protobranch and pteriomorph bivalves from early Oligocene seep deposits from the Cerro La Salina (block 1, A; block 6, D; block 9, C) and Belén seep deposit (B), Talara Basin, northern Peru. **A**. Malletiid *Neilo altamirano* sp. nov. (NRM Mo187001, holotype), internal mold in lateral view (A_1); external mold in lateral view (A_2), arrows indicating the posterior ridge; view on the dorsal side (A_3); close-up on the taxodont hinge dentition (A_4). **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_1), arrow indicating the taxondont teeth; close-up on taxodont teeth on posterodorsal shell margin (C_2). **D**. Propeamussiidae indet. (NRM Mo187004), uncoated specimen showing internal radial ridges (D_1); specimen coated with ammonium-chloride, highlighting external sculpture (D_2).

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

Dimensions.—The holotype is 20 mm long, 12 mm high and the single valve is 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, width 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 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, length 4 mm) from the Oligocene Cerro La Salina block 9, northern Peru.

Remarks.—The single specimen consists of a right valve 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.

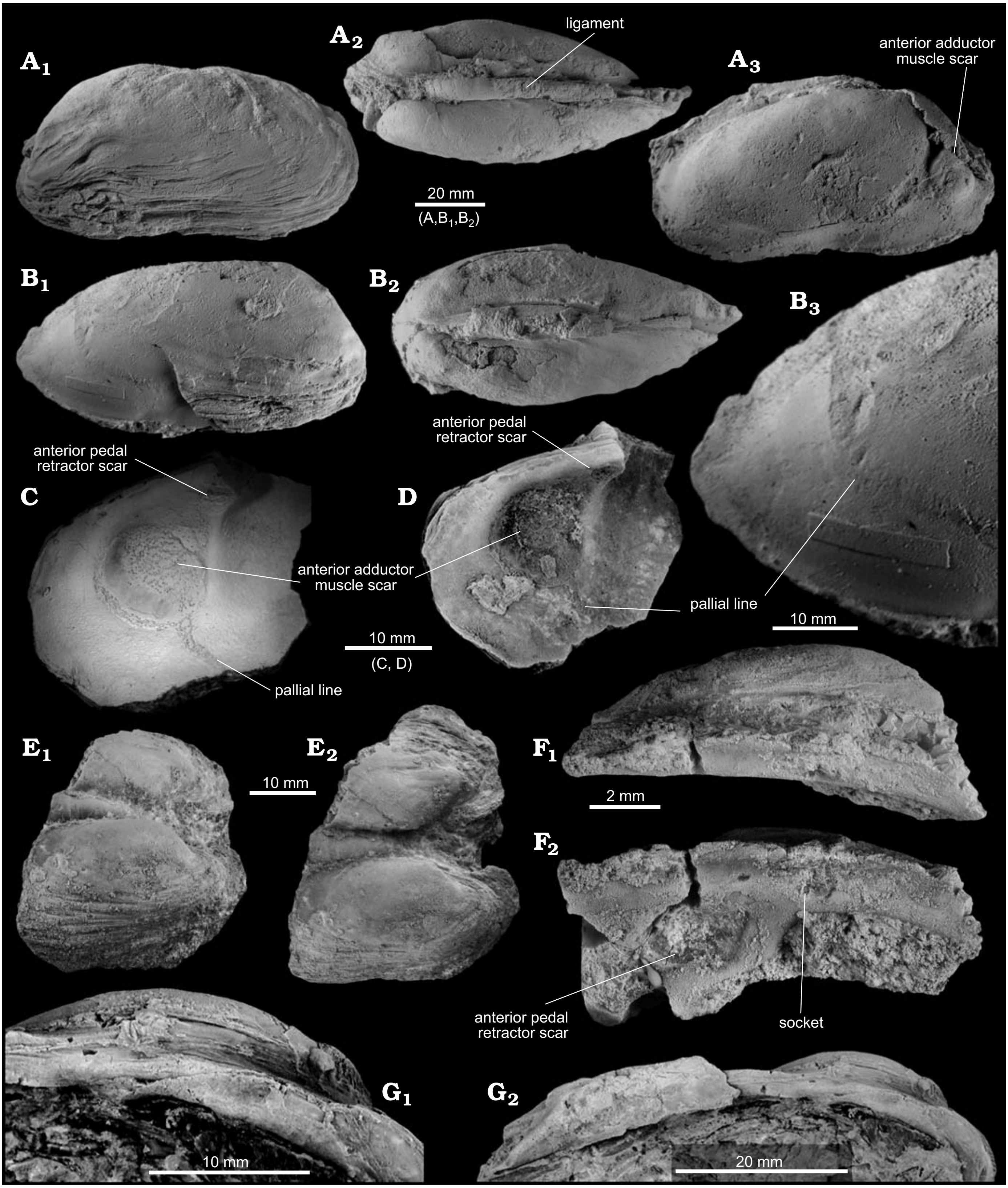
Etymology: For its superficial similarity to the vesicomyid genus *Pleurophopsis*.

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 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 *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 Vesicomyidae (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$_1$) 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$_1$), the long and thick ligament (A$_2$) and deep anterior adductor muscle scar (A$_3$). **B**. Large articulated specimen (USNM PAL 728208) →



showing posterior half of pallial line (B_1, B_3) and thick ligament (B_2). **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_1) and dorsal view (E_2). **F**. Fragment (NRM Mo187028) preserving edentulous hinge area (F_1) and large anterior pedal retractor scar (F_2). **G**. Dorsal shell margin of large left valve (USNM PAL 530295), showing edentulous hinge. 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 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 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 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 genus {?} (max. 35 mm in length), 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 the following dif-

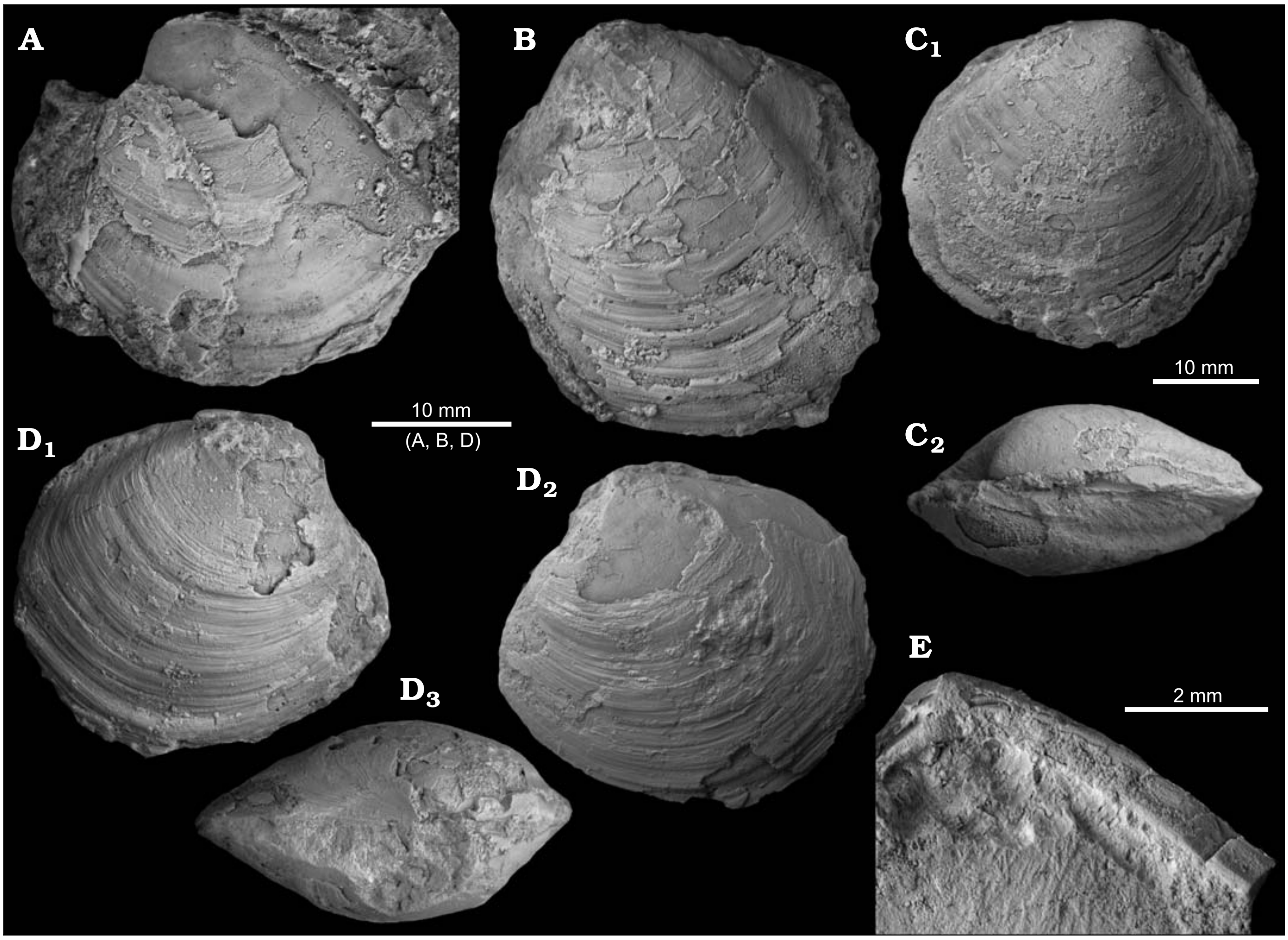


Fig. 4. The thyasirid *Conchocele tessaria* (Olsson, 1931) from early Oligocene seep deposits at Cerro La Salina (block 1, E; block 7, A–C; block 8, D), Talara Basin, northern Peru. **A**, **B**. Left valve of large specimen (**A**, NRM Mo187005; **B**, NRM Mo187006). **C**. Medium-sized specimen (NRM Mo187007), right valve showing fine growth increments (C_1), dorsal view showing lunule (C_2), left valve showing dorsal sulcus (C_3). **D**. Small specimen (NRM Mo187008), left valve showing a healed shell injury (D_1), right valve showing dorsal sulcus (D_2) and dorsal view showing lunule posterior area (D_3). **E**. Small specimen (NRM Mo187010) showing hinge of right valve.

ferences 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. kiritachiensis* 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 the left valve, 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.

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 [22–27 mm length] specimens, 0.33–0.40 of the five largest [32–40 mm length] 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.

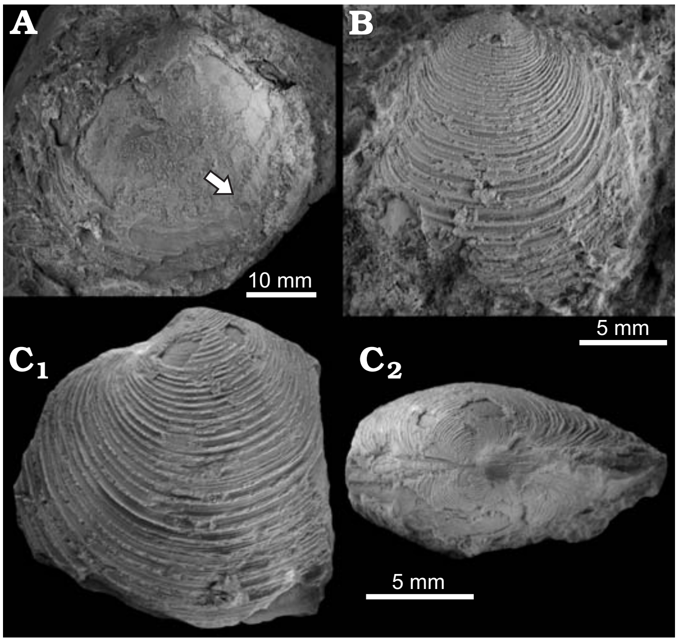


Fig. 5. The lucinid *Lucinoma zapotalensis* (Olsson, 1931) from early Oligocene seep deposit at Cerro La Salina (block 1, C; block 9, A) and Cerros El Pelado (block 2, B), Talara Basin, northern Peru. **A**. Internal mold of large left valve (NRM Mo187011), left valve showing anterior adductor muscle scar (arrow). **B**. NRM Mo187012, external sculpture on right valve. **C**. Articulated specimen (NRM Mo187013), showing external sculpture on left valve (C_1) and lunule and ligament in dorsal view (C_2).

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

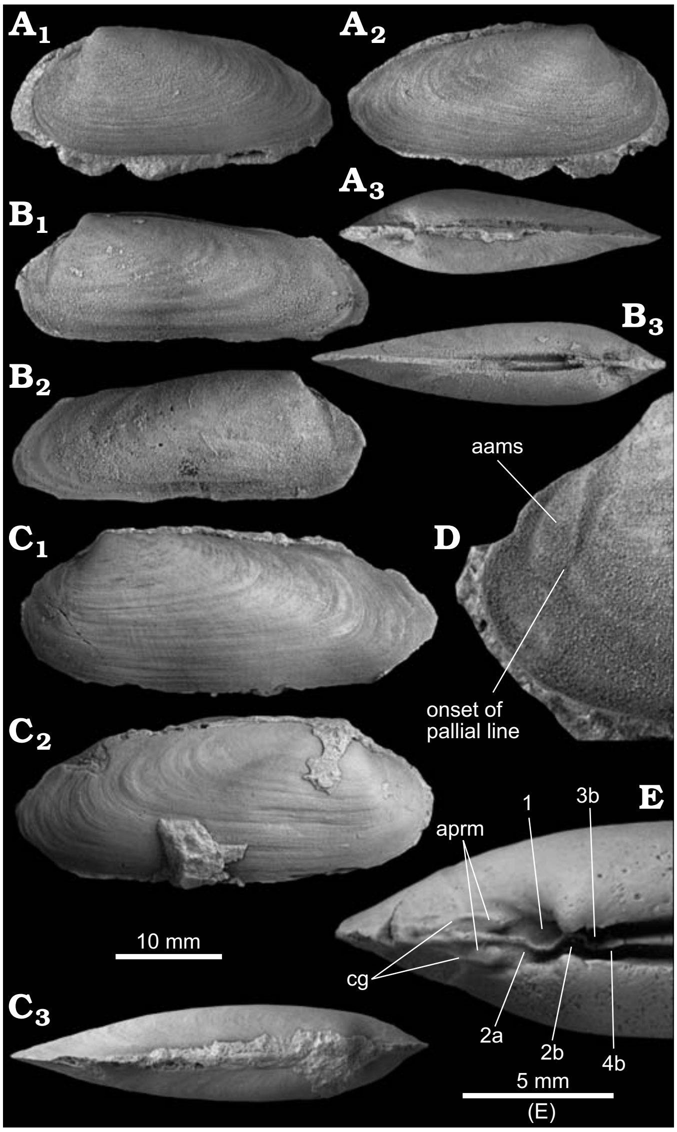


Fig. 6. The vesicomyid *Pleurophopsis lithophagoides* Olsson, 1931, from the early Oligocene Belén seep site, Talara Basin, northern Peru. **A**. Specimen with strongly sloping posterodorsal margin (NRM Mo187014), left valve (A_1), right valve (A_2), and dorsal view (A_3). **B**. Specimen with rather straight posterodorsal margin (NRM Mo187015), left valve (B_1), right valve (B_2), and dorsal view (B_3). **C**. Large specimen (NRM Mo187016), left valve (C_1), right valve (C_2), and dorsal view (C_3). **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 grove between aams and aprs; LV, left valve.

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 left valve (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

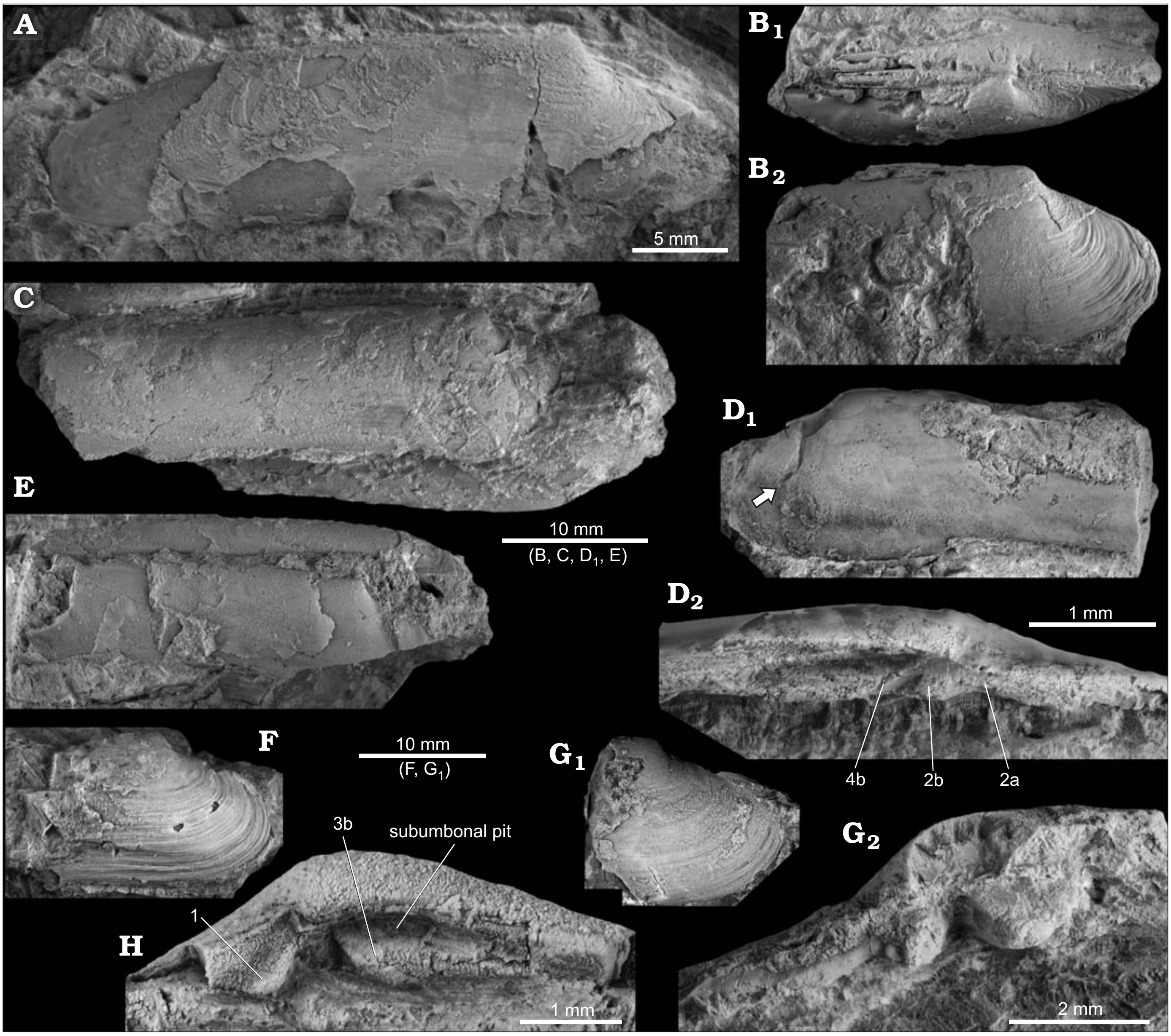


Fig. 7. The vesicomyid *Pleurophopsis talarensis* sp. nov., from early Oligocene seep deposits at Cerro La Salina (block 6, A, D, F–H; block 7, E; block 9, B, C), Talara Basin, northern Peru. **A**. Holotype (NRM Mo187019), right valve showing shell outline. **B**. Paratype (NRM Mo187022), posteriorly 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 fight 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.

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 Humptulips 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

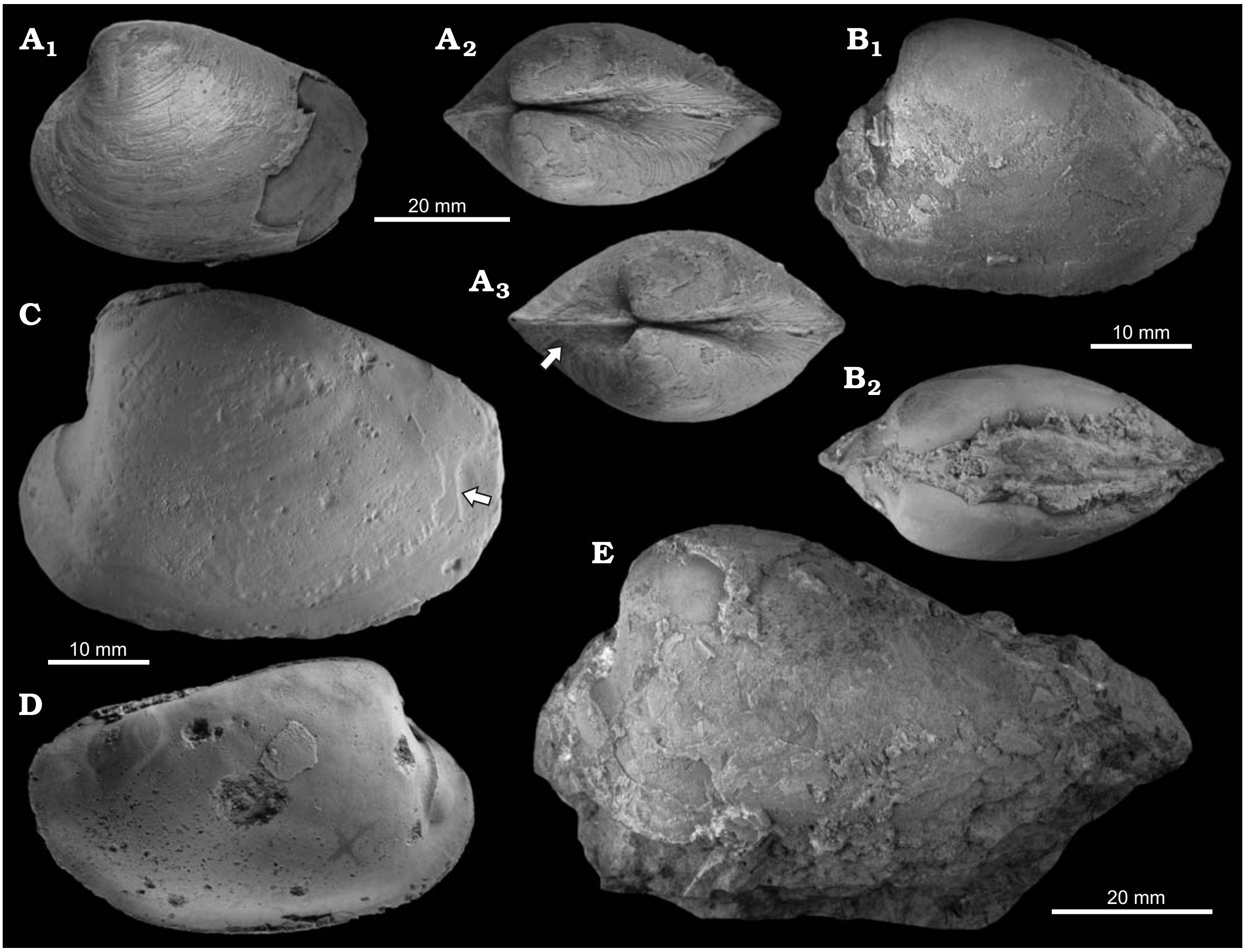


Fig. 8. The vesicomyids "*Vesicomya*" *tschudi* Olsson, 1931 (A–C, E) and "*Vesicomya*" *ramondi* Olsson, 1931 (D), from early Oligocene seep deposits in the Talara Basin, northern Peru. **A**. Small specimen (NRM Mo187029) from Cerro La Salina block 1, view on left valve (A_1), dorsal view (A_2), view on anterodorsal side showing lunular incision (A_3, arrow). **B**. Medium-sized specimen (NRM Mo187030) from Cerro La Salina block 5, view on left valve (B_1) and dorsal view (B_2). **C**. Holotype (PRI 1965) from Pajarabobo, view on left valve showing posterior end of pallial line (arrow); deposited at PRI. **D**. Holotype (PRI 1962), from Pajarabobo, view on right valve; deposited at PRI. **E**. Large left valve (NRM Mo187031) from Cerro La Salina block 5, view of the outer side.

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.

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
P. akanudaensis	71.1	32.9	0.39	0.24–0.4	concave	turns to anterior	Japan Sea	middle Miocene	Miyajima et al. 2017
P. chinookensis	90	27	0.3	0.73	straight to slightly convex	turns postero-dorsally	Washington state, USA	late Eocene–Oligocene	Squires and Goedert 1991
P. chitanii	70.4	21	0.3	0.7	straight to concave	turns to anterior	Japan	early to early middle Miocene	Amano and Kiel 2011
P. hamuroi	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
P. hokkaidoensis	66.2	22.6	0.34	weakly inflated	slightly concave	turns to anterior	Japan Sea	early middle Miocene	Amano and Kiel 2007
P. kuroiwaensis	66.7	24.6	0.34	0.6	slightly convex	turns to anterior	Japan Sea	latest middle Miocene	Amano and Kiel 2011
P. lithophagoides	40	15	0.33	0.58–0.66	straight to slightly convex	?	northern Peru	early Oligocene	Olsson 1931; and this paper
P. matsumotoi	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
P. talarensis	37	9.5	0.26	0.61–0.63	straight	?	northern Peru	early Oligocene	this paper
P. uchimuraensis	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
P. unioides	77	33	0.43	0.55	straight to slightly convex	slight turn to anterior	Trinidad	middle Miocene	Van Winkle 1919; Kiel 2007

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 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.

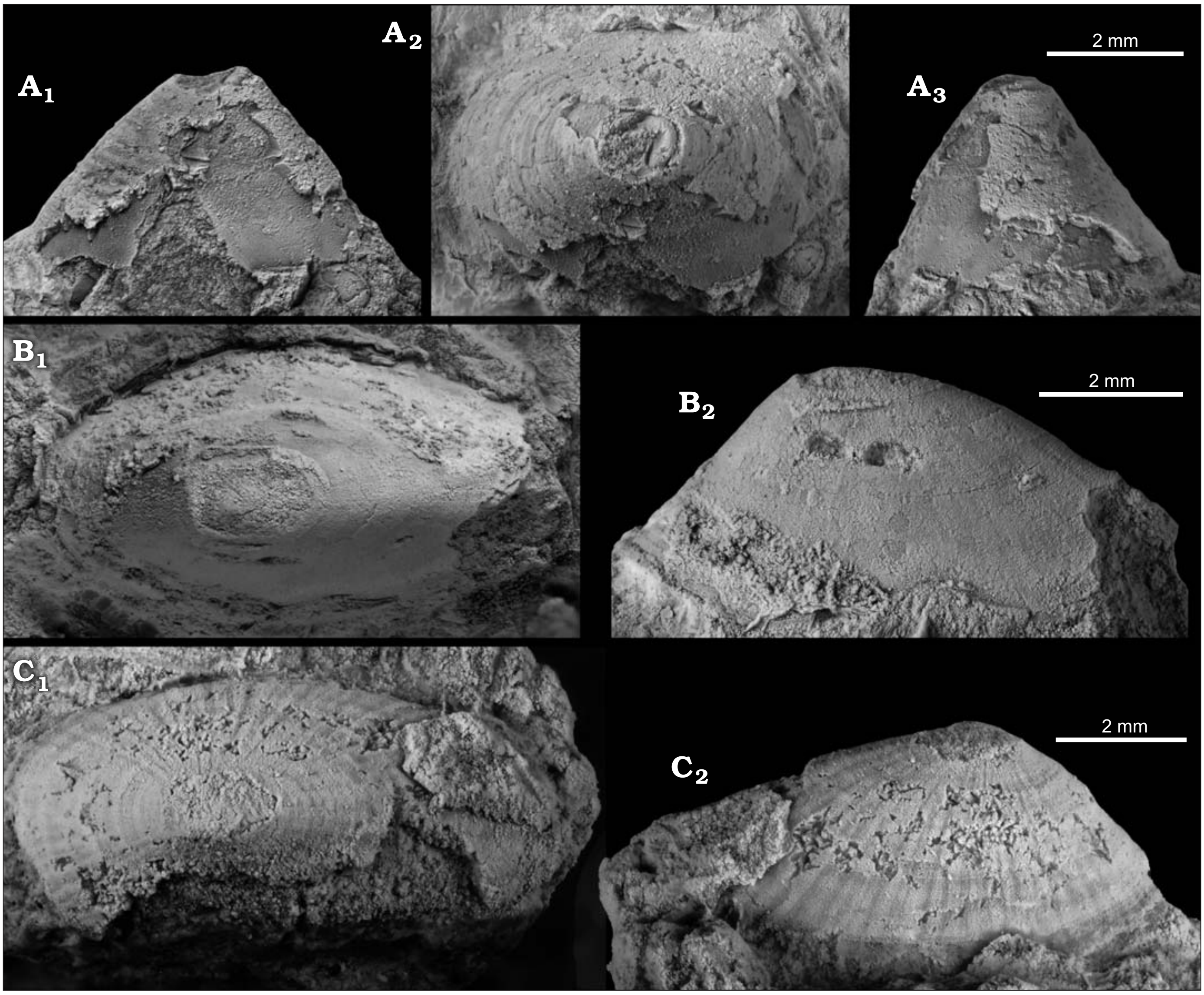


Fig. 9. Limpet gastropods from early Oligocene seep deposits at Cerro La Salina (block 6, B, C; block 9, A) Talara Basin, northern Peru. **A**. Limpet indet. 1 (NRM Mo187032) in lateral view (A_1), apical view (A_2) and seen from anterior view (A_3). **B**. Limpet indet. 2 (NRM Mo187033) in apical (B_1)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

Retiskenea? sp.

Fig. 10.

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

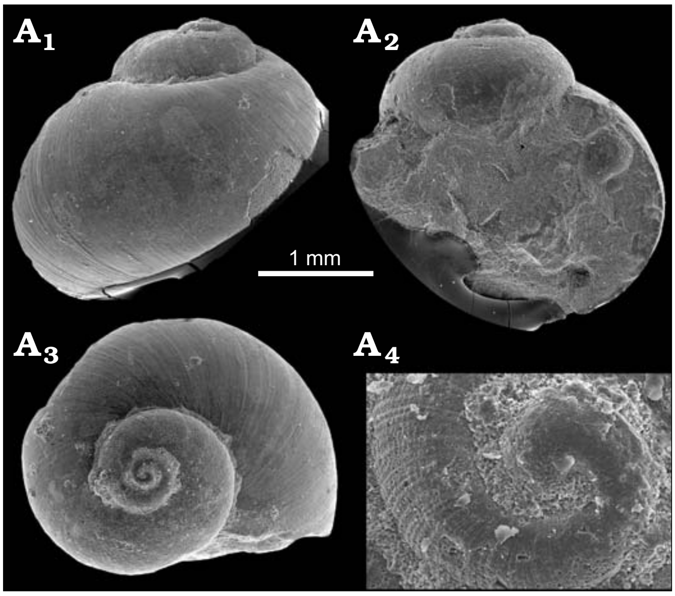


Fig. 10. The possible neomphalid *Retiskenea*? sp. (PRI 80014) from the early Cenozoic Lomitos cherts seep deposits near Negritos, Talara Basin, northern Peru.

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 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

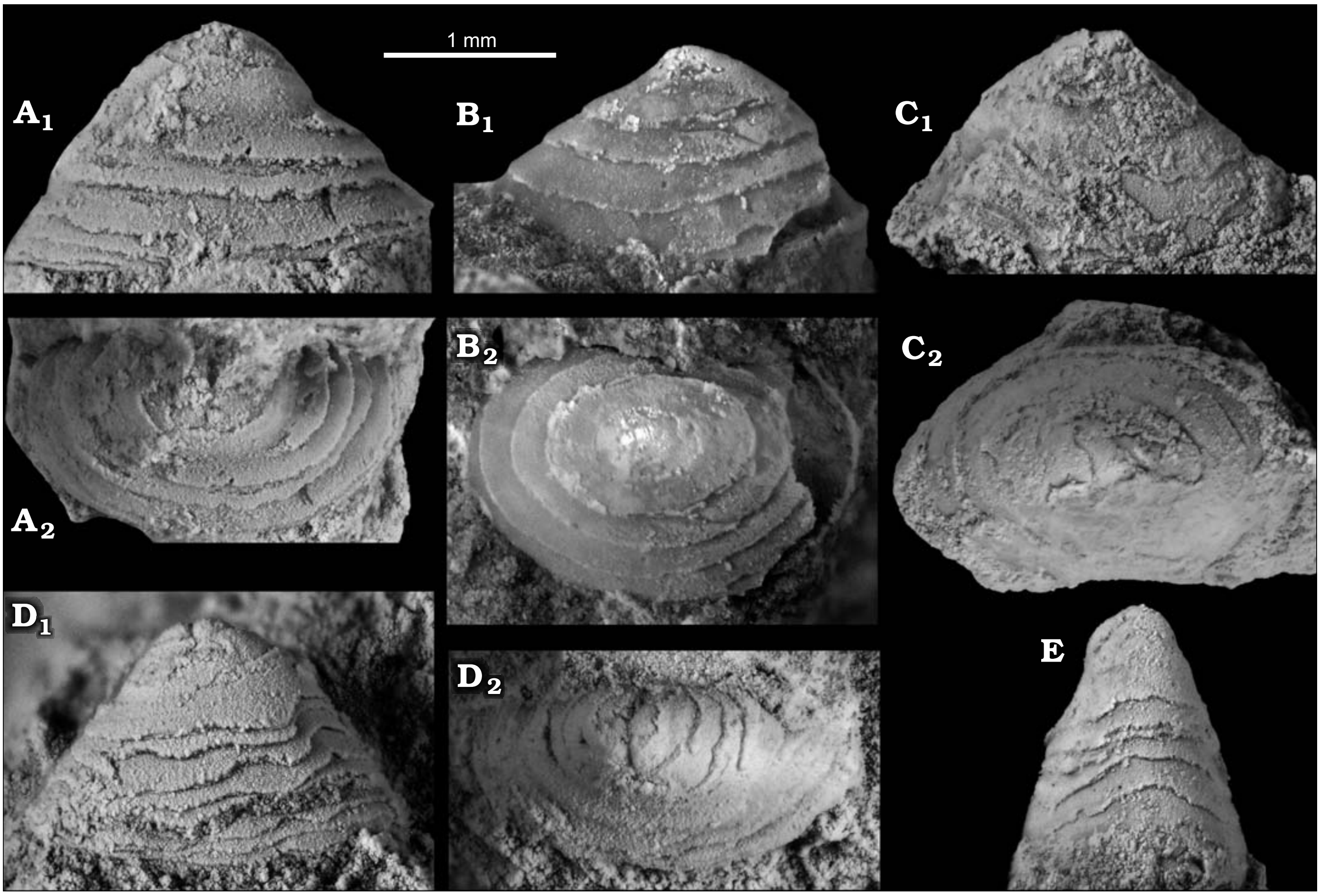


Fig. 11. The vetigastropod *Pyropelta seca* sp. nov. from early Oligocene seep deposits at Cerro La Salina block 6, Talara Basin, northern Peru. **A**. Paratype (NRM Mo187035) in lateral (A_1) and apical (A_2) views. **B**. Holotype (NRM Mo187036) in lateral (B_1) and apical (B_2) views. **C**. Paratype (NRM Mo187037) in lateral (C_1) and apical (C_2) views. **D**. Paratype (NRM Mo187038) in lateral (D_1) and apical (D_2) views. **E**. Paratype (NRM Mo187039) in anterior view.

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 *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.

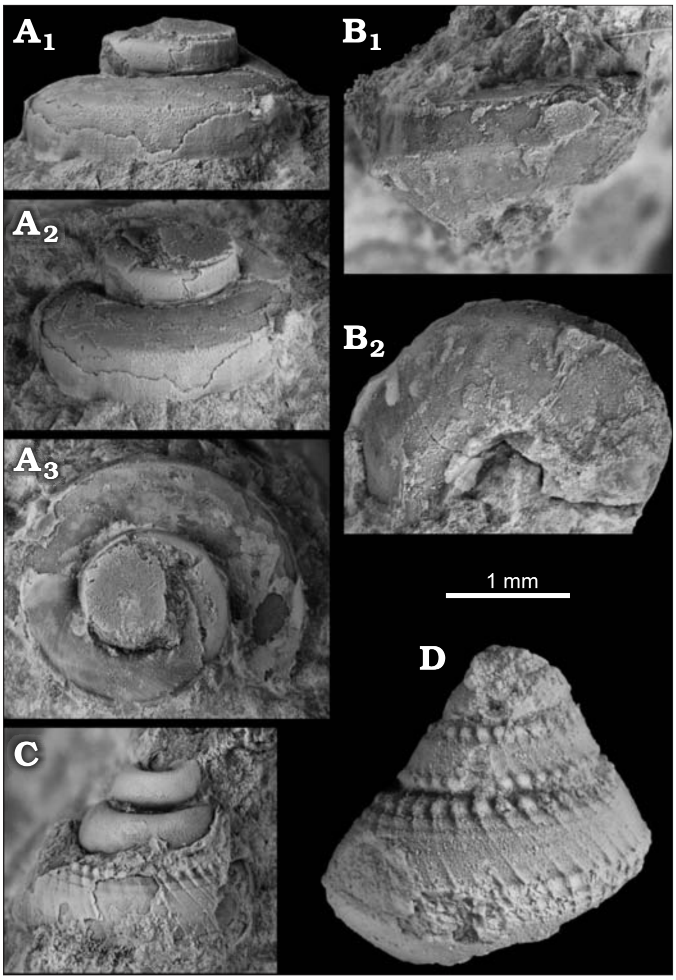


Fig. 12. Vetigastropoda from early Oligocene seep deposits at Cerro La Salina (block 1, A, D; block 2, C; block 9, B) Talara Basin, northern Peru. **A**, **B**. The colloniid *Cantrainea* sp. **A**. NRM Mo187040, specimen with base embedded in rock matrix in lateral (A_1), oblique (A_2) and apical (A_3) views. **B**. NRM Mo187041, specimen with exposed base in lateral (B_1) and basal (B_2) views. **C**, **D**. The trochoid incertae sedis. **C**. NRM Mo187042. **D**. NRM Mo187043.

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.

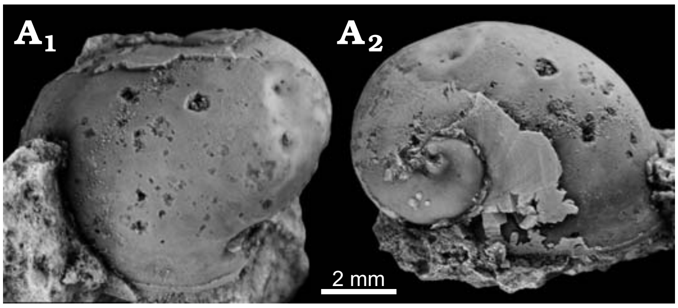


Fig. 13. Neritimorpha indet. (PRI 80015) from the early Cenozoic Lomitos cherts seep deposits near Negritos, Talara Basin, northern Peru.

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.

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 is about 8 mm high.

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 hi-*

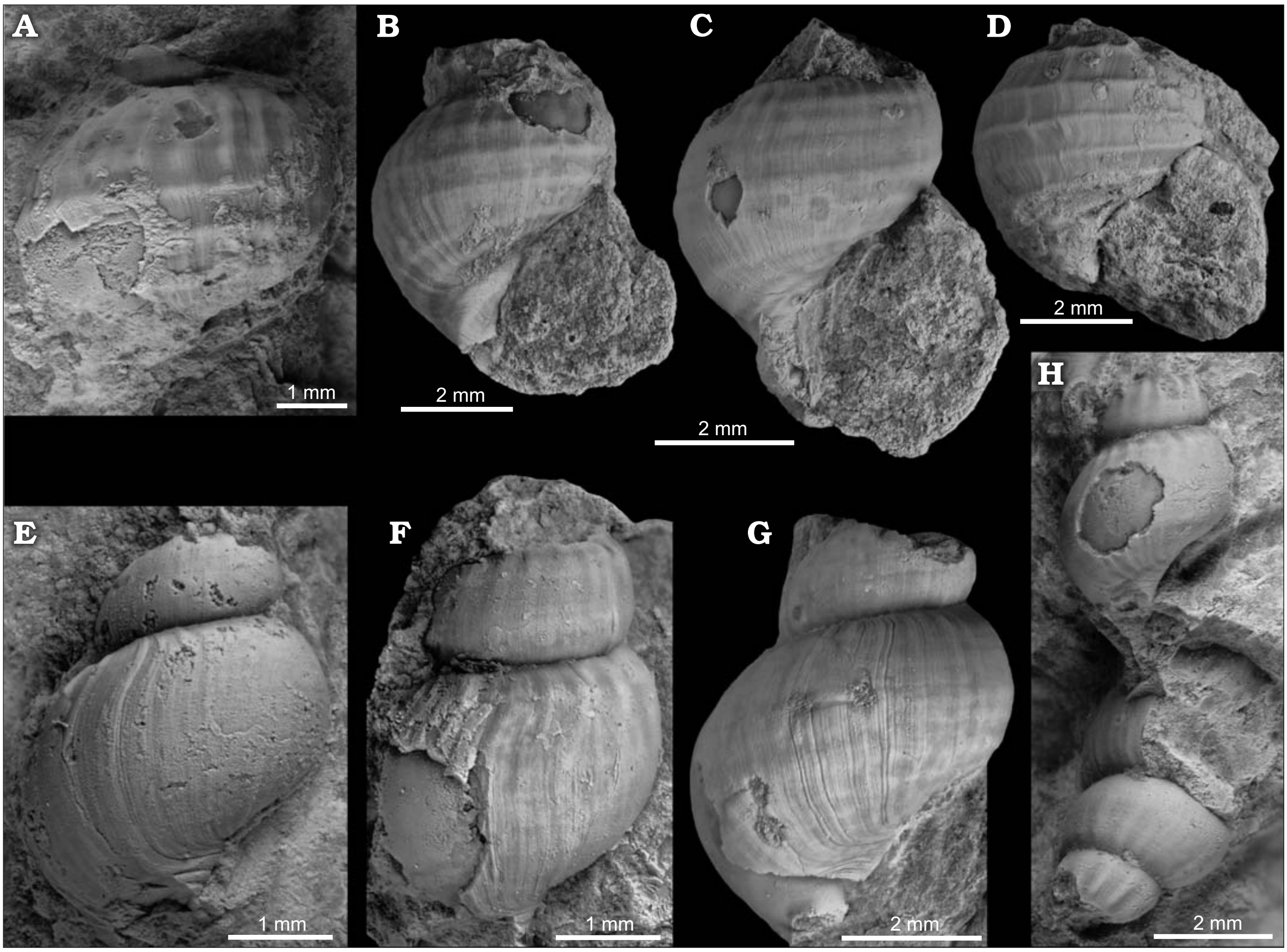


Fig. 14. The provannid gastropod *Provanna antiqua* Squires, 1995, from early Oligocene seep deposits at Cerro La Salina (block 1, A, F; block 4, H; block 6, B, C, D, G; block 8, E), Talara Basin, northern Peru. **A**. NRM Mo187044, specimen with distinctive axial and spiral sculpture, in abapertural 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..

rokoae 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 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*.

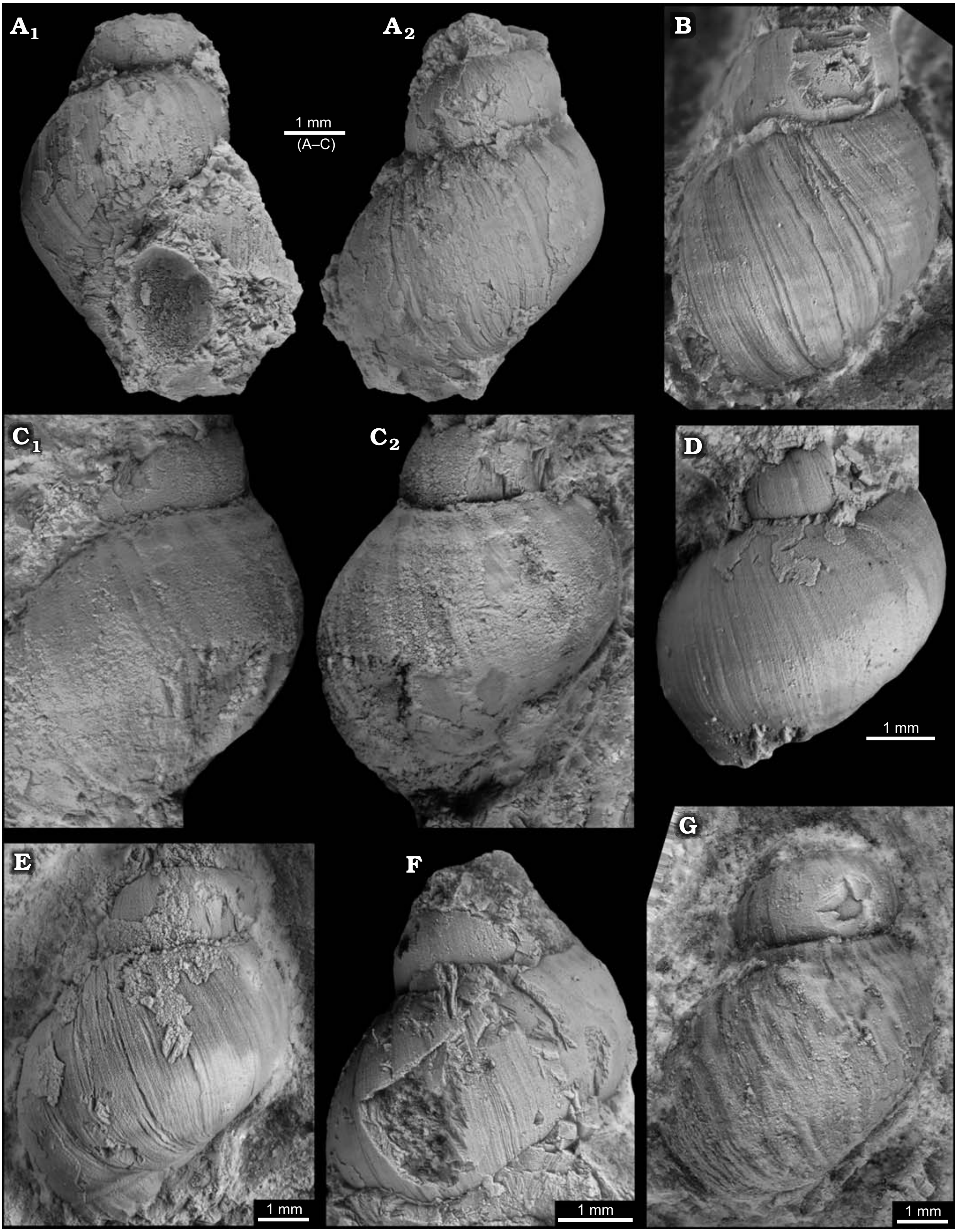
Stratigraphic and geographic range.—Type locality and horizon only.

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


A_1
A_2
1 mm
(A–C)
B
C_1
C_2
D
1 mm
E
1 mm
F
1 mm
G
1 mm

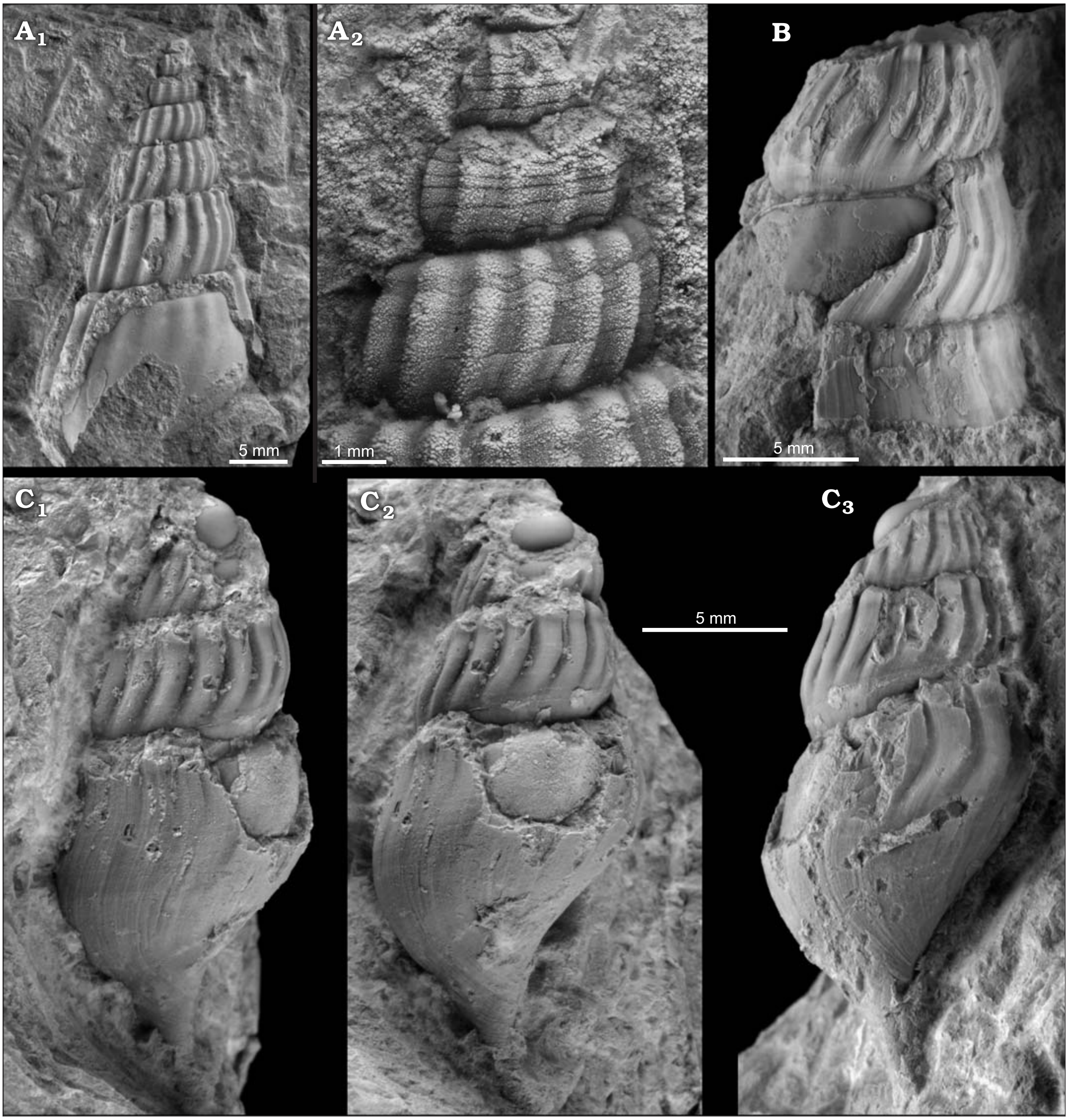


Fig. 16. The hokkaidoconchid gastropod *Ascheria salina* sp. nov. from early Oligocene seep deposits at Cerro La Salina (block 1, B, C; block 2, A) Talara Basin, northern Peru. **A**. Paratype (NRM Mo187059) showing fine spiral sculpture on early whorls. **B**. Paratype (NRM Mo187060) large fragmentary specimen. **C**. Holotype (NRM Mo187061) showing opisthocline axial ornament and faint spirals on last whorl. 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_1) and abapertural (A_2) 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_1, C_2). **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.

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 raui* (Goedert and Kaler, 1996) from seep 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 with missing early whorls H = 22 mm, W = 9 mm wide; 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) 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) 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).

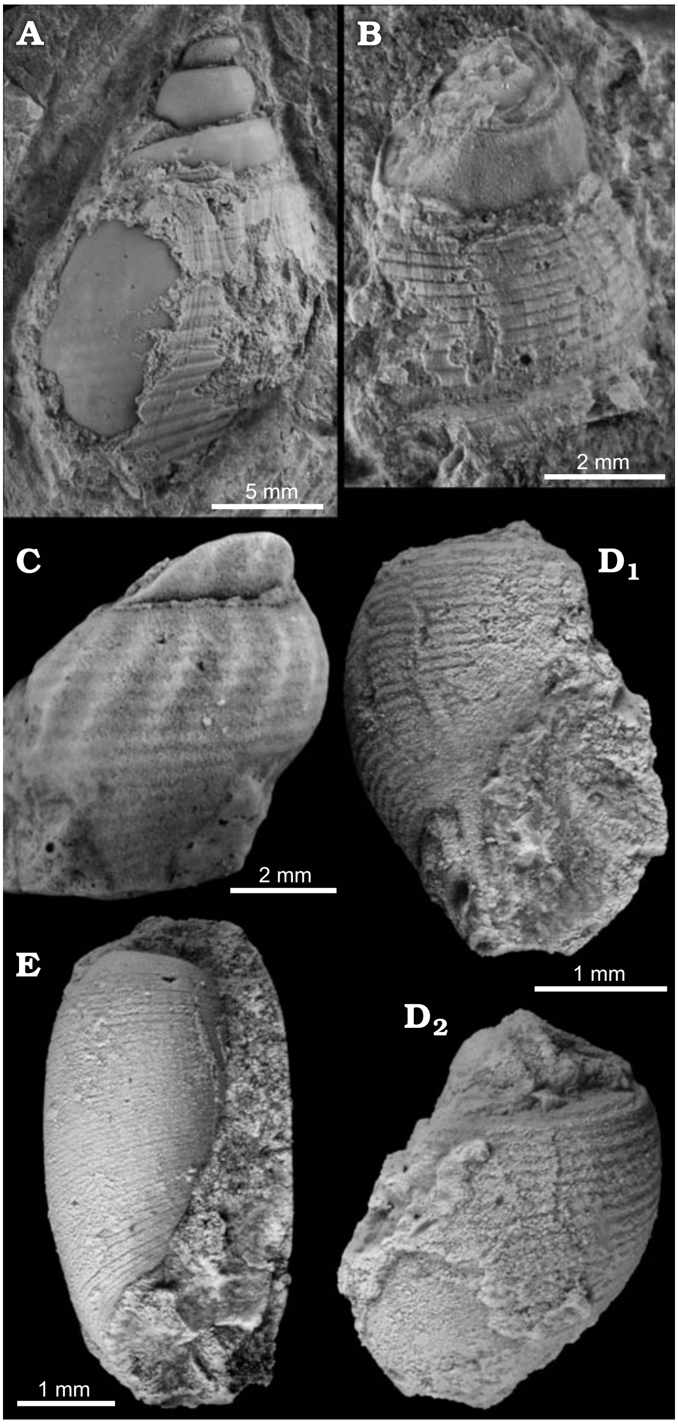


Fig. 17. Neogastropod and opisthobranch gastropods from early Oligocene seep deposits at Cerro La Salina (block 2, A; block 4, B; block 6, E; block 7, D) and Belén seep site (C), Talara Basin, northern Peru. **A**, **B**. The buccinid *Colus sekiuensis* Kiel and Goedert, 2007. **A**. Large specimen (NRM 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. **E**. The opisthobranch *Cylichna* sp. (NRM Mo187066).

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 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.

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 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 tuberculate 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 capsulated setae. They are not uncommon in hermit crabs

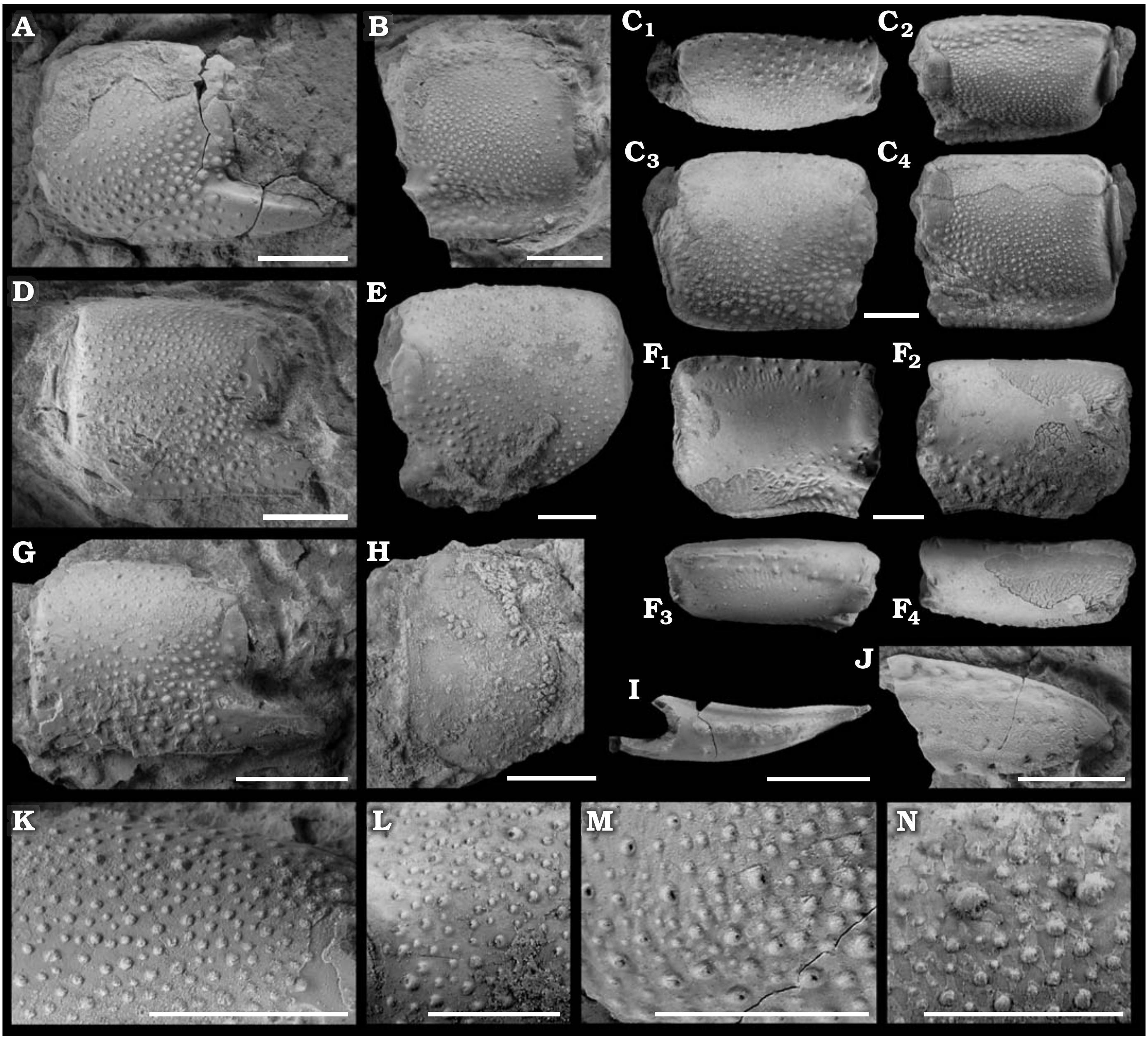


Fig. 18. The callianassid ghost shrimp *Eucalliax capsulasetaea* sp. nov. from early Oligocene seep deposits at Cerro La Salina, blocks 2, 4, 6, 7, in the Talara Basin, northern Peru. **A**. Holotype (NRM Ar69394), right propodus in outer lateral view. **B**. Paratype (NRM Ar69376), right propodus in inner lateral view. **C**. Paratype (NRM Ar69383), right propodus in dorsal (C_1), dorso-lateral (C_2), outer lateral (C_3), and inner lateral (C_4) 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_1), outer lateral (F_2) and dorso-lateral (F_3, F_4) 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.

(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 shrimp species described to date, to our knowledge. The new species is morphologically closest to *Eucalliax burckhardti* (Böhm, 1911) from the Maastrichtian and Danian

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
Bivalvia							
Solemya lomitensis Olsson, 1931						×	
Solemya (*Acharax*) *belenensis* Olsson, 1931					×		
Nucula paboensis Olsson, 1931					×		
Acila paita Olsson, 1931				?	×		possibly same as *Acila* sp. in this paper
Acila piura Olsson, 1931				?	×		possibly same as *Acila* sp. in this paper
Neilo altamirano sp. nov.	×						
Idas sp.	×						
Propeamussiidae indet.	×						
Pseudophopsis peruviana (Olsson, 1931)	×	×	×		×	×	
Conchocele tessaria (Olsson, 1931)	×				×		as *Thyasira* in Olsson (1931)
Thyasira peruviana Olsson, 1931						×	
Thyasira staufti Olsson, 1931						×	
Myrtaea? *cookei* Olsson, 1931			×				
Myrtaea? sp.						×	
Lucinoma zapotalensis (Olsson, 1931)	×	×					as "*Phacoides* (*Lucinoma*)" in Olsson (1931)
Nipponothracia lomitensis (Olsson, 1931)						×	as "*Lucina*? *lomitensis*" in Olsson (1931)*
Pleurophopsis lithophagoides Olsson, 1931				×	×		
Pleurophopsis talarensis sp. nov.	×		×		×		reported as *P. lithophagoides* by Olsson (1931)
"*Vesicomya*" *tschudi* Olsson, 1931	×				×	×	
"*Vesicomya*" *ramondi* Olsson, 1931					×		
Gastropoda							
Limpet 1	×						
Limpet 2	×						
Coccopigya sp.	×						
Retiskenea? sp.	×						
Pyropelta seca sp. nov.	×	×					
Cantrainea sp.	×	×					
Trochoid incertae sedis	×						
Neritimorpha indet.					×	×	listed as "*Nerita*" by Olsson (1931)
Ampullina or *Polinices*						×	internal casts
Provanna antiqua Squires, 1995	×			×			
Provanna pelada sp. nov.		×					
Ascheria salina sp. nov.	×						
Colus sekiuensis Kiel and Goedert, 2007	×						
Buccinidae indet.				×			
Austrofusus? *belenensis* Olsson, 1931					×		nomen dubium
Siphonalia? *belenensis* Olsson, 1931					×		
Siphonalia? *tessaria* Olsson, 1931					×		
Acteon sp.	×						
Cylichna sp.	×						
Decapoda							
Eucalliax capsulasetaea sp. nov.	×						

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*

(Lőrenthey in Lőrenthey 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. yoshihiroi* 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 *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*, *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 vesicomyid 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 vesicomyid bivalves from the North Pacific region. *The Veliger* 49: 270–293.

Amano, K. and Kiel, S. 2010. Taxonomy and distribution of fossil *Archivesica* (Vesicomyidae, Bivalvia) in Japan. *The Nautilus* 124: 155–165.

Amano, K. and Kiel, S. 2011. Fossil *Adulomya* (Vesicomyidae, Bivalvia) from Japan. *The Veliger* 51: 76–90.

Amano, K. and Kiel, S. 2012. Two Neogene vesicomyid 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 abyssochrysoid 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 vesicomyid 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 vesicomyid 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. Aggiornamento 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. *Bayerische 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 burckhardti* 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 *Retiskenea*? (Gastropoda: Neomphalidae) from Lower Cretaceous hydrocarbon seep-carbonates of northern California. *Journal of Paleontology* 82: 140–153.

Cantraine, F.J. 1835. Diagnoses ou descriptiones 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-Berríos, 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*, I85–I169. 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. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts* 2: 433–449.

d'Orbigny, A. 1842–43. *Paléontologie Française, terrains crétacés. Vol. 2, Gastèropodes*. 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 supervision 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, Teleodemacea: *Solen* to *Di-*

plodonta. *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 vesicomyid 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 kempi* 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. (Enoplometopoidea, 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]. *Rezul'taty biologičeskih issledovanij sovetskih antarktičeskih èkspedicij 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 Albian 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 *Abyssochrysos* (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: Vesicomyidae). *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–ccxlvi 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. *Madrynomya bruneti* n. gen. and sp. (Bivalvia: ?Modiomorphoidae): 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., Klompmaker, 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: Eucalliacinae), a ghost shrimp from the Middle Miocene of Europe, with reappraisal of the fossil record of Eucalliacinae. *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 taphonomy 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 vesicomyid 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: Abyssochrysoidea). *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 Withham, 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 vesicomyid 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. *Palaios* 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.

Klompmaker, 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.

Klompmaker, 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. Vesicomyidae 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. Vesicomyidae (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 Vesicomyidae (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: Callianassidae): 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, Ctenochelidae) in the West Pacific, with the description of a new species from Taiwan. *Crustaceana* 80: 1193–1203.

Linnaeus, C. 1758. *Systema naturæ per regna tria naturæ, 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-Akademien Förhandlingar* 3: 134–160, 182–204.

Lőrenthey, 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 Callianassidae (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 vesicomyid species (Bivalvia) from the middle Miocene Bessho Formation in Nagao Prefecture, central Japan, with notes on vesicomyid 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 arrengement générique, leur description charactéristiques, 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, Publicacion 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 Ingemmet. 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 phylogenetique des pélécypodes. *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 organisées*. 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 chemoautosynthesis-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'Elía, G. 2013. Phylogenetic position of vesicomyid clams from a methane seep off central Chile (~36°S) with a molecular timescale for the diversification of the Vesicomyidae. *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.