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LATE CRETACEOUS HYDROTHERMAL VENT COMMUNITIES FROM THE TROODOS OPHIOLITE, CYPRUS: SYSTEMATICS AND EVOLUTIONARY SIGNIFICANCE

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Abstract: Modern hydrothermal vent communities are based on chemosynthesis by microbial primary producers. Molecular phylogenetic divergence estimates indicate that many of the dominant vent taxa arose during the Cenozoic and Cretaceous; however, the fossil record of vent communities from these time periods is poor. One occurrence of such Cretaceous vent communities pertains to six volcanogenic massive sulphide deposits in the Troodos ophiolite of Cyprus. These deposits represent hydrothermal activity on deep (2500–5000 m) arc-related spreading ridge(s) in the Neotethyan Ocean over several million years during the late Cenomanian and earliest Turonian. The Cyprus vent communities consist of worm tubes, representing possible vestimentiferans and serpulids, together with a moderate diversity of abyssochrysoid gastropods, belonging to eight new species (*Desbruyeresia kinousaensis* sp. nov., *Desbruyeresia memiensis* sp. nov., *Desbruyeresia kambiaensis* sp. nov., *Hokkaidoconcha morisseaui* sp. nov., *Ascheria canni* sp. nov., *Cyprioconcha robertsoni* gen. et sp. nov., *Paskentana xenophontosi* sp. nov. and *Paskentana dixoni* sp. nov.) in five genera and three families; none of the species is shared between vent sites. A single gaudryceratid ammonite from one of the vent sites most likely represents a water-logged shell that sank from surface waters. The gastropod fauna contains the first representatives of the genera *Desbruyeresia*, *Hokkaidoconcha*, *Ascheria* and *Paskentana* from hydrothermal vents, and also the youngest representative of the last-named genus in any environment. The Cypriot vent communities share tube worms with slightly older (Cenomanian) and younger (Turonian–Santonian) vent communities elsewhere in the western part of the Neotethyan Ocean.

Key words: Upper Cretaceous, hydrothermal vent communities, Provannidae, Hokkaidoconchidae, Paskentanidae, Gaudryceratidae.

SINCE their discovery in the late 1970s (Lonsdale 1977), hydrothermal vents have now been recorded from all of the world's oceans, and are associated with sea-floor spreading and submerged volcanoes in a wide variety of tectonic settings, including mid-ocean ridges, forearc and back-arc basins, and island arc volcanoes, and at water depths ranging from the intertidal to 5200 m (InterRidge Global Database of Active Submarine Hydrothermal Vent Fields, Version 3.4; Beaulieu & Szafranski 2020). Most vent sites are located on bare-rock substrates, but where they are close to continental margins, such as in the Guaymas Basin, they can vent through thick sediment sequences (e.g. Teske *et al.* 2016). Hydrothermal fluid issuing onto the sea floor at these vent sites is hot (up to 398°C), anoxic, acidic, and enriched in sulphide, hydrogen, methane, and various metals (especially Fe, Zn, Cu, and Mn). When vent fluid mixes with ambient seawater, minerals (mainly metal sulphides) rapidly precipitate to form sea-floor structures, often in the form of chimneys, which over time collapse and reform to produce mound-like structures, termed sea-floor massive sulphides (SMS) (Beaulieu *et al.* 2015; German *et al.* 2016). Individual vent sites are highly heterogeneous both over a variety of scales, and in terms of temporal duration. For SMS on spreading ridges, the deposit size, along-ridge spacing and temporal duration are controlled to a great extent by the ridge spreading rate, such that SMS on slow-spreading ridges (e.g. the Mid-Atlantic Ridge) are large, widely

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spaced (hundreds of kilometres) and active over tens of thousands of years, while those on fast-spreading ridges (e.g. the East Pacific Rise) are small, spaced as little as 6 km apart, and are active only on decadal scales (Beaulieu *et al.* 2015; Baker *et al.* 2016; German *et al.* 2016).

Communities of organisms living at hydrothermal vents have radically altered our ideas about life in the deep sea, because the primary energy source in the vent environment is geochemical and not solar (Van Dover 2000). This geochemical energy comes in the form of reduced chemical compounds coming directly from vent fluid (hydrogen sulphide, methane and elemental hydrogen being particularly important) and is used by a diversity of bacteria and archaea for nutrition, a process called chemosynthesis. These microbes are the primary producers in vent communities and are utilized by animals either directly (e.g. grazing of microbial mats), or by forming exosymbiotic or endosymbiotic relationships (termed chemosymbiosis; e.g. Dubilier *et al.* 2008). Chemosymbiotic animals tend to predominate in terms of biomass at the vent sites they inhabit, but often the diversity in vent communities is found among the smaller animals, especially polychaete worms and gastropods (Van Dover 2000). The presence and diversity of chemosymbiotic species in vent communities has a bathymetric control, such that above *c.* 200 m they are not present (Tarasov *et al.* 2005), with very few exceptions (e.g. *Bathymodiolus* mussels in the photic zone (100 m) on Volcano 1 on the Kermadec-Tonga Arc; Metaxas 2015). Several invertebrate groups that are conspicuous deep-sea benthos (e.g. sponges, corals, bryozoans, brachiopods, echinoderms and tunicates) are rare in or are absent from vent communities. Vent communities contain a very high percentage of endemic (or more properly: obligate) species, not found in any other marine community (e.g. McArthur & Tunnicliffe 1998). Ecologically, communities that are most similar to vent communities are those found at hydrocarbon ('cold') seeps on active and passive continental margins. Seep communities are also based on microbial chemosynthetic primary production, and share a few species and many genera with hydrothermal vent communities (Sibuet & Olu 1998; Kiel 2016).

In an analysis of the distribution of modern vent faunas (Rogers *et al.* 2012 and references therein) 11 biogeographic provinces have been recognized: one on the Mid-Atlantic Ridge, one on the East Scotia Ridge, four in the western Pacific, one on the Juan de Fuca Ridge, three along the East Pacific Rise, and one in the Indian Ocean. For the most part these provinces are delimited by a lack of inter-connecting spreading ridges (e.g. between the provinces in the East and West Pacific), but also by major discontinuities along contiguous ridges, such as microplates. Some chemosymbiotic taxa are near ubiquitous in global vent communities (e.g. bathymodiolin mussels), while others have a more restricted distribution (e.g. vestimentiferan siboglinid tubeworms in the Pacific and Caribbean, the provannid gastropod genera *Ifremeria* in the West Pacific and *Alviniconcha* in the West Pacific and Indian Ocean, the neomphaline gastropod genus *Chrysomallon* in the Indian Ocean, as well as the shrimp genus *Rimicaris* in the Atlantic and Indian oceans). The reasons for the distribution patterns of these important taxa are not currently well-understood. Adjacent vent fields (loosely defined as clusters of active vents on a volcano or spreading ridge) in each vent biogeographic province share a regional species pool, and genetic connectivity along active ridges can be in the order of hundreds of kilometres in some vent taxa (e.g. Coykendall *et al.* 2011). This gene flow comes from the dispersal of larvae (Tyler & Young 1999; Mullineaux *et al.* 2010) rather than adults, given that most benthic vent taxa are either sessile (e.g. vestimentiferans), or have limited motility (e.g. molluscs). However, individual vent sites commonly do not have all the species in a regional species pool. Occasionally this is because of successional ecological changes after disturbance by volcanic activity (Fornari *et al.* 2012; Sen *et al.* 2014), and sometimes this is due to small differences in the physical vent environment, such as fluid chemistry, substrate or bathymetry (Desbruyères *et al.* 2001; Plouviez *et al.* 2015). Modern vent communities display highly distinctive patterns of zonation, in which the distribution of macrofauna is controlled by the heterogeneous physiochemical conditions around the active hydrothermal vents (Mullineaux *et al.* 2018). In turn, the zonation occurs because of nutritional requirements of the different animal species, such that taxa with chemosymbionts (e.g. vestimentiferans, bathymodiolin and vesicomyid bivalves, and some alvinocaridid shrimp, as well as provannid, peltospirid and lepetodrilid gastropods) and those that graze microbial mats (e.g. many vent gastropods) live in places where the concentration of vent fluid (and thus temperature) is higher, whereas filter-feeding animals (e.g. serpulid tube worms, eolepadid barnacles) and sessile predators (e.g. anemones, carnivorous sponges) live at the periphery of active vent sites (Mullineaux *et al.* 2018).

In recent years molecular phylogenetic studies of vent taxa have yielded important insights into their evolutionary origins. Vrijenhoek (2013) presented a review of divergence estimates available at that time and showed that of 14 important vent taxa, 6 had origins in the Cenozoic (i.e. the polychaete genus *Amphisamytha*, vesicomyids and bathymodiolins, lepetodriliid gastropods, bresiliid shrimp and bythograeid crabs) and 9 (vestimentiferan and alvinellid polychaetes, neomphaline gastropods, abyssochrysoid gastropods as a whole, plus the genera *Provanna*, *Desbruyeresia* and the *Alviniconcha*/*Ifremeria* doublet, and the neolepadine and neoverrucid barnacles) had origins in the Mesozoic (all but one in the

Cretaceous). Subsequently, Herrera *et al.* (2015) reanalysed the vent barnacles and were able to distinguish two clades, one with likely origins in the Late Cretaceous and one with origins in the Cenozoic. Furthermore, Roterman *et al.* (2018) gave divergence estimates of the vent and seep squat lobster family Kiwaidae as being in the Early Cretaceous, with a radiation of living species in the Cenozoic. Thus, the Mesozoic (and the Cretaceous in particular) appears to have been a critical period for the evolution of modern vent animals. However, finding fossil evidence for this evolutionary history is difficult because there are only very few known Mesozoic vent communities in the geological record (Little *et al.* 1998). These are found in volcanogenic massive sulphides (VMS), which are the ancient analogues of modern SMS. A single Lower Jurassic vent community is on record from the Figueroa VMS in California; this consists of vestimentiferan worm tubes, a species of trochoid vetigastropod and a species of dimerelloid brachiopod (Little *et al.* 1999*a*, 2004; Georgieva *et al.* 2019). More fossil vent communities are known from the Upper Cretaceous, with examples coming from six VMS in Cyprus, one from Oman, one from Turkey and one from the Republic of Georgia (Oudin & Constantinou 1984; Haymon *et al.* 1984; Haymon & Koski 1985; Little *et al.* 1999*b*, 2007; Revan *et al.* 2014). All of these fossiliferous VMS formed in the Neotethys, a largely destroyed ocean, which is represented today by the Mediterranean and western Indian Ocean. These Upper Cretaceous vent communities all include worm tube fossils, but only those from Cyprus have additional taxa, involving a diversity of gastropods (Little *et al.* 1999*b*). To date, only the worm tube fossils from the Cypriot vent communities have received systematic treatment (Georgieva *et al.* 2019). In the present paper we formally describe the Cypriot vent gastropod taxa. In addition, we reconstruct the palaeoecology of the Cypriot vent communities and discuss the evolutionary and palaeobiogeographic significance of Neotethyan vent communities.

GEOLOGICAL SETTING

The Troodos ophiolite is a fragment of oceanic crust that formed at a sea-floor arc-related spreading centre in the Neotethys ocean, near a subduction zone (e.g. Robertson *et al.* 1991; Robertson & Xenophontos 1993; Pearce & Robinson 2010; Woelki *et al.* 2020). The ophiolite is deformed into an anticlinal dome structure (Fig. 1), which, at its core, preserves a basal unit of upper mantle rocks, surrounded by stratigraphically overlying units consisting of a crustal sequence of gabbroic and ultramafic cumulates (collectively indicated as a plutonic and mantle sequence; Fig. 1), followed by a sequence of sheeted dykes, and, at the top, an extrusive unit comprising mostly pillow lavas, with sheet flows, hyaloclastites, and *c.* 90 VMS, which formed at sites of sea-floor hydrothermal activity. The age of the Troodos ophiolite is constrained, first, by zircons from plagiogranite plutons at the top of the cumulate sequence that are dated at 94.3 ± 0.5 Ma (Morag *et al.* 2020), corresponding to the late Cenomanian to earliest Turonian in version 2020/01 of the International Chronostratigraphic Chart (Cohen *et al.* 2020); and second, by middle–late Turonian to latest Santonian radiolarians in the pelagic sedimentary rocks overlying the ophiolite (Bragina 2012). The top of the extrusive unit of the ophiolite has a low-amplitude sea-floor topography that indicates formation at intermediate or fast spreading rates (>70 mm/year total spreading rate) (Carbotte & Macdonald 1994). At a full spreading rate of 70 mm/year, the 110 km across-strike total extent of the ophiolite would have taken 3 myr to form, if it all lay on one side of a spreading axis. However, there are three major graben structures in the ophiolite outcrop that are likely to be extinct spreading axes (Moores *et al.* 1990), the presence of which suggests that the outcropping area of the ophiolite formed over a shorter time period, perhaps 2 myr, or less. Depth estimates during ophiolite formation vary from 2500 ± 300 m (based on homogenization temperatures in fluid inclusions from quartz veins in the Mathiati VMS; Spooner 1980) to *c.* 5000 m (based on H_2O contents of Troodos volcanic glasses; Woelki *et al.* 2020).

The Troodos ophiolite VMS consist largely of pyrite with small amounts of chalcopyrite and sphalerite, and formed from hydrothermal fluids that were *c.* 500–525°C at depth and which underwent phase separation into low-salinity and high-salinity fluids (brines) (e.g. Cowan & Cann 1988; Hannington *et al.* 1998; Humphris & Cann 2000; Martin *et al.* 2019). The VMS occur at all depths within the Troodos extrusive rocks, from close to the sheeted dyke complex at the base (e.g. Peristerka and Kapedhes) to one deposit that lies at the interface between volcanic rocks and overlying sedimentary units. This shows that the hydrothermal activity from which the VMS formed occurred sometimes at the spreading ridge axis (for those at the base of the extrusive unit) and sometimes at some distance from it (Humphris & Cann 2000). Worm tube and gastropod macrofossils occur in six of the Troodos ophiolite VMS (Fig. 1), and the present-day distances between the fossiliferous VMS are between 1.5 and 47.5 km (Little *et al.* 1999*b*).

MATERIAL AND METHOD

Most of the Cypriot VMS macrofossils were collected by one of us (CTSL) in 1997 and were reported on by Little *et al.* (1999*b*) and Georgieva *et al.* (2019).

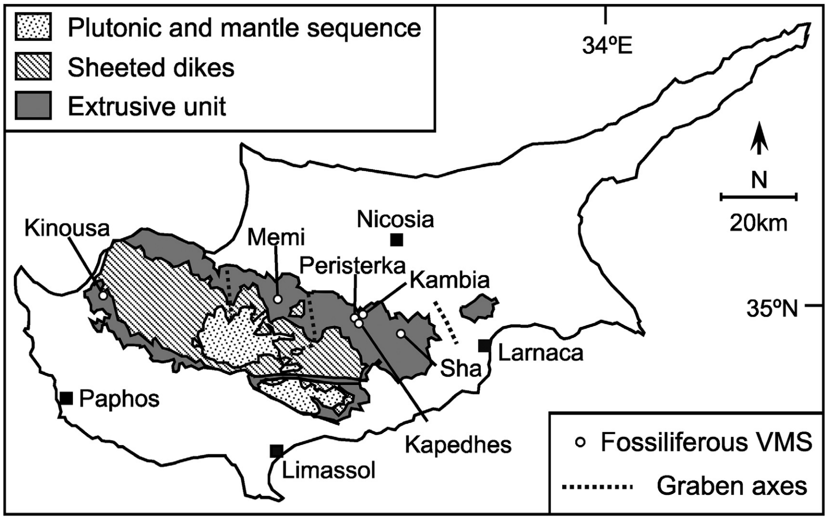

FIG. 1. Simplified geological map of the Troodos ophiolite (Cyprus), showing the location of the fossiliferous volcanogenic massive sulphides (VMS) (modified from Little *et al.* 1999*b*).

Subsequently, specimens were recovered between 1997 and 2014 by CTSL and students from the University of Leeds. Additional specimens were collected from the Kambia VMS by LMA and John Dixon, University of Edinburgh. All specimens were extracted from blocks of massive pyrite containing sulphide textures and structures indicative of primary mineralization (e.g. colloform pyrite and fluid conduits; Little *et al.* 1999*b*) on open-pit ore dumps and spoil heaps. The majority of the Cypriot VMS macrofossils consist of thin external moulds of very fine crystalline pyrite, preserving ornament details, but lacking any original shell or organic tube-wall material. Some of the gastropods are preserved as external moulds only; from these, silicone rubber casts were produced. The specimens were imaged either by digital camera or scanning electron microscopy (SEM) at 15–20 keV, using an FEI Quanta 650 FEG-ESEM at the Leeds Electron Microscopy and Spectroscopy Centre, University of Leeds, UK.

Institutional abbreviations. GSD, Geological Survey Department, Lefkosia, Cyprus; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

DISCUSSION

Cyprus hydrothermal vent community: taphonomy, palaeoecology and endemism

The Cyprus vent communities contain examples of shelly taxa (gastropods, ammonites and possibly serpulids as 'Troodos attached tubes') and taxa forming organic tubes (as 'Troodos collared tubes' and 'Troodos wrinkled tubes') (Table 1). With the exception of the ammonite (see below), it is most probable that these taxa represent animals that were living in areas of active mineralization; around or on hydrothermal vent chimneys. Extremely rapid (a year or less) replacement of alvinellid and vestimentiferan worm tubes, and molluscan shells by sulphide minerals (mostly pyrite) and silica is known from vent chimneys at modern hydrothermal sites (Cook & Stakes 1995; Georgieva *et al.* 2015). This rapid replacement process is probably a prerequisite for preservation of vent macrofauna in the fossil record, because a number of sea-floor experiments have shown that the organic tubes of vestimentiferans, crab carapaces and bivalve shells are dissolved and/or microbially degraded in only a few years at modern vent sites (Kennish & Lutz 1999; Ravaux *et al.* 2003). For bivalve shells the rate of shell dissolution is controlled by mineralogy, with aragonitic microstructures dissolving before those made of calcite, and also by proximity to active venting, because vent fluid is usually acidic. Even bivalve shells away from active venting are estimated to dissolve entirely in *c.* 300 years, due to undersaturation of aragonite in the water at the experimental sites of Kennish & Lutz (1999), which are at 2600 m on the East Pacific Rise. In the context of the Cyprus vent communities the rate of carbonate shell dissolution would have been similar close to active vents, and likely to be more rapid away from the vents (compared with the modern experimental sites), because of the estimated 2500–5000 m water depth during Troodos ocean crust formation and the fact that carbonate compensation depths (ccd) in Cretaceous oceans were probably shallower than today, because of higher CO_2 atmospheric concentrations (global estimate of 3500 m during the Late Cretaceous; Zeebe & Tyrrell 2019). Furthermore, the first biogenic sediments deposited on the Troodos ocean crust (the

TABLE 1. Fossil occurrences from Cypriot volcanogenic massive sulphides (VMS).

Taxon/VMS	Kinousa	Memi	Kambia	Peristerka	Kapedhes	Sha
Desbruyeresia kinousensis sp. nov.	2					
Desbruyeresia memiensis sp. nov.		8				
Desbruyeresia kambiaensis sp. nov.			30			
Hokkaidoconcha morisseaui sp. nov.			1			
Ascheria canni sp. nov.			6			
Cyprioconcha robertsoni gen. et sp. nov.			2			
Paskentana xenophontosi sp. nov.		1 (+1)*				
Paskentana dixoni sp. nov.			1			
Gaudryceratidae indet.			1			
Worm tube indet.[1]				X		
Troodos attached tubes[2]	X	X				
Troodos wrinkled tubes[2]			X		X	
Troodos collared tubes[2]		X	X		X	X

[1] Oudin & Constantinou (1984); [2] Georgieva *et al.* (2019). X, present.
*One certain + one uncertain specimen (see species description).

middle–late Turonian to latest Santonian radiolarian cherts of the Perapedhi Formation) lack carbonate, showing that even *c.* 11 myr after the formation of the Troodos ophiolite the sea floor was still below the palaeo-ccd.

In modern vent communities the majority of animals with chemosymbionts live close to the active part of vent systems and are consequently those more likely to be preserved (see above). We use these observations and comparisons with modern taxa to reconstruct the Cypriot vent communities. The commonest element in the Cypriot communities, both in terms of abundance (Little *et al.* 1999*b*) and geographic distribution (Table 1), are the possible vestimentiferan tube worms (the Troodos collared tubes and Troodos wrinkled tubes of Georgieva *et al.* 2019). If these are indeed vestimentiferans then they would have been dependent for their nutrition on sulphide-oxidizing chemosymbionts, as are all modern vent siboglinids (Hilário *et al.* 2011; Karaseva *et al.* 2016). The Troodos attached tubes may have been the attached juveniles of siboglinids, or, if serpulids, would have been filter-feeders, although serpulids with methanotrophic symbionts have recently been described from hydrocarbon seeps in the Pacific Ocean (Goffredi *et al.* 2020). The Cypriot vent gastropods lived alongside the worm tube taxa, because they often co-occur in the same blocks of sulphide. We infer that the Cypriot vent abyssochrysoids were grazers on microbial mats, like the majority of extant vent abyssochrysoids. However, some modern vent abyssochrysoids have methantrophic and sulphide-oxidizing symbionts (e.g. species belonging to the genera *Ifremeria* and *Alvinochoncha*), housed in hypertrophied gills. These taxa are large and have a globular morphology to contain their expanded gill tissue (Dubilier *et al.* 2008). The Cypriot species of *Paskentana*, in particular *P. dixoni* sp. nov., approach the shape of some of the modern species of *Ifremeria*, but suggesting that these fossil species had chemosymbionts is speculative, given that there are no living representatives of *Paskentana* for comparison.

The conspicuous indentation on two of the upper whorls of the holotype of *Paskentana xenophontosi* from Memi (see below) could be attributed either to predation damage or to a growth defect. Another alternative is that it represents mechanical damage of a very thin shell with high organic content, leading to ductile rather than brittle damage behaviour. Similar folds have been seen in the shells of abyssochrysoid shells from Jurassic and Cretaceous hydrocarbon seeps in California, USA (Kiel *et al.* 2008*a*). In the context of hydrothermal vents, one further explanation for the indentations in *Paskentana xenophontosi* could be that this was an area where the shell was completely dissolved, leaving the more flexible periostracum to deform into the space left behind. This interpretation is supported by the common observation at modern vent sites of extreme shell dissolution of bivalve and gastropod shells (especially protoconchs) leaving only periostracum, even while animals are still alive (e.g. Warén & Ponder 1991; Warén & Bouchet 1993). Three of the Cyprus gastropod specimens from two vent sites (*Hokkaidoconcha morisseaui* (Fig. 4B) and *Cyprioconcha robertsoni* (Fig. 4I) from Kambia, and *Desbruyeresia memiensis* (Fig. 3U) from Memi) have smooth, domed structures on their shell surfaces, which are roughly circular and *c.* 1–2 mm in diameter. There are 1–4 of these per shell. These structures do not belong to the shells themselves, so are not palaeo-pathologies, but rather represent epizoans that attached to the shell surfaces. There are several possibilities as to their origin, including gastropod egg capsules, or the very early settlement structures of vestimentiferan worm tubes (Southward *et al.* 2005).

The presence of a single gaudryceratid ammonite in the Kambia VMS is surprising for two reasons. First, this is the first cephalopod discovered in any ancient vent community; and second, it is related to the water depth at which the Cypriot vent communities lived (see 'Geological setting' above). It seems highly improbable that the ammonite inhabited the Kambia vent site at depths of 2500–5000 m, because the thin shells of a gaudryceratid would have imploded even at much shallower depths. Indeed, Hewitt (1996) calculated an implosion depth of 328 m for gaudryceratids. Even modern *Nautilus* shells, which are substantially thicker than those of gaudryceratids, and have thicker septae, implode at a maximum depth of 785 m (Kanie *et al.* 1980). For this reason, we suggest that the gaudryceratid represents a post-mortem water-logged shell that sank from surface waters and settled fortuitously close to the active Kambia vent site, where its shell was rapidly replaced by pyrite. Thus, the ammonite was not part of that vent community.

Worm tubes are found in all six of the fossiliferous Cypriot VMS (Table 1). This was to be expected considering that they are the commonest macrofossils in Phanerozoic VMS (Haymon *et al.* 1984; Oudin *et al.* 1985; Boirat & Fouquet 1986; Little *et al.* 1997, 1998, 1999*a*, *b*, *c*, 2007; Revan *et al.* 2014; Georgieva *et al.* 2019); it also reflects the fact that in many modern vent communities, particularly those in the East Pacific, tube-forming polychaetes (e.g. siboglinids and alvinellids) are abundant, and also tend to live in proximity to areas of active mineralization (Shank *et al.* 1998; Hilário *et al.* 2011; Karaseva *et al.* 2016). Gastropods are found in three of the fossiliferous Cypriot VMS (Table 1). Their absence from the Peristerka and Sha VMS is likely to be due to collection failure given that fewer than 10 macrofossils were found at each site (Oudin & Constantinou 1984; Little *et al.* 1999*b*, table 1). More worm tube fossils were found in the Kapedhes VMS (*n* = 77; Little *et al.* 1999*b*, table 1), but the absence of other taxa may also be an artefact of collection failure, or of the selective preservation of only worm tubes at this site. There are no shared gastropod species between the Kinousa, Memi and Kambia VMS (Table 1). This is intriguing, because there would be an expectation of at least some shared species, given the small distances between the sites (Fig. 1; Little *et al.* 1999*b*, table 1) and the lack of obvious differences in fluid chemistry, substrate and palaeobathymetry. However, a major caveat is that there is no proof that any of the Cypriot VMS were active at the same time, and indeed they could have been separated temporally over as much as 3 myr (see 'Geological setting' above). In this case the faunal differences may reflect evolutionary changes in vent gastropod lineages over time.

Macroevolutionary considerations

The gastropod fauna of the Cypriot hydrothermal vent communities consists of five genera and eight species in three abyssochrysoid families: Provannidae, Hokkaidoconchidae and Paskentanidae. Provannids are ubiquitous at modern hydrothermal vent sites (e.g. Warén & Bouchet 1993; Desbruyères *et al.* 2006; Linse *et al.* 2019); hokkaidoconchids and paskentanids are extinct taxa. Species of *Desbruyeresia*, *Hokkaidoconcha*, *Ascheria* and *Paskentana* from Cyprus are the first representatives of these genera to be recorded from any hydrothermal vent sites, and those of the last-named genus are also the youngest representatives from any environment. Provannids, hokkaidoconchids and paskentanids are common constituents of Mesozoic hydrocarbon seep communities (Fig. 2), including representative species of the genera *Desbruyeresia*, *Hokkaidoconcha*, *Ascheria* and *Paskentana* (Kaim *et al.* 2008, 2014, 2017; Kiel *et al.* 2008*a*). *Desbruyeresia* is relatively rare in the fossil record. In addition to the Cypriot record, the genus is known from Cenomanian seep deposits in Japan (Kaim *et al.* 2008) and Eocene seeps in Washington State, USA (Hybertsen & Kiel 2018). *Hokkaidoconcha* is a cosmopolitan genus with the oldest occurrence in the Oxfordian seeps in France (Kiel *et al.* 2010) and the youngest from the Eocene seeps of Barbados ('zygopleurid sp. A' of Gill *et al.* 2005, reinterpreted as ?Hokkaidoconchidae by Kaim *et al.* 2008). *Ascheria* is known from Lower Cretaceous seeps of California and the Czech Republic (Kaim *et al.* 2013, 2014) and ranges temporally to Oligocene seeps in Peru (Kiel *et al.* 2020). The genus *Paskentana* might be as old as Late Triassic (i.e. the *Paskentana*-like gastropod of Kiel *et al.* 2017 from Turkey), and its youngest occurrences at seeps are from the Hauterivian of the Crimea and California (Kiel *et al.* 2008*a*, 2010; Kaim *et al.* 2014). We suggest that the latest Cenomanian to earliest Turonian age of the Cypriot vent species of *Paskentana* might indicate a habitat switch for this gastropod taxon from hydrocarbon seeps to hydrothermal vents between the Lower and Upper Cretaceous. However, the lack of other Cretaceous vent sites with gastropod fossils makes this inference quite speculative. From a wider palaeobiogeographic perspective, in the Mesozoic the representative species of *Hokkaidoconcha*, *Ascheria* and *Paskentana* occurred both at vents (Cyprus) and at seeps (France, Crimea and Czech Republic; Kiel *et al.* 2010; Kaim *et al.* 2013, 2014) in the Tethys, while *Desbruyeresia* has so far been found only at the Cypriot vents for this time period and area. All four genera occurred in seeps in the

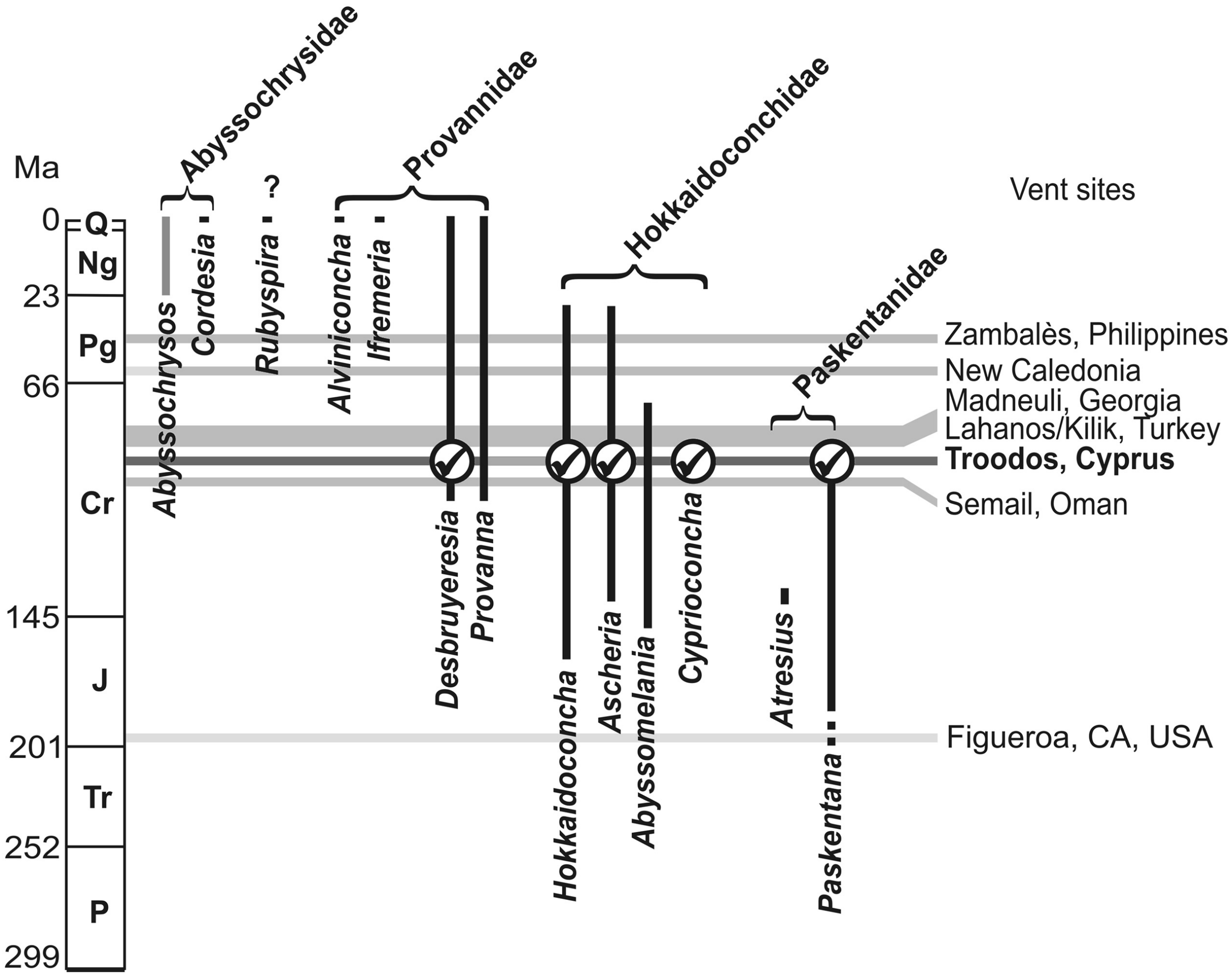

FIG. 2. Range chart of abyssochrysoid genera from hydrothermal vent and hydrocarbon seep sites, and fossiliferous Mesozoic and Cenozoic hydrothermal vent deposits. Family groupings are after Souza *et al.* (2020). Note that the genus *Abyssochrysos* (in grey) is not known from chemosynthetic environments, but is included here for completeness.

North Pacific, now California and/or Japan (Kaim *et al.* 2008, 2014), during the Mesozoic. Today, a high diversity of species of *Desbruyeresia* is known from the West Pacific vent sites and serpentinization-related seeps, and there is a single species on record from Indian Ocean vents (Sasaki *et al.* 2010; Chen *et al.* 2016).

Compared with modern vent sites and contemporary seeps, many ecologically important and speciose major taxa are missing from the Cyprus vent communities, in particular vetigastropod and neomphaline snails, bivalves and arthropods. It may be that these taxa were originally present, but have not been found in the Cypriot VMS deposits, either because of simple collection failure or through contemporary taphonomic loss. It seems very unlikely that the absence of bivalves has a taphonomic explanation, because bivalves are present in other (older) vent communities (Devonian; see Little *et al.* 1999*c*), and they can be preserved in modern vent deposits (CTSL pers. obs.) Contemporary seep deposits contained numerous bivalve taxa, particularly those with supposed chemosymbionts: solemyids, lucinids and thyasirids (Kiel *et al.* 2008*b*, 2010; Kiel 2013; Kaim *et al.* 2014; Hryniewicz *et al.* 2017). The absence of these families and of the extinct modiomorphid seep genus *Caspiconcha* may have been related to substrate availability, given that the Cypriot vent sites consisted exclusively of hard substrates (as deposits of metal sulphides and basaltic pillow lavas), whereas solemyids, lucinids, thyasirids and *Caspiconcha* were infaunal or semi-infaunal (Kelly *et al.* 2000; Kiel & Peckmann 2008; Jenkins *et al.* 2013, 2018), and would have required at least some soft substrate to burrow into. Indeed, at most modern vent sites solemyids, lucinids and thyasirids are either absent or highly localized to small patches of sediment (e.g. Glover *et al.* 2004; Desbruyerès *et al.* 2006; Oliver & Holmes 2006, 2007), the exception being sedimentcovered vent sites, where soft substrate is abundant (e.g. Lartaud *et al.* 2010; Bell *et al.* 2016). The two chemosymbiotic bivalve groups that are nearly ubiquitous and often numerically dominant at modern vent sites are the large vesicomyid clams and bathymodiolin mussels (e.g. Taylor & Glover 2010), which are either epifaunal where no soft substrate is available, or semi-infaunal where there is. These taxa have Paleocene divergence estimates of 63 and 58 Ma, respectively (Vrijenhoek 2013), dates that are largely supported by the Eocene appearance of these taxa in seep deposits (Amano & Kiel 2007; Kiel & Amano 2013). In consequence, neither the vesicomyids nor the bathymodiolins would be expected to be present at Upper Cretaceous vent sites.

The lack of vetigastropods or neomphalines in the Cyprus vent communities also cannot be explained by taphonomic loss either, and these groups have numerous representative taxa in contemporary and other Mesozoic seep deposits (Kiel *et al.* 2008*a*; Kaim *et al.* 2009, 2014). Therefore, their absence from the Cyprus vents could have been a real phenomenon, perhaps a function of Late Cretaceous biogeography and/or environmental preference.

In contrast, taphonomic loss may explain the absence of arthropods from the Cyprus vent communities, because many modern vent arthropods, such as bresiliid shrimp, have only lightly calcified carapaces, with low preservation potential, and in experiments even the more robustly shelled taxa, such as bythograeid crabs, have been shown to disappear very quickly (36 days or less) in the modern vent environment (Ravaux *et al.* 2003). However, age is also a likely explanation for the absence of arthropods from the Cyprus vents because the arthropod groups that occur abundantly in modern vent communities appear not to have evolved by the Late Cretaceous. Phylogenetic analyses of bresiliid shrimp, bythograeid crabs and vent cirripedes resulted in Cenozoic divergence estimates for all of these (Vrijenhoek 2013; Herrera *et al.* 2015).

The Cypriot vent communities share worm tube macrofossils with other Neotethyan hydrothermal vent sites of Late Cretaceous age. The Troodos ophiolite lies at one end of a belt of Upper Cretaceous ophiolites that stretches from Cyprus, through Syria, Iraq and Iran, to the Semail ophiolite of Oman and the United Arab Emirates. These ophiolites probably represent a series of small back-arc or forearc basins lying above a subduction zone within the gradually closing Neotethys Ocean (Robertson *et al.* 1991). The Semail ophiolite formed between 96.1 and 95.5 Ma (Rioux *et al.* 2016), corresponding to the Cenomanian in version 2020/01 of the International Chronostratigraphic Chart (Cohen *et al.* 2020), and thus is around 1–2 myr older than the Troodos ophiolite. One of the many VMS in the Semail ophiolite has been shown to contain worm tube fossils (Bayda; Haymon *et al.* 1984; Haymon & Koski 1985). These are morphologically quite similar to the Troodos collared tubes and the Troodos wrinkled tubes (Georgieva *et al.* 2019), being sinuous with an external ornament of longitudinal ridges and concentric annulations, between 1 and 5 mm in diameter (Little *et al.* 1998), and may also have been formed by vestimentiferan worms. A little later in the Late Cretaceous, to the north of this belt of ophiolites in the Neotethys, were a series of Turonian–Santonian-aged volcanic arcs with associated hydrothermal activity, represented today by VMS in the southern Transcaucasus – eastern Pontides orogenic belt in Georgia and Turkey. Three of these VMS contain worm tube fossils. From the Madneuli VMS of Georgia are three smooth-walled tubes that are considerably larger than any of the Cypriot tubular fossils, being between 6.8 and 11.9 mm in diameter (Little *et al.* 2007). The Lahanos and Killik VMS of Turkey contain tubular fossil-like structures that are even larger than the Madneuli tubes, being 20–25 mm in diameter (based on Revan *et al.* 2014, figs 4c, 5). There are not sufficient morphological features in the tubular fossils from the Georgian and Turkish VMS to identify them with any certainty, but their presence, along with the Cyprus and Oman examples, provides a record of hydrothermal vent communities in the western part of the Neotethyan Ocean for *c.* 10 myr, from the Cenomanian to the Santonian, from a variety of tectonic settings (Little *et al.* 2007). The presence of worm tube fossils in the Upper Cretaceous Neotethyan vent communities is intriguing given the absence of large tube-dwelling worms (e.g. vestimentiferans) from modern vent sites in the modern-day Indian Ocean, and their occurrence, often in great abundance, in Caribbean, West and East Pacific vent communities (Karaseva *et al.* 2016). This, together with the distribution of modern and fossil species of *Desbruyeresia* (see above), is suggestive of a biogeographic link in the Late Cretaceous between the western Neotethys and the Pacific via spreading ridges(s) in the central and eastern Neotethys, since destroyed by the Cenozoic collision of India into Asia and the continued movement northwards of Africa and Arabia (e.g. Moix *et al.* 2008; Gibbons *et al.* 2015). This would have caused a regional extinction of hydrothermal communities, and the Neotethyan vent faunal combination of provannid, hokkaidoconchid and paskentanid gastropods, and tube worms is likely to have disappeared. However, only the discovery of other Mesozoic and Cenozoic vent communities from the Neotethys, Indian and West Pacific will corroborate this hypothesis.

CONCLUSION

Hydrothermal vent communities were present at six locations on arc-related spreading ridge(s) in the

Neotethyan Ocean over several million years during the late Cenomanian to earliest Turonian (Late Cretaceous). While they were extant, water depths are estimated to have been between 2500 and 5000 m. The communities consisted of worm tubes with three different morphologies, representing possible vestimentiferans and serpulids, together with a moderate diversity of abyssochrysoid gastropods, belonging to eight species in five genera and three families. The gastropods and tube worms probably lived close to active venting and some of the tube worms and species of *Paskentana* may have had chemosymbionts. Epizoans on a few of the gastropod shells may have been gastropod egg capsules, or the very early settlement structures of vestimentiferan worm tubes. It is most likely that a single gaudryceratid ammonite found in one of the Cypriot vent sites represents a waterlogged shell that sank down from surface waters. Among the Cypriot vent gastropod taxa there are no shared species, despite the fact that the vent locations are relatively closely spaced; this may indicate that the communities were not living at the same time during the formation of the Troodos ophiolite. The Cypriot vent gastropod fauna contains the first representatives of the genera *Desbruyeresia*, *Hokkaidoconcha*, *Ascheria* and *Paskentana* at hydrothermal vents, and also the youngest representative of the last-named genus in any environment. The Cypriot vent fauna is taxonomically similar to Cretaceous hydrocarbon seep communities, but lacks vetigastropod and neomphaline gastropods, bivalves and arthropods. Potential explanations for these absences are varied, including ecological, environmental, palaeogeographic and taphonomic. The Cypriot vent communities shared tube worms with slightly older (Cenomanian) and younger (Turonian–Santonian) vent communities elsewhere in the western part of the Neotethyan Ocean, and these may have had faunal connections with contemporary (but currently unknown) vent communities in the western Pacific. However, all the Neotethyan vent communities vanished during the destruction of that ancient ocean during the early Cenozoic.

SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA Linnaeus, 1758
Class GASTROPODA Cuvier, 1795
Order CAENOGASTROPODA Cox, 1959
Superfamily ABYSSOCHRYSOIDEA Tomlin, 1927
Family PROVANNIDAE Warén & Ponder, 1991
Genus DESBRUYERESIA Warén & Bouchet, 1993

Type species. Desbruyeresia spinosa Warén & Bouchet, 1993, by original designation. Recent; North Fiji Basin.

Remarks. Desbruyeresia is a small-sized abyssochrysoid gastropod that is similar in several morphological and anatomical respects to *Provanna* (Chen *et al.* 2016), but has a slender shell profile, and a multispiral and decollated protoconch (Kaim *et al.* 2008). *Desbruyeresia* is invariably a distinct taxon in molecular phylogenetic trees (Johnson *et al.* 2010; Chen *et al.* 2016; Souza *et al.* 2020) and is more closely related to other abyssochrysoideans than to *Provanna*.

Desbruyeresia kinousaensis sp. nov.
Figure 3A–E

1999*b* Cerithioid sp. B; Little *et al.*, p. 1028, fig. 2G.

LSID. urn:lsid:zoobank.org:act:5137EC6B-2AC0-4829-A7BB-6CA71559BB45

Derivation of name. After the type locality.

Type material. Holotype, and sole specimen known, is ZPAL Ga.20/1 (Fig. 3A–C); specimen broken into two pieces (ZPAL Ga.20/1a and b) during collection.

Type locality. Kinousa massive sulphide deposit, Cyprus.

Type horizon. Pillow lava sequence of Troodos ophiolite, late Cenomanian to earliest Turonian age (Late Cretaceous).

Additional material. A fragmentary specimen, ZPAL Ga.20/2 (Fig. 3D, E).

Diagnosis. Slim shell of medium size and melanoid in shape with strong reticulate ornament; the distance between the first and second spiral ribs is bigger than between the other ribs.

Description. High-spired specimen. Broken in two parts (upper part, ZPAL Ga.20/1a; lower part, ZPAL Ga.20/1b). Visible portions of each part show opposite shell surfaces, due to the way the specimens were prepared. Upper part poorly preserved with all ornamentation worn away and consisting of six preserved whorls. Lower part well-preserved and with three whorls ornamented by five spiral ribs, with sixth located just at the abapical suture. First and second spiral ribs more widely spaced than the others. Whorls slightly angulated at the most adapical rib. Axial ribs prosocyrt, moderately high, and running from suture to suture. Spiral ribs cross the axial ribs without any break. Intersections of spiral and axial ribs accentuated by well-developed knobs. Suture fairly deeply incised. The demarcation with the base angular and enhanced by a spiral rib. The base ornamented by three strong spiral ribs. Protoconch and aperture unknown.

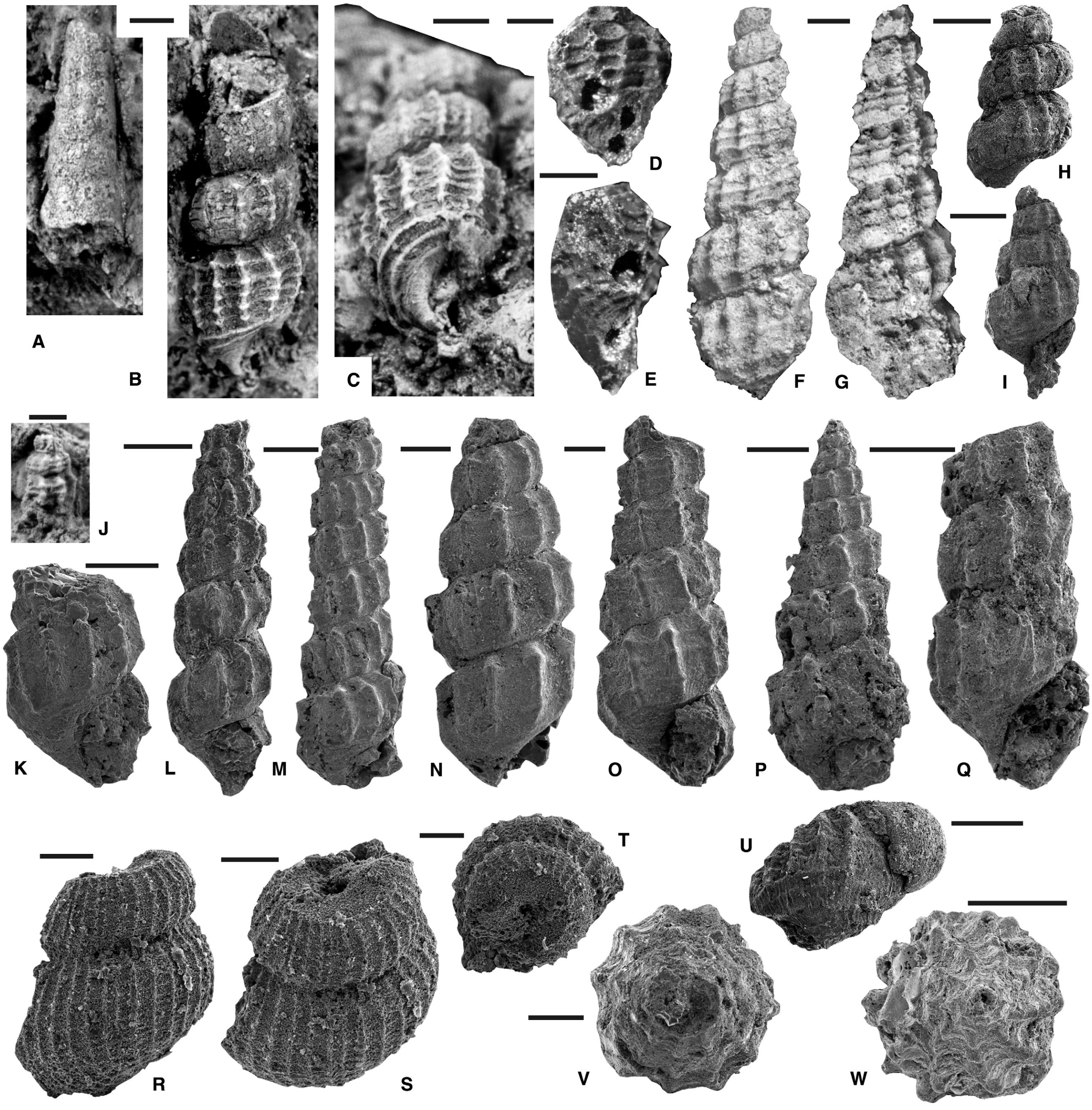

FIG. 3. A–E, *Desbruyeresia kinousaensis* sp. nov.: A–C, ZPAL Ga.20/1: A, apical part, lateral view; B–C, apertural part, adapertural lateral and oblique adapical views; D–E, ZPAL Ga.20/2: D, adapertural lateral view; E, oblique adapical view. F–J, U–V, *Desbruyeresia memiensis* sp. nov.: F–G, GSD-Ga.01 (holotype): F, adapertural lateral view; G, apertural lateral view; H, ZPAL Ga.20/4, adapertural lateral view; I, V, ZPAL Ga.20/5: I, adapertural lateral view; V, apical view; J, ZPAL Ga.20/3, lateral view; U, ZPAL Ga.20/6, lateral view of ultimate whorl with epizoon. K–T, W, *Desbruyeresia kambiaensis* sp. nov.: K, ZPAL Ga.20/24, apertural lateral view; L, ZPAL Ga.20/25, apertural lateral view; M, ZPAL Ga.20/26 (holotype), apertural lateral view; N, ZPAL Ga.20/27, adapertural lateral view; O, ZPAL Ga.20/28, apertural lateral view; P, W, ZPAL Ga.20/29: P, lateral view; W, apical view; Q, ZPAL Ga.20/30, apertural lateral view; R–T, ZPAL Ga.20/32, protoconch: R, lateral view; S, oblique apical view, T, apical view. Scale bars represent: 1 mm (A–E, I, K–M, P–Q, U, W); 0.5 mm (F–H, J, N–O, V); 0.1 mm (R–T). A–G, J, optical photographs; H–I, K–W, SEM micrographs.

Dimensions. Holotype: lower piece (ZPAL Ga.20/1b): height, 7.4 mm; width, 2.9 mm; upper part (ZPAL Ga.20/1a): height, 5.2 mm. Specimen ZPAL Ga.20/2: height, 3.3 mm; width, 3.3 mm.

Remarks. Desbruyeresia kinousaensis is remarkably similar to *D. kanajirisawensis* from Cenomanian hydrocarbon seep deposits in Hokkaido (northern Japan), but it is slightly slimmer than that species and the distance between the first and second spiral ribs is greater than that between the other ribs. In *D. kanajirisawensis* the distances between the spiral ribs are nearly equal in all instances. Of the other Cypriot species (see below), *D. memiensis* sp. nov. and *D. kambiaensis* sp. nov. possess only three spiral ribs, in contrast to *D. kinousaensis*, which has five. The most closely similar Recent form is *D. melanioides* Warén & Bouchet, 1993, but this has only three spiral ribs.

Desbruyeresia memiensis sp. nov.
Figure 3F–J, U, V

1999*b* Cerithioid sp. A; Little *et al.*, p. 1028, fig. 2H.

LSID. urn:lsid:zoobank.org:act:CD9C250E-B190-4EC3-9F96-5C988B63AB7E

Derivation of name. After the type locality.

Type material. Holotype is GSD-Ga.01 (Fig. 3F, G).

Type locality. Memi massive sulphide deposit, Cyprus.

Type horizon. Pillow lava sequence of Troodos ophiolite, late Cenomanian to earliest Turonian age (Late Cretaceous).

Additional material. ZPAL Ga.20/4 (Fig. 3H), ZPAL Ga.20/5 (Fig. 3I, V), ZPAL Ga.20/6 (piece of ultimate whorl) (Fig. 3U); ZPAL Ga.20/3 (Fig. 3J); and three additional fragmentary specimens (ZPAL Ga.20/7-9).

Diagnosis. Shell slender with six or more convex whorls, slightly angulated at first and third spiral ribs. Axial ribs strong and clearly elevated over the whorl surface.

Description. Shell high-spired, consisting of seven preserved whorls on the holotype. Ramp absent, whorls fairly convex, suture deeply incised. Axial ribs orthocline to weakly opisthocline, clearly elevated, and running from suture to suture. Three closely spaced spiral ribs located in median part of flank, crossing axial ribs without any break and forming blunt knobs at the intersections. Demarcation with the last whorl base angular and enhanced by a spiral rib. Base, aperture and protoconch not observed.

Dimensions. Holotype: height, 4.3 mm; width, 1.5 mm. For other specimens see Table 2.

Remarks. Desbruyeresia memiensis sp. nov. most closely resembles the Recent species *D. melanioides* Warén & Bouchet, 1993, which differs in having weaker spiral and axial ornamentation, and a non-angular whorl profile. In additions, it is also less slender and never has more than 3.5 whorls (Warén & Bouchet 1993), in contrast to *D. memiensis* sp. nov., which grows more than six whorls. The new species differs from *D. kambiaensis* sp. nov. (see below) in being less slender and less angular.

Desbruyeresia kambiaensis sp. nov.
Figure 3K–T, W

LSID. urn:lsid:zoobank.org:act:22D7E5FC-3E15-4622-AE0E-B57F795AE7A7

TABLE 2. Additional measurements of gastropod specimens from Cypriot volcanogenic massive sulphides (VMS).

Species	Specimen code	Height (mm)	Width of last preserved whorl (mm)
Desbruyeresia memiensis	ZPAL Ga.20/3	1.5	0.8
	ZPAL Ga.20/4	3.2	2
	ZPAL Ga.20/5	3.6	2
	ZPAL Ga.20/6	2.6	2.3
	ZPAL Ga.20/7	2.8	1.6
	ZPAL Ga.20/8	3.1	1.4
	ZPAL Ga.20/9	4.5	2
Desbruyeresia kambiaensis	ZPAL Ga.20/10	2.8	1.4
	ZPAL Ga.20/11	2.8	1.3
	ZPAL Ga.20/12	4.5	1.8
	ZPAL Ga.20/14	3.4	1.6
	ZPAL Ga.20/15	5.2	1.9
	ZPAL Ga.20/17	4.2	1.8
	ZPAL Ga.20/19	2.9	1.3
	ZPAL Ga.20/20	2.8	1.5
	ZPAL Ga.20/21	n.m.	1.9
	ZPAL Ga.20/22	n.m.	1.5
	ZPAL Ga.20/24	2.6	2.1
	ZPAL Ga.20/25	6	2.1
	ZPAL Ga.20/27	3.9	1.5
	ZPAL Ga.20/28	4.6	1.9
	ZPAL Ga.20/29	6.3	2.2
	ZPAL Ga.20/30	4.6	2.2
	ZPAL Ga.20/31	5.3	1.6
Ascheria canni	ZPAL Ga.20/42a	4.2	1.8
	ZPAL Ga.20/42b	4.2	1.8
	ZPAL Ga.20/43	3.1	2.4
	ZPAL Ga.20/44	24.3	8.2
	ZPAL Ga.20/45	18.2	9
	ZPAL Ga.20/46	24.7	6.7

n.m., not measured due to poor preservation.

Derivation of name. After the type locality.

Type material. Holotype, ZPAL Ga.20/26 (Fig. 3M); the largest specimen available, with seven whorls and a broken apex.

Type locality. Kambia massive sulphide deposit, Cyprus.

Type horizon. Pillow lava sequence of Troodos ophiolite, late Cenomanian to earliest Turonian age (Late Cretaceous).

Additional material. ZPAL Ga.20/24 (Fig. 3K), ZPAL Ga.20/25 (Fig. 3L), ZPAL Ga.20/27 (Fig. 3N), ZPAL Ga.20/28 (Fig. 3O), ZPAL Ga.20/29 (Fig. 3P, W), ZPAL Ga.20/30 (Fig. 3Q), eight protoconchs (ZPAL Ga.20/32–39) with the best-preserved of these, ZPAL Ga.20/32 illustrated (Fig. 3R–T), and 15 additional complete and partial specimens (ZPAL Ga.20/10–23 and 31).

Diagnosis. Shell very slender with strongly orthocline axial ribs producing shell profile with angulate appearance. Whorl flanks nearly flat.

Description. Protoconch multispiral ornamented with numerous axial ribs and weaker spiral riblets with no knobs at the intersections. Apex decollated. Teleoconch high-spired, very slim, consisting of seven preserved whorls in the holotype. Ramp absent, whorls flat-sided to weakly convex, suture deeply incised. Axial ribs orthocline, strongly elevated, and running from suture to suture, but becoming weaker next to the suture (both ab- and adapically). Three weak and evenly distributed spiral ribs cross the axial ribs without any break and form blunt knobs at the intersections. Demarcation with base angular and enhanced by a spiral rib. Base and aperture not observed.

Dimensions. Holotype: height, 6.7 mm; width, 2.1 mm. For other specimens see Table 2.

Remarks. None of our teleoconch specimens has a protoconch attached; however, all of the protoconch specimens are associated with numerous specimens of *D. kambiaensis* sp. nov. in the same horizon and on the same block of sulphide. It is therefore most parsimonious to consider them conspecific. The new species is the most slender of the Cypriot species of *Desbruyeresia* and the only one for which protoconch details are known. The protoconchs are cancellate, multispiral and decollated, which are features that are typical of the genus (Kaim *et al.* 2008). The flattened teleoconch whorl flanks are reminiscent of *Hokkaidoconcha tanabei* (Kaim *et al.* 2008), but that species has opisthocyrtic axial ribs rather than orthocline ones.

Family HOKKAIDOCONCHIDAE Kaim *et al.*, 2008
Genus HOKKAIDOCONCHA Kaim *et al.*, 2008

Type species. Hokkaidoconcha tanabei Kaim *et al.*, 2008, by original designation; Cenomanian, Kanajirisawa (Hokkaido, Japan).

Remarks. Hokkaidoconchids form an extinct group of abyssochrysoid gastropods that were previously known only from ancient hydrocarbon seeps (e.g. Kaim *et al.* 2008, 2014, 2017; Kiel *et al.* 2008*a*, 2010).

Hokkaidoconcha morisseaui sp. nov.
Figure 4A, B

LSID. urn:lsid:zoobank.org:act:07E6D3E2-760C-4FE6-86A1-3828FB53069E

Derivation of name. After geologist Michel Morisseau (formerly Geoconsult Ltd Cyprus), who first found gastropod fossils from the Cyprus VMS.

Type material. Holotype is ZPAL Ga.20/40 (Fig. 4A, B), a specimen in two pieces, lacking both apex and aperture.

Type locality. Kambia massive sulphide deposit, Cyprus.

Type horizon. Pillow lava sequence of Troodos ophiolite, late Cenomanian to earliest Turonian age (Late Cretaceous).

Material. The holotype is the sole specimen known to date.

Diagnosis. Shell strongly elongate with weakly convex to nearly flat whorl flanks ornamented with strong, opisthocyrtic axial ribs and five well-expressed spirals. Intersections of axial ribs with adapical spiral rib appended by pointed knob. Axial ribs run from suture to suture.

Description. Shell strongly elongate, cylindrical. The two preserved parts of the shell consist of five whorls in total (three and two, respectively). Whorls weakly convex to nearly flat. Ornamentation consists of strong opisthocyrtic axial ribs, although some ribs nearly orthocline. Axial ribs run from suture to suture without a break in the abapical portion of the shell. Spiral ribs well-expressed with adapical spiral rib forming pointy knobs at the intersections with axial ribs. Aperture not preserved; protoconch unknown.

Dimensions. Holotype ZPAL Ga.20/40: height, 4.5 mm; width, 1.5 mm.

Remarks. Hokkaidoconcha morisseaui sp. nov. is most closely similar to *H. hikidai* Kaim *et al.*, 2008 from a

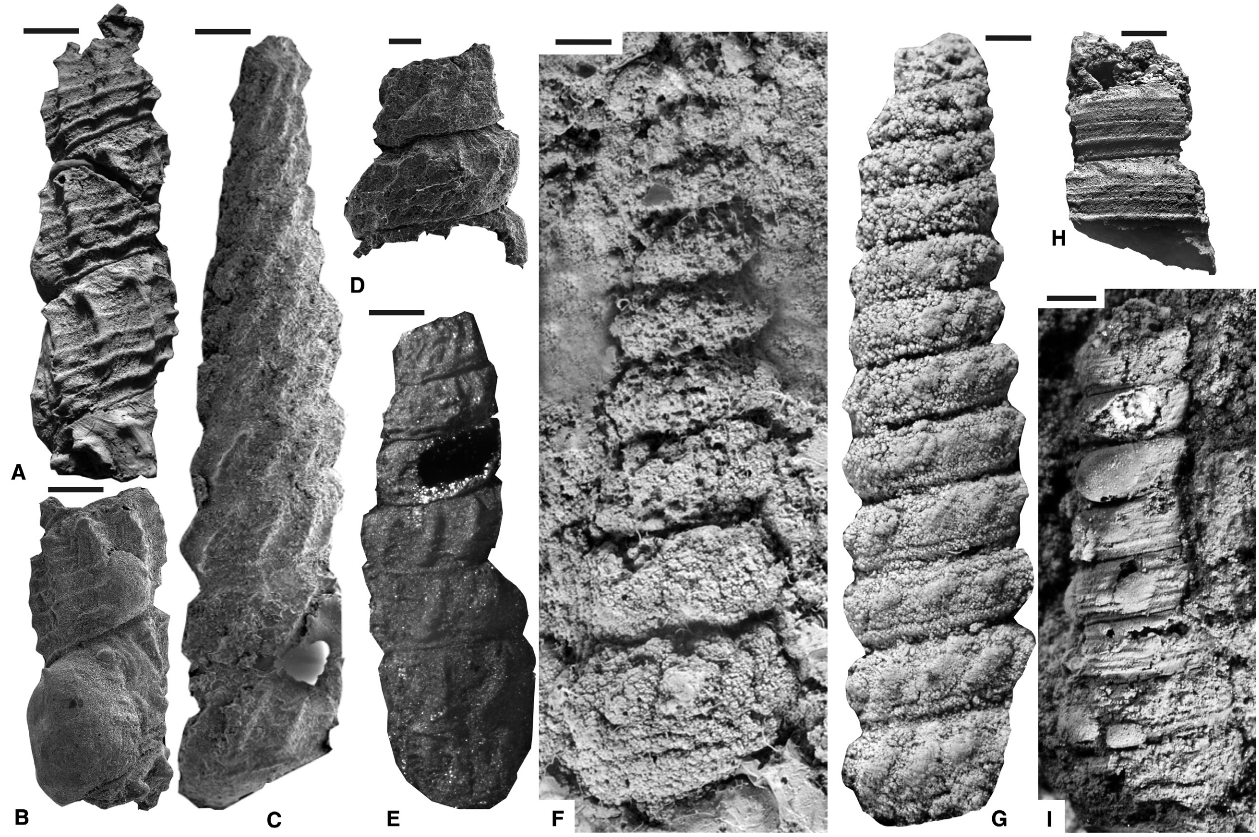

FIG. 4. A–B, *Hokkaidoconcha morisseaui* sp. nov. ZPAL Ga.20/40, lateral views of two parts of same specimen; note epizoons on B. C–F, *Ascheria canni* sp. nov.: C, ZPAL Ga.20/41 (holotype), silicone rubber cast, adapical lateral view; D–E, ZPAL Ga.20/42: D, detail of apex; E, lateral view of entire specimen; F, ZPAL Ga.20/44, silicone rubber cast, lateral view. G–I, *Cyprioconcha robertsoni* gen. et sp. nov.: G, ZPAL Ga.20/49 associated with *A. canni* sp. nov. (Fig. 4F), silicone rubber cast, lateral view; H, ZPAL Ga.20/47c (adapical part of holotype), lateral view; I, ZPAL Ga.20/47b (abapical part of holotype), lateral view; note epizoons. Scale bars represent: 2 mm (A–C, E, F, H); 1 mm (G, I); 0.2 mm (D). E–G, I, optical photographs; A–D, H, SEM micrographs.

Campanian hydrocarbon seep in Yasukawa (Hokkaido, Japan), but the former differs in having less convex whorls, having axial ribs running from suture to suture, and in possessing pointed knobs on the intersections of axial ribs and the most adapical spiral rib. In addition, the axial ribs in the new species are more widely set than in *H. hikidai*.

Genus ASCHERIA Kaim *et al.*, 2014

Type species. Abyssochrysos? *giganteum* Kiel *et al.*, 2008*a*, by original designation; Lower Cretaceous; East Berryessa (California, USA).

Ascheria canni sp. nov.
Figure 4C–F

LSID. urn:lsid:zoobank.org:act:8367DAF0-A858-4079-8374-CABD6417AA48

Derivation of name. After Professor Joe Cann (University of Leeds, emeritus) for his pioneering work on the geology of the Troodos ophiolite.

Type material. Holotype is ZPAL Ga.20/41 (Fig. 4C), an external mould and associated silicone rubber cast.

Type locality. Kambia massive sulphide deposit, Cyprus.

Type horizon. Pillow lava sequence of Troodos ophiolite, late Cenomanian to earliest Turonian age (Late Cretaceous).

Additional material. ZPAL Ga.20/42 (Fig. 4D, E); ZPAL Ga.20/44 (Fig. 4F) as well as three additional fragmentary specimens (ZPAL Ga.20/43, 45 and 46).

Diagnosis. Very elongate shell with strong, markedly opisthocline axial ribs, and numerous much weaker spiral ribs.

Description. Turreted shell with 12 whorls preserved in the holotype. Whorls weakly convex and ornamented by strong, markedly opisthocline axial ribs in all preserved whorls. Spiral ribs weak and the strongest being the most abapical. Suture weakly incised. Axial ribs start at the adapical suture and end up at the most abapical spiral rib. Base delimited by a rib and angulation. Base ornamented with delicate spiral ribs. Aperture and protoconch unknown.

Dimensions. Holotype: height, 6.7 mm; width, 1.6 mm. For other specimens see Table 2.

Remarks. Ascheria is a genus of abyssochrysoid gastropods that resembles the extant *Abyssochrysos* (see Kaim *et al.* 2014 for a discussion) and the only abyssochrysoid known to have strongly opisthocline axial ribs throughout ontogeny; species of *Abyssochrysos* (e.g. Bouchet 1991; Killeen & Oliver 2000) also have opisthocline axial ribs, but only early in ontogeny. In view of the fact that the present specimens have opisthocline axial ribs on all whorls we place them into *Ascheria*. However, due to poor preservation we cannot determine whether an umbilical constriction is present in *A. canni* sp. nov.; such a constriction would be diagnostic of *Ascheria*. *Ascheria canni* sp. nov. differs from its congeners in being much more elongated and slimmer. Here we tentatively assign the largest specimen (Fig. 4F) to *A. canni* sp. nov. because of poor preservation. The juvenile whorls (Fig. 4D) of the new species display a spiral and axial ornament that is typical of juvenile hokkaidoconchids.

Genus CYPRIOCONCHA nov.

LSID. urn:lsid:zoobank.org:act:3BB576F7-6902-4303-9208-08F254001EFE

Derivation of name. After Cyprus and *concha*, Latin for 'shell'.

Type species. Cyprioconcha robertsoni sp. nov., see below; by monotypy.

Diagnosis. As for type species.

Cyprioconcha robertsoni sp. nov.
Figure 4G–I

LSID. urn:lsid:zoobank.org:act:3635EA5F-394B-4C6A-B298-9D33B19DECB0

Derivation of name. After Professor Alastair Robertson (University of Edinburgh, emeritus) for his influential work on the geology of Cyprus and the eastern Mediterranean.

Type material. Holotype: ZPAL Ga.20/47 in three pieces: external mould ZPAL Ga.20/47a; abapical part of the shell ZPAL Ga.20/47b (Fig. 4I); and adapical part of the whorls ZPAL Ga.20/47c (Fig. 4H).

Type locality. Kambia massive sulphide deposit, Cyprus.

Type horizon. Pillow lava sequence of Troodos ophiolite, late Cenomanian to earliest Turonian age (Late Cretaceous).

Additional material. ZPAL Ga.20/49 (Fig. 4G), a large external mould associated with *Ascheria canni* sp. nov. (Fig. 4F) on the same sulphide block.

Diagnosis. Very elongate shell with numerous, short whorls. Numerous spiral ribs and axial ornament of opisthocline growth lines and blunt opisthocline axial ribs present only on terminal whorls.

Description. Shell turreted with approximately 12 whorls preserved on all parts of the holotype and 12 whorls preserved on slightly ontogenetically older ZPAL Ga.20/49 (Fig. 4G). Whorls very low and weakly convex, ornamented by six spiral ribs crossed by numerous opisthocline growth lines. Blunt opisthocline axial ribs present only on the latest whorls. The abapical spiral rib is the strongest and the remaining ones are of similar strength. Suture weakly incised. Aperture and protoconch not known.

Dimensions. Holotype: height, 9.9 mm; width, 4.3 mm; specimen ZPAL Ga.20/49: height, 18.3 mm; width, 5.3 mm.

Remarks. The strongly turreted shell and the appearance of spiral ribs with the rounded and relatively wide tops suggest a relationship with hokkaidoconchids. *Cyprioconcha* gen. nov. differs, however, from the other genera in this family in lacking axial ornamentation on early whorls and in having exceptionally narrow whorls with a nearly flat-topped profile and its continuous bend towards the sutures. The most closely similar genus is *Ascheria*, which possesses, however, wider whorls and the opisthocline axial ribs throughout its ontogeny.

Family PASKENTANIDAE Kaim *et al.*, 2014
Genus PASKENTANA Kiel *et al.*, 2008*a*

Type species. Turbo paskentaensis Stanton, 1895, by original designation; Upper Jurassic to Lower Cretaceous seep carbonates in California, USA.

Paskentana xenophontosi sp. nov.
Figure 5B–E

1999*b* Epitoniid; Little *et al.*, p. 1028, fig. 2I.

LSID. urn:lsid:zoobank.org:act:4CA1BC92-6432-4580-9943-4B5048B1C49F

Derivation of name. After Costas Xenophontos (retired chief geologist of the Cyprus Geological Survey) for his influential work on Cypriot geology and assistance to visiting geologists over many years.

Type material. Holotype is ZPAL Ga.20/51, a specimen broken in the middle with the two parts inclined towards each other.

Type locality. Memi massive sulphide deposit, Cyprus.

Type horizon. Pillow lava sequence of Troodos ophiolite, late Cenomanian to earliest Turonian age (Late Cretaceous).

Material. The holotype is the sole specimen known to date.

Description. The abapical part of the specimen consists of five turbiniform whorls (seven in total). Whorls continuously convex up to a weak ramp at the adapical suture. Ornament of six spiral ribs and orthocline axial ribs (*c.* 30 per whorl), with scaly elaborations at the intersections with spiral ribs on early whorls. The hollow part of the scales is directed anteriorly. Axial ribs change direction to prosocline at the ramp. Whorl surfaces also with thin spiral lirae. Demarcation to base without angulation. Base smooth. Aperture and protoconch unknown.

Dimensions. Holotype: height, 19.3 mm; width, 10.2 mm.

Remarks. In having a scaly sculpture, the new species is most closely similar to a congener from the California Bear Creek seep site (Valanginian) that was described by Kiel *et al.* (2008*a*) as *Paskentana paskentaensis* (Stanton, 1895), but is likely to represent an undescribed species. *Paskentana xenophontosi* sp. nov. differs from this taxon in being higher spired and having thin spiral lirae on the whorl surfaces.

Paskentana dixoni sp. nov.
Figure 5A

LSID. urn:lsid:zoobank.org:act:BC7570FF-7E57-4F79-A3C9-45E043EA9A91

Derivation of name. After Dr John Dixon (University of Edinburgh, emeritus), who donated the type specimen.

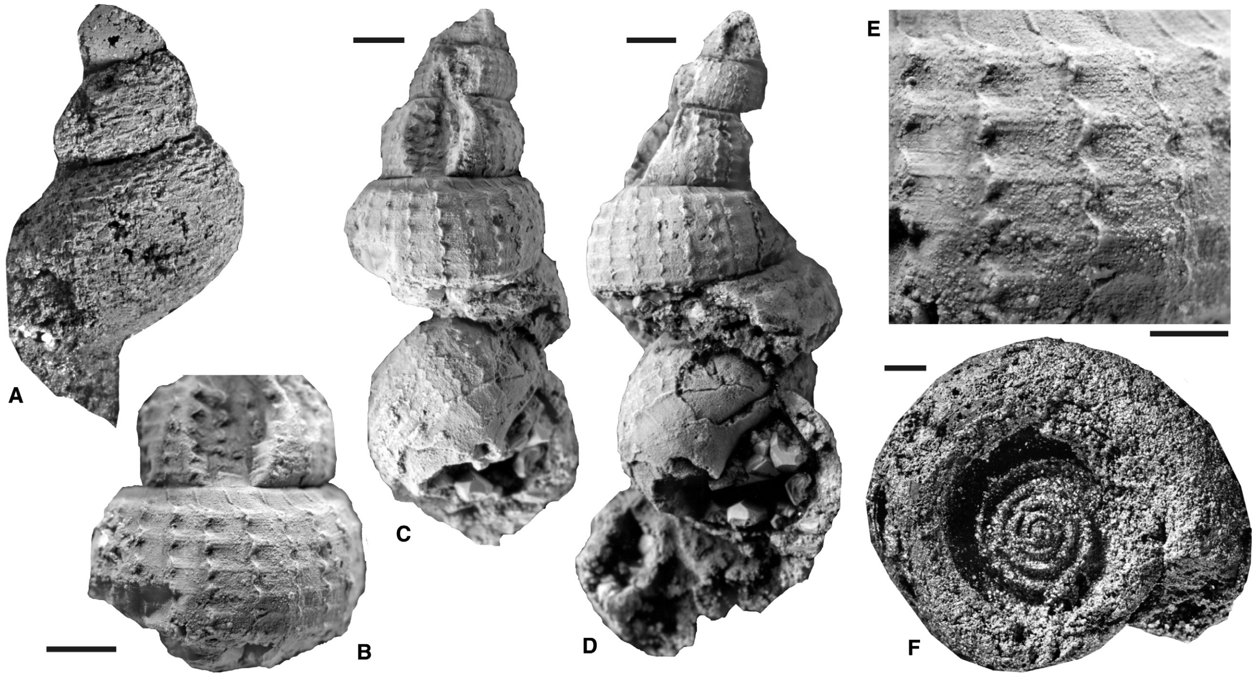

FIG. 5. A, *Paskentana dixoni* sp. nov. ZPAL Ga.20/49 (holotype), adapertural lateral view. B–E, *Paskentana xenophontosi* sp. nov. ZPAL Ga.20/51 (holotype): B, lateral view detail showing whorl indentation; C, lateral view; D, apertural lateral view; E, detail of ornament. F, Gaudryceratidae indet. ZPAL Ga.20/52. Scale bars represent: 2 mm (A–D, F); 1 mm (E). All optical photographs.

Type material. Holotype is ZPAL Ga.20/49.

Type locality. Kambia massive sulphide deposit, Cyprus.

Type horizon. Pillow lava sequence of Troodos ophiolite, late Cenomanian to earliest Turonian age (Late Cretaceous).

Material. An additional specimen, possibly belonging here, is ZPAL Ga.20/50, which comprises a partially preserved shell base.

Diagnosis. Shell turbiniform with moderately incised suture, flanks continuously rounded and angulated at the mid-flank. The whorls are ornamented by numerous thin spirals but no axial ribs.

Description. Turbiniform shell with three whorls visible. Whorl flanks continuously rounded. No angulation at the demarcation with base. Suture fairly incised. No axial ornament apart from prosocline growth lines. Spiral ornament of very fine lirae, those on the abapical part of lateral flank slightly stronger.

Dimensions. Holotype: height, 8.5 mm; width, 5.8 mm.

Remarks. The most closely similar species is *P. umbilicata* Kiel *et al.*, 2010 from the Oxfordian-age seeps of Beauvoisin, southeastern France (Kiel *et al.* 2010), but that species differs from *P. dixoni* sp. nov. in having the whorl angulation close to the base demarcation rather than in the mid-flank position. The new species also resembles *P. wilburensis* (Stanton, 1895) from the Hauterivian Wilbur Springs seep (California, USA), but has more convex and lower whorls. *Paskentana anistratenkorum* Kiel *et al.*, 2010 from Hauterivian seeps in Crimea is also similar, but has more expanded whorls and less incised sutures than *P. dixoni* sp. nov.

Class CEPHALOPODA Cuvier, 1795
Suborder LYTOCERATINA Hyatt, 1889
Superfamily TETRAGONITOIDEA Hyatt, 1900
Family GAUDRYCERATIDAE Spath, 1927
GAUDRYCERATIDAE indet.
Figure 5F

Material. A single, poorly preserved specimen (ZPAL Ga.20/52) from the Kambia massive sulphide deposit, Cyprus, consisting of seven whorls and measuring 45.2 mm in diameter.

Description. Outer 1.25 whorls have a maximum preserved diameter of 45.2 mm, and are preserved in finely crystalline pyrite; there is no trace of ornament, external shell surface or surface of the internal mould surviving. Inner 5.5 whorls preserved as an external mould in coarsely crystalline pyrite, also with no details of ornament preserved. Coiling very evolute, serpenticone, the umbilicus wide, comprising 57.7% of the diameter, with a broad, convex umbilical wall. The whorl section is depressed, with a broadly convex inner flank region, convergent outer flanks and ventrolateral shoulders, and a broad, convex venter. No preserved sutures.

Remarks. Given the late Cenomanian to earliest Turonian date of the Kambia VMS, the sole contemporaneous ammonite group with the coiling and whorl section of the Kambia specimen is the family Gaudryceratidae. Two gaudryceratid genera are known from the Turonian: *Anagaudryceras* Shimizu, 1934 and *Gaudryceras* de Grossouvre, 1894. The Kambia gaudryceratid is 45 mm in diameter; adult *Anagaudryceras* are up to 110 mm in diameter (Kennedy & Klinger 1979, pl. 11, fig. 1), and adult *Gaudryceras* exceed 180 mm in diameter (de Grossouvre 1894, pl. 39; see also Matsumoto 1995). The Kambia specimen is thus either a juvenile, or represents the inner whorls of a larger individual. There are records of *Anagaudryceras* from western Europe, Austria, Romania, Algeria, Tunisia, KwaZulu-Natal in South Africa, Madagascar, Tamil Nadu in South India, Japan, Sakhalin, Kamchatka, Alaska, British Colombia, California, New Zealand, and Seymour Island on the Antarctic Peninsula; *Gaudryceras* is equally widely distributed. At the species level, *Anagaudryceras sacya* (Forbes, 1846) ranges from the middle Albian to the Coniacian, and is known from Tamil Nadu in South India, Madagascar, KwaZulu-Natal in South Africa, Mozambique, Japan, Alaska, British Columbia, California, central and southern Europe, and the Balkans. Clearly, gaudryceratid ammonites could achieve wide distribution, either by passive drifting or more active locomotion, to cross Cretaceous oceans, so that their presence in the water column above the Kambia vent system is unexceptional.

Worm tubes

The worm tubes from the Cypriot VMS were described in detail by Georgieva *et al.* (2019). We here reiterate only the most important information. Georgieva *et al.* (2019) distinguished three groups of tubes: Troodos collared tubes from the Kambia, Kapedhes, Memi and Sha VMS; Troodos wrinkled tubes from the Kambia and Kapedhes VMS; and Troodos attached tubes from the Kinousa and Memi VMS. The collared and wrinkled tubes were considered by Georgieva *et al.* (2019) to be possible vestimentiferan siboglinids, while the attached tubes are possibly serpulids, although a siboglinid affinity could not be ruled out. The worm tubes figured by Oudin & Constantinou (1984) from the Peristerka VMS do not show sufficient characters to be compared to the worm tubes from the other Troodos VMS (Little *et al.* 1999).

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This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/879323E5-8659-4C7B-9735-1B3A38C16EA1

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