The pre-Messinian deep-sea Neogene echinoid fauna of the Mediterranean: Surface productivity controls and biogeographical relationships

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A B S T R A C T

Autochthonous deep-water echinoid faunas are very rare in the fossil record. A well-preserved bathyal echinoid assemblage is described from the middle Miocene Pakhna Formation of southern Cyprus. This low-diversity fauna is dominated by just two genera of spatioadnoid (Palaeobrissus and Heteropneustes), and implies a water depth of 200–1000 m. Echinoids occur in modest abundance but are restricted to a small number of intervals where sapropels are numerous and thick, although never in the sapropels themselves. This suggests that echinoids in the deep pre-Messinian Mediterranean were surviving at depth by exploiting raised levels of nutrient input driven by Milankovitch forcing, but being excluded at times of peak carbon settlement. In contrast to the modern depauperated deep-water fauna of the Mediterranean, which has Atlantic affinities, these two species show strongest phylogenetic affinities with bathyal Caribbean fauna. Caribbean and Mediterranean deep-sea macrobenthic faunas were thus closely connected until just before the Gibraltar Sill formed.

1. Introduction

The Mediterranean is both the youngest and the most unusual of deep-sea basins (reviewed by Emig and Geistdoerfer, 2004). Early in the Miocene the eastern marine gateway connecting the Mediterranean and Indo-Pacific closed. Shortly after, at the end of the Miocene, the marine gateway between the Mediterranean and Atlantic also closed, isolating the basin and leading to the Messinian crisis, a desiccation event that generated high-salinity deep water and led to widespread extinction (Duggan et al., 2003). After this short-lived event the western marine connection to the Atlantic basin was re-established, but only through a narrow opening with a high sill, which thus continued to act as a barrier isolating the deep-sea basin and its fauna. Today the Mediterranean shelf break barrier exists at 100–110 m, which makes the shelf narrow and strengthens the overall oligotrophy of the sea. At depths greater than 200–300 m temperatures remain constant and high at 13.5 °C (west) to 15.0 °C (east). Additionally, the deep water is very saline with values up to 38.5–39 psu. Both temperature and salinity create a very strongly stratified water body, which further enhances the oligotrophy of the Mediterranean. As a consequence the Mediterranean deep-sea echinoid fauna is sparse and appears to have arisen through post-Miocene colonisation by relatively shallow Atlantic forms. In contrast to other deep-sea basins, the Mediterranean has no echinoid species that are confined to bathyal depths: all species found at depth in the Mediterranean today are also present in shelf settings (Table 1). Unfortunately there is very little direct evidence of the composition and affinities of the deep-water echinoid fauna of the Mediterranean basin prior to the Messinian.

The fossil record of echinoids is overwhelmingly that of shallow continental shelf faunas. Indeed true ancient deep-sea echinoid faunas are exceedingly rare and confined to tectonic regions where there has been convergence, notably in island arc settings, or to seamounts such as Barbados. As a consequence our knowledge of the evolution of deep-sea echinoid faunas is pitifully small and has largely been pieced together through a combination of molecular clock studies and inference from our knowledge of the history of shelf faunas (e.g. Smith, 2004, Smith and Stockley, 2005). Yet those few windows into the deep-sea fossil record can provide key data.

In the Mediterranean region deep-water echinoid faunas of Neogene age come from just two regions, the southern Cyprus fauna described here, and the middle Miocene (’Helvetian’) fauna described by Manzoni (1879), Stefanini (1908) and Lambert (1915) from the northern Apennines. This latter region is well known for its upper bathyal sediments of Serravallian age, which include hydrocarbon-vent deposits (“calcaria Lucini”) and yield chemosymbiont faunas deposited no shallower than 200–250 m (Aharon and Gupta, 1994). However it is not yet known how the echinoid-bearing levels relate in the sequence to these hydrocarbon-seep deposits.

Although echinoids have been recorded from deep-water settings of Neogene age in the Caribbean, these are almost exclusively composed of allochthonous faunas transported downslope from shallow...
water settings. Donovan et al. (2005) described a deep-water echinoderm fauna from chalks and mass mud flows of the lower Miocene Montpelier formation of Jamaica. The echinoids however, are typical shallow-water taxa (Echinometra, Clypeaster, Pricinidae) and co-occur with derived scleractinian debris. So although the beds themselves may be 200 m or more in depth (Underwood and Mitchell, 2004), the echinoid fauna is very definitely not. Only the cidaroid Histocidaris, represented by isolated spines, may be truly autochthonous to this setting. The same conclusions hold true for the echinoids from the Bowden Shell Bed, a Pliocene deeper water deposit in Jamaica (Donovan and Paul, 1998). Bathyal taxa that are widely distributed in the Caribbean today, such as Heteropneustes and Palaeopneustes, have never been recorded from the fossil record of that region (Donovan and Rowe, 2000, table 2). There are therefore only two records of bathyal echinoids in the Cenozoic and Quaternary of the region: Palaeopneustes cf. cristatus from the Pleistocene Manchioneal Formation, estimated to be deposited at depths of at least 100 m (Donovan and Embden, 1996), and Cheilechinus crassus from the Palaeogene radiolarian marls of Barbados (Gregory, 1889).

Elsewhere in the world the most unambiguous Neogene deep-sea echinoid faunas come from the radiolarian oozes in Fiji and Java (Bather, 1934) of early Pliocene age (Rodda et al., 1985), and the middle Miocene Tatsukuroiso mudstone in north-western Honshu, Japan, where endemic deep-sea echinoid taxa, including Pourtalesia and echinothurioids are found (Kitakazi and Nikaido, 1985).

Given this sparsity of information, the middle Miocene Lophos Beds of Cyprus, which yield a deep-sea echinoid fauna takes on importance. This fauna comes from a key time in the evolution of the Mediterranean, after its connection to the Indian Ocean through the Red Sea had finally been cut but before the western closure at the Gibraltar straights had effectively been sealed off. This fauna offers a window into the conditions that prevailed in the deep Mediterranean just prior to the Messinian extinctions.

2. Geological setting

The Miocene Pakhna Formation of southern Cyprus comprises a diverse suite of dominantly carbonate sediments, deposited in shallow- to deep-marine settings and showing strong tectonic controls on deposition. The Pakhna Basin was bounded to the north by the ophiolitic terrain of the Troodos Massif, and to the south by the exotic Mesozoic succession of the Akrotiri Peninsula (Eaton and Robertson, 1993). During the early to mid-Miocene, the ophiolitic terrain to the north of the Pakhna Basin was thrust progressively southwards over Cenozoic sediments, creating a series of emergent east-west structural lineaments over which shallow marine carbonates formed. In the Khalassa Sub-Basin (Eaton and Robertson, 1993), immediately to the south, deep-water hemipelagic sedimentation dominated, but turbidity currents brought shallow-water carbonate sediments to the basin floor (Fig. 1). The material described in this paper comes from this setting.

The succession from which the echinoids were collected falls within the Lophos Beds, comprising the lower 400 m of the Pakhna Formation (Greitzer & Constantinou 1969, cited in Martill and Baker, 2006). These strata are well exposed in road cuttings along the major road (B8, Limassol-Troodos) east and west of Alasia New Village (Fig. 2). The stratigraphically lower group of exposures is immediately west of the new Kouris Bridge, 2–3 km north east of Alasia (34°46.0.49’N, 32°56.3.52’E); the higher is 1–1.5 km west of Alasia, adjacent to the minor road to Lophos (34°46.2.31’N, 32°55.6.46’E). This latter exposure

| Table 1 | List of species of echinoid recorded from depths of 100 m or more in the Mediterranean. |
|----------|--------------------------------|----------------|----------------|----------------|----------------|----------------|
| Genus    | Species | Taxon | Min depth (m) | Max depth (m) | Distribution |
| Stylocidaris | affinis | Cidarid | 50 | 1000 | Atlantic, Mediterranean |
| Centrostephanus | longispinus | Diademoid | 50 | 208 | Atlantic, Mediterranean |
| Echinus | melo | Echinoid | 25 | 1100 | Atlantic, Mediterranean |
| Genocidaris | maculata | Temnoeureid | 12 | 420 | Atlantic, Mediterranean |
| Neolampas | rostellata | Cassiduloid | 145 | 1260 | Mediterranean |
| Pinnomechinus | microtuberculatus | Echinoid | 5 | 100 | Mediterranean |
| Schizaster | canaliculatus | Spatangoid | 0 | 100 | Mediterranean |
| Rhabdobrissus | costae | Spatangoid | 25 | 200 | East Atlantic, Mediterranean |
| Brixius | unicolor | Spatangoid | 0 | 240 | N. Atlantic, Caribbean, Mediterranean |
| Echinocardium | flavescens | Spatangoid | 5 | 325 | Mediterranean |

Fig. 1. Block diagram reconstructing the palaeogeography of southern Cyprus during the Miocene, based upon Eaton and Robertson (1993: fig. 16) with modifications. T = turbidites; * = likely echinoid habitat.
was described in some detail by Gaudant et al. (2000), who recorded a well-preserved fish fauna and provided a detailed stratigraphical log. Subsequently, Martill and Barker (2006) described an *Argonauta* from this exposure.

The Lophos Beds of the Pakhna Formation comprise thinly and rhythmically bedded, strongly bioturbated hemipelagic nanofossil chalks and marls, which display a highly variable bed thickness. They contain numerous graded calciturbidites with a mean thickness of about 0.1 m, some of which have basal lags containing larger foraminifera, fragments of corals, rhodoliths and calcite-shelled molluscs. Many contain abundant sand-grade benthic foraminifera, derived from shallow marine environments (Gaudant et al., 2000). Very thin (<0.01 m) sand-grade turbidites are also common, and a single metre-thick turbidite with a slumped base was present. Finely laminated marl beds (0.1–0.6 m thick) containing fossil fish were interpreted by Gaudant et al. (2000) as distal argillaceous turbidites; however, the elevated organic content, lamination and abundant plant debris in these beds indicate that they are in fact sapropels. Sapropels are widely developed in the Neogene and Quaternary of the Mediterranean region, and represent humid climatic periods forced by the precession cycle (21 ka; Rossignol-Strick, 1983; Rohling and Hilgen, 1991; Diester-Haass et al., 1998; Kroon et al., 1998).

Two sedimentological logs of the Lophos Beds were constructed to place the echinoids described herein into their sedimentological context. The lower of these (Fig. 3) was drawn in the cutting adjacent to Krouos Bridge, the higher encompasses the succession in cuttings west of Alassa described by Gaudant et al. (2000) and Martill and Barker (2006). The age of these sections has been determined as middle Miocene. The locality west of Alassa has yielded a nanoflora indicative of a NN6 Zone age, and planktic foraminifera of a N10 Zone age (Gaudant et al., 2000). Together, these suggest a late Serravallian age (Gaudant et al., 2000). These are housed in the Natural History Museum, London (BMNH). Except for one unidentifiable cassisulid fragment (*Echinolampas*), all echinoids belong to just two species, *Heteropneustes monteisi* Manzioni and Mazzetti, 1877, and *Palaeobrissus canaverii* (De Lornoi, 1882) (Figs. 4–8). These are generally well preserved, though crushed to a greater or lesser degree. Both species are autochthonous: their extremely thin tests are so fragile that they would certainly never have withstood any transportation intact.

*Heteropneustes* and *Palaeobrissus* are spatangoids that today are found only in bathyal settings. Both are detritivore feeders, using specialized tube-feet that surround the mouth to pick organic-rich material selectively from the sediment. *Palaeobrissus*, like most specialist deep-sea echinoids, lacks respiratory tube-feet and is exceptionally thin-tested. Its rather rounded proTERM (Fig. 3) marks the distribution and abundance of echinoids in section B, along with the distribution of sapropels.

### 4. Discussion

#### 4.1. Palaeodepth of the Pakhna Formation

Determining the water depth at time of deposition when the sea urchins were living is fraught with difficulty. Palaeoenvironmental interpretation of the Pakhna succession at Alassa is complicated by the abundance of exotic elements in the fauna. Thus, the pipefish *Syngnathus* sp., common in the sapropels, is a denizen of Mediterranean subtidal seagrass meadows, and much of the detritus in the turbidites was derived from shallow marine carbonate environments (Gaudant et al., 2000).
The indigenous fauna associated with the echinoids comprises the nautiloid *Aturia* (common), the argonaut *Argonauta* (1 specimen), pteropod gastropods (diverse, common), rare, small, aragonitic bivalves (*Nuculidae*), a pholadomyid bivalve in life position (3 specimens), oysters (probably originally attached to driftwood), and siphonal tubes of a wood-boring bivalve (*Teredinidae*). Most of these records are of nektonic, planktic or pseudoplanktic taxa, and the indigenous macrobenthos is represented by only two species of bivalves and three species of echinoids. Although part of this low abundance and diversity could be attributed to early diagenetic dissolution of aragonite (as suggested by Kennedy, 1969 for Upper Cretaceous deep water settings), the relative scarcity and low diversity of the fauna most likely is indicative of an oligotrophic deep water environment in which organic flux to the sea floor from primary productivity was mostly low (comparable with Turonian Chalks; Gale et al., 2000). However, the abundance of plant debris...
preserved in the dysaerobic sapropels, plus the presence of tubes of wood boring teredinid bivalves in the chalks, is an indication of an original high input of plant detritus at some intervals. This probably provided nutrition for the detritivorous spatangoid echinoid species and explains their concentration close to these horizons. Gaudant et al. (2000) inferred a depositional depth for the Pakhna Formation at...
Alassa at a maximum of 150 m, based on the benthic foraminifera. However, most if not all of these forms are probably derived from shallow-water sea grass settings.

Evidence from the echinoids suggests a somewhat deeper palaeodepth. The two spatangoid echinoid species have closest living relatives that are bathyal in distribution. The living sister species of _Palaeobrissus canaverii_ is _P. hilgardi_, which is found from Barbados to Colombia living at depths of 300–1025 m (Serafy, 1979; Borrero-Perez et al., 2002), though at least one individual has been captured as shallow as 150 m (Mortensen, 1950). The closest living sister species of _Heterobrissus montesii_ is _H. hystrix_, which also comes from the Gulf of Mexico, Cuba and Colombia and is found living at depths of 220 to 1610 m (Mortensen, 1950; Serafy, 1979; Borrero-Perez et al., 2002). Other, more distantly related species of _Heterobrissus_ alive today are _H. niasicus_ (Indian Ocean, Norfolk Islands and New Caledonia: 420–475 m), _H. erinaceus_ (Australia: 183–457 m) and _H. gigas_ (Australia: 128–503 m) (Mortensen, 1950; Baker and Rowe, 1990).

We can also use other somewhat more indirect evidence from the echinoids that are absent from this environment. Deep-water spatangoid echinoids in the Gulf of Mexico and Atlantic fall into three broad categories: (i) primarily continental shelf taxa that extend into upper slope settings that can be found as deep as ca. 600 m...
(Schizaster, Agassizia, Moira, Brissopsis, Echinocardium and Brissus); (2) bathyal taxa that are largely confined to the upper continental slope from 150–800 m but which rarely migrate into shelf settings (Plethotaenia [150–623 m], Palaeopneustes [76–805], Linopneustes [55–710], Heteropneustes [220–1610 m], Palaeobrissus [150–1025 m]); and (iii) primarily abyssal plain dwellers (Aceste [550–5220 m], Araeolampas [1920–3595 m] and Holanthus [380–4833 m]). The early and middle Miocene continental shelf echinoid fauna of the Mediterranean contains numerous species of the first category (Schizaster, Agassizia, Brissopsis, Echinocardium, Brissus), and their complete absence from the Pakhna Formation suggests that we are dealing with a depositional setting that is significantly deeper than the shelf-break at 150 m. Similarly true abyssal species are absent from the Mediterranean today and have never been recorded from the circum-Mediterranean region as fossils. Of the five bathyal taxa in category (ii) two occur in the middle Miocene of the Mediterranean (Heteropneustes and Palaeopneustes) and a third, Linopneustes, is closely related to the taxon Mazzettia, which co-occurs with Heteropneustes and Palaeobrissus in the middle Miocene deep-water marls of the north Apennines. These were deposited during a rapid shelf-drowning interval in the region and overlie shallow shelf deposits (Amorosi, 1996). They include upper bathyal sediments of Serravallian age (“calcari a Lucini”), which represent hydrocarbon-vent deposits deposited no shallower than 200–250 m (Aharon and Gupta, 1994). Linopneustes in the Gulf of Mexico is a somewhat shallower water taxon that overlaps in range with Palaeobrissus or Heteropneustes today but does not extend as deep as either. Thus the absence of Mazzettia from the Pakhna Formation may indicate that it represents a somewhat deeper water setting than in the northern Apennines. In summary, comparison with living sister taxa and their bathymetric ranges suggests that the Parkha Formation was deposited somewhere in the range of 200–1000 m water depth, and most probably not in the uppermost part of this range.

4.2. Echinoid distribution and nutrient influx to the deep sea

Sapropels are a common feature of the Pliocene and Quaternary sedimentary record of the Mediterranean. These are dark grey or black coloured organic-rich silts and clays that form during periods of higher surface water productivity generated by increased precipitation periods and run-off. Cycles of arid and humid phases in the Mediterranean climate associated with Earth precession have created 21,000 year cycles of enhanced surface productivity and more sluggish deep water circulation, and it is during these periods that organic-rich sapropel layers form. These have been extensively studied and shown to cause a drop of diversity in benthic foraminifera when productivity reaches a critical level and bottom waters become less oxygenated.

Echinoids in the Pakhna Formation occur at levels in which sapropels are numerous and thick, but are absent from the sapropels themselves which represent episodes of sea-floor anoxia (e.g. Fig. 3). Plotted against the density of sapropels in the section it is clear that echinoids are present only during intervals when sapropels are also common, and that the abundance of sapropel levels and the abundance of echinoid tests are strongly correlated ($r^2 = 0.603$). Diester-Haass et al. (1998) described sapropels and associated sediments of Pliocene to Quaternary age seen in deep-sea cores taken south of Cyprus, and showed quantitatively how the abundance of echinoid debris changes in relation to palaeoproductivity. They showed that echinoids are most common beneath and above sapropels, and generally absent in them, coincident with high productivity as calculated from benthic foraminifera (Diester-Haass et al., 1998). The occurrence of stratigraphical clusters of sapropels in Cyprus, as seen west of Alassa (Fig. 3) is suggestive of an eccentricity control modulating the precessional signal, as demonstrated by Lourens et al. (1992) in their tuned timescale for the Neogene based on astrochronology. They demonstrated that sapropels mostly formed during periods of high eccentricity on the 100 and 400 Ka cycles. Thus, it is likely that echinoid distribution in the Miocene of the eastern Mediterranean was strongly controlled by productivity changes driven by Milankovitch forcing. Note that, although the sapropel intervals may have caused local short-term extinction through anoxia as often occurs today (Stachowitsch et al., 2007), the area was repopulated after each event by communities of identical structure. The repeated occurrence of the same species shows that we are just dealing with local extinction and recolonisation presumably from adjacent regions.
4.3. Biogeographical affinities

The middle Miocene marks a critical time interval in Mediterranean deep-sea evolution. Closure of the Red Sea link between the eastern Mediterranean and the Indo-Pacific was complete by the early Miocene (Burdigalian) [Steininger and Rögl, 1984] although deep-sea faunal exchange had probably ceased much earlier than this. Then in the late Miocene the Messanian crisis brought about a dramatic drop in sea level and led to high temperature, hypersaline and stagnant bottom water conditions and the wholesale extinction of the deep-sea fauna. Today the Mediterranean shelf break barrier exists at 100–110 m, which makes the shelf narrow and strengthens the overall oligotrophy of the sea. The Mediterranean displays homothermy, such that depths greater than 200–300 m exhibit constant warm temperatures of 13.5 (west) to 15.0 °C (east). Additionally, the deep water is very saline with values up to 38.5–39 psu. Both temperature and salinity create a very strongly stratified water body, which further enhances the oligotrophy of the Mediterranean. [Emig and Geistdoerfer, 2004]. Current Mediterranean physical oceanography is thus unusual and may have started to develop from the mid-Miocene onwards. The modern deep-sea fauna of the Mediterranean is very young and atypical, having arisen through gradual colonisation since the Pliocene by immigration from the Atlantic deep sea through the Strait of Gibraltar [Taviani, 2002]. Thus the middle Miocene faunas of northern Apennines and Cyprus are very important as they provide

Fig. 8. Heterobrissus montesii Manzoni and Mazzetti, 1877, Lophos Beds, Pakhna Formation, Serravallian, Alessa, near Limossol, Cyprus. A, BMNH EE13527; apical view; B, D, E, BMNH EE13526, lateral, apical and oral views; C, BMNH EE13528, apical view. Scale bar 10 mm.
evidence of the nature of the deep-Mediterranean fauna post-closure of the basin but pre-Messinian crisis.

Although only three taxa of middle Miocene bathyal echinoid are known, a strong Caribbean link clearly exists. *Palaeobrissus* is known only from the Caribbean region today and, other than the Serravallian records discussed here, is unreported from the fossil record. *Heterobrissus* is more widely represented with species in the Caribbean, Indian Ocean, and around Australia, the Norfolk Islands and New Zealand. However, the Miocene species is most closely related to the Caribbean *H. hystrix*, sharing with that species a more derived plastron plating pattern. The third taxon *Mazzettia*, although endemic to the Mediterranean, is a probable sister to *Linopenues*, which occurs in both the Caribbean and the Indo-Pacific. This mirrors a strong biogeographical similarity of shallow marine echinoid faunas (e.g. Stefani, 1924; Poddubik and Rose, 1985) and suggests that deep- as well as shallow-water connections between the Mediterranean and Caribbean were retained until well into the Miocene.

5. Systematic palaeontology

Order Spatangoidea L. Agassiz, 1840, p. 15
Family Palaeotrotopidae Lambert, 1896, p. 324
Genus *Palaeobrissus* A. Agassiz, 1883, p. 56

*Palaeobrissus canaverii* (De Loriol, 1882) (Figs. 4, 5)
1882 *Cleistechinus canaverii* De Loriol, 1882, p. 27.
1931 *Cleistechinus canaverii* De Loriol: Callegari, p. 15, pl. 1, fig. 6.
1935 *Neopenues* sp. Currie, p. 34, pl. 4, figs 2, 3.


Occurrence: The type material comes from the middle Miocene (‘Helvetic’) of Camerino, Tuscany, Italy. Material described here comes from the Lophos Beds, Pakhna Formation, Serravallian, middle Miocene, of the Limassol region, Cyprus.

Diagnosis: An apetaloid spatangoid with two gonopores in its ethmolytic apical disc, a circular subanal fasciole, no anterior sulcus and with both columns of ambulacral plates reaching the apex. Labral plate elongate, extending to the second ambulacral plate.

Description: Tests relatively small, never exceeding 30 mm in length; thin shelled. The rare specimens that are not badly crushed and distorted are approximately oval in outline, 85% as wide as long, and depressed in profile with a rounded ambitus set a little below mid-height (Fig. 4); test height is approximately 45–50% of length. In lateral profile the posterior face is probably steeply truncated, and the upper surface weakly domed, though all material is crushed to a greater or lesser extent.

The apical disc lies a little anterior of centre. Plating is probably ethmolytic with a narrow wedge-shaped genital plate 2 present between the posterior genital plates (Fig. 5B). The two posterior genital plates each bear a large gonopore, surrounded by a prominent raised rim (Fig. 4C). Genital plate 2 bears a small cluster of hydropores, six or seven in number, positioned immediately in front of the two gonopores (Fig. 5C). Genital plate 3 is small and usually perforate (in one specimen G3 has a rudimentary gonopore), slightly sunken and triangular in outline.

Ambulacral zones are flush on the aboral surface. The anterior ambulacrum is relatively narrow and constructed of plates that are pentagonal or hexagonal in shape and taller than wide. These bear only microscopic pores. The paired ambulacra are also constructed of plates that are approximately as wide as tall, bearing a distinctly enlarged pore-pair, which lies at some distance in from the lower plate suture (Fig. 5E). These pore-pairs are largest in the more adapical region and decrease in size and become single and rudimentary approximately half-way towards the ambitus. On the oral surface the ambulacral regions become very slightly depressed as they approach the peristome and there are enlarged pores; three or four in the anterior and paired posterior ambitus, and six in the paired lateral ambulacra.

The interambulacral zones on the aboral surface are composed of large pentagonal plates that are only slightly wider than tall (Fig. 4F). On the oral surface the labral plate is relatively small (2.9 mm in a 28 mm long individual) and slightly longer than wide (Figs. 4D and 5A). It extends to half-way down the second adjacent ambulacral plate in ambulacrum 1. The succeeding sternal plates are long and relatively narrow, with a vertical median suture. The posterior suture of plate 5.b.2 coincides with the fifth plate in ambulacrum 1. The episternal plates are paired and elongate, tapering to a very narrow posterior tip, and crossed by the lower half of the subanal fasciole (Fig. 5D). Plates 4a and 4b are paired adorally but extend to different lengths aborally, and bear the upper half of the subanal fasciole (Fig. 5D). Three ambulacral plates are wedged between the episternal and post-episternal plates and carry the lateral parts of the subanal fasciole. There are no enlarged subanal pores on these plates.

The peristome is slightly wider than long, faces directly downwards and is not surrounded by any rim (Fig. 4D). The periproct is relatively large and framed by plates 5 to 7 in each column.

The upper surface is covered in a uniform array of small rather widely spaced tubercles that are crenulate and perforate (Fig. 4C). Sparse uniform granules are scattered amongst these. On the oral surface the sternal and episternal plates are densely covered in tubercles and the paired interambulacra slightly less densely tuberculate (Fig. 4D). The periproct is rimmed by dense tubercles. The subanal fasciole is well defined in all specimens, subcircular in outline and four or five tubercles wide. Larger tubercles lie inside the subanal fasciole. No other fascioles are present.

Remarks: *Palaeobrissus* is a genus established by Agassiz (1883) for a single species *P. hilgardi* that is found living today in the waters of the Caribbean, from Barbados to Colombia at depths of 300–1025 m (Seraphy, 1979; Borroto-Perez et al., 2002). This is a member of a primarily deep-sea group of spatangoinds, the *Palaeotrotopidae*, characterized by having thin tests, a subanal fasciole and apetaloid ambulacra. *Palaeobrissus canaverii* differs from *P. hilgardi* in having a well-preserved subanal fasciole at all test sizes, in having the periproct set slightly higher and framed by plates 5a, 5b orally, and having the tallest point set to the posterior of the test. In *P. hilgardi* a subanal fasciole is present only in juveniles, the periproct is framed by plates 4a, 4b on the oral side, and the test is uniformly domed and tallest at mid-height. The labral plate in *P. canaverii* is also slightly longer, extending about a third of the way along the second plate in the adjacent ambulacrum whereas in *P. hilgardi* it only just touches plate 2. In all other aspects the two taxa are indistinguishable.

This species was first described by De Loriol (1882) under the name *Cleistechinus canaverii* from the middle Miocene of Camerino, Tuscany. His species was based on a single 20 mm test, which shows no plating details (illustrated in Smith et al., 2005). *Cleistechinus* was a genus established by De Loriol solely for this species, and thus differs in no significant way from *Palaeobrissus*. Callegari (1931) reillustrated the specimen but could add no further information. Currie (1935) attributed some poorly preserved material of this species from Cyprus to Duncan’s genus *Neopenues*. However, that genus has a peripetalous fasciole and a short and wide labral plate, neither of which are evident in Currie’s material.

Family Heterobrissiidae nov.

[= Incertae sedis B Smith et al., 2005]

*Diagnosis: Spatangoids lacking all fascioles and with an ethmolytic apical disc. Petals without occluded plates at their ends. Labral plate elongate, extending to reach the second ambulacral plate or beyond.

Range: Oligocene to Recent; Antarctic, Caribbean, Mediterranean.

Genus *Heterobrissus* Manzoni & Mazzetti, 1877, p. 354
[= *Archaeopenues* Gregory, 1892, p. 163; ?= *Brissolampas* Pomel, 1883]

*Heterobrissus montesii* Manzoni and Mazzetti, 1877 (Figs. 6–8)
1877 *Heterobrissus montesii* Manzoni & Mazzetti, p. 350, pl. 19, fig. 2. 1879 *Heterobrissus montesii* Manzoni, p. 162.
1908 Heterobrissus montesi Manzoni & Mazzetti; Stefanini p. 95, pl. 14, figs 4, 5, pl. 15, fig. 1.
1935 Heterobrissus cypriotes Currie, p. 32, pl. 3, fig. 1.
71935 Heterobrissus sp. Currie, p. 33, pl. 4, fig. 1.

Types. The whereabouts of Manzoni’s specimen is not stated in the original description, and has not been traced. Currie’s holotype of Heterobrissus cypriotes is the specimen figured by Currie, 1935, pl. 3, fig. 1, deposited in the Sedgwick Museum, Cambridge.

Occurrence. The type material comes from the Miocene of Montese, Italy. Currie’s type comes from the Lophos beds of the Pahnka Formation Serravallian, middle Miocene, north of Limassol, Cyprus. The material described here also comes from this horizon and locality.

Description. Test moderately thick-shelled and large, up to 110 mm in length; ovate in outline with convex anterior and weakly pointed posterior (Fig. 6). Test width 75–80% of test length, widest just in front of mid-length. Tests rather depressed in profile with low domal upper surface and rather flat lower surface, sinking towards the peristome. Ambitus rounded and below mid-height (Fig. 8C).

Apical disc subcentral, small, plating ethmolitic with genital plate 2 extending a short distance to the posterior of the posterior ocular plates (Fig. 7C). Four gonopores, the anterior pair placed closer together than the posterior pair. Hydro pores well developed and covering all of genital plate 2 behind the gonopore.

Ambulacrum III flush over aboral surface becoming slightly depressed only as it approaches the peristome (Fig. 6B); narrow, composed of small, hexagonal or pentagonal plates (Fig. 7A). Adapically these plates bear a small but distinct slit-like pore oriented almost vertical to the lower suture. These pores become reduced and lost towards the ambitus. The paired ambulacra are petaloid adapically and very slightly depressed in their upper half (Fig. 8B, D). Petals extend almost to the ambitus, diverging slightly and remaining open distally; pore-pairs become slightly smaller towards the end. In the anterior petals the anterior column of pore-pairs are significantly smaller and reduced compared to those in the posterior column as they approach the apex. Pore-pairs are isopores, the two pores tear-drop-shaped with a narrow, flush interporal zone. The anterior petals are very slightly flexed to the anterior, and diverge from each other at 130°. The posterior petals are more or less straight and diverge at about 65°. There are no enlarged subanal pore-pairs. The lateral and posterior ambulacra enlarge and widen as they approach the peristome, and plating becomes crowded. These plates bear large, ovate anisopores, with the more adoral pore large and circular and the adradial pore much smaller and more slit-like. In some the adradial pore may be completely lacking. There are some 8 phylloide pores in a column in the posterior and anterior ambulacra, and some 12 phylloide pores in a column in the lateral ambulacra.

The interambulacral zones have a standard plating pattern aborally. On the oral surface the labral plate is subrectangular, about twice as long as wide, and with a strongly convex oral face (Fig. 7A). It extends to half-way along the third plate in the adjacent ambulacral column (ambulacrum I). The succeeding sternal plates are twice as long as the labral plate and symmetrical with a sagittal median suture. Sternal plate 5.b.2 extends to plate 9 in the adjacent ambulacral column. The episternal plates are also paired and symmetric and are about half as long as the sternal plates. They are also separated by a sagittal median suture. Plates 5.a.4 and 5.b.4 are weakly offset and form the posterior part of the oral surface. These plates are L-shaped and form the oral border of the periproct (Fig. 8E). All other interambulacral zones are amphisternous. In the lateral paired interambulacra plates 6a and 6b form the ambitus.

The peristome is sunken, angular, and with a strongly projecting labrum (Figs. 6B and 8E). The periproct is inframarginal to almost oral, ovate in outline, almost as wide as long (Figs. 6B and 8E). It is framed by plates 5.a.4, 5.b.4 to 5.a.7, 5.b.7.

The upper surface has a scattering of larger primary tubercles which are perforate and crenulate (Fig. 8A, B, D). These become denser approaching the apex and along the mid-line of the posterior interambulacrum. However, they are found sparcely over the entire upper surface, including on occasional anterior ambulacral plates. They are prone to loss by abrasion but, when missing, the large circular scars on the plate surface mark their position (as in the extant H. nicosius: David and Néraudeau, 1989). All plates have a covering of sparse miliary granules and occasional smaller tubercles. Some small tubercles also occur within the more distal parts of the petals. On the oral surfaces tubercles are denser, although never contiguous and always separated by zones of fine granules, even on plastron plates. Ambulacral zones have identical tuberculation to that in the interambulacral zones with scattered primary tubercles, except in the phylloides. Oral tubercles have asymmetric areoles. Primary spines are more or less straight, with a hollow lumen. There are no fascioles.

Remarks. Heterobrissus is here treated as a senior synonym of Archaeopneustes Gregory, 1892, p. 163. Gregory based this genus on the Recent Caribbean bathyal species Palaeoepinaste hystrix A. Agassiz, 1881, p. 82 without considering its differentiation from Heterobrissus. Mortensen (1950) maintained the two genera as separate, arguing that Heterobrissus had a shorter labral plate (extending to plate 2 in Heterobrissus, but to plate 3 in Archaeopneustes), and a more marginal periproct (submarginal in Archaeopneustes). However, he had only Stefanini’s pictures and descriptions of the type species, and so largely based his concept of Heterobrissus on two Indo-Pacific species H. niassicus and H. hemingi, which do differ from Archaeopneustes hystrix in the ways described. Furthermore, Stefanini’s specimen shows a rather more central peristome, but the specimen is damaged and foreshortened making the position seem more central than it really is. However, the Miocene Mediterranean species (which is the type of Heterobrissus) has a submarginal periproct and an elongate labrum that extends to ambulacral plate 3 and so shares all the diagnostic features of Archaeopneustes.

Heterobrissus montesi closely resembles the living H. hystrix (Agassiz, 1881) but the peristome is a little more anterior in H. hystrix and the peristome more rounded and C-shaped (see illustration in Smith et al., 2005). In H. montesi the labral plate also projects less strongly and the peristome is distinctly angular. Other extant species of Heterobrissus have a shorter and wider labral plate that extends only to the second ambulacral plate. Baker and Rowe (1990) gave a key to distinguish the Recent species.

The Cypriot material described by Currie (1935: 32) was differentiated from Manzoni and Mazzetti’s Italian material by “the interambulacra being relatively shorter, the periproct being larger and pyriform, and the ambital outline of the test contracting more rapidly towards the posterior”. However, her material was not well preserved, being crushed and slightly distorted. With access to much better material it turns out that there is no significant difference between the specimens from Cyprus and the type material from Italy.

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References


