ALL CHANGE AT THE CRETACEOUS–TERTIARY BOUNDARY? ECHINOIDS FROM THE MAASTRICHTIAN AND DANIAN OF THE MANGYSHLAK PENINSULA, KAZAKHSTAN

by CHARLOTTE H. JEFFERY

ABSTRACT. The Maastrichtian and Danian echinoid fauna of the Mangyshlak Peninsula, Kazakhstan is revised on the basis of new collections from three localities representing both a shallow water calcarenite facies and a deeper water chalk facies. The two chalk sections sampled have no biostratigraphically detectable breaks across the Cretaceous–Tertiary boundary.

Sixteen species in 11 genera are recognized, including one new species, *Cyclaster galei*. Of these, 13 species are found only in Maastrichtian strata. The remaining three are found only in the Danian giving an apparent species extinction rate of 100 per cent. across the Cretaceous–Tertiary boundary in Mangyshlak. However, inspection of occurrence data from localities outside Kazakhstan shows that many of these species are in fact longer ranging than the Mangyshlak occurrences alone suggest. If this global data is taken into account the species extinction rate drops to 60 per cent. and the generic extinction rate to 25 per cent. This pattern of local extinction and replacement is repeated in other Cretaceous–Tertiary sections (e.g. in Denmark and at Maastricht).

The Maastrichtian chalk of Mangyshlak contains a diverse echinoid fauna and includes some taxa indicative of shallower water conditions. In contrast, the Danian contains only a small number of exclusively deep water forms. This change in local faunal content may be explained either in terms of a facies shift from shallower to deeper water conditions or by the recolonization of shelf habitats by surviving deep water clades.

GENERATIONS of studies investigating taxonomic diversity through time have identified periods when there was a significant and rapid loss of biological diversity on a global scale. Where the loss has been of large enough geographical and taxonomic proportions, these periods have been dubbed mass extinction events. In all, five extinction events justify this rank. All five have generated a great deal of research interest, both in documenting and in postulating causes for the biological changes. The most recent mass extinction, the end-Cretaceous extinction, is probably the most comprehensively studied. Research has been particularly intensive over the past 20 years, especially since debate was stimulated by Alvarez *et al.*'s (1980) claim that iridium anomalies at the boundary were produced as a result of an extraterrestrial bolide impact.

Previous work on the Cretaceous–Tertiary boundary

Sedimentological and geochemical evidence. Research to date has followed two main avenues. The first has concentrated on the sedimentological and geochemical evidence for an impact and its location (e.g. Bhandari *et al.* 1994). Possible impact sites so far discovered include the Chicxulub crater off the coast of Mexico (Hildebrand *et al.* 1991) and another smaller site off the Indian coast (Negi *et al.* 1993). Further evidence of extraterrestrial bolide bombardment comes from the presence of shocked quartz (Officer 1990), tektites (Smit 1990) and a minimum in the osmium isotope ratio (Peucker-Ehrenbrink *et al.* 1994) in boundary sections. There has also been a great deal of speculation over the way in which the bolide impact and end-Cretaceous extinctions are linked.

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Many differing 'killing mechanisms' have been proposed. Hypotheses have included global darkness caused by debris thrown up by the impact and an associated breakdown of the food chain (Alvarez *et al.* 1980), global cooling again due to the presence of dust in the atmosphere (Pollack *et al.* 1983), and greenhouse warming produced by the volatilization of carbon dioxide from carbonate target rocks (O'Keefe and Ahrens 1989). There have also been suggestions that sulphate, originating from an impact in evaporitic deposits, may have caused acid rain (Weil 1994; Robinson 1995) and surface water acidification (D'Hondt *et al.* 1994). Impact-induced volcanism has also been proposed as a cause of the extinctions (Negi *et al.* 1993; Sutherland 1994).

Palaeontological evidence. The second approach to study of the Cretaceous–Tertiary boundary has focused on the palaeontological evidence for the magnitude and duration of the mass extinction event and how this relates to proposed extinction scenarios. To date, the documentation of biological change has followed two lines: detailed investigations of sections across the boundary, and analysis of regional or global taxonomic compilations. Both approaches have their own inherent problems.

A large amount of work documenting taxonomic change has concentrated on patterns of relative abundances of taxa within so-called complete sections across the boundary (e.g. Hansen *et al.* 1993; Keller *et al.* 1993; van Fossen *et al.* 1995), the aim being to find evidence for the rapidity and duration of the extinction event. However, there are several major problems with this approach. The first is simply that only a small number of continuous boundary sections exist and that many of these are barren of macrofossils. If research was limited to the study of these sections alone, knowledge of taxonomic change across the Cretaceous–Tertiary boundary would be severely restricted. One explanation for this paucity of boundary sections stems from the major sea-level fluctuations and consequent facies changes in the latest Cretaceous. Facies-dependent taxa disappear from the studied section giving a false extinction signal, and it is only by looking in more recent deposits elsewhere where facies similar to those below the boundary occur that the survival of these taxa can be confirmed. Even if a section appears complete and free from facies changes there may still be hiatuses 'hidden' within the section with no lithological expression, and this also can give the impression of many simultaneous extinctions. Indeed, the absence of intervals close to the boundary has been demonstrated by microfaunal studies for many of the classic 'continuous' sections across the Cretaceous–Tertiary boundary (MacLeod and Keller 1991). A further drawback encountered when working at the mm scale is that of reworking. This is particularly pertinent in microfossil studies where arguments continue as to whether fossils collected are still in their original depositional settings (MacLeod and Keller 1992).

The second line of palaeontological investigation has sought to assess the extent of diversity change regionally or globally but with far lower temporal resolution. Such studies have often drawn on data in the form of compendia of occurrences. Compilations of this type very often suffer from problems of inconsistent taxonomic usage (Wingard 1993). Taxonomic disappearances due to artefacts of nomenclature (i.e. the naming of species solely on the basis of their occurrence in a particular stratigraphical level or geographical location) produce 'pseudoextinctions'. A thorough taxonomic revision is therefore a prerequisite for studies of biological turnover. Accordingly, a taxonomic revision of all the echinoid species recorded in the literature from Maastrichtian and Paleocene deposits world-wide is currently underway. This will produce a global database with a uniform taxonomy and with each occurrence as stratigraphically constrained as possible. In order to investigate which clades survived the end-Cretaceous extinction, the data will be set into a sound phylogenetic framework. Inferences about the selectivity of echinoid survivorship at the end-Cretaceous can then be made.

Survivorship selectivity patterns. Despite the volume of work that has been published on the end-Cretaceous mass extinction, relatively little is known in detail about how the marine benthic macrofauna was affected, in terms of both geographical and biological selectivity patterns. Work to date has concentrated on molluscan faunas with varying degrees of extinction selectivity

recognized by different workers. No latitudinal bias in extinction intensity has been found among the molluscan groups studied, but only by excluding rudists from the analysis (Raup and Jablonski 1993). This is in contrast to recent microfaunal studies which show a correlation between high latitudes and lower extinction intensities (Keller *et al.* 1993; Elliot *et al.* 1994). However, geographically widespread taxa were less affected over this time period than those with narrow geographical ranges (Jablonski 1986; Jablonski and Raup 1995). Sheehan and Hansen (1986) and Jablonski and Raup (1995) have recorded differences in extinction intensity among bivalve feeding types. In both studies, deposit feeders showed significantly lower extinction rates than did suspension feeders. However, this low overall rate is due to extremely low extinction levels in just two groups, Nuculoida and Lucinoidea (Jablonski and Raup 1995). The preferential survivorship exhibited by these taxa is thus attributable to factors other than, or in addition to feeding strategy (Levinton 1996). Some studies have recorded higher rates of extinction among infaunal and semi-infaunal organisms (e.g. Gallagher 1991). This result is not corroborated by Jablonski and Raup (1995) but it should be noted that rudists were again excluded from their analysis. It has also been suggested that taxa with a planktotrophic mode of larval development fared badly over the Cretaceous–Tertiary boundary (Gallagher 1991). In contrast, Jablonski (1986) recorded similar levels of extinction in gastropods across the Cretaceous–Tertiary boundary regardless of developmental strategy. These examples clearly demonstrate the lack of consensus so far recorded in survival selectivity patterns at this boundary.

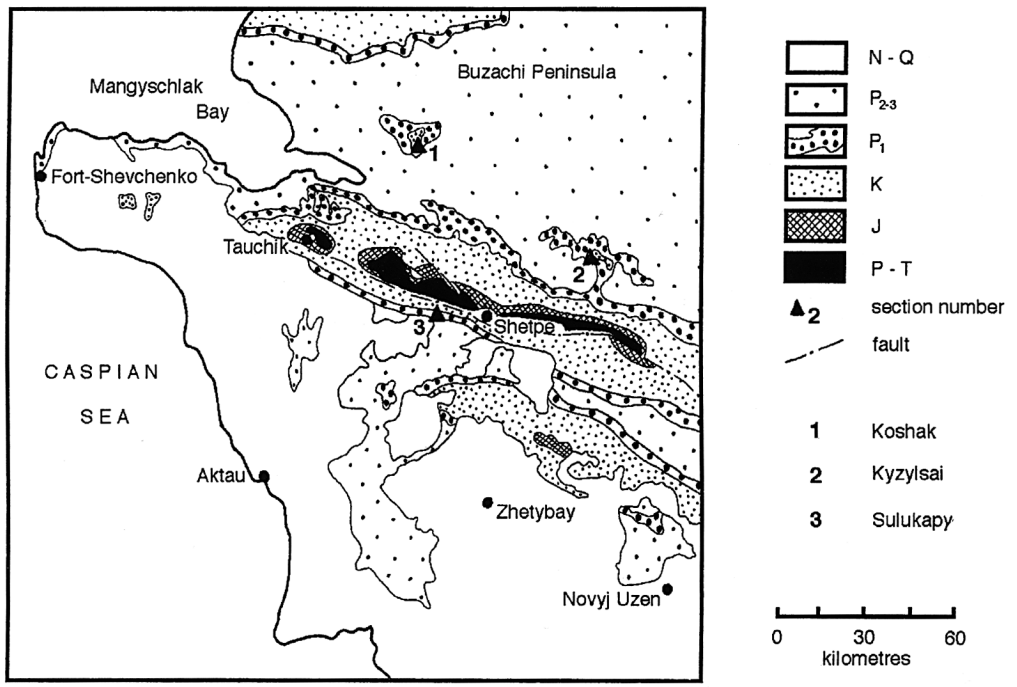
Why study echinoids at the Cretaceous–Tertiary boundary?

Research into other groups of marine benthic macrofauna is necessary if patterns of selectivity are to be clarified. Echinoids are perfect for this type of study: they form an important and diverse component of the marine benthos both before and after the extinction, with some clades surviving; and they are morphologically complex, making them relatively simple to classify taxonomically and phylogenetically. Correlation between morphology and palaeobiology is also good (e.g. Kanazawa 1992), enabling survivorship selectivity of key biological traits to be investigated. Due to a high preservation potential, the fossil record of post-Palaeozoic echinoids is good especially amongst the irregulars (Kier 1977) and fossil echinoids are abundant in differing facies types from the poles to the equator in late Cretaceous and early Tertiary strata. Despite this, the echinoids have yet to be studied extensively outside Russia (e.g. Poslavskaya and Moskvin 1960; Moskvin *et al.* 1980; Moskvin 1989).

Why study the Mangyshlak Peninsula?

The Mangyshlak Peninsula of Kazakhstan is one of only a few localities worldwide where sections without detectable breaks across the Cretaceous–Tertiary boundary contain preserved macrofauna. The other 'complete' sections where echinoid faunas are preserved represent different palaeolatitudes and in some cases depositional environments. Deposits in Denmark, Belgium and the Netherlands have a well-constrained stratigraphy and represent both deep- and shallow-water shelf deposition in northern temperate palaeolatitudes (Scotese *et al.* 1988). Sediments accumulated in southern temperate latitudes are represented by fossiliferous sections in Madagascar, but unfortunately there has been very little recent research in this area and detailed stratigraphical work on these sections is yet to be done. Sections across the Cretaceous–Tertiary boundary which represent deposition in the palaeotropics are known from Algeria (Amard *et al.* 1981). However, accurate dating of these sedimentologically undifferentiated sections is exceptionally difficult because of sparse microfossil data and the presence of only a single ammonite species.

In fact, no widely applicable ammonite zonation exists for the Maastrichtian (Hancock *et al.* 1992; Kennedy and Henderson 1993) and the two most widely used biostratigraphical schemes for this stage are based on belemnites (see Christensen 1990) and planktic foraminifera (e.g. Caron 1985). Use of the belemnite scale is restricted to north-west Europe and parts of the former Soviet



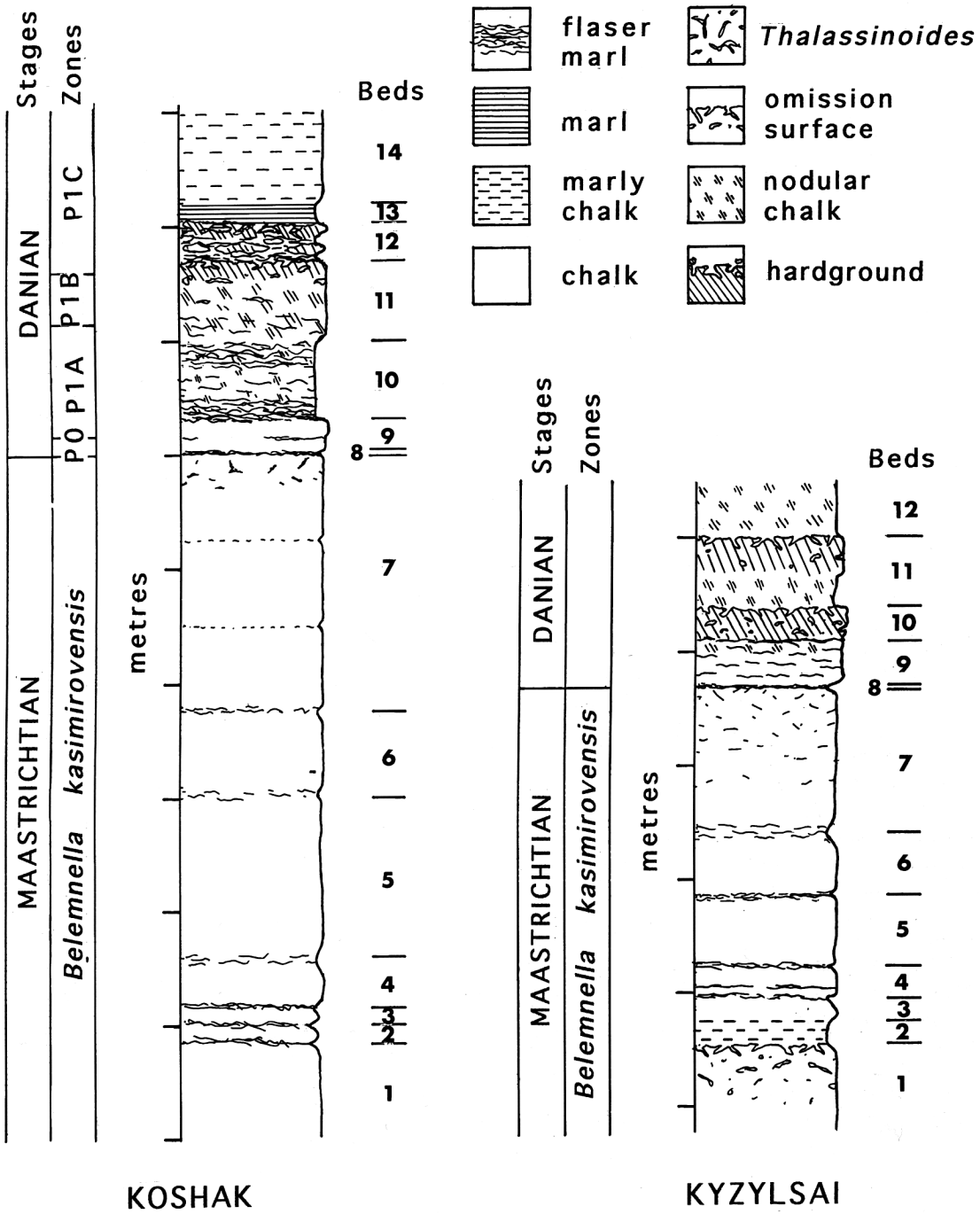
TEXT-FIG. 1. Map of the Mangyshlak Peninsula, Kazakhstan showing the location of the three sections studied. Abbreviations: N–Q, Neogene–Quaternary; P_{2-3}, Eocene–Oligocene; P_1, Paleocene; K, Cretaceous; J, Jurassic; P–T, Permo–Trias.

Union (boreal region) whilst the planktonic foraminiferal zonation is essentially Tethyan. As yet, no direct correlation between the two schemes exists. However, it is known that the Campanian–Maastrichtian boundary as defined by planktonic foraminifera is older than that based on belemnites. In addition, it has been suggested that the Lower/Upper Maastrichtian boundary in the belemnite scheme lies close to the base of the *Abathomphalus mayaroensis* Zone (Kennedy and Henderson 1993). The four-fold division of the Maastrichtian based on belemnites (Christensen 1979) is used throughout this paper for discussion purposes. All the Maastrichtian echinoids described here were collected from the latest Maastrichtian *Belemnella casimirovensis* Zone which, if the assertion of Kennedy and Henderson (1993) is correct, lies within the *A. mayaroensis* Zone.

The Mangyshlak sections have been well dated on the basis of abundant micropalaeontological data. Like the Danish, Belgian and Dutch sections, they represent shelf deposition in northern temperate latitudes. However, the Mangyshlak Peninsula lies much further to the east and at the time of sediment deposition was situated almost in the Paratethys (see Scotese *et al.* 1988). Thus sections here show a somewhat different faunal composition from those in north-west Europe. To date, all the taxonomic work on echinoids from this area has been published in Russian. Standardization with European taxonomy is essential if information on echinoids is to be integrated into a global database.

LOCALITIES AND STRATIGRAPHY

The Mangyshlak Peninsula is situated on the north-east side of the Caspian Sea, 80–100 km north-east of the city of Aktau. A group of three Permo-Triassic inliers form hills running north-north-east–south-south-west along the peninsula. These inliers are surrounded by a periclinal region of Jurassic, Cretaceous and Paleogene strata (Text-fig. 1). The region is semi-arid and provides abundant natural exposures of fossiliferous Cretaceous and Tertiary strata (Naidin 1987). In the



TEXT-FIG. 2. Lithological successions across the Maastrichtian–Danian boundary at Koshak and Kyzylsai (by A. S. Gale). The planktic foraminiferan zones at Koshak were determined by Alfonso Pardo (pers. comm.).

core of the pericline (Sulukapy), close to the outcrops of Permo-Trias, latest Cretaceous and earliest Paleocene sediments were deposited as shallow-water calcarenite facies. Northwards, the succession passes into deeper water chalk facies, which are exposed at Koshak and Kyzyslai.

The material described herein was collected by A. S. Gale, D. J. Ward and J. M. Hancock in May 1994 during an international field symposium on the Cretaceous organized by Russian and Kazakh geologists and led by Professor D. P. Naidin.

Koshak (44° 36′ 55″ N 51° 36′ 45″ E) (Text-fig. 2)

The section at Koshak Hill comprises dry gullies (lower part) and a cliff (upper part) and exposes a total of nearly 20 m of Maastrichtian and 18 m of Paleocene strata. The section was described by Naidin *et al.* (1982) and Naidin (1987). Material for the present work was collected from the lower part of the Maastrichtian section, and from the 9 m straddling the Cretaceous–Tertiary boundary (Text-fig. 2).

The Maastrichtian is developed in a fine white chalk facies, and displays marked rhythmicity on a decimetre scale, probably representing climatic cyclicity in the Milankovitch band. Couplets are defined by burrowed omission surfaces which rest on white chalk, overlain by flaser marl seams. The entire section falls within the latest Maastrichtian *Belemnella casimirovensis* Zone (upper Upper Maastrichtian in the German sense).

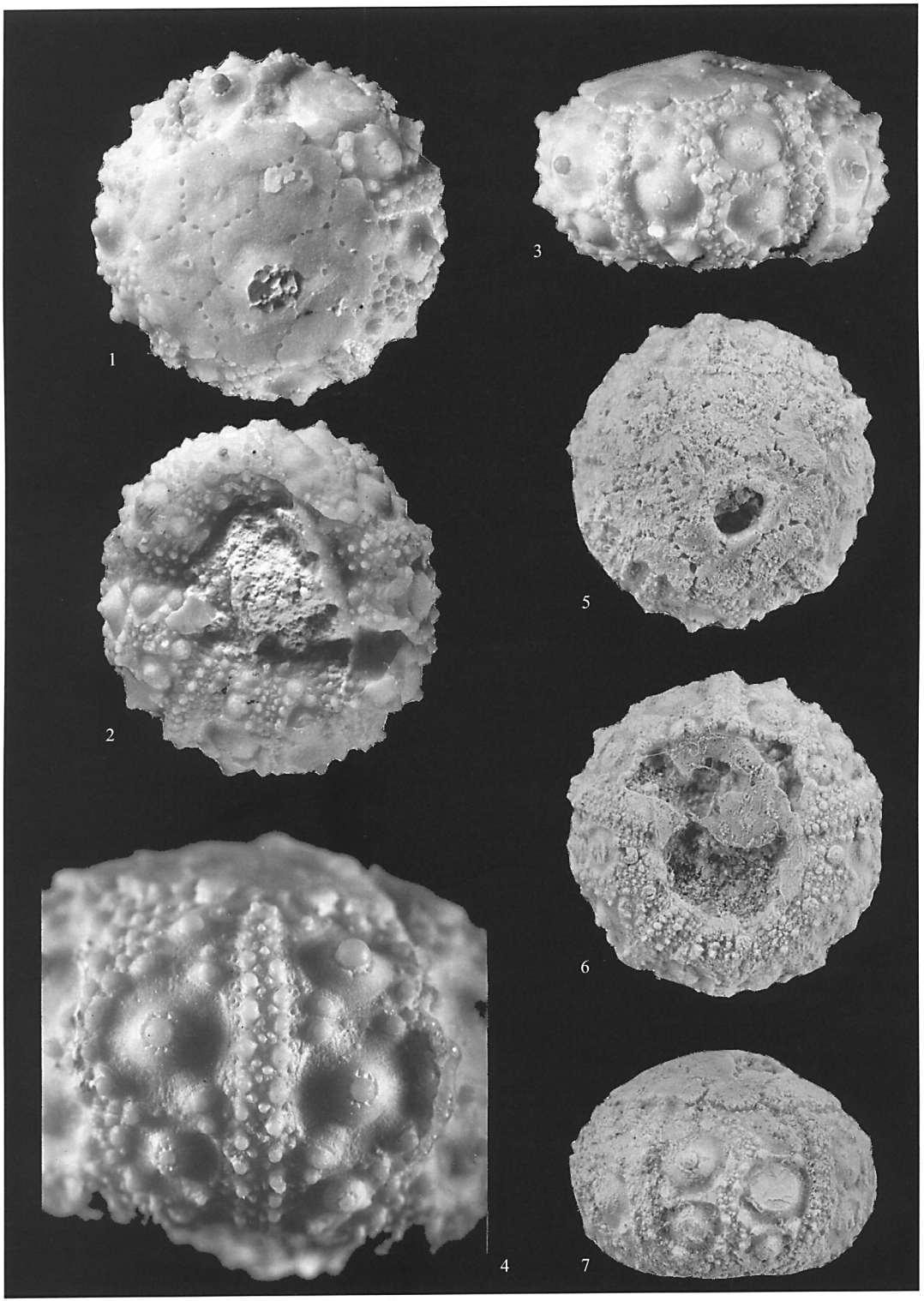
The Maastrichtian chalk is overlain by a 10–20 mm thick flasered grey marl (Bed 8) which rests on an omission surface. Nazarov *et al.* (1983) recorded an iridium 'spike' within this bed. *Thalassinoides* burrows (idiomorphic, omission-suite) which contain a dark marl fill, penetrate 0·3 m down into the Maastrichtian Bed 7. Bed 9 comprises firm white chalk containing discontinuous flaser marl partings and is rather unfossiliferous. Bed 10 is a chalk containing many thin wispy flaser marls and abundant echinoids. Beds 11 and 12 are pinkish-grey chalkstone containing abundant debris of calcite fossils and underlie a sharply defined hardground which does not show evidence of boring. Beds 13 and 14 are yellow and marly. Planktic foraminiferan zones were determined by Alfonso Pardo (pers. comm.), and show the Early Danian to be thin but completely represented (P0–P1C). It is not presently possible to determine if any Maastrichtian is missing at Koshak, although the presence of a burrowed omission surface immediately beneath the Danian is suggestive of a minor break at least.

Kyzylsai (Text-fig. 2)

This remote section, exposing approximately 45 m of Maastrichtian chalk and 35 m of Danian chalk and calcarenites, was described by Naidin *et al.* (1982). The upper part of the succession straddling the Cretaceous–Tertiary contact was measured by ASG in 1994 and is shown in Text-figure 2. As at Koshak, the Maastrichtian *B. casimirovensis* Zone is represented by white nannofossil chalks (Beds 1–7) containing flaser marls and an omission surface. The boundary marl is thin and flasered (Bed 8) and is underlain by an omission surface; small limonitized burrows are abundant in the upper 0·65 m of the Maastrichtian. Bed 9 is a chalk containing flaser marls and abundant echinoids, and is overlain by two yellow-pink hardgrounds (Beds 10–11). I have no microfaunal data for this section.

EXPLANATION OF PLATE 1

Figs 1–7. *Salenia belgica* Lambert, 1897; Upper Maastrichtian, Mangyshlak, Kazakhstan. 1–3, BMNH EE5624; 1·0 m below Cretaceous–Tertiary boundary, Kyzylsai. 1, apical view; 2, oral view; 3, lateral view; all ×4, BMNH EE5623; 1·8 m below Cretaceous–Tertiary boundary, Kyzylsai; detail of ambulacrum in lateral view; ×7. 5–7, BMNH EE5629; middle *B. casimirovensis* Zone, Sulukapy. 5, apical view; 6, oral view; 7, lateral view; all ×4.



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Sulukapy (44° 08′ 27″ N 51° 54′ 57″ E)

The Late Maastrichtian succession at Sulukapy is exposed where a small stream cuts the Maastrichtian–Danian scarp obliquely. The *B. casimirovensis* Zone (29 m thick) is here developed as a massive calcarenite, a shallow water facies which contrasts strikingly with the chalks at Koshak and Kyzylsai. This facies accumulated over the relatively shallow basement of the Aktau Ridge. The fauna is dominated by belemnites (the zonal species), oysters and echinoids. The contact with the overlying Danian was determined biostratigraphically in the field by finding the upper limit of belemnite records. A sedimentary hiatus is not visible. Echinoids were collected from 10 to 20 m below the Cretaceous–Tertiary boundary.

Institutional abbreviation. BMNH: The Natural History Museum, London.

SYSTEMATIC PALAEONTOLOGY

Order CALYCINA Gregory, 1900
Family SALENIIDAE Agassiz, 1838

Genus SALENIA Gray, 1835

Type species. Salenia scutigera Goldfuss, 1829, by monotypy.

Salenia belgica Lambert, 1897

Plate 1, figures 1–7; Text-figures 3C–D, 4A

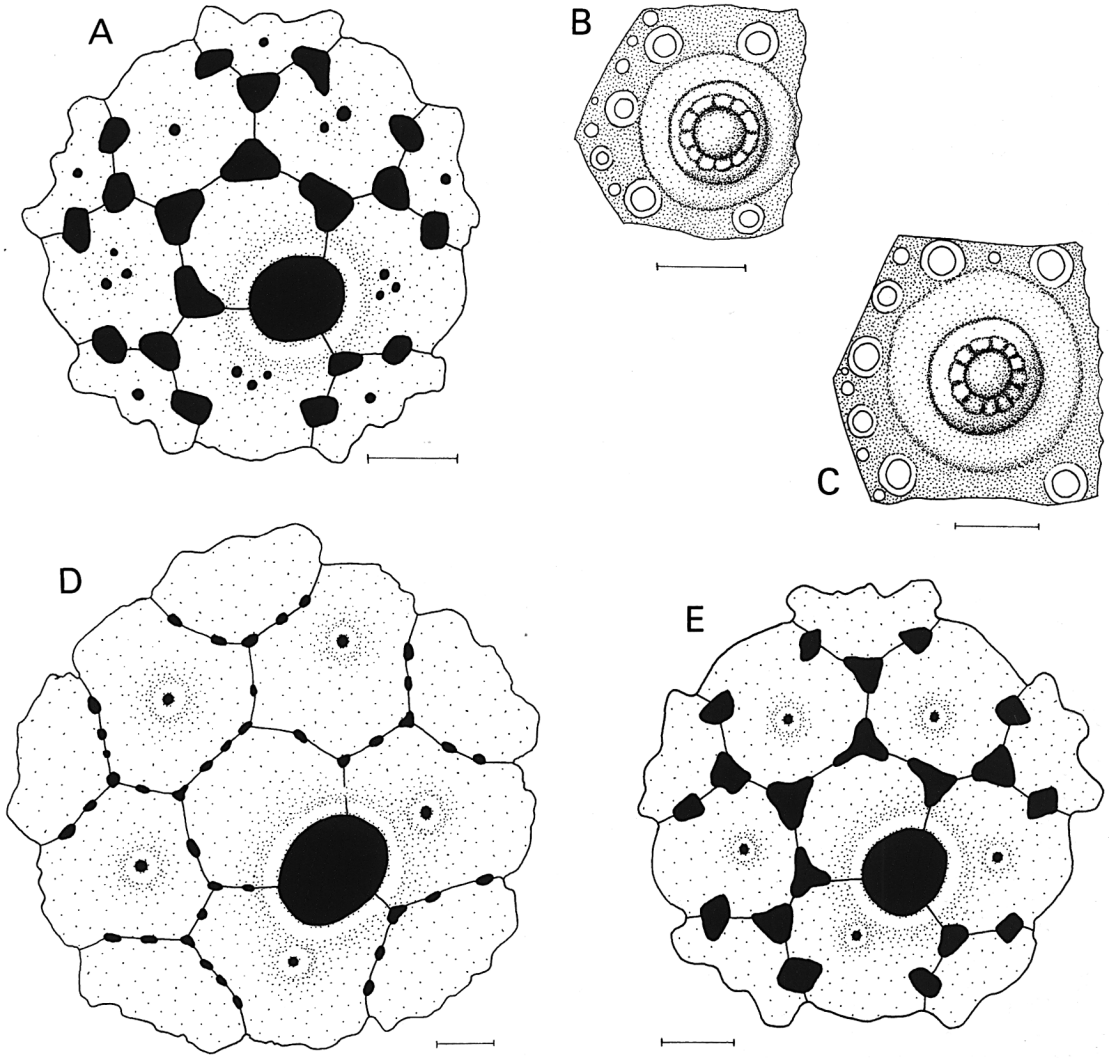
1897	*Salenia belgica* Lambert, p. 150, pl. 3, figs 1–6.
1911	*Salenia belgica* Lambert; Lambert and Thiéry, p. 211.
1979	*Salenia belgica* Lambert; Geys, p. 316 (*pars*), figs 11.3–6.
1982	*Salenia minima* Geys (*non* Desor), p. 266, pl. 29, figs 1–4.
non 1983	*Salenia belgica* Lambert; Kutscher, p. 892, pl. 1, figs 2, 5; pl. 2, fig. 1; pl. 4, figs 3–8 [= *Salenia hagenowi* Nestler].
1987	*Salenia belgica* Lambert; van der Ham *et al.*, p. 21, pl. 2, fig. 2.
1988	*Salenia belgica* Lambert; van der Ham, p. 139, pl. 3, figs 1–4.

Material. Four specimens: BMNH EE5623–EE5624, EE5628–EE5629.

Occurrence. Upper Maastrichtian strata, 1·0–1·8 m below the Cretaceous–Tertiary boundary at Kyzylsai and middle *B. casimirovensis* Zone of Sulukapy, Mangyshlak, Kazakhstan. Elsewhere, the species is recorded from the early Danian of Limburg, the Netherlands and the Mons Basin, Belgium.

Description. Test diameter 13·3–16·4 mm and height 8·5–11·2 mm (64–69 per cent. of test diameter). The ambitus is at mid-height with the test smoothly rounded above and below. The test has broad and flat upper and lower surfaces with the apical disc only slightly convex.

Ambulacra are narrow (13–14 per cent. of test diameter at the ambitus) and almost straight. The plating is predominantly bigeminate with occasional unigeminate plates near the ambitus (Text-fig. 4A). Ambulacral pores are uniserial throughout and are small, well spaced and obliquely positioned. The primary tubercles are uniformly large from the apex to the peristome although they are not contiguous. There are 15 primary tubercles and 24 or 25 pore-pairs per column at 13·3 mm diameter rising to 16 or 17 primary tubercles and 26 or 27 pore-pairs at 16 mm diameter. Smaller secondary tubercles are developed perradially and these form a central zigzag line between the rows of primary tubercles. Sparse miliary tubercles are also present on some plates. The tuberculate zone occupies 67 per cent. of ambulacral width.



TEXT-FIG. 3. *Camera lucida* drawings of *Salenia pygmaea* von Hagenow, 1840, *Salenia belgica* Lambert, 1897 and *Salenia anthophora* Müller, 1846. A–B, *Salenia pygmaea*; BMNH EE5620. A, apical disc; B, single ambital interambulacral plate. C–D, *Salenia belgica*. C, BMNH EE5623; single ambital interambulacral plate. D, BMNH EE5624; apical disc. E, *Salenia anthophora*; BMNH EE5630; apical disc. A and E, scale bars represent 2 mm. B–D, scale bars represent 1 mm.

Interambulacra are approximately three times as wide as ambulacra (41–44 per cent. of test diameter at the ambitus). There are five interambulacral plates per column and all except the most adapical plate carry a fully formed primary tubercle. The primary interambulacral tubercles are large with broad areoles which are confluent throughout, although they decrease in size dramatically towards the peristome. Each primary tubercle is surrounded by seven widely spaced smaller tubercles (Text-fig. 3C). The interradial zone is fairly narrow containing only a few scattered miliary tubercles.

The apical disc is approximately circular in outline, but with the ocular plates protruding slightly beyond the genital plates. There are notches at the margin of the disc between ocular and genital plates. Ocular plate I is always exsert. The disc is 9·4 mm to 12·2 mm in diameter (69–74 per cent. of test diameter) and is fairly

thin, although clearly standing above the coronal plates. It is almost flat, although raised a little towards the periproct where there is a distinct rim. The surface of the disc appears smooth, but fine striated ornamentation is apparent under the microscope. Small sutural pits are developed at all triple junctions and additionally at points in between (Text-fig. 3D). Pores are centrally positioned on the genital plates and are surrounded by raised rims. The periproct is almost circular to oval with its longest diameter 13–17 per cent. of test diameter.

The peristome is 38–39 per cent. of the test diameter across. It is very slightly sunken and has small and insignificant buccal slits.

Remarks. This is the first Maastrichtian record of this species despite Geys' (1979) claim that the species is also found in the Maastrichtian of Belgium. The Belgian strata in which *S. belgica* occurs are almost certainly Danian (van der Ham, 1988, p. 139). Despite the slight difference in age between the specimens described here and those already recorded, there are no significant morphological differences.

This species is very similar in overall appearance to *S. hagenowi* Nestler from the Lower Maastrichtian of Denmark and the Isle of Rügen. However, *S. hagenowi* has a more distinctly sculptured apical disc with corrugation towards the margins of the plates, more obvious sutural pits along plate boundaries, and the disc margin is markedly indented at the sutures between the plates.

Salenia pygmaea von Hagenow, 1840

Plate 2, figures 1–4; Text-figures 3A–B, 4B

1840 *Salenia pygmaea* von Hagenow, p. 650, pl. 9, fig. 4.
1911 *Salenia pygmaea* von Hagenow; Lambert and Thiéry, p. 211.
1928 *Salenia pygmaea* von Hagenow; Krenkel, p. 29, pl. 3, figs 14–15.
non 1928 *Salenia pygmaea* von Hagenow; Ravn, p. 41, pl. 5, figs 1–2 [= small specimens of *Salenia anthophora* or *S. selandica*].
1965 *Salenidia pygmaea* von Hagenow; Nestler, p. 982, pls 1–3; pl. 4, figs 1–3.
1973 *Salenidia pygmaea* von Hagenow; Kutscher, p. 111, figs 11–12.
1983 *Salenidia pygmaea* von Hagenow; Kutscher, p. 889, pl. 1, fig. 3; pl. 2, figs 7–11.

Material. Three specimens: BMNH EE5620–EE5622.

Occurrence. Upper Maastrichtian strata, 0·5–2·5 m below the Cretaceous–Tertiary boundary at Kyzylsai, Mangyshlak, Kazakhstan. This species is also recorded from the lower Maastrichtian of the Isle of Rügen, northern Germany.

Description. Test diameter 10·4–13·2 mm and height 6·6–8·6 mm (61–64 per cent. of test diameter). The ambitus lies at approximately 40 per cent of test height from the base and the test is smoothly rounded both above and below. The oral surface is broad and flat whilst the apical surface is somewhat domed (Pl. 2, fig. 3).

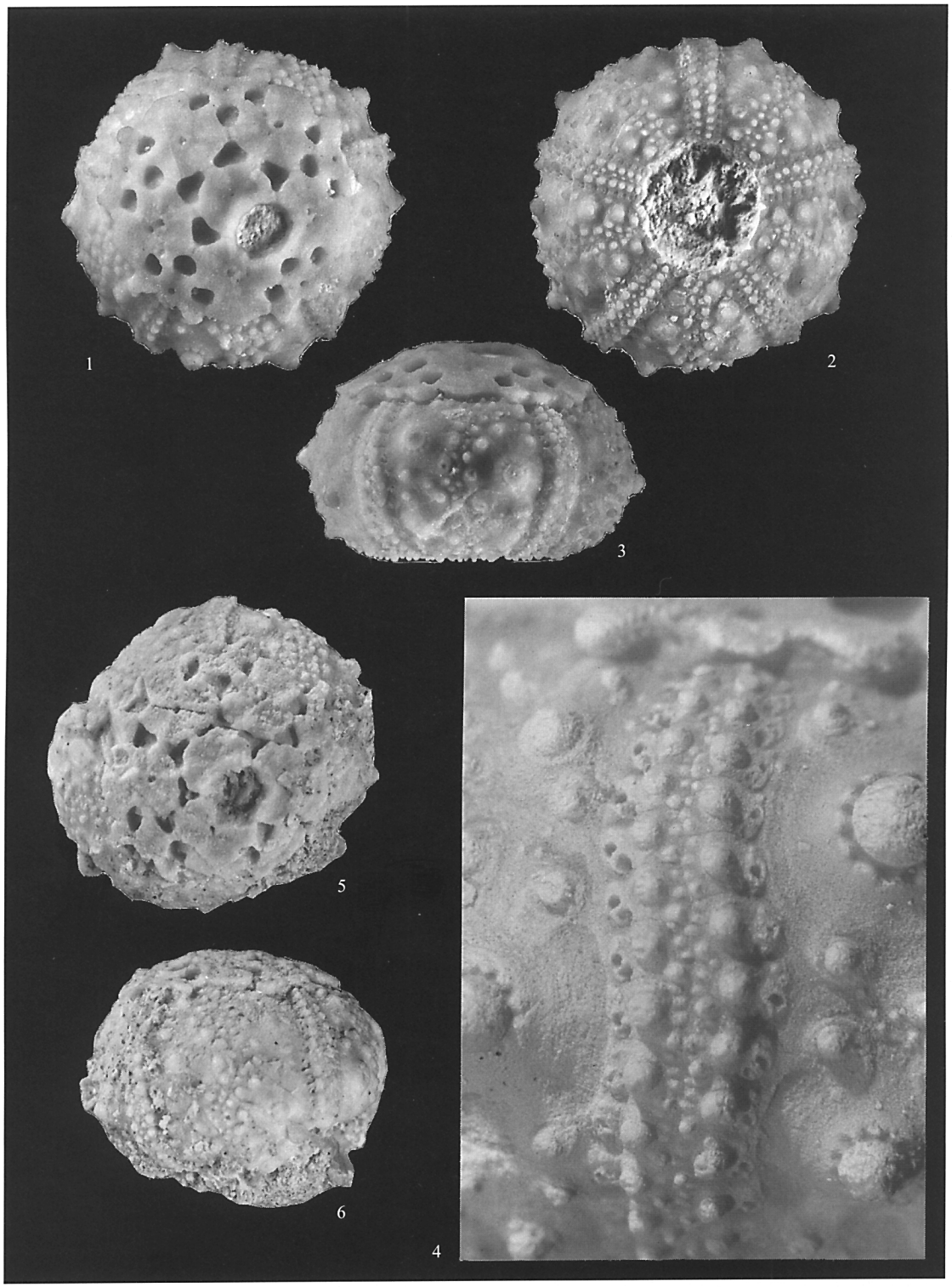
The ambulacra are narrow (13–16 per cent. of test diameter at the ambitus) and are approximately straight although becoming slightly sinuous towards the apex. Plating is unigeminate throughout and pore-pairs are arranged in a single column from apex to mouth (Text-fig. 4B). The pore-pairs are well spaced and set very obliquely, becoming smaller on the lower surface. Primary tubercles diminish in size both adorally and adapically away from the ambitus, although they form a fairly contiguous straight line throughout. There are

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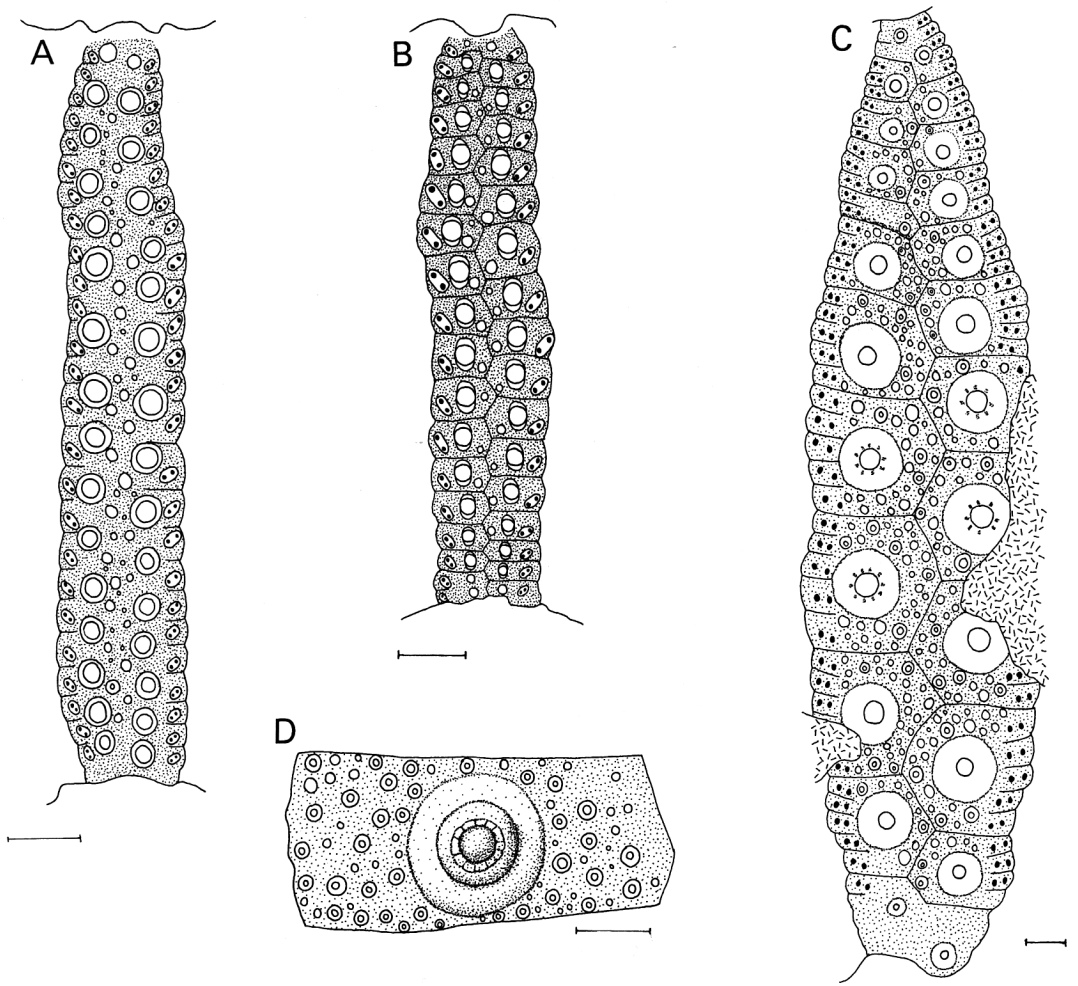
EXPLANATION OF PLATE 2

Figs 1–4. *Salenia pygmaea* von Hagenow, 1840; BMNH EE5621; Upper Maastrichtian, 0·5 m below Cretaceous–Tertiary boundary, Kyzylsai, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view; 4, detail of ambulacrum in lateral view. 1–3, ×4; 4, ×16.

Figs 5–6. *Salenia anthophora* Müller, 1846; BMNH EE5630; Upper Maastrichtian, middle *B. casimirovensis* Zone, Sulukapy, Mangyshlak, Kazakhstan. 5, apical view; 6, lateral view; both ×3.



JEFFERY, *Salenia*



TEXT-FIG. 4. *Camera lucida* drawings of *Salenia belgica* Lambert, 1897, *Salenia pygmaea* von Hagenow, 1840 and *Micropsis* cf. *leridensis* Cotteau, 1856. A, *Salenia belgica*; BMNH EE5623; ambulacral plating. B, *Salenia pygmaea*; BMNH EE5621; ambulacral plating. C–D, *Micropsis* cf. *leridensis*; BMNH EE5631; C, ambulacral plating; D, single interambulacral plate. Scale bars represent 1 mm.

16–18 primary tubercles and 17–19 pore-pairs per column in the ambulacra. Small secondary tubercles are developed perradially and form a zigzag line between the primary tubercles. The tuberculate zone covers 62 per cent. of the ambulacral width.

The interambulacra are 2·7 to 3·2 times wider than the ambulacra (39–43 per cent. of test diameter at the ambitus). There are four interambulacral primary tubercles per column, although the most adapical plate does not carry a fully developed primary tubercle. The primary tubercles are largest at the ambitus and diminish in size substantially towards the mouth. They have broad areoles although these are not confluent. Five well spaced scrobicular tubercles surround the areole of the primary tubercles (Text-fig. 3B) and beyond these is a fairly broad interradial zone with secondary tubercles two abreast and additional scattered miliaries.

The apical disc is approximately circular in outline although with the ocular plates protruding distinctly beyond the genital plates. It measures 77–82 per cent. of test diameter. The disc is fairly thin although obviously elevated above the surrounding coronal plates. The ocular plates are 'bat-shaped' with a distinct central protrusion. Large, subangular sutural pits are developed at all triple junction points and at mid-points where

ocular and genital plates are adjacent (Text-fig. 3A). Ocular plate I is exsert in all specimens. The genital plates are slightly sunken centrally where the genital pores lie without distinct rims. Near to each genital pore are two other distinct pits. Pits are also visible at the centres of the ocular plates and the suranal plate. The plates appear smooth but under the microscope show faint radial striations from the sutural pits. The surface is also finely granulated. The periproct is oval with its major axis 14–17 per cent. of test diameter. It is surrounded by a distinct elevated rim.

The peristome measures 77–81 per cent. of test diameter and is slightly sunken. Small buccal slits are present around the margin.

Remarks. S. pygmaea is an easily recognized species due to its unigeminate ambulacra and pitted apical disc.

Salenia anthophora Müller is most similar in overall appearance, but differs in having no small central pits on the ocular and genital plates of the apical disc, and the sutural pits are smaller and less rounded. *Salenia scabra* Nestler has wider ambulacra than either *S. anthophora* or *S. pygmaea* and displays a narrow zone of miliaries separating the vertical columns of primary and secondary tubercles.

Salenia anthophora Müller, 1846

Plate 2, figures 5–6; Text-figure 3E

1846 *Salenia anthophora* Müller, p. 7, pl. 1, fig. 1.
1866 *Salenia bonissenti* Cotteau, p. 202, pl. 15, figs 4–7.
1897 *Salenidia bonissenti* (Cotteau); Lambert, p. 148, pl. 2, figs 13–16.
1911 *Salenia anthophora* Müller; Lambert and Thiéry, p. 211.
1911 *Salenida bonissenti* (Cotteau); Lambert and Thiéry, p. 212.
1928 *Salenia anthophora* Müller; Ravn, p. 44, pl. 5, fig. 4.
1935 *Salenida bonissenti* Cotteau; Smiser, p. 29.
1950 *Salenidia bonissenti* (Cotteau); Kongiel, pp. 311, 321, pl. 1, figs 1–4.
1979 *Salenidia anthophora* (Müller); Geys, p. 313, figs 10.5–6, 11.1–2.
1979 *Salenidia* cf. *bonissenti* (Cotteau); Geys, p. 306, figs 6.3–6.
1983 *Salenidia anthophora* (Müller); Kutscher, p. 891, pl. 1, fig. 1; pl. 2, fig. 2; pl. 3, figs 6–8; pl. 4, figs 1–2.
1983 *Salenidia bonissenti* (Cotteau); Kutscher, p. 890, pl. 1, fig. 4; pl. 2, figs 3–6; pl. 3, figs 1–5.
1987 *Salenidia bonissenti*? (Cotteau); van der Ham *et al.*, p. 21.
1992 *Salenidia anthophora* (Müller); van der Ham and van Birgelen, p. 143, pl. 1, figs 1–3.

Material. BMNH EE5630.

Occurrence. One specimen, collected at Sulukapy, Mangyshlak, Kazakhstan (middle *B. casimirovensis* Zone). Elsewhere the species is recorded from the Lower Maastrichtian of the Isle of Rügen, the Ciply district of Belgium and the Maastricht area and from the Upper Maastrichtian of Poland and Denmark.

Description. The specimen is incomplete, missing the whole of the lower surface of the test as well as some of the sides. Measurements are therefore approximate. The test diameter is *c.* 17 mm and the height *c.* 13 mm (76 per cent. of test diameter). The ambitus appears to be a little below mid-height with the upper surface of the test domed in profile. Ambulacra are narrow, 2·2 mm wide at the ambitus (13 per cent. of test diameter) and slightly sinuous. Plating is unigeminate throughout with the pore-pairs placed obliquely and forming a single series. Primary tubercles are all of a similar size and form a continuous column along the ambulacral length. The tuberculate zone covers 77 per cent. of the ambulacral width. Alternating secondary tubercles are present within the perradial region. Due to the state of preservation, it is impossible to tell the number of tubercles or pore-pairs in each column.

The interambulacra are very broad, 3·7 times wider than the ambulacra (50 per cent. of test diameter at the ambitus). It is impossible to discern the number of primary tubercles in each interambulacral column, but three are discernible in each column between the apex and the ambitus. The tubercles which are visible show broad areoles which do not appear to be confluent. A wide interradial zone covers 35 per cent. of the interambulacral width and this forms a zigzag swathe of secondary tuberculation.

The apical disc is massive. In diameter it occupies 78 per cent. of overall test diameter. It is approximately pentagonal in outline with the 'bat-shaped' ocular plates protruding beyond the genital plates. Large, angular sutural pits are developed at all triple junctions and at mid-points between (Text-fig. 3E). Ocular plate I is exsert. The surface of the apical plates is granular and under magnification shows slight radial corrugation. The genital plates are slightly sunken in the centre where a rim surrounds each centrally placed genital pore. There are no ancillary pits on any of the plates. A rim also surrounds the periproct which is sub-circular in outline. The longest dimension of the anus is 2·5 mm (15 per cent. of test diameter).

The size and degree of invagination of the mouth are not visible.

Remarks. Salenia pygmaea von Hagenow is closest in appearance to *S. anthophora* but differs in having small central pits on the ocular and genital plates, and larger and more angular sutural pits on the apical disc.

Salenia anthophora shows a similar pattern of sutural pitting to that of *S. maestrichtensis* Schlüter, but may be distinguished by its more conical profile and domed apical disc.

Both *S. anthophora* and *S. pygmaea* are easily distinguished from the only other saleniid found in the Mangyshlak sections, *S. belgica* Lambert. This differs markedly in its apical disc structure, predominantly bigeminate ambulacral plate arrangement, thinner, flatter disc with far smaller and less angular sutural pits, and lack of pits on the ocular and genital plates.

Order PHYMOSOMATOIDA Mortensen, 1904
Family PHYMOSOMATIDAE Pomel, 1883

Genus PHYMOSOMA Haime, *in* d'Archiac and Haime, 1853

Type species. Cidaris koenigii Mantell, 1822, by subsequent designation of Lambert and Thiéry, 1911.

Phymosoma granulosum (Goldfuss, 1829)

Plate 3, figures 1–5; Text-figure 5A–B

1829	*Cidarites granulosus* Goldfuss, p. 122, pl. 40, fig. 7.
1855	*Phymosoma granulosum* Goldfuss; Desor, p. 87.
1911	*Phymosoma granulosum* Goldfuss; Lambert and Thiéry, p. 225.
1928	*Phymosoma subconicum* Ravn, p. 59, pl. 6, fig. 5.
?1928	*Phymosoma granulosum* Goldfuss; Ravn, p. 55, pl. 6, figs 3, 6–10.
1934	*Cyphosoma granulosum* (Goldfuss); Tzankov, p. 194.
1973	*Phymosoma koenigi* (Mantell); Kutscher, p. 114, fig. 22 (*pars*).
?1974	*Phymosoma granulosum* (Goldfuss); Savchinskaya, p. 312, pl. 95, figs 7–10.
1980	*Phymosoma granulosum* (Goldfuss); Geys, p. 204, figs 2.1–2.4.
1985	*Rachiosoma granulosa* (Goldfuss); Kutscher, p. 525, pl. 2, figs 7–12 (*pars*).
1985	*Phymosoma koenigi* (Mantell); Kutscher, p. 521, pl. 2, figs 1–6 (*pars*).

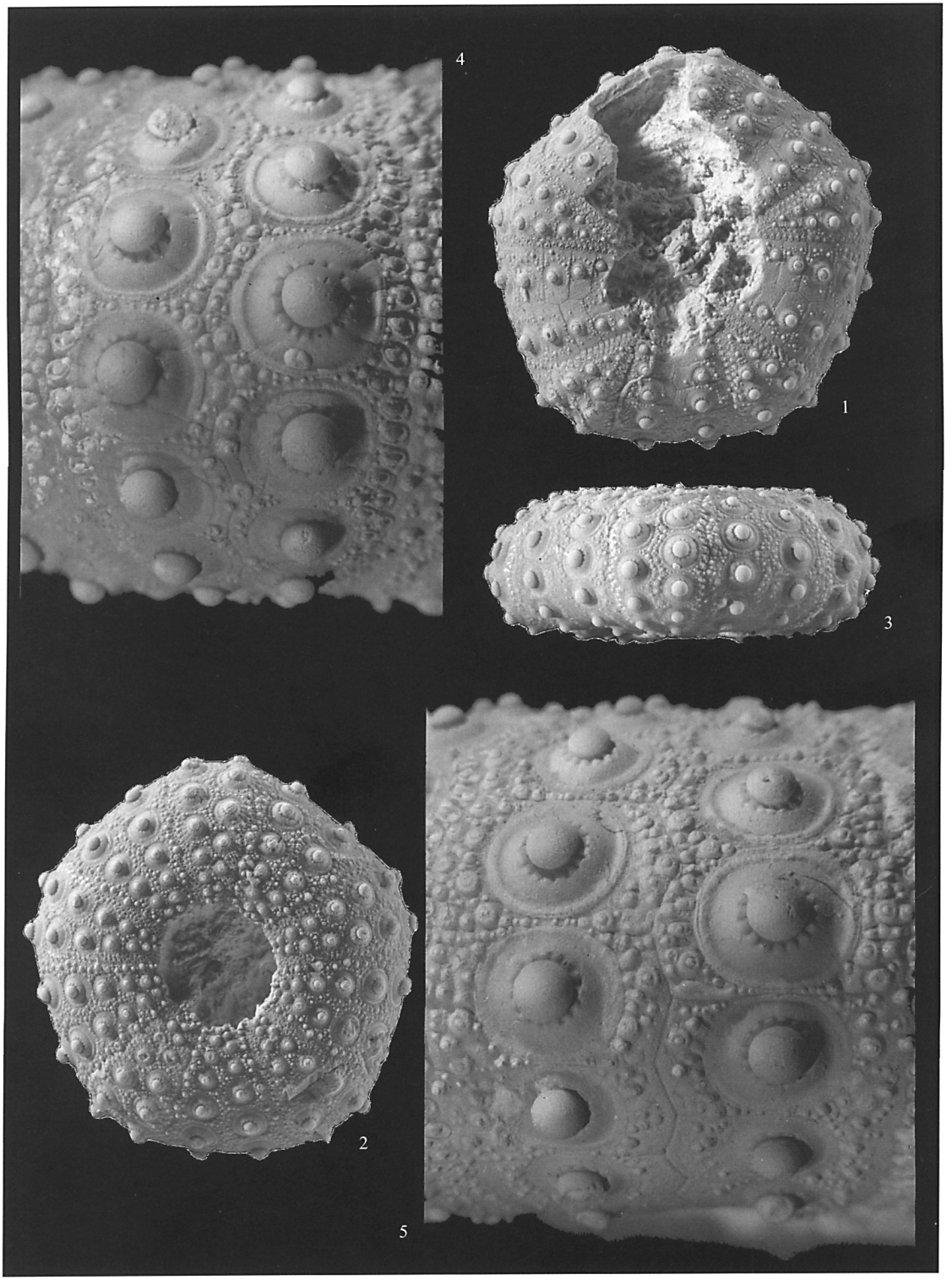
Material. Two specimens: BMNH EE5560–EE5561.

Occurrence. Uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan: 14–16 m below the Cretaceous–Tertiary boundary. This is a long-ranging species known from the

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EXPLANATION OF PLATE 3

Figs 1–5. *Phymosoma granulosum* (Goldfuss, 1829); BMNH EE5560; uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view; 4, detail of ambulacrum in lateral view; 5, detail of interambulacrum in lateral view. 1–3, ×2; 4–5, ×7.



JEFFERY, *Phymosoma*

Maastrichtian and Paleocene of Denmark. Elsewhere it is found in the Lower Maastrichtian of the Isle of Rügen and in the Lower to Upper Maastrichtian of the Don Basin, Bulgaria, Belgium and the Netherlands.

Description. The specimens are 30·3 mm and 19·2 mm in diameter respectively, and are circular to subpentagonal in outline, with ambulacra at the angles of the pentagon. The test is somewhat flattened with a height 37–38 per cent. of test diameter, and with broad, flat oral and apical surfaces. The sides are uniformly curved with the ambitus at approximately mid-height or slightly above. Ambulacral and interambulacral tubercles are equally developed.

Ambulacra are straight and moderately broad measuring 25–26 per cent. of test diameter at the ambitus. They show phymosomatoid compound plating with five elements in each compound plate at the ambitus (Text-fig. 5A). There is a single large tubercle on each compound plate. These primary tubercles are crenulate and non-perforate and are largest adambitally, becoming smaller both adapically and adorally. In the most adapical plates, the primary tubercle is too small to cover all of the compounding elements and overlies only two or three. There are 11 or 12 compound plates and approximately 53 pore-pairs at 19·2 mm test diameter increasing to 13 or 14 compound plates and 68 pore-pairs per column at 30·3 mm test diameter. The pores are noticeably crowded adorally and adapically where the pore zones also become less sinuous. The pores are partitioned isopores and at the ambitus the pore zone covers 17–18 per cent. of the width of the plates. Miliary tubercles run along the perradius.

Interambulacral zones are 1·3 to 1·5 times wider than ambulacral zones at the ambitus (33–36 per cent. of test diameter). There are 11 or 12 plates per column in both specimens examined. A single large crenulate, non-perforate tubercle with a circular areole is present on each interambulacral plate (Text-fig. 5B). In addition, from the ambitus to the mouth there is a line of small tubercles running along the edge of the plates adjacent to the ambulacra. In the three or four most adoral plates of each column these secondary tubercles are larger and more prominent. Miliary tubercles cover the remainder of each plate. Adapically there are far fewer tubercles and those which are present are appreciably smaller than on the oral surface. A naked interradial zone develops towards the apex.

Apical disc plates are not preserved in either specimen. In diameter, the apical disc occupies 36–39 per cent. of test diameter. Notches are apparent at the interradial sutures.

The peristome is circular with a diameter of 33–41 per cent. of test diameter. A proportionally larger mouth is present in the smaller specimen. Buccal slits are present at the margins of the peristome.

Remarks. Phymosoma corneti Cotteau is closest in appearance to *P. granulosum*. Both have distinctly crenulate primary tubercles and no well developed secondary tubercles. *P. corneti*, however, has extensive zones of miliary tubercles both adradially and interradially, whilst *P. granulosum* has poorly developed miliary granulation and its plates are almost entirely covered by primary tubercles.

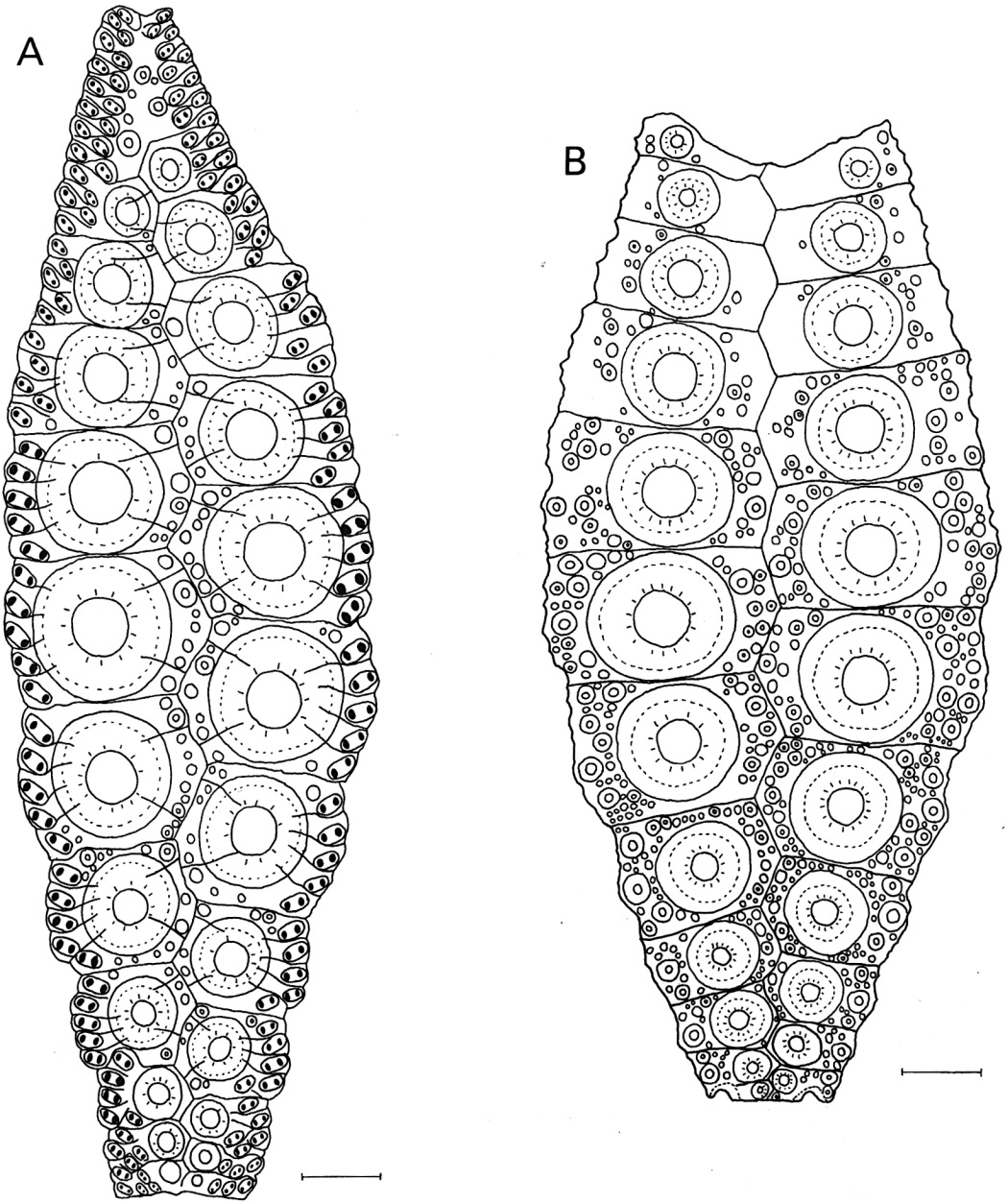
Genus GAUTHIERIA Lambert, 1888

Type species. Cyphosoma radiatum Sorignet, 1850, by original designation.

Gauthieria pseudoradiata (Schlüter, 1883)

Plate 4, figures 1–5; Text-figure 6A–B

1881 *Phymosoma pseudoradiatum* Schlüter, p. 216 [*nomen nudum*].
1883 *Phymosoma pseudoradiatum* Schlüter, p. 24.
1897 *Gauthieria Broecki* Lambert, p. 52, pl. 4, figs 1–5.
1911 *Gauthieria Broecki* Lambert, p. 65.
1911 *Phymosoma pseudoradiatum* Schlüter; Lambert and Thiéry, p. 225.
1928 *Phymosoma pseudoradiatum* Schlüter; Ravn, p. 58, pl. 6, fig. 4.
1935 *Gauthieria radiata* (Sorignet); Smiser, p. 30 (*pars*).
1935 *Gauthieria corneti* (Cotteau); Smiser, p. 31 (*pars*).
1935 *Gauthieria broecki* Lambert; Smiser, p. 32 (*pars*).
1950 *Gauthieria*(?) *pseudoradiata* (Schlüter); Kongiel, p. 314, pl. 1, figs 5–8.
1966 *Gauthieria radiata* (Sorignet); Nestler, p. 1214, figs 1–4.



TEXT-FIG. 5. *Camera lucida* drawings of *Phymosoma granulosum* (Goldfuss, 1829); BMNH EE5560. A, ambulacral plating; B, interambulacral plating. Scale bars represent 2 mm.

1980 *Gauthieria radiata broecki* Lambert; Geys, p. 210, figs 3.3–3.6.
1980 *Gauthieria pseudoradiata* (Schlüter); Geys, p. 212, figs 3.7–3.9, 4.1–4.2.

Material. BMNH EE5625.

Occurrence. Maastrichtian of Kyzylsai, Mangyshlak, Kazakhstan: 2·1 m below the Cretaceous–Tertiary boundary. Elsewhere, it is present in the Lower Maastrichtian of the Isle of Rügen, Belgium and the Netherlands and in the Upper Maastrichtian of Denmark and Poland.

Description. The test is circular in horizontal outline, with a diameter of 12·0 mm and a height of 4·1 mm (34 per cent. of test diameter). The ambitus is a little above mid-height and the test curves smoothly both above and below. Upper and lower surfaces are both broad and flat, although the oral surface is a little less so as the peristome is slightly sunken.

The ambulacra are 3·1 mm wide at the ambitus (26 per cent. of test diameter), tapering orally and ambitally. Compound plates contain three or four elements. Each compound plate carries a large, crenulate, non-perforate primary tubercle covering almost the entire surface of the plate. The compound plates show distinct radial ornamentation, especially close to the ambitus (Text-fig. 6A). Simple plates with densely packed small tubercles alternate with the compound plates. A single row of miliaries separates the primary tubercles ambitally along the perradius. Pore-pairs are uniserial throughout with no phyllode development. There are 35 pore-pairs in each column and these are positioned in weak arcs of five or six along the column length.

Interambulacra are 1·4 times wider than ambulacra at the ambitus (36 per cent. of test diameter). As in the ambulacra, interambulacral plates show distinct radial striations (Text-fig. 6B). Each plate carries a large crenulate, non-perforate tubercle. The primary tubercles on the most ambital plates have broad areoles covering virtually the whole plate. Around the plate margin is a single row of miliary granules. Primary tubercles decrease dramatically in size both apically and orally.

The apical disc is pentagonal and 5·2 mm in diameter (43 per cent. of test diameter), but no plates remain.

The peristome is circular with weak buccal slits. It measures 4·6 mm in diameter (38 per cent. of test diameter) and is very slightly sunken.

Remarks. A distinguishing feature of this species is the pronounced radial ornamentation on both ambulacral and interambulacral plates. Such radial striae are known to be a characteristic of juveniles of several other species of *Gauthieria*, and as all known specimens of *G. pseudoradiata* are small it is possible that they merely represent juveniles of another species. Another characteristic of *G. pseudoradiata* is the marked enlargement of the tubercles on the two or three most ambital plates, a feature also present in *G. middletoni* (Woodward). However, at a similar size to specimens of *G. pseudoradiata*, *G. middletoni* shows less enlargement of the ambital interambulacral tubercles, more developed miliary granulation and no radial ornamentation. It is therefore probable that they do represent two separate species.

Gauthieria pseudoradiata is easily distinguished from the only other phymosomatid found in these Mangyshlak sections, *Phymosoma granulosum*. *P. granulosum* has far coarser tuberculation, moderately strong phyllodes with distinct pore crowding near the mouth and a peristome which is flush with the test. Ambulacral plating also differs. In *Phymosoma*, compound plates are present throughout the ambulacral columns, whereas in *Gauthieria* compound plates alternate with simple elements.

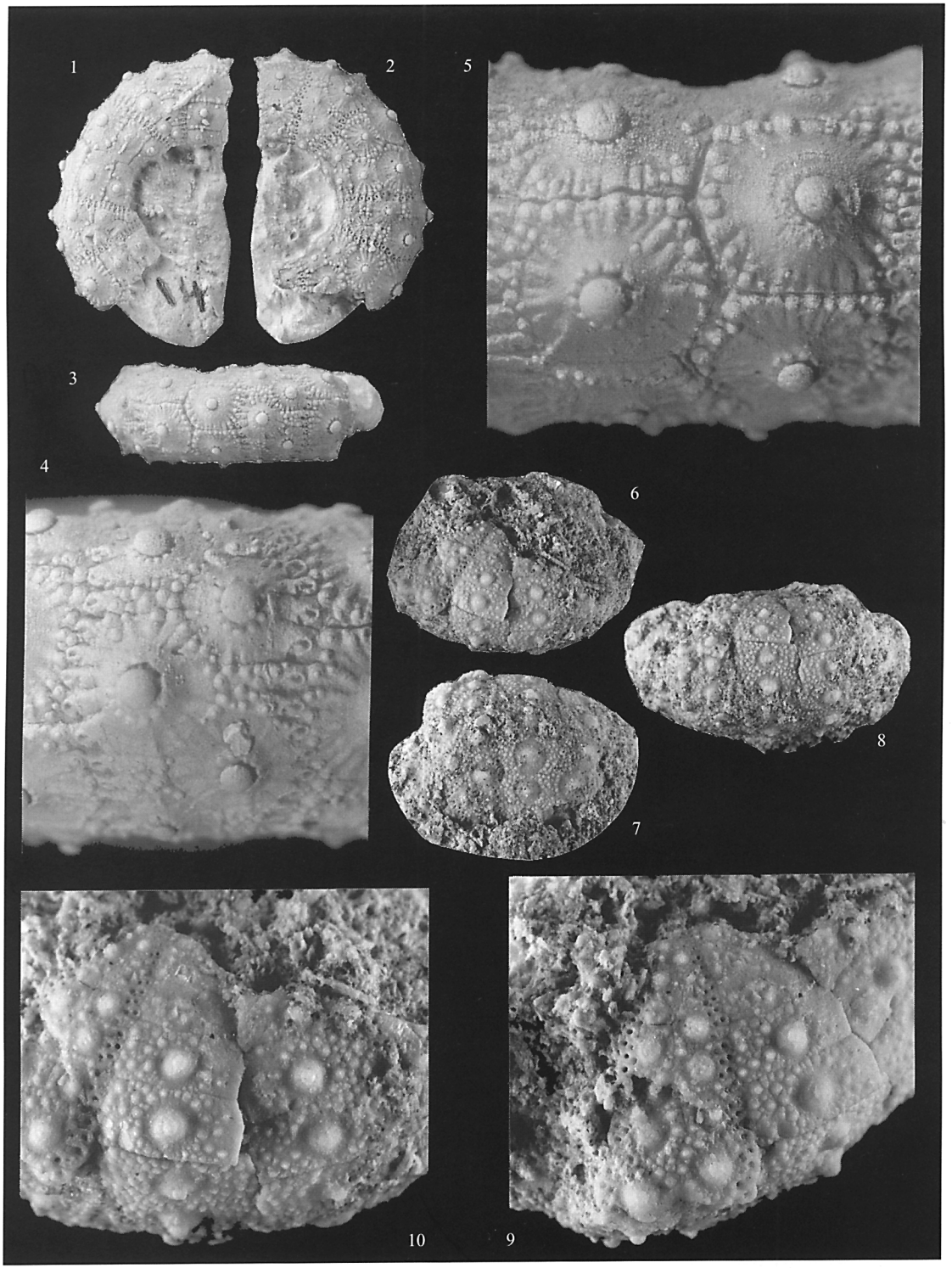
Genus MICROPSIS Cotteau, *in* Leymerie and Cotteau, 1856

Type species. Micropsis desorii Cotteau, *in* Leymerie and Cotteau, 1856, by original designation.

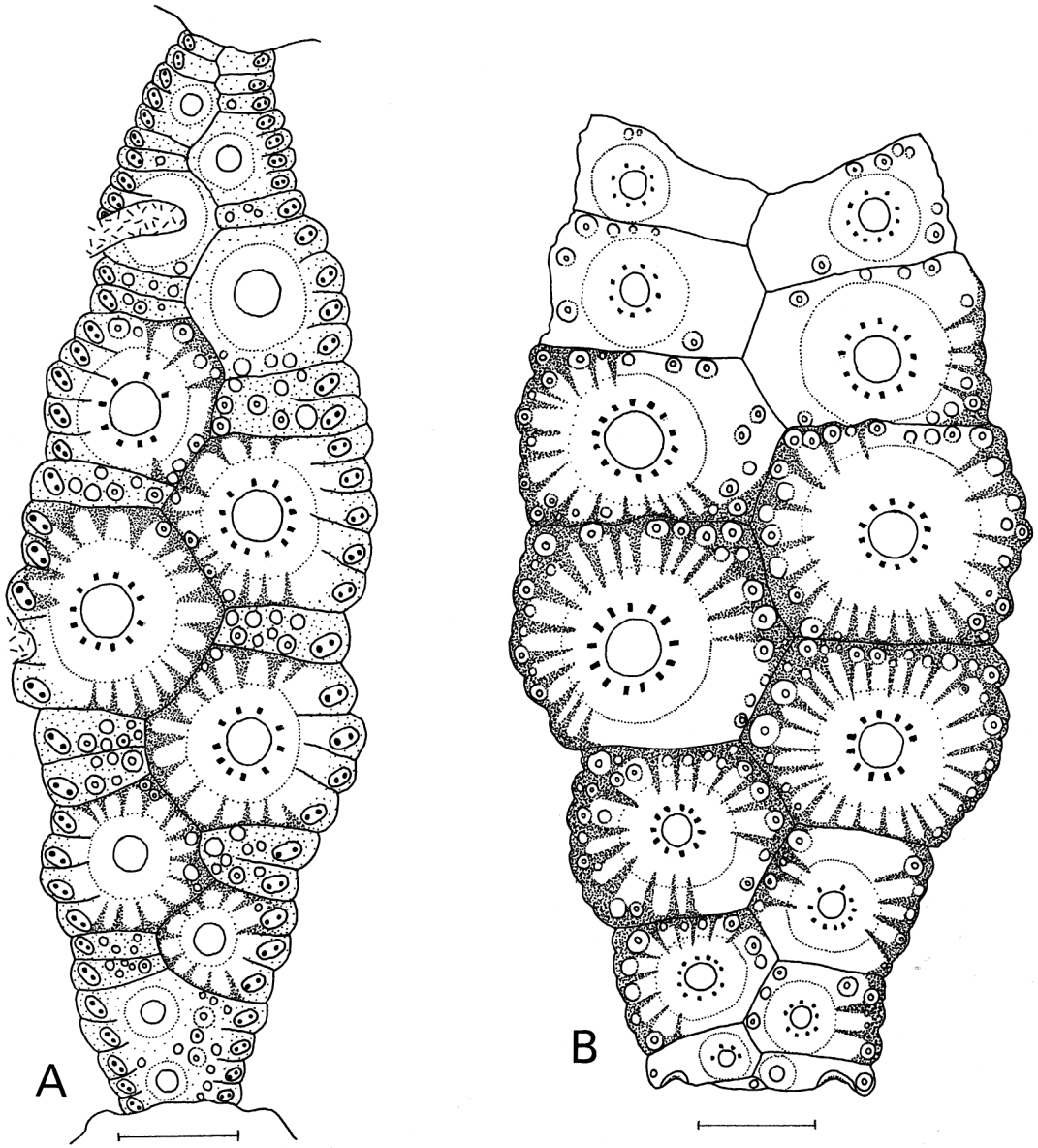
EXPLANATION OF PLATE 4

Figs 1–5. *Gauthieria pseudoradiata* (Schlüter, 1883); BMNH EE5625; Upper Maastrichtian, 2·1 m below Cretaceous–Tertiary boundary, Kyzylsai, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view; 4, detail of ambulacrum in lateral view; 5, detail of interambulacrum in lateral view. 1–3, ×4; 4–5, ×16.

Figs 6–10. *Micropsis* cf. *leridensis* Cotteau, *in* Leymerie and Cotteau, 1856; BMNH EE5631; Upper Maastrichtian, middle *B. casimirovensis* Zone, Sulukapy, Mangyshlak, Kazakhstan. 6, apical view; 7, oral view; 8, lateral view; 9, detail of ambulacrum in apical view; 10, detail of interambulacrum in apical view. 6–8, ×2; 9–10, ×5.



JEFFERY, *Gauthieria*, *Micropsis*



TEXT-FIG. 6. *Camera lucida* drawings of *Gauthieria pseudoradiata* (Schlüter, 1883); BMNH EE5625. A, ambulacral plating; B, interambulacral plating. Scale bars represent 1 mm.

Micropsis cf. *leridensis* Cotteau, 1882

Plate 4, figures 6–10; Text-figure 4C–D

cf. 1882 *Micropsis leridensis* Cotteau, p. 12, pl. 2, figs 8–10.
cf. 1911 *Rachiosoma leridense* (Cotteau); Lambert and Thiéry, p. 221.

Material. BMNH EE5631.

Occurrence. Collected in Late Maastrichtian strata (middle *B. casimirovensis* Zone) of Sulukapy, Mangyshlak Peninsula, Kazakhstan. *Micropsis leridensis* is known only from the Lower Senonian of Lérida Province, Spain.

Description. Only about one-third of the test is preserved. The test measures about 35 mm in diameter and 11·5 mm in height (33 per cent. of test diameter). It is circular in horizontal outline with broad, flat upper and lower surfaces giving it a somewhat wheel-like appearance.

Ambulacral width is 5·7 mm at the ambitus (16 per cent. of test diameter). Compound plates are made up of five elements ambitally but this number is reduced to four and then three adapically (Text-fig. 4C). There are 11 or 12 compound plates per ambulacral column. Each compound plate carries a single primary tubercle. These are non-perforate and only very weakly crenulate. They are of a similar size along the whole of the ambulacral length with an areole of similar width to the diameter of the mammelon. Surrounding the primary tubercles, and especially along the perradius are small secondary tubercles of approximately equal size. There are approximately 53 pore-pairs in each ambulacral column arranged uniserially in weak arcs.

The interambulacra are 1·8 times broader than the ambulacra at the ambitus (29 per cent. of test diameter). The interambulacral plates are of similar height to those in the ambulacra. They are, however, much broader, so that each interambulacral plate is about twice as broad as it is high. Primary tubercles in both ambulacra and interambulacra are equally developed and of similar dimensions. As in the ambulacra, their size diminishes only slightly away from the ambitus with the smallest tubercles adapically. Secondary tuberculation is similar to that found in the ambulacra giving the test an overall granular appearance (Text-fig. 4D).

The apical disc is not preserved, and it is not possible to tell what proportion of test diameter it made up. The shape of the apical system is likewise unknown.

The mouth is small (about 20 per cent. of test diameter), circular and invaginated.

Remarks. Micropsis seems to be closely related to *Porosoma* and *Rachiosoma*. Distinctions between these three genera are based mostly on the structure of the apical system. Consequently, when the apical disc is missing it is difficult to determine the true generic position of a specimen. However, another distinguishing feature of *Micropsis* is its small primary tubercles developed equally in both ambulacral and interambulacral fields. Of described *Micropsis* species, *M. leridensis* Cotteau, from the Senonian of Spain, most closely resembles the specimen from Kazakhstan. It is the only *Micropsis* species to have polyporous plates with five compounding elements near to the ambitus, and shows no enlarged secondary tubercles. Due to age and locality differences between *M. leridensis* and the species described herein, I refer the specimen from Kazakhstan to *M.* cf. *leridensis*.

Order HOLECTYPOIDA Duncan, 1889
Family CONULIDAE Lambert, 1911
Genus CONULUS Leske, 1778

Type species. Conulus albogalerus Leske, 1778, by original designation.

Conulus magnificus (d'Orbigny, 1854)

Plate 5, figures 1–4; Text-figure 7A–B

1854 *Echinoconus magnificus* d'Orbigny, p. 540, pl. 1004.
1921 *Conulus conicus* Breynius var. *grimmensis* Nietsch, p. 41, pl. 11, figs 1–2.
1927 *Conulus magnificus* (d'Orbigny); Ravn, p. 323, pl. 1, fig. 9.
1934 *Echinoconus Raulini* (d'Orbigny); Tzankov, p. 195, pl. 1, fig. 5.
1959 *Conulus magnificus* (d'Orbigny); Poslavskaya and Moskvin, p. 251, pl. 3, fig. 3.
1979 *Conulus grimmensis* Nietsch; Asgaard, table 2.
1986 *Conulus magnificus* (d'Orbigny); Kutscher, p. 325, pl. 1, figs 1–5, text-figs a–b.

Material. Two specimens: BMNH EE5562–EE5563.

Occurrence. Uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan: 14–16 m below the Cretaceous–Tertiary boundary. This species is also recorded from the Lower Maastrichtian

of northern Germany and the Isle of Rügen, and the Upper Maastrichtian of Denmark, Bulgaria, Crimea and the northern Caucasus.

Description. The test is slightly egg-shaped in horizontal outline, tapering posteriorly and with the widest point 40 per cent. of test length from the anterior margin. The specimens are 42·4 mm and 43·7 mm long and 39·5 mm and 40·1 mm wide respectively. In profile the test has a conical upper surface and a flat base.

The ambulacra are all alike. They are straight, narrow and non-petaloid, with a width approximately 13 per cent. of test length at the ambitus, and tapering towards the apex. Ambulacral pores are alike from the apical system to the peristome except that they become more sunken adorally. On the upper surface of the test, pore-pairs are arranged uniserially and the ambulacral plating is simple. Below the ambitus the pore-pairs form oblique arcs of three and plating is trigeminate.

The interambulacra are approximately three times as wide as the ambulacra at the ambitus (about 43 per cent. of test length). There are four to five ambulacral pore-pairs adjacent to each interambulacral plate and 19 or 20 plates per column in each interambulacrum. There are eight plates separating the peristome from the periproct.

The apical system lies at the highest point of the test. It is slightly longer than wide and tetrabasal (Text-fig. 7B). Gonopores are present on all four genital plates, and the madreporite has numerous additional hydropores. The madreporite is the largest of the plates and is in contact with all three other genital plates. Oculars II, III and IV are well separated. Oculars I and V meet at the midline and are larger than the other three ocular plates.

The peristome is oval in outline and is 1·25 times longer than wide. The axis of elongation runs from the top right to the bottom left. It lies a little anterior of the centre of the oral surface (44 per cent. of test length from the anterior margin) and is very slightly sunken.

The periproct lies in a marginal position, visible both from the posterior and from the oral surface. It is a large transverse oval and is approximately 1·3 times broader than long.

Tubercles are crenulate and perforate. They are denser, coarser, more distinctly sunken and of differing sizes on the oral surface with no differentiation between the ambulacra and the interambulacra. On the upper surface the tubercles from distinct diagonal rows in the interambulacra. Tuberculation is far finer and sparser than on the lower surface.

Remarks. *C. magnificus* is very similar in size and shape to *C. gigas* Cotteau from the Maastrichtian of the Pyrenees. However, *C. gigas* has a consistently smaller periproct with a longitudinally elongate oval shape which differs markedly from that of *C. magnificus* (Text-fig. 7A, C).

The German specimens described by Nietsch (1921) were larger and less conical than those previously assigned to *C. conicus* (Breynius) and a new subspecies was erected to accommodate them. I have not examined Nietsch's original material. Specimens in the Copenhagen Geological Museum labelled *Conulus grimmensis* are indistinguishable from *C. magnificus*.

Family GALERITIDAE Gray, 1825

Genus GALERITES Lamarck, 1801

Type species. *Echinites vulgaris* Leske, 1778, by original designation.

Galerites stadensis (Lambert, 1911)

Plate 6, figures 1–9; Text-figures 7D–E, 8

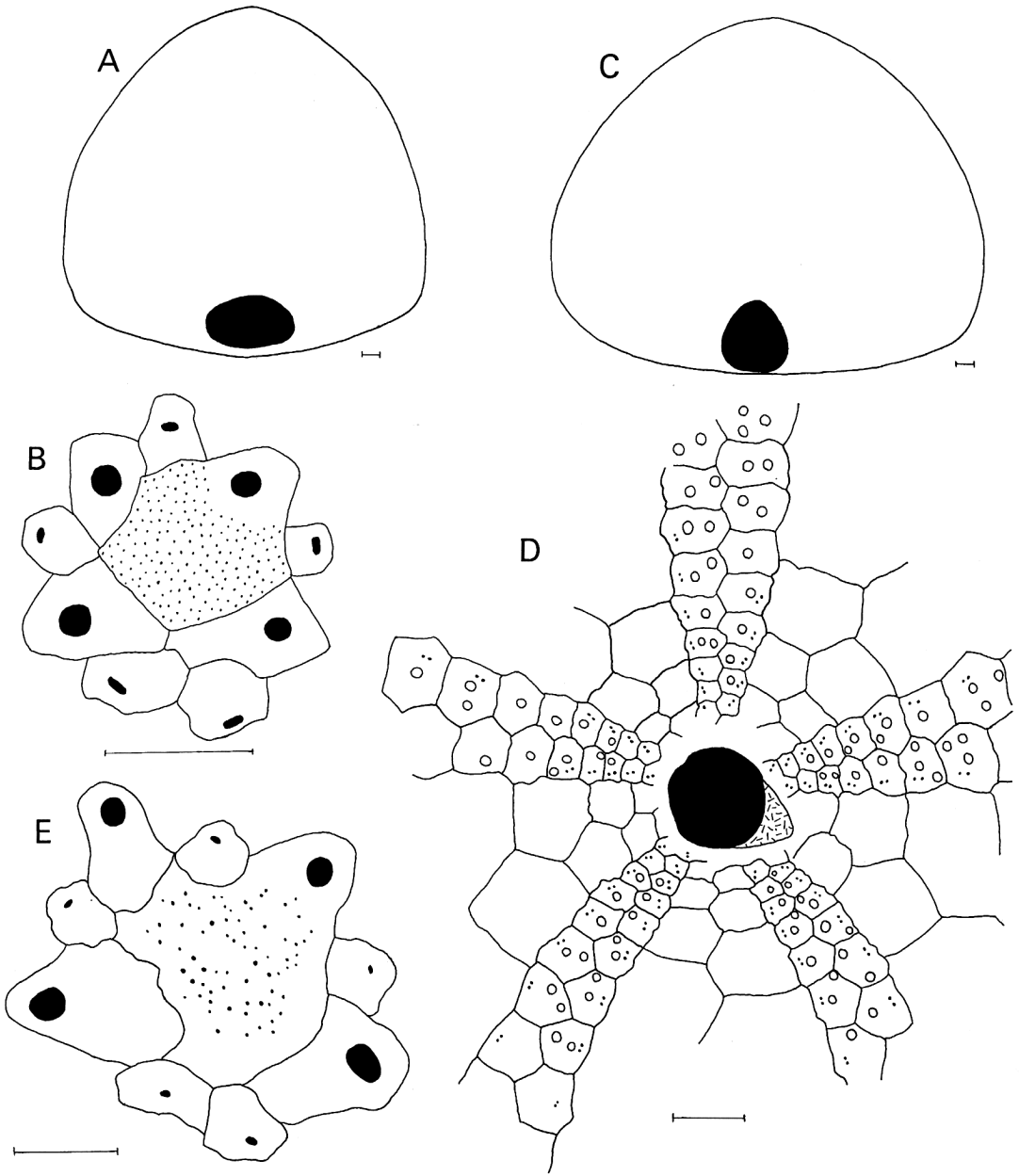
1911 *Echinoconus wollemanni* Lambert, p. 62, pl. 3, figs 19–21.

EXPLANATION OF PLATE 5

Figs 1–4. *Conulus magnificus* (d'Orbigny, 1854); BMNH EE5563; uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view; 4, posterior view; all ×2.



JEFFERY, *Conulus*



TEXT-FIG. 7. *Camera lucida* drawings of *Conulus magnificus* (d'Orbigny, 1854), *Conulus gigas* Cotteau and *Galerites stadensis* (Lambert, 1911). A–B, *Conulus magnificus*; BMNH EE5563; A, posterior view; B, apical disc plating. C, *Conulus gigas*; Maastrichtian of the Pyrenees; BMNH EE4835; posterior view. D–E, *Galerites stadensis*; BMNH EE5567; D, oral surface plating; E, apical disc plating. A–D, scale bars represent 2 mm. E, scale bar represents 1 mm.

1911 *Echinoconus globulus* var. *stadensis* Lambert, p. 75.
1921 *Echinoconus vulgaris* Leske; Nietsch, p. 33, pl. 9, figs 1–12; pl. 10, figs 1–7, 11.
1927 *Conulopsis globulus* Klein var. *goldfussi* (Lambert); Ravn, p. 326, pl. 2, fig. 3.
1927 *Conulopsis wollemanni* (Lambert); Ravn, p. 327, pl. 2, fig. 8.

1935 *Echinoconus wollemanni* Lambert; Smiser, p. 45.
1959 *Echinoconus vulgaris* Leske; Poslavskaya and Moskvin, p. 252, pl. 3, fig. 4.
?1979 *Galerites globulus* (Klein); Gongadze, p. 70, pl. 6, fig. 3.
1979 *Galerites vulgaris* (Leske); Kutscher, p. 564, pl. 2, figs 6–8.
1985 *Galerites* (*Galerites*) *stadensis* (Lambert); Schulz, p. 54, pl. 6, fig. 2; pl. 10, figs 10–15; pl. 11, fig. 4; pl. 15, figs 1–6.
1987 *Galerites stadensis*?; van der Ham *et al.*, p. 28.
1992 *Galerites* cf. *stadensis*; van der Ham and van Birgelen, p. 149.

Material. Eight specimens: BMNH EE5564–EE5571.

Occurrence. Uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan: 14–16 m below the Cretaceous–Tertiary boundary. *G. stadensis* has also been recorded from the Lower Maastrichtian of northern Germany and the Isle of Rügen and the Lower to Upper Maastrichtian of the Maastricht area, Denmark, Georgia, Crimea and the northern Caucasus.

Description. Tests are approximately circular to very slightly elongate oval in horizontal outline. They are more or less domed to conical in profile with a flat base and the ambitus situated just above this. They are 21·3–31·8 mm long and 15·5–26·8 mm high (61–84 per cent. of test length; Text-fig. 8).

Ambulacra are flush and all alike. They are straight and narrow, tapering towards the apex and towards the mouth on the oral surface. At the ambitus they measure between 2·6 mm and 4·1 mm (12–15 per cent. of test length). Pores are small and round with pairs very obliquely positioned especially adjacent to the peristome (Text-fig. 7D). They are identical from apex to mouth except for becoming slightly smaller adorally. Plating is simple throughout and pore-pairs are uniserial along the whole column. Each column contains 37 or 38 plates. The adoral pore angle, as defined by Schulz (1985, p. 14), ranges from 140° to 175°.

Interambulacra are all alike, 2·7–3·5 times broader than ambulacra at the ambitus, measuring between 8·3 mm and 13·3 mm (39–44 per cent. of test length). At the ambitus each interambulacral plate is adjacent to three ambulacral plates. Interambulacrum 5 forms a raised narrow triangular platform between the mouth and anus. There are six or seven plates separating the peristome and the periproct.

The apical system is situated centrally at the highest point on the test. In more conical specimens, it may be sunken slightly below the level of the surrounding coronal plates. It has a greatly enlarged madreporite which is in contact with the remaining three genital plates (Text-fig. 7E). All four genital plates are roughly triangular and carry a gonopore, and the madreporite has numerous additional small hydropores. The apical system is broadest posteriorly where the posterior genital plates are separated by the posterior oculars which meet at the midline.

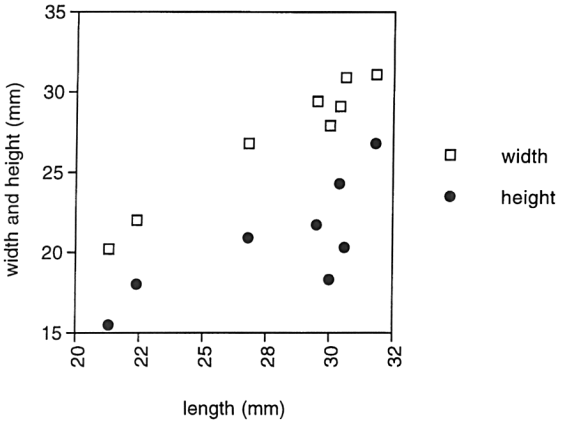
The mouth is situated 37–44 per cent. of test length from the anterior margin. It is circular or very slightly broader than long and is positioned in a deep peristomal well with vertical walls covered by small miliary tubercles. The peristome is fairly small, 1·9–2·8 mm long (7–9 per cent. of test length).

The periproct is situated inframarginally, 28–39 per cent. of test length posterior of the mouth on the raised platform of interambulacrum 5. It is rounded triangular to teardrop-shaped with the widest point posteriorly and is 0·9–1·2 times longer than wide. The length of the periproct is 10–12 per cent. of test length.

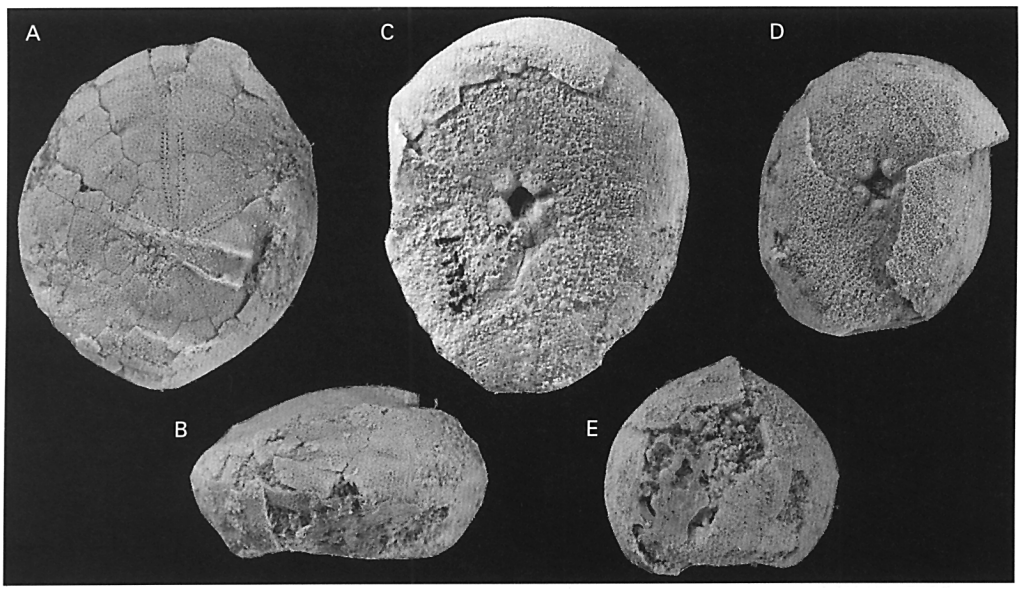
All tubercles are crenulate, perforate and sunken. Over the whole test, primary tubercles with sunken areoles are interspersed with secondary tubercles with mammelons. Dense miliary tuberculation fills all the gaps. On the oral surface the tubercles are larger and more deeply sunken and approximately twice as densely packed as on the upper surface. Tubercles are especially dense immediately adjacent to the mouth.

Remarks. The specimens from Mangyshlak have the vertical peristomal wall characteristic of *G.* (*G.*) *stadensis* which easily distinguishes this species from *G.* (*G.*) *abbreviatus* and *G.* (*G.*) *vulgaris* (Schulz 1985, p. 54).

The adoral 'pore angle' in *Galerites* (Schulz 1985) is a quantitative measure of the straightness of the ambulacra near to the mouth. According to Schulz, the size of this angle is of diagnostic value. Some of the specimens studied have pore angles somewhat smaller than those given for *G.* (*G.*) *stadensis* but within the range given by Schulz (p. 47) for *G.* (*G.*) *vulgaris*. Relative heights and the ratio of ambulacral to interambulacral plates at the ambitus also fall within the range for *G.* (*G.*) *vulgaris*. Schulz described a large number of species and subspecies based upon these characters. However, the diagnostic values of pore angle and relative height often have greatly overlapping ranges and further study may show that many of these taxa should be synonymized.



TEXT-FIG. 8. Biometric data for *Galerites stadensis* (Lambert, 1911).



TEXT-FIG. 9. *Zuffardia* sp.; Upper Maastrichtian, middle *B. casimirovensis* Zone, Sulukapy, Mangyshlak, Kazakhstan. A–B, BMNH EE5634; A, apical view; B, posterior view. C, BMNH EE5632; oral view. D–E, BMNH EE5633; D, oral view; E, posterior view. All ×2.

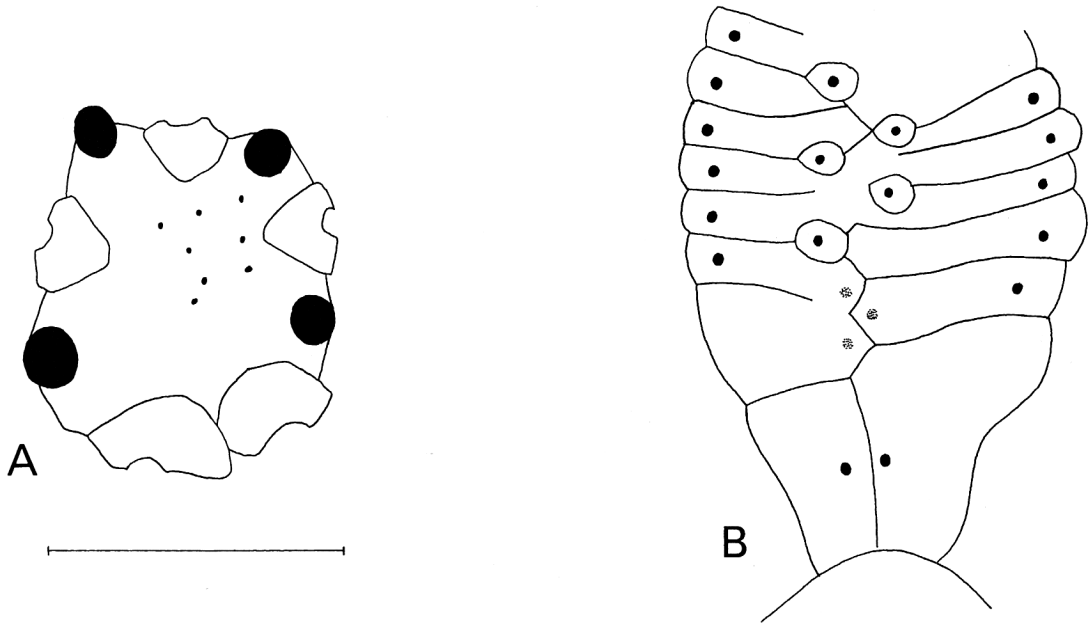
Galerites sulcatoradiatus Goldfuss is extremely similar to *G. stadensis* in overall appearance. They differ only in the larger 'pore angle' of the pore-pairs on the oral surface of *G. stadensis* and in the more distinctly raised triangular area around the periproct. *G. sulcatoradiatus* also has distinct surface tuberculation: primary tubercles are interspersed with pits containing pedicellarial bases which often coalesce.

EXPLANATION OF PLATE 6

Figs 1–9. *Galerites stadensis* (Lambert, 1911); uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1–3, BMNH EE5564; 1, apical view; 2, oral view; 3, lateral view. 4–6, BMNH EE5570; 4, apical view; 5, oral view; 6, lateral view. 7–9, BMNH EE5566; 7, apical view; 8, oral view; 9, lateral view. All ×2.



JEFFERY, *Galerites*



TEXT-FIG. 10. *Camera lucida* drawings of *Zuffardia* sp. A, BMNH EE5634; apical disc. B, BMNH EE5632; detail of phyllode V. Scale bar represents 1 mm.

Galerites stadensis is easily distinguished from *Conulus magnificus*, the only other holectypoid found in these Mangyshlak sections. *C. magnificus* has its periproct in a marginal position, visible both from behind and below. In addition, the ambulacral plating becomes trigeminate adorally in *Conulus* with the pore-pairs forming arcs of three. Tuberculation also differs: in *Conulus* tubercles are arranged in semi-regular diagonal rows.

Order CASSIDULOIDA Claus, 1880
Family PLIOLAMPADIDAE Kier, 1962

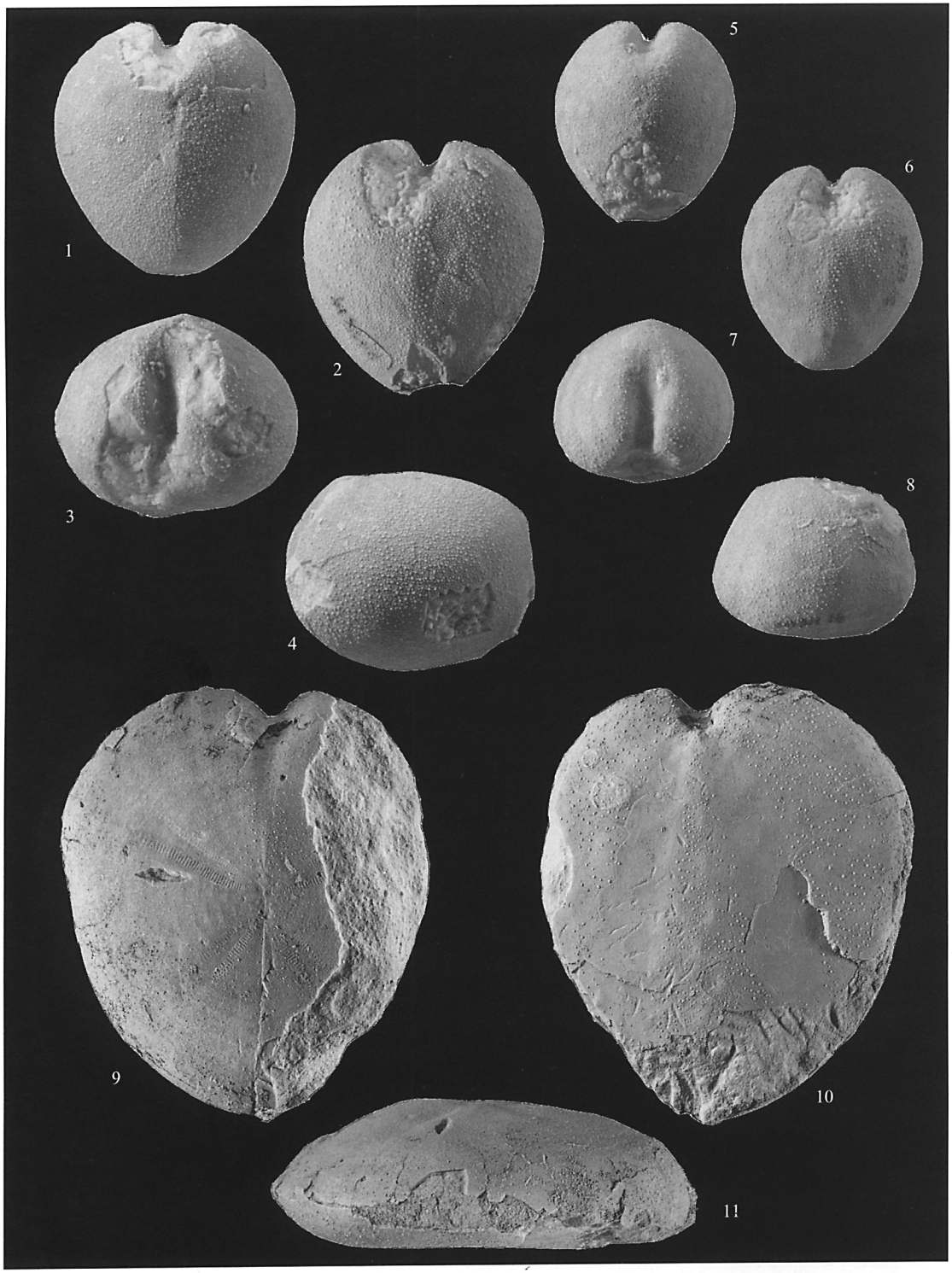
Genus ZUFFARDIA Checchia-Rispoli, 1917

Type species. Pseudocatopygus sanfilippoi Checchia-Rispoli, 1914, by original designation.

EXPLANATION OF PLATE 7

Figs 1–8. *Galeaster bertrandi* Seunes, 1889; Danian, 0·38 m above Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1–4, BMNH EE5596; 1, apical view; 2, oral view; 3, anterior view; 4, lateral view. 5–8, BMNH EE5595; 5, apical view; 6, oral view; 7, anterior view; 8, lateral view. All ×2.

Figs 9–11. *Cardiotaxis heberti* (Cotteau, *in* Cotteau and Triger, 1860); BMNH EE5627; Upper Maastrichtian, 0·4 m below Cretaceous–Tertiary boundary, Kyzylsai, Mangyshlak, Kazakhstan. 9, apical view; 10, oral view; 11, lateral view. All ×1.



JEFFERY, *Galeaster*, *Cardiotaxis*

Zuffardia sp.

Text-figures 9A–F, 10A–B

Material. Three specimens: BMNH EE5632–EE5634.

Occurrence. Upper Maastrichtian (middle *B. casimirovensis* Zone) of Sulukapy, Mangyshlak, Kazakhstan. Representatives of *Zuffardia* are known from the Maastrichtian of Libya, Algeria, Oman and the United Arab Emirates as well as from the upper Senonian of southern Iran. It has also been recorded from the upper Paleocene to Eocene of Oman.

Description. The specimens are more or less crushed. They are 19·3–24·6 mm long and 15·1–19·7 mm wide (78–87 per cent. of test length). The test is ovoid in horizontal outline with a smoothly rounded anterior margin and a tapered posterior. In profile, the test is somewhat inflated with the ambitus at about mid-height. The base is flat with slightly rounded margins.

The ambulacra are alike and of equal length. They are flush with the test surface and form long, narrow, poorly developed petals with almost parallel rows of pore-pairs. The petals are open distally and ambulacral plates beyond the ends of the petals are single-pored. Within the petaloid region, the pores of each pair differ in size, the outer pore being more elongate than the inner.

The apical system is situated at the highest point on the test, slightly anterior of centre. The apical region is poorly preserved. However, the apical disc appears to be monobasal with four small gonopores (Text-fig. 10A).

The peristome is positioned a little anterior of centre (43–46 per cent. of test length from the anterior margin). It is pentagonal and invaginated, with the floscelle well developed. There are strong bourrelets and broad single-pored phyllodes with two series of pores in each half ambulacrum (Text-fig. 10B). The phyllodes have six or seven pores in the outer series and three in the inner series. Buccal pores are also present.

The periproct is marginal and of elongate oval shape. It is positioned high on the truncate posterior with a slight projection above it.

Tuberculation on the upper surface is uniform and fairly dense. The tubercles are small with deeply sunken areoles. On the oral surface tubercles are more densely packed and are very slightly larger.

Remarks. This genus appears to be very facies dependent. It is recorded only from the calcarenite deposits at Mangyshlak and from the more sandy, coarse grained calcareous strata of localities outside Kazakhstan.

The specimens available for study are rather more flat-based and have narrower petals than the *Zuffardia* species previously described. However, none of the material is well enough preserved to be designated as holotype of a new species and so is here determined only to generic level.

Order HOLASTEROIDA Durham and Melville, 1957
Family HOLASTERIDAE Pictet, 1857

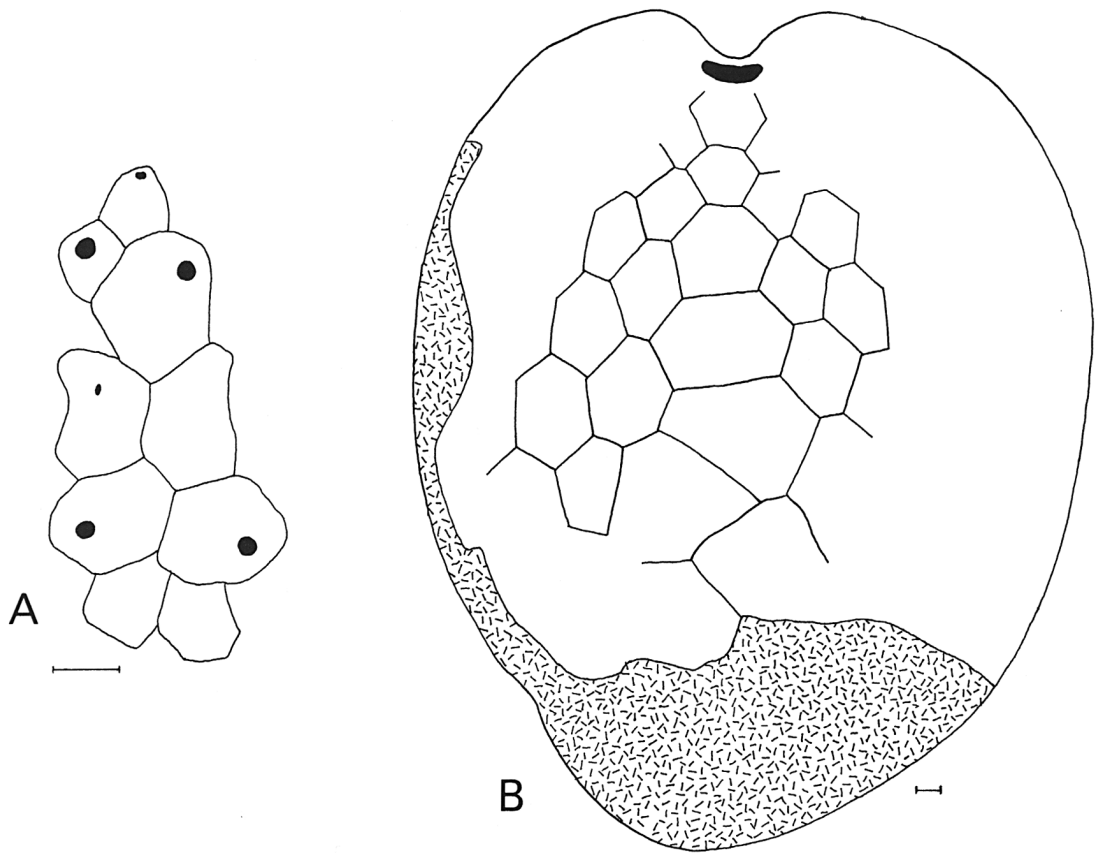
Genus CARDIOTAXIS Lambert, 1917

Type species. Cardiaster peroni Lambert, *in* Peron 1887, by original designation.

Cardiotaxis heberti (Cotteau, *in* Cotteau and Triger, 1860)

Plate 7, figures 9–11; Text-figure 11A–B

1860 *Cardiaster heberti* Cotteau, p. 240.
1874 *Cardiaster heberti* Cotteau, p. 655.
1897 *Cardiaster heberti* Cotteau; Lambert, p. 176, pl. 2, figs 11–12.
1911 *Cardiaster heberti* Cotteau; Lambert, pp. 19, 45, pl. 1, figs 7–9.
1927 *Cardiaster heberti* Cotteau; Ravn, p. 341.



TEXT-FIG. 11. *Camera lucida* drawings of *Cardiotaxis heberti* (Cotteau, *in* Cotteau and Triger, 1860); BMNH EE5627. A, apical disc plating; B, oral surface plating. A, scale bar represents 1 mm. B, scale bar represents 2 mm.

1978 *Cardiotaxis heberti* (Cotteau); Kutscher, p. 627, pl. 1.
1979 *Cardiotaxis heberti* (Cotteau); Asgaard, table 2.

Material. BMNH EE5627.

Occurrence. Upper Maastrichtian white chalk of Kyzylsai, Mangyshlak, Kazakhstan: 1·4 m below the Cretaceous–Tertiary boundary. It is also recorded from the Lower Maastrichtian of the Isle of Rügen, Belgium and the Netherlands, and from the Lower to Upper Maastrichtian of Denmark.

Description. The test is large and heart-shaped. It is 68·9 mm long and *c.* 61 mm wide (86 per cent. of test length). There is a broad and distinct frontal groove which runs all the way to the mouth. The adjoining interambulacra form rounded keels. The test is low (34 per cent. of test length) and flattened, with broad flat oral and apical surfaces. The ambitus is 21 per cent. of test height above the base. The specimen has a very thin test.

The anterior ambulacrum is sunken in the frontal groove and has small, round, non-sunken pores. Each pair is positioned obliquely. The paired ambulacra are flush with the test surface. They are broad at the ambitus and taper substantially towards the apex. The pores are slightly elongate and are identical in both series of the anterior and posterior paired ambulacra. There is a wide, granulated interporiferous zone.

The plastron is made up of a series of single plates placed one behind the other. The labrum is followed by four large single plates which in turn are followed by pairs of alternating plates (Text-fig. 11B).

The apical system is of typical elongate holasteroid structure with four gonopores and ocular plates II and IV meeting at the midline (Text-fig. 11A). The madreporite carries numerous hydropores in addition to its genital pore.

The peristome is situated in an extremely anterior position (8 per cent. of test length from the anterior margin). It is oval, 1·1 times broader than long, and faces anteriorly at the end of the frontal groove. The periproct is not visible.

There is fine and sparse (though regularly spaced) tuberculation on the upper surface. Granulation in between is equally fine and sparse. Larger, more numerous tubercles are present on the oral surface especially along the edges of the plastron and around the anterior margin of the test.

A fairly broad marginal fasciole is visible in parts. It is approximately six miliaries wide and contains inclusions of small tubercles.

Remarks. *Cardiotaxis heberti* is the only representative of this genus found in Maastrichtian strata of Denmark, Rügen, the Maastricht area and the former USSR. It is often found in association with *Cardiaster granulosus* (Goldfuss) from which it may be easily distinguished by its larger, lower and extremely thin test and lack of large adapical interambulacral tubercles. In addition, the plastron of *C. heberti* is made up of the labrum followed by four single plates whilst that of *Cardiaster granulosus* has two single plates after the labrum before the plates become paired and alternate. In *C. heberti*, the peristome is more anterior, situated at the end of the frontal sulcus.

Genus ECHINOCORYS Leske, 1778

Type species. *Echinocorys scutatus* Leske, 1778, by subsequent designation of Lambert 1897.

Echinocorys obliqua Ravn, 1927

Plate 8, figures 1–3; Text-figures 12, 14B

1927 *Echinocorys obliquus* Ravn, p. 336, pl. 4, fig. 2; pl. 5, fig. 2; text-figs 4–5.
1935 *Echinocorys obliquus* Ravn; Kongiel, p. 36, pl. 3(6), figs 2–3.
1959 *Echinocorys obliquus* Ravn; Poslavskaya and Moskvin, p. 262, pl. 11, figs 3–4, text-fig. 4.
1979 *Echinocorys obliquus* Ravn; Asgaard, tables 1–2.
1979 *Echinocorys obliquus* Ravn; Gongadze, p. 91, pl. 20, fig. 2.

Material. Eighteen specimens: BMNH EE5590–EE5594, EE5600–EE5601, EE5605–EE5613, EE5618–EE5619.

Occurrence. Present in strata from 50 mm below to 0·8 m above the Cretaceous–Tertiary boundary (i.e. predominantly Danian strata) at Kyzylsai and Koshak, Mangyshlak, Kazakhstan. Elsewhere, *Echinocorys obliqua* is known from the Danian of Denmark, Poland, Georgia, Crimea and the northern Caucasus.

Description. This species is remarkably consistent in shape. The test is egg-shaped in horizontal outline with a smoothly rounded anterior margin, tapering towards the posterior. The test is 26·6–44·0 mm long and 23·3–38·7 mm wide (81–91 per cent. of test length). It has a highly vaulted upper surface and a flat base giving it a somewhat rounded sub-conical profile. The height is 16·0–29·8 mm (60–74 per cent. of test length). There is a weak keel running from the apex to the periproct.

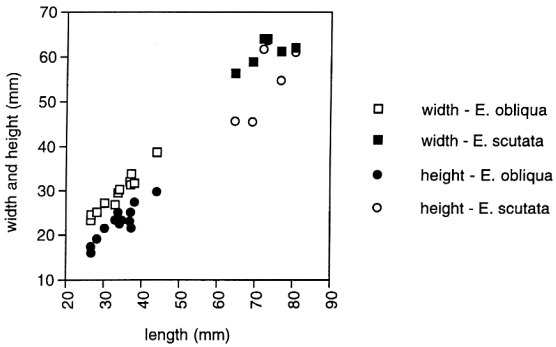
EXPLANATION OF PLATE 8

Figs 1–3. *Echinocorys obliqua* Ravn, 1927; BMNH EE5609; Danian, 0·75 m above Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view. All ×2.

Figs 4–7. *Pseudoffaster caucasicus* (Dru, 1884); BMNH EE5573; uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 4, apical view; 5, oral view; 6, posterior view; 7, lateral view. All ×2.



JEFFERY, *Echinocorys*, *Pseudoffaster*



TEXT-FIG. 12. Biometric data for *Echinocorys scutata* Leske, 1778 and *Echinocorys obliqua* Ravn, 1927.

All ambulacra are alike. They are straight and narrow and taper towards the apex. Pores are small and round, becoming smaller still towards the ambitus. They are arranged in slightly oblique pairs at the centre of the ambulacral plates. The interporiferous zone is approximately three times wider than each series of pores. Plating is simple throughout.

The plastron is meridosternous with the labral plate followed by a large single plate and then biserial plating.

The apical system is positioned on the highest part of the test. It is elongate with the anterior and posterior genital plates separated by ocular plates II and IV meeting at the midline (Text-fig. 14B). All four genital plates are similar sized and carry a gonopore. The madreporite also has numerous hydropores.

The peristome is transversely oval and situated anteriorly on the lower surface of the test, 15–19 per cent. of test length from the anterior margin. It is roughly 1·5 times broader than long and is slightly sunken. The mouth is not labiate.

The periproct is marginally positioned, visible both from behind and below. It is small and circular.

Tuberculation is sparse and regularly spaced on the upper surface. The tubercles are small, perforate and crenulate. Granulation in between is equally sparse. On the oral surface tubercles are more abundant. The plastron and anterior and lateral margins show fairly close-packed tuberculation whilst the posterior ambulacral zones are naked.

There are no fascioles.

Echinocorys scutata Leske, 1778

Plate 9, figures 1–6; Text-figures 12, 13A–D, 14A

1959 *Echinocorys pyramidatus* (Portlock); Poslavskaya and Moskvin, p. 259, pl. 8, fig. 2; pl. 9, fig. 1; text-fig. 61.
1959 *Echinocorys ciplyensis* Lambert; Poslavskaya and Moskvin, p. 259, pl. 9, fig. 2; text-fig. 62.
1959 *Echinocorys perconicus* (von Hagenow); Poslavskaya and Moskvin, p. 260, pl. 9, fig. 3; pl. 10, fig. 1; text-fig. 63.
1959 *Echinocorys edhemi* Boehm; Poslavskaya and Moskvin, p. 260, pl. 10, fig. 3; pl. 11, fig. 1; text-fig. 64.
1959 *Echinocorys renngarteni* Poslavskaya and Moskvin, p. 260, pl. 10, fig. 2; text-fig. 65.
1959 *Echinocorys sulcatus* (Goldfuss); Poslavskaya and Moskvin, p. 261, pl. 11, fig. 5; text-fig. 66.
1959 *Echinocorys pyrenaicus* Seunes; Poslavskaya and Moskvin, p. 262, pl. 11, fig. 2; text-fig. 67.
1974 *Echinocorys ovatus* Leske; Savchinskaya, p. 325, pl. 108, figs 2–3.
1974 *Echinocorys ciplyensis* Lambert; Savchinskaya, p. 325, pl. 109, figs 1–4.
1979 *Echinocorys ovatus* Leske; Gongadze, p. 76, pl. 7, fig. 1.
1979 *Echinocorys* cf. *pyramidatus* (Portlock); Gongadze, p. 77, pl. 8, fig. 1.
1979 *Echinocorys conoideus* (Goldfuss); Gongadze, p. 78, pl. 9, fig. 1.
1979 *Echinocorys elatus* Arnaud; Gongadze, p. 79, pl. 10, fig. 1.
1979 *Echinocorys kharagoulensis* Gongadze, p. 80, pl. 11, fig. 1; pl. 12, fig. 1.
1979 *Echinocorys perconicus* von Hagenow; Gongadze, p. 82, pl. 13, fig. 1.
1979 *Echinocorys renngarteni* Poslavskaya and Moskvin; Gongadze, p. 83, pl. 14, fig. 1.
1979 *Echinocorys pyrenaicus* Seunes; Gongadze, p. 84, pl. 15, fig. 1.
1979 *Echinocorys ciplyensis* Lambert; Gongadze, p. 85, pl. 16, fig. 1.

1979 *Echinocorys subglobosus* var. *fonticola* Arnaud; Gongadze, p. 86, pl. 17, fig. 1.
1979 *Echinocorys conicus* (Agassiz); Gongadze, p. 88, pl. 18, fig. 1.
1979 *Echinocorys edhemi* Böhm; Gongadze, p. 89, pl. 19, fig. 1.
1979 *Echinocorys depressus* (Eichwald); Gongadze, p. 90, pl. 20, fig. 1.
1979 *Echinocorys katscharavai* Tsagareli; Gongadze, p. 93, pl. 20, fig. 3.

Material. Six specimens: BMNH EE5577–5579 and EE5615–5617.

Occurrence. Upper Maastrichtian strata (*B. casimirovensis* Zone) of Mangyshlak, Kazakhstan, 12–16 m below the Cretaceous–Tertiary boundary. Elsewhere, *Echinocorys scutata* is known from chalk facies world-wide, ranging throughout the Maastrichtian and Danian.

Description. Tests are oval in horizontal outline and 64·6–80·5 mm long. Maximum width is 77–89 per cent. of test length and occurs just anterior of centre. Test profile is highly variable: it ranges from flat-based and conical to low and exceptionally rounded. Height varies from 66 to 87 per cent. of test length. None of the specimens shows a marked keel.

Ambulacra are as those described for *Echinocorys obliqua* above except that the pore-pairs are not positioned obliquely and the interporiferous zone is much broader in *Echinocorys scutata*. This, however, may just be a function of larger size. Interambulacral plating is also as described above for *E. obliqua*. The plastron is meridosternous.

The apical system is positioned on the highest part of the test. It is of typical elongate holasteroid structure.

The peristome is situated anteriorly, 15–21 per cent. of test length from the anterior margin. It is transversely elongate with no labral projection.

The periproct is situated inframarginally and is visible only from below. It is circular and approximately half the size of the mouth.

Tuberculation on the apical surface is so fine and sparse that the test appears superficially to be tubercle-free. On the oral surface tubercles are far larger and more abundant. As in *Echinocorys obliqua*, tubercles are restricted to the plastron and anterior and lateral margins of the test.

No fascioles are present.

Remarks. The specimens described here are very variable in shape: from flat-based and conical to exceptionally globular (Text-fig. 13). Previous authors have erected a large number of species to accommodate such differently shaped 'varieties'. The six specimens available appear, however, to form a gradational series and, as no structural differences can be distinguished, they are here treated as a single species complex, following van der Ham *et al.* (1987).

Echinocotys scutata and *E. obliqua* are found in different stratigraphical horizons in the Mangyshlak sections (Maastrichtian and Danian respectively). Apart from *E. scutata* always being much larger than *E. obliqua*, they differ most noticeably in the presence of a distinct carina in *E. obliqua* running from the apex to the posterior on the upper surface of the test. *E. obliqua* also has oblique pairs of ambulacral pores and a periproct that is visible both from behind and from below. As noted above some of these character differences may be size-related. However, the studied specimens of *E. obliqua* show a strikingly consistent morphology despite their size differences, and appear to represent a single growth series.

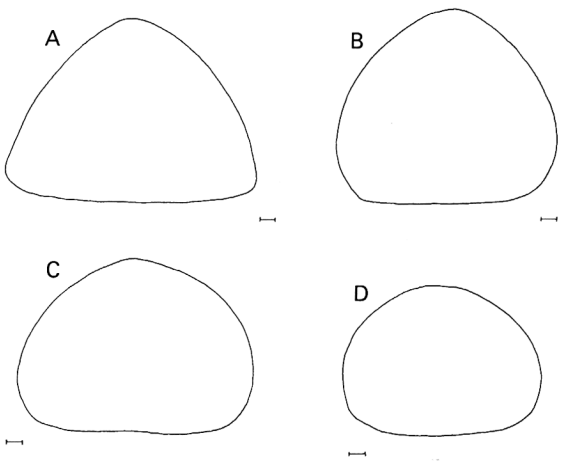
Genus GALEASTER Seunes, 1889

Type species. Galeaster bertrandi Seunes, 1889, by original designation.

Galeaster bertrandi Seunes, 1889

Plate 7, figures 1–8; Text-figures 14F–H, 15

1889 *Galeaster bertrandi* Seunes, p. 822, pl. 27, figs 2–3.
1959 *Galeaster minor* Poslavskaya; Poslavskaya and Moskvin, p. 273, pl. 17, figs 9–10.
1959 *Galeaster sumbaricus* Poslavskaya; Poslavskaya and Moskvin, p. 273, pl. 17, figs 7–8.
1960 *Galeaster minor* Poslavskaya; Poslavskaya and Moskvin, p. 58, pl. 2, figs 3–4, 7.



TEXT-FIG. 13. *Camera lucida* drawings of *Echinocorys scutata* Leske, 1778; lateral views. A, BMNH EE5615. B, BMNH EE5579. C, BMNH EE5616. D, BMNH EE5617. Scale bars represent 5 mm.

1960 *Galeaster sumbaricus* Poslavskaya; Poslavskaya and Moskvin, p. 57, pl. 2, figs 1–2.
?1960 *Galeaster dagestanensis* Poslavskaya and Moskvin, p. 59, pl. 2, fig. 6.
1979 *Galeaster* cf. *bertrandi* Seunes; Gongadze, p. 107, pl. 25, fig. 2.
1979 *Galeaster* cf. *minor* Poslavskaya and Moskvin; Gongadze, p. 108, pl. 25, fig. 3.

Material. Five specimens: BMNH EE5588–EE5589, EE5595–EE5596, EE5614.

Occurrence. Danian strata (0·38–0·95 m above the Cretaceous–Tertiary boundary) at Koshak, Mangyshlak, Kazakhstan. *Galeaster bertrandi* was recorded previously from the Maastrichtian of Georgia and the Danian of the eastern Pyrenees. *G. sumbaricus* is also found in the Lower to Upper Maastrichtian of the northern Caucasus and the Transcaspian region, whilst *G. minor* and *G. dagestanensis* are known from the Lower to Upper Danian of Georgia, the northern Caucasus and the Transcaspian region.

Description. The test is heart-shaped in horizontal outline, broadest anteriorly and tapering towards the vertically truncate posterior. The specimens are 15·9–21·2 mm long and 14·2–20·0 mm wide (88–96 per cent. of test length; Text-fig. 15). The distinct frontal groove is deepest at the ambitus and runs all the way to the mouth. On the upper surface it shallows towards the apex. The test is 13·1–16·9 mm high (77–83 per cent. of test length). The ambitus is at one-quarter to one-third height from the base. The test is globular in profile with the upper surface highly vaulted. Both the oral and apical surfaces are weakly keeled posteriorly.

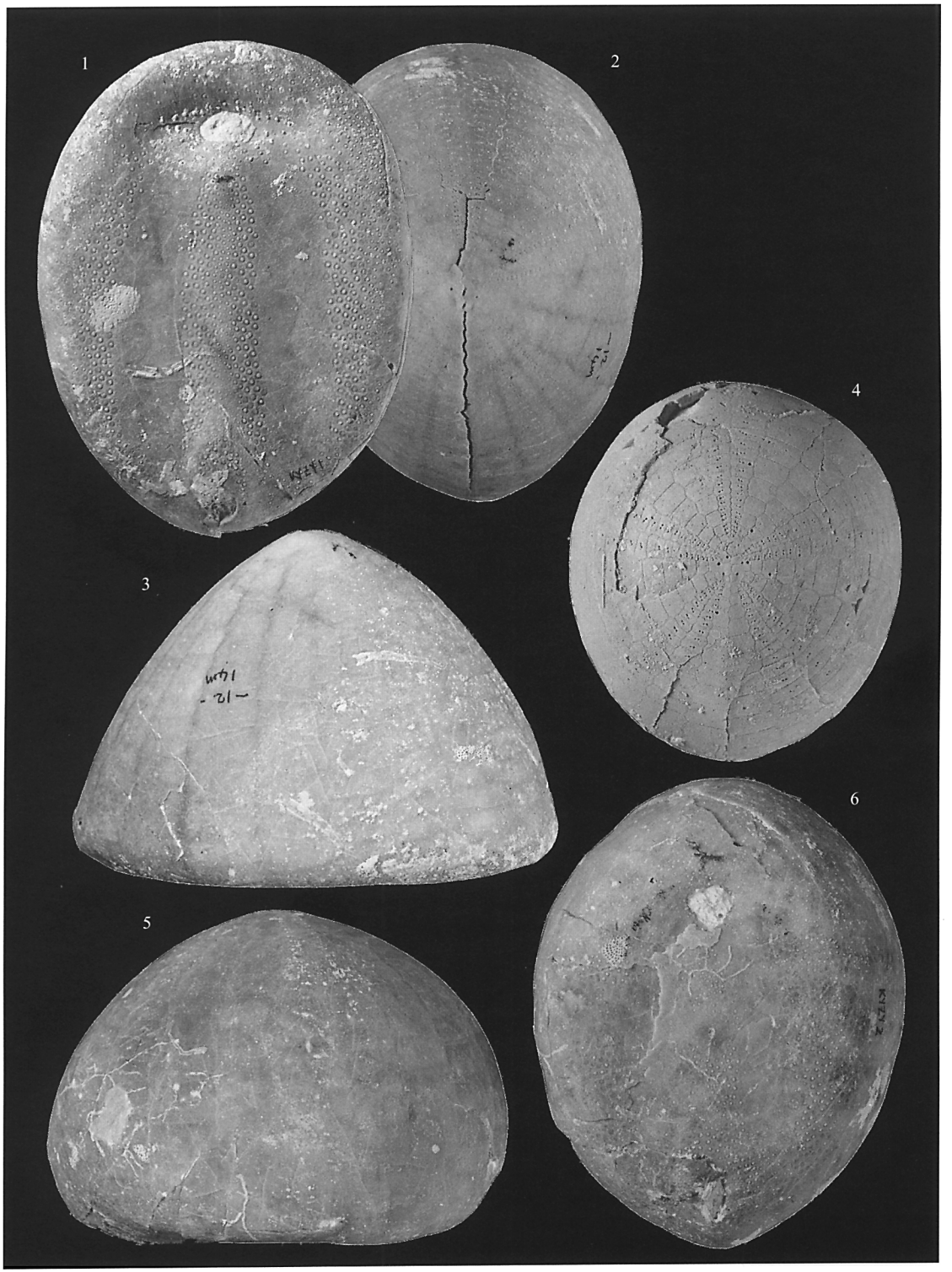
The anterior ambulacrum is sunken in the frontal groove. Its pores are round and minute with each pair situated very obliquely at the adoral centre of the plate. Interambulacral and ambulacral plates of the paired ambulacra are of similar dimensions with one interambulacral plate adjacent to each ambulacral plate. Ambulacral plates are high. Pores in the paired ambulacra are only slightly larger than those of the frontal ambulacrum. The pores of each pair are very close together. Pore-pairs are positioned as in the frontal ambulacrum although a little less obliquely.

The plastron is orthosternous with labral and sternal plates having a fairly broad contact surface (Text-fig. 14H).

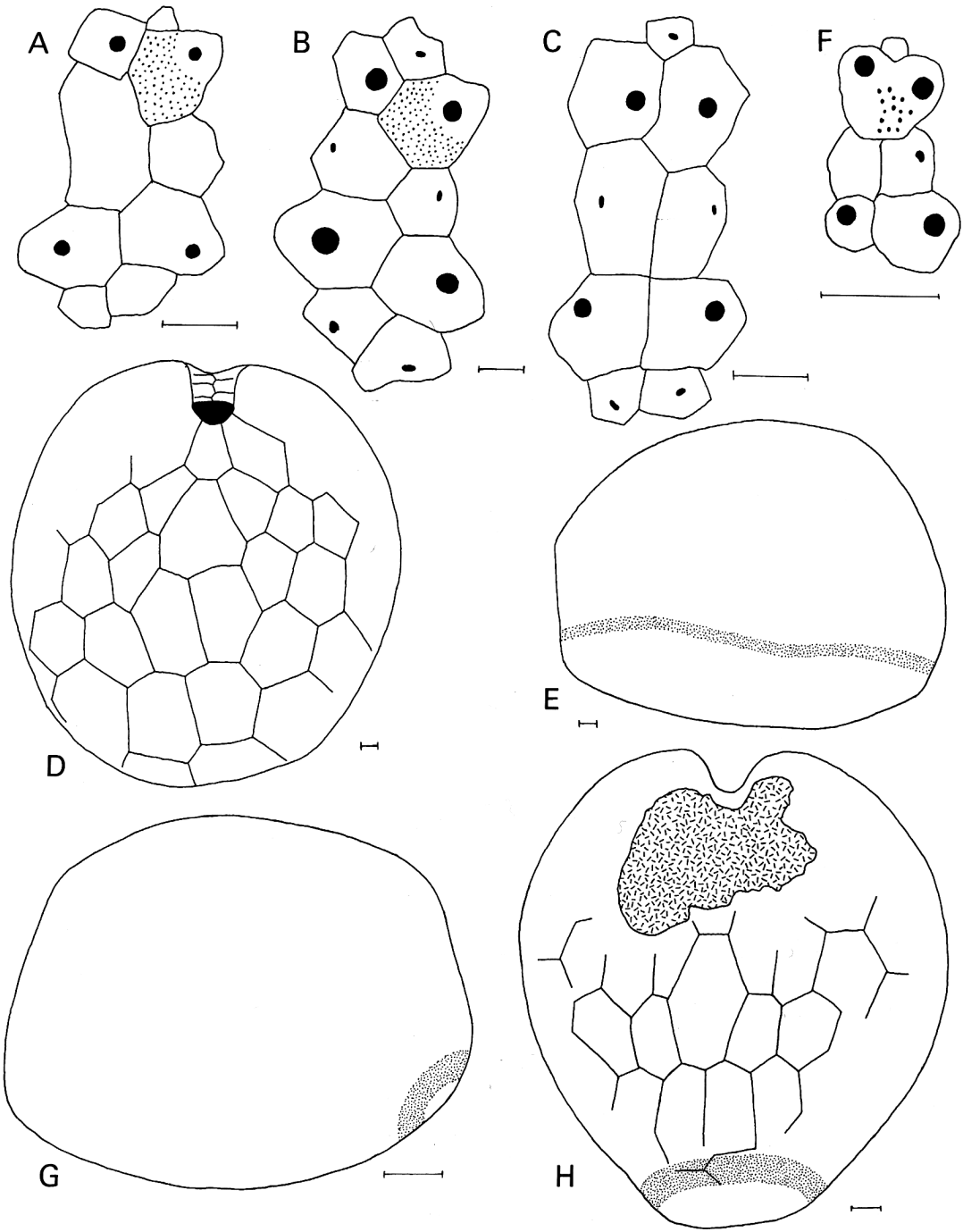
The apical system is situated at the highest point on the test, 32 per cent. of test length from the anterior margin. It is of elongate structure with ocular plates II and IV separating the anterior and posterior genital plates. It is difficult to ascertain the position of the posterior ocular plates in many of the specimens. However,

EXPLANATION OF PLATE 9

Figs 1–6. *Echinocorys scutata* Leske, 1778; Upper Maastrichtian, 12–14 m below Cretaceous–Tertiary boundary, Kyzylsai, Mangyshlak, Kazakhstan. 1–3, BMNH EE5615; 1, apical view; 2, oral view; 3, lateral view. 4, BMNH EE5578; apical view. 5–6, BMNH EE5616; 5, lateral view; 6, oral view. All ×1.

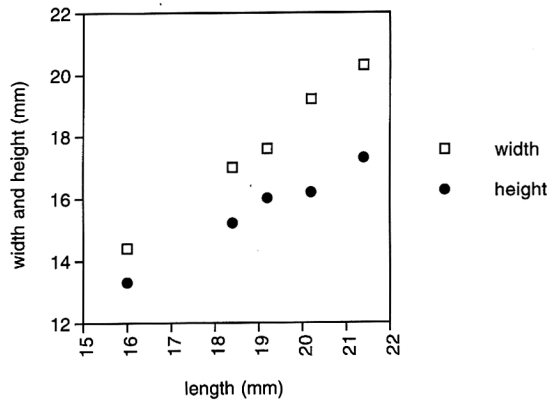


JEFFERY, *Echinocorys*



TEXT-FIG. 14. *Camera lucida* drawings of *Echinocorys scutata* Leske, 1778, *Echinocorys obliqua* Ravn, 1927, *Pseudoffaster caucasicus* (Dru, 1884) and *Galeaster bertrandi* Seunes, 1889. A, *Echinocorys scutata*; BMNH EE5579; apical disc plating. B, *Echinocorys obliqua*; BMNH EE5609; apical disc plating. C–E, *Pseudoffaster caucasicus*; BMNH EE5573; C, apical disc plating; D, oral view showing plastron plating; E, lateral view

TEXT-FIG. 15. Biometric data for *Galeaster bertrandi* Seunes, 1889.



where visible, they appear to be disjunct, and not in contact with the posterior genital plates (Text-fig. 14F). Genital plates 2 and 3 are fused and carry several hydropores in addition to the two gonopores. Gonopores are also present on the remaining two genital plates.

The peristome is circular to elongate oval in outline with its greatest diameter 11 per cent. of test length. It is flush with the test and is situated at the end of the deep frontal groove, visible from both the anterior and lower surfaces.

The periproct is situated high on the truncate posterior. It is of similar dimensions to the mouth (10–13 per cent. of test length) and is also circular in outline.

A broad and distinct subanal fasciole is present (Text-fig. 14G–H). It is oval in shape, crossing at the posterior of the sternal plates. It measures 12–15 miliaries across with no inclusions of larger tubercles.

Tuberculation is relatively sparse on the upper surface of the test. Small scattered tubercles are interspersed with fine granulation. Larger tubercles are present immediately adjacent to the apex and dense granulation extends along the centre of the frontal groove. On the lower surface, tuberculation is far denser and the individual tubercles are of greater dimensions. All are perforate, crenulate and not sunken. The largest tubercles are situated along the outer edges of the plastron where their areoles show a preferred enlargement towards the midline and posterior. The ambital area is intermediate in its size and density of tuberculation.

Remarks. G. bertrandi differs from *Galeaster carinatus* Ravn in the structure of the plastron. The plastron of *G. bertrandi*, as described above, is orthosternous in construction with the labral plate in broad contact with the following unpaired plate. *G. carinatus*, on the other hand, has a disjunct plastron, with the labrum and sternum separated by the adjoining ambulacra meeting at the midline. However, it has been postulated (David 1988, p. 336) that slight breaks between the labrum and sternum may represent intraspecific variation. In modern taxa, such variation in the degree of separation has been shown to occur with growth (David 1987). Specimens of *G. carinatus* tend to be larger and it could be that this pattern of increasing disjunction is a function of increased size and that the two 'species' form part of the growth series of a single species. Poslavskaya and Moskvin (1960) described an even larger species, *Galeaster dagestanensis*. Unfortunately, no details of plastron plating were given. If, with further study, it transpires that this species has a widely disjunct plastron, all nominal species may prove to form part of a single growth series.

The taxonomic confusion surrounding this genus is due in part to the absence of reliable plating information for the named species. Poslavskaya and Moskvin (1960) provided the same text-figures

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showing position of marginal fasciole. F–H, *Galeaster bertrandi*. F, BMNH EE5614; apical disc plating. G–H, BMHN EE5595; G, lateral view showing position of subanal fasciole; H, oral view showing plastron plating. A and G, scale bars represent 2 mm. B–F and H, scale bars represent 1 mm.

with their descriptions of both *G. minor* and *G. sumbaricus*. In this paper, *G. bertrandi* Seunes, *G. minor* Poslavskaya, *G. sumbaricus* Poslavskaya and *G. dagestanensis* Poslavskaya (tentatively) are synonymized as they are distinguished only by subtleties of test shape with no discernible structural differences.

Genus PSEUDOFFASTER Lambert, 1927

Type species. *Holaster caucasicus* Dru, 1884, by original designation.

Pseudoffaster caucasicus (Dru, 1884)

Plate 8, figures 4–7; Text-figure 14C–E

1884 *Offaster caucasicus* Dru, p. 514, pl. 26, figs 5–10.
1927 *Pseudoffaster caucasicus* (Dru); Lambert 1927, p. 42.
1938 *Pseudoffaster caucasicus* (Dru); Schmidt, p. 78, pl. 25, figs 6–9; pl. 26, figs 6–7.
1938 *Pseudoffaster renngarteni* Schmidt, p. 80, pl. 25, figs 1–5; pl. 26, figs 1–3.
1959 *Pseudoffaster caucasicus* (Dru); Poslavskaya and Moskvin, p. 270, pl. 7, fig. 2.
1959 *Pseudoffaster renngarteni* Schmidt; Poslavskaya and Moskvin, p. 271, pl. 17, fig. 3.
1959 *Pseudoffaster schmidti* Poslavskaya and Moskvin, p. 270, pl. 17, fig. 1.
1979 *Pseudoffaster* cf. *caucasicus* (Dru); Gongadze, p. 104, pl. 24, fig. 2.
1979 *Pseudoffaster renngarteni* Schmidt; Gongadze, p. 105, pl. 24, fig. 3.

Material. Three specimens: BMNH EE5572–EE5574.

Occurrence. Uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan: 14–16 m below the Cretaceous–Tertiary boundary. Elsewhere, *P. caucasicus* is known from the Maastrichtian of Spain and *P. schmidti* and *P. renngarteni* from the Lower to Upper Maastrichtian of the former USSR. *P. caucasicus* and *P. schmidti* are also recorded from Campanian strata of the former USSR.

Description. The test is oval in horizontal outline with a shallow frontal notch and slight posterior truncation. The specimens are 18·9 to 23·3 mm long, with the greatest width, 92–96 per cent. of test length, centrally. The frontal notch is deepest at the ambitus and is traceable all the way to the peristome. The test is somewhat gibbous in profile with a highly inflated upper surface and convex lower surface and with an approximately vertically truncated posterior. The greatest height is 78–82 per cent. of test length, 38 per cent. of test length from the anterior margin. The ambitus is positioned at 27–32 per cent. of test length above the base.

The frontal ambulacrum is sunken. Paired pores are minute, no more than 0·1 mm in diameter, and are positioned obliquely and towards the adoral centre of the plates. The paired ambulacra are flush with the test. The pores are small, round and again positioned towards the adoral centre of the plates. They are hardly oblique. All ambulacra are non-petaloid, straight and taper a little towards the apex.

Ambulacra and interambulacra are of approximately the same width at the ambitus (39 per cent. of test length). The plates are also of roughly the same size with each interambulacral plate adjacent to a single ambulacral plate. The plastron is orthosternous in structure (Text-fig. 14D).

The apical system is positioned at the highest point on the test. It is of typical holasteroid structure – elongate with the anterior oculars meeting at the midline and with four gonopores (Text-fig. 14C).

The peristome is anterior facing, visible from the anterior and lower surfaces and positioned 6–7 per cent. of test length from the anterior margin. It is small and circular, with no labral projection.

The periproct is situated high on the truncate posterior, 49–53 per cent. of test height from the base, under a slight projection. It is circular and of similar dimensions to the peristome.

A distinct narrow marginal fasciole, six to eight miliaries wide, runs below the periproct and is discernible around the complete test margin (Text-fig. 14E). It contains no inclusions of larger tubercles.

Tuberculation on the apical surface is extremely sparse and inconspicuous, although there are tubercles present near the apex, around the ambitus and low down on the interambulacra adjoining the frontal groove. Dense granulation covers the remainder of the upper surface. On the oral surface larger tubercles are present along the edges of the plastron with areoles enlarged latero-posteriorly. Further large tubercles are situated in the remaining interambulacra. Dense granulation fills the spaces between the tubercles. All tubercles are perforate, crenulate and not sunken.

Remarks. *P. caucasicus* (Dru) and *P. schmidti* Moskvin are both recorded previously only from the Campanian of the former Soviet Union, whilst *P. renngarteni* Schmidt has been collected exclusively from Maastrichtian strata. However, all three have been distinguished merely on subtleties of shape and size and form a gradational series. There appear to be no structural differences on which to distinguish them and consequently they are synonymized in this paper.

Order SPATANGOIDA Claus, 1876
Family MICRASTERIDAE Lambert, 1920

Genus CYCLASTER Cotteau, *in* Leymerie and Cotteau, 1856
[= *Brissopneustes* Cotteau, 1887 (type species *Brissopneustes vilanovae* Cotteau, by original designation); *Isopneustes* Seunes, 1888 (*non Isopneustes* Pomel, 1883)]

Type species. *Cyclaster declivus* Cotteau, *in* Leymerie and Cotteau, 1856, by original designation.

Remarks. Despite being placed in separate families (*Cyclaster* in Brissidae and *Brissopneustes* in Micrasteridae), *Cyclaster* and *Brissopneustes* differ in their original definitions only in the presence or absence of a peripetalous fasciole. However, several of the species studied have either a partial peripetalous fasciole, which is distinct posteriorly and completely absent anteriorly, or an indistinct peripetalous fasciole most obvious at the ends of the petals and elsewhere made up of miliary tubercles crowded together to varying degrees. There is a complete gradation between those forms with a fully developed peripetalous fasciole and those without. The presence of a peripetalous fasciole is therefore not a reliable diagnostic feature and consequently, *Cyclaster* and *Brissopneustes* are synonymized.

The presence of subanal and peripetalous fascioles has been used as a diagnostic character for Brissidae. As the presence of a peripetalous fasciole has been demonstrated to be impersistent this character is no longer sufficient by itself for familial differentiation. Other differences between Micrasteridae and Brissidae include an ethmophract apical system and mesamphisternous plastron structure in micrasterids compared with an ethmolytic arrangement and an ultramphisternous plastron in the brissids. Since plastron plating is consistently mesamphisternous and the apical system always ethmophract within the *Cyclaster* species studied, *Cyclaster* is here assigned to the Micrasteridae.

The genus *Isopneustes* Pomel (type species *Cyclaster bourgeosi* Cotteau) has four gonopores and a petaloid unpaired ambulacrum. However, Seunes (1888) assigned three-gonopored Cretaceous spatangoids to *Isopneustes*, claiming that the name *Cyclaster* was only applicable to post-Cretaceous species. *Isopneustes* Seunes is thus synonymized with *Cyclaster*.

Cyclaster integer (Seunes, 1888)

Plate 10, figures 1–4; Text-figures 16, 17A–C

1888 *Isopneustes integer* Seunes, p. 798, pl. 28, fig. 1.
1888 *Isopneustes munieri* Seunes, p. 798, pl. 28, fig. 4.
1897 *Brissopneustes danicus* Schlüter, p. 18, pl. 1, figs 1–4.
1926 *Brissopneustes danicus* Schlüter; Ødum, p. 163.
?1926 *Cyclaster brünnichi* Ravn; Ødum, p. 163.
1927 *Brissopneustes danicus* Schlüter; Ravn, p. 349, pl. 4, figs 5–6.
1927 *Cyclaster brünnichi* Ravn, p. 345, pl. 5, fig. 5.
?1933 *Brissopneustes decaryi* Lambert, p. 19, pl. 3, figs 9–10.
1940 *Cyclaster pygmeus* Rouchadze, pp. 129, 155, 176, pl. 3, fig. 7.
1959 *Cyclaster integer* (Seunes); Poslavskaya and Moskvin, p. 291, pl. 26, figs 4–5; text-fig. 107.
1959 *Cyclaster danicus* (Schlüter); Poslavskaya and Moskvin, p. 291, pl. 26, fig. 6; text-fig. 108.
1960 *Cyclaster danicus* (Schlüter); Poslavskaya and Moskvin, p. 70, pl. 5, fig. 6; text-fig. 21.
1960 *Cyclaster integer* (Seunes); Poslavskaya and Moskvin, p. 69, pl. 5, figs 4–5; text-fig. 20.

1979 *Cyclaster danicus* (Schlüter); Gongadze, p. 131, pl. 33, figs 1–2.
1979 *Cyclaster bruennichi* Ravn; Asgaard, tables 1–2.
1979 *Cyclaster danicus* (Schlüter); Asgaard, tables 1–2.
?1979 *Brissopneustes decaryi* Lambert; Tanaka, p. 44, pl. 3, fig. 8.

Material. Thirteen specimens: BMNH EE5581–EE5587, EE5597–EE5599, EE5602–EE5604.

Occurrence. Danian strata (0·37–0·8 m above the Cretaceous–Tertiary boundary) at Koshak, Mangyshlak, Kazakhstan. Elsewhere, this species is recorded from the Maastrichtian of Azerbeijan, the Maastrichtian and Danian of the Pyrenees, the Georgian Republic, the northern Caucasus and the Transcaspian region as well as from the Danian of Denmark and Madagascar.

Description. The test is coffin-shaped with the widest point anteriorly. It is 20·4–28·8 mm long and 16·1–24·3 mm wide (79–89 per cent. of test length; Text-fig. 16). The broad, shallow frontal groove is deepest adapically and shallows to become flush by the ambitus. The anterior margin is smoothly rounded. The upper surface of the test is more strongly vaulted than the lower surface and has a weak keel running posteriorly from the apex to the periproct. The test is 12·2–18·8 mm high (60–70 per cent. of test length).

The unpaired ambulacrum is non-petaloid and lies in a shallow flat-based furrow. Its pores are round, very small and oblique, with those of each pair lying very close together in a hollow separated by a granule. The distance between pore-pairs becomes greater away from the apex and the pore zones diverge strongly. Further from the apex, the pores are situated very low on each plate. The paired ambulacra are petaloid and very slightly sunken. Anterior petals diverge at 110–115° and contain 10–14 pore-pairs. Posterior petals diverge at an angle of 50–60° and comprise 14–18 pore-pairs. Anterior and posterior petals are approximately equal in length. In both pairs of petals, pores are round in the anterior series and a little elongated in the posterior series. Pores are present in ambulacral plates beyond the distal ends of the petals. The interporiferous zone is broader than each poriferous zone.

The plastron is mesaphisternous with a long, narrow labrum (Text-fig. 17B).

The apical system is positioned centrally. It is ethmophract with three gonopores, the madreporite being imperforate but carrying numerous hydropores (Text-fig. 17C).

The peristome is small and transversely oval to kidney-shaped with a thickened rim. It is weakly labiate and lies anteriorly, 25 per cent. of test length from the anterior margin.

The small circular periproct is positioned very high on the truncate posterior.

A distinct subanal fasciole is present. It is six to seven miliaries across and has a simple oval shape in smaller specimens. In larger specimens there is a marked bend under the periproct. A more-or-less distinct peripetalous fasciole is visible in the larger specimens indenting distinctly between the anterior and posterior paired ambulacra (Text-fig. 17A). It is also six to seven miliaries wide although it contains inclusions of large tubercles. This fasciole is lost forward of the anterior paired petals.

The upper surface of the test is covered in dense and quite coarse granulation with sparse, small tubercles interspersed. Tuberculation is denser and coarser on the oral surface especially around the anterior margin of the test and on the edges of the plastron where areoles show a preferred direction of enlargement.

Remarks. Cyclaster vilanovae (Cotteau) is similar in overall appearance, but tapers a little more towards the posterior in horizontal outline. It appears to be slightly more inflated, although the ranges of height as a percentage of test length do overlap between the two species (68–77 per cent. in *C. vilanovae* and 60–70 per cent. in *C. integer*). *C. vilanovae* has a less labiate mouth and paired

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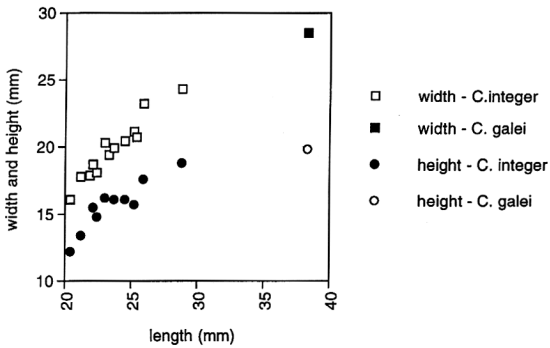
EXPLANATION OF PLATE 10

Figs 1–4. *Cyclaster integer* (Seunes, 1888); BMNH EE5585; Danian, 0·6–0·8 m above Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 5, apical view; 6, oral view; 7, lateral view; 8, posterior view. All ×2.

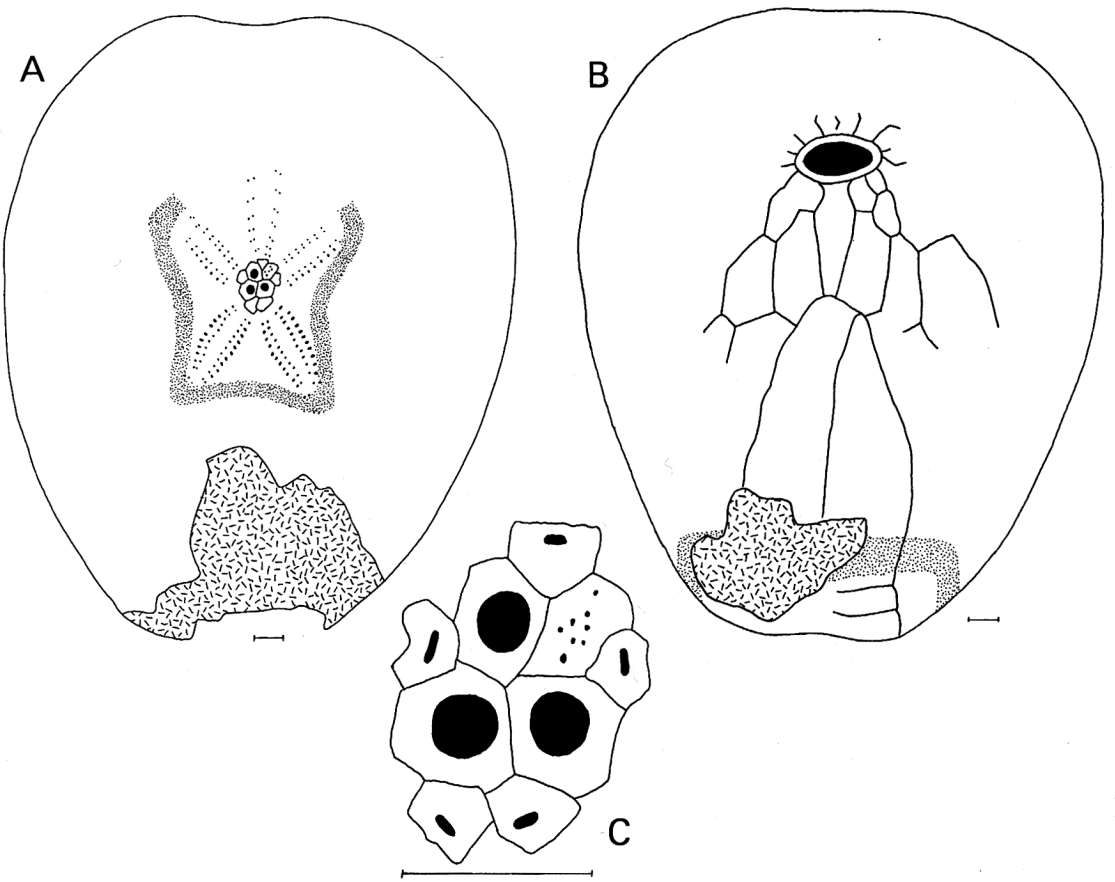
Figs 5–8. *Cyclaster galei* sp. nov.; BMNH EE5575, holotype; uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view; 4, posterior view. All ×2.



JEFFERY, *Cyclaster*

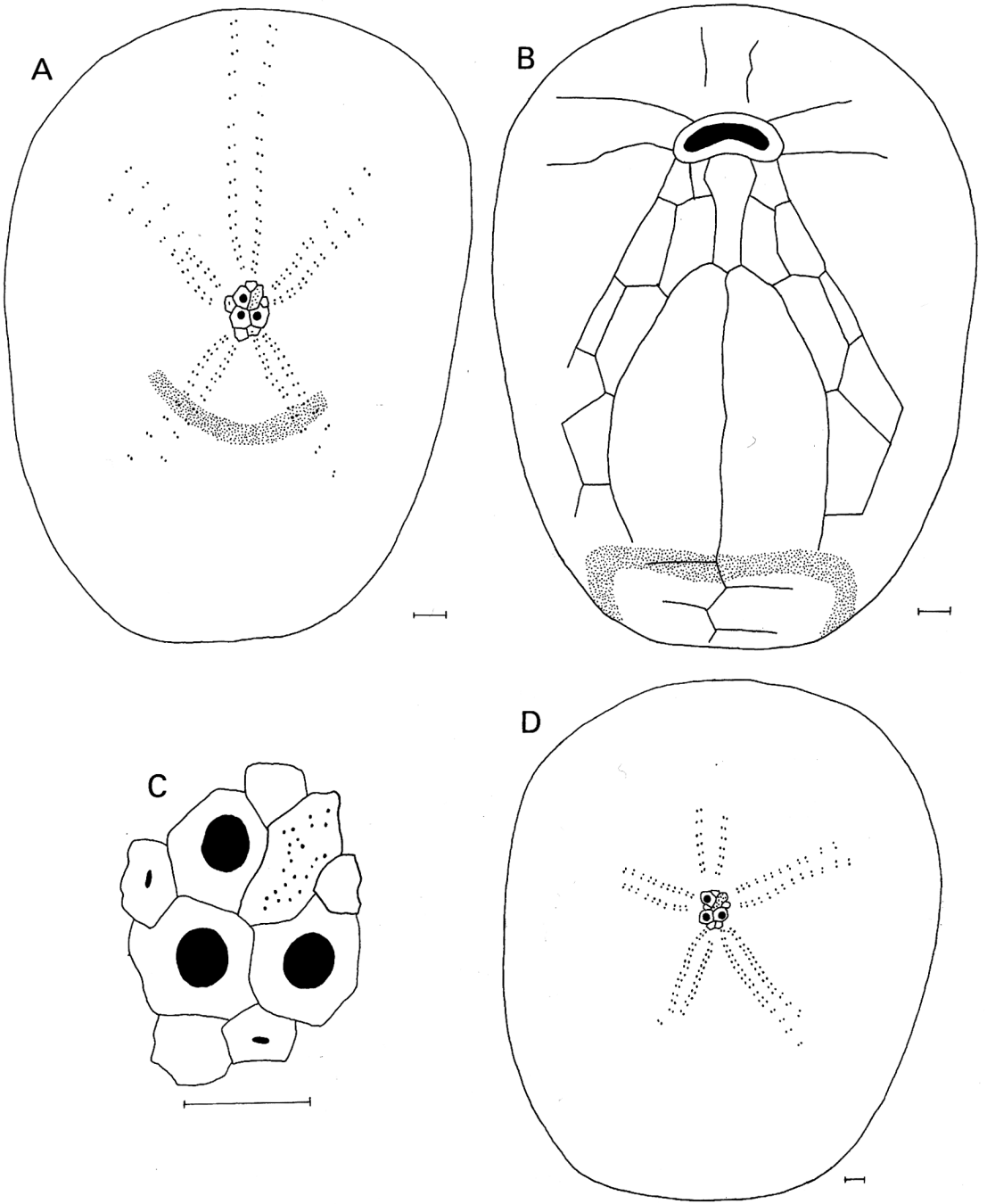


TEXT-FIG. 16. Biometric data for *Cyclaster integer* (Seunes, 1888) and *Cyclaster galei* sp. nov.



TEXT-FIG. 17. *Camera lucida* drawings of *Cyclaster integer* (Seunes, 1888). A–B, BMNH EE5585; A, apical view showing position and extent of peripetalous fasciole; B, apical disc plating. C, BMNH EE5581; oral view showing plastron plating. Scale bars represent 1 mm.

ambulacra that differ from those of *C. integer*. The petals are broader with more elongate pores and a narrower interporiferous zone. Additionally, *C. vilanovae* shows only an indistinct and incomplete peripetalous fasciole which is clearest posteriorly.



TEXT-FIG. 18. *Camera lucida* drawings of *Cyclaster galei* sp. nov. and *Cyclaster suecicus* (Schlüter). A–C, *Cyclaster galei*; BMNH EE5575, holotype; A, apical view showing position and extent of peripetalous fasciole; B, oral view showing plastron plating; C, apical disc plating. D, *Cyclaster suecicus*; Geological Museum, Copenhagen specimen number 2455; lower Danian of Denmark; apical view. A–B, scale bars represent 2 mm. C–D, scale bars represent 1 mm.

Cyclaster galei sp. nov.

Plate 10, figures 5–8; Text-figures 16, 18A–C

Material. Three specimens: holotype, BMNH EE5575, and paratypes, BMNH EE5576 and EE5626.

Occurrence. Two specimens, including the holotype, were collected from the uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan, 14–16 m below the Cretaceous–Tertiary boundary. The third specimen was collected from the Maastrichtian (165 m below the Cretaceous–Tertiary boundary) at Kyzylsai, Mangyshlak, Kazakhstan.

Description. The most complete test is 38·3 mm long, with a rounded rectangular shape in horizontal outline. Its greatest width is 28·5 mm (74 per cent. of length) at 9 mm from the smoothly rounded anterior margin, and it tapers a little posteriorly. The greatest height is 19·8 mm (52 per cent. of test length) at the posterior margin. The ambitus is at approximately mid-height. In profile, the test has a truncate posterior and the broad, flattened upper surface of the test has a slight downward slope towards the smoothly convex anterior. The base is slightly convex at the margins.

All five ambulacra are sunken adapically and taper towards the apical system. The anterior ambulacrum is non-petaloid. It runs along a shallow groove adapically which shallows and broadens, becoming flush by the ambitus. Pores are paired throughout but only about 12 sets in the upper 8 mm of the ambulacrum are enlarged. The paired ambulacra are petaloid and open distally. The anterior pair are straight with a very slight forward sweep and are 6·1 mm (EE5575) to 8·3 mm long and 1·2–1·4 mm wide. They diverge at 90°. There are ten pore-pairs in each anterior petal. The posterior paired ambulacra are straight and are 5·3 mm (EE5575) to 7·3 mm long (87–88 per cent. length of anterior petals) and 1·4–1·7 mm wide. They diverge at 60°. There are nine pore-pairs in each petal. Paired pores are apparent beyond the end of the petals although they are much smaller and more widely spaced.

The interambulacral areas are slightly elevated, forming ridges between the petals. All five interambulacra reach the peristome. The plastron is mesamphisternous (Text-fig. 18B) and is 16·8 mm long (44 per cent. of test length). The labrum is elongate measuring approximately 20 per cent. of test length and projects prominently over the peristome.

The apical system is slightly sunken below the surrounding interambulacral areas and lies 17·8 mm (47 per cent. of test length) from the anterior margin. It is approximately twice as long as broad, with the madreporite in contact with the other three genital plates. Oculars I and V abut at the posterior. The apical system is ethmophract and has three large gonopores: the madreporite lacks a genital pore but has hydropores densely distributed over its surface (Text-fig. 18C).

The peristome is positioned anteriorly at 20 per cent. of test length from the anterior margin and is visible in anterior view. It is kidney-shaped with the long axis running transversely and is 4·8–5·6 mm wide and 2 mm long. It has a distinct thickened rim and a labrum that extends prominently over the peristome. The ambulacra are slightly sunken adjacent to the peristome.

The periproct is approximately circular, 3·6 mm high by 3·2 mm wide. It is positioned high on the truncate posterior end of the test.

A broad subanal fasciole is present running below the periproct and composed of 12–14 rows of closely packed miliary tubercles. Within the fasciole is a pair of densely tuberculated areas and three enlarged pore-pairs are present at each lateral edge. Only a short portion of a peripetalous fasciole is visible running just beyond the ends of the posterior petals (Text-fig. 18A). This is an original feature as the tuberculation is well preserved over the whole surface of the test.

Tubercles on the aboral surface are so minute that the test looks superficially tubercle-free. However, the adapical interambulacra are slightly more coarsely tuberculated than the remainder of the upper surface and larger and more closely packed tubercles also run along the borders of the anterior ambulacrum. On the oral surface, the plastron has large, fairly densely packed tubercles with posteriorly enlarged areoles although these do not extend onto the labrum. The periplastronal zones are also tubercle-free but are granular in appearance. All tubercles are perforate and crenulate and slightly sunken.

Remarks. Cyclaster galei has a characteristic oblong outline seen only in two other species: *Cyclaster ruegensis* (Kutscher) and *Cyclaster suecicus* (Schlüter).

Cyclaster ruegensis, from the Lower Maastrichtian of the Isle of Rügen, also has a low test of rectangular horizontal outline and short, virtually flush petals. However, it is much broader than

C. galei with its widest dimension 91–95 per cent. of test length compared with 74 per cent. in *C. galei*. It also has more divergent anterior petals (110° compared with 90° in *C. galei*). All known specimens of *C. ruegensis* are somewhat crushed and damaged with details of the oral surface unclear. *C. ruegensis* has no trace of a peripetalous fasciole.

Cyclaster suecicus (Schlüter), from the Danian of Denmark, is also rectangular in horizontal outline and has paired petals of approximately equal lengths that are open distally. However, the test of *C. suecicus* is broader and more inflated, with a test width of 85–91 per cent. of test length compared with 74 per cent. in *C. galei*. The paired ambulacra are less depressed and the anterior pair are far more divergent in *C. suecicus* (130° compared with 90° in *C. galei*) (Text-fig. 18D). The mouth is also smaller, less labiate and situated in a more posterior position, 24–25 per cent. of test length from the anterior margin. No peripetalous fasciole, however faint or incomplete, is found in *C. suesicus*.

Cyclaster integer (Seunes) is the only other spatangoid found in the Mangyshlak sections. The two species are never found in association, however, as *C. integer* is found exclusively in the Danian and *C. galei* only in the Maastrichtian. The new species differs from *C. integer* in its larger size, more rectangular outline and broader, flatter apical and oral surfaces. The paired ambulacra appear to be open distally in *C. galei* sp. nov. and are also far less divergent than those of *C. integer*. They diverge at an angle of 90° in *C. galei* compared with 110–115° in *C. integer*. The peristome in *C. integer* has a far narrower rim, is less distinctly labiate and is more posteriorly placed at 25 per cent. of test length from the anterior margin. In addition, the labral plate of *C. integer* is far narrower than that of *C. galei* (the labrum is 2·3 times longer than wide in *C. galei* compared with 2·9 times in *C. integer*). A further difference is the presence of a near complete peripetalous fasciole in *C. integer*.

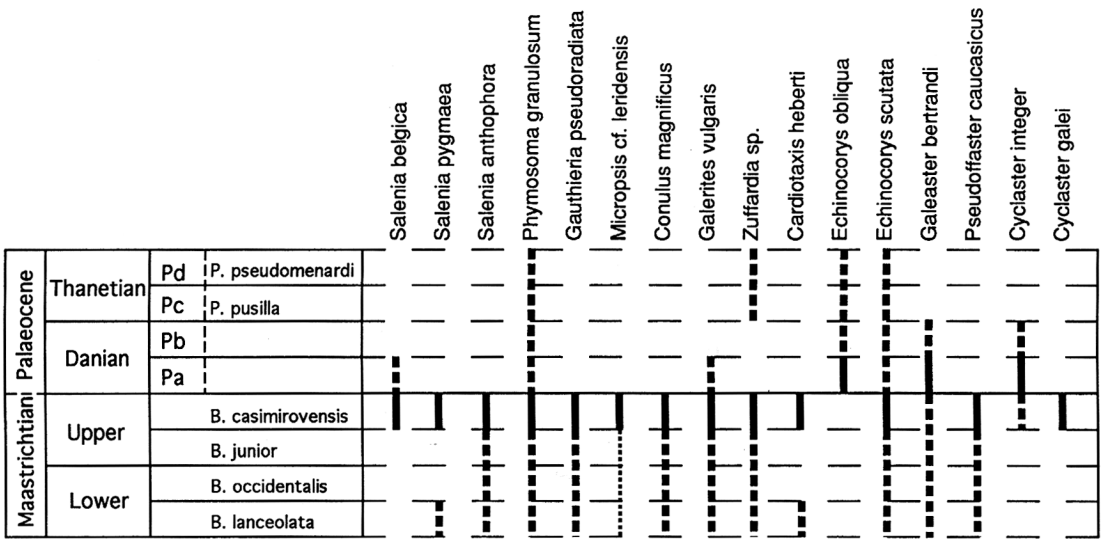
DISCUSSION

All of the taxa described in this paper are stratigraphically confined to either the uppermost Maastrichtian or the lowermost Paleocene in the Mangyshlak sections. Only two genera (*Cyclaster* and *Echinocorys*) appear to pass through the boundary. However, inspection of occurrence data from other localities world-wide shows that many of these species are in fact longer ranging than the Mangyshlak occurrences would suggest (Text-fig. 19).

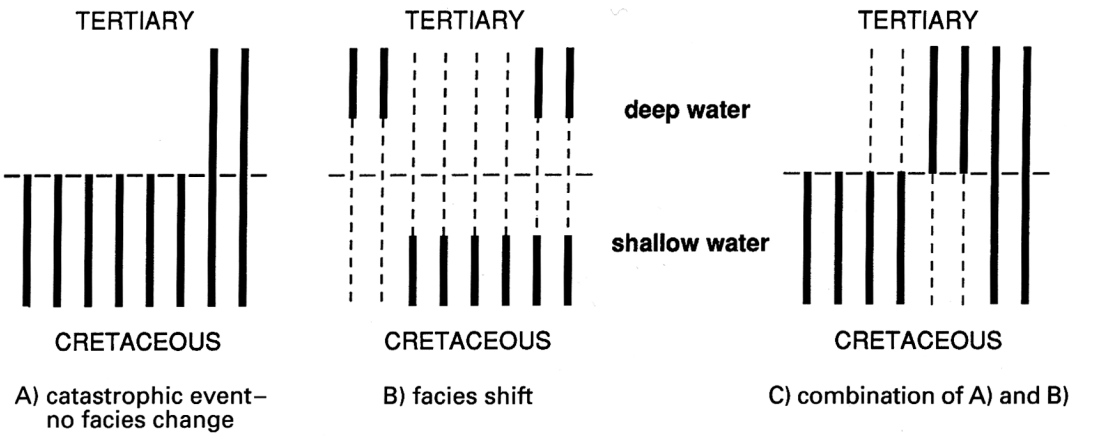
Of the 16 species described, only *Cyclaster galei* sp. nov. is endemic and, if occurrences outside Kazakhstan are taken into account, six of the 15 species present in the Maastrichtian (40 per cent.) survive into the Danian. Thus, the species extinction rate for this fauna at the Cretaceous–Tertiary boundary drops from 100 per cent. to 60 per cent. Although this is lower than some previous estimates for the reduction in marine biodiversity at the species level (eg. 70–80 per cent. extinction estimated by Jablonski and Raup 1995), it is still significant. It should also be noted that the figure of 60 per cent. species extinction is based on actual species occurrence data and not interpolated from rarefaction curves, as in many previous studies (e.g. McKinney 1995). One problem with species data, however, is that species tend to demonstrate a higher level of endemicity than genera, so that generic data may prove more informative.

Of the 11 genera present below the boundary in Mangyshlak, two are also present in the Danian (82 per cent. extinction) but, if world-wide data is considered, this figure drops to 25 per cent. (three out of 12). Again, this is significantly lower than the 50 per cent. generic reduction estimated by Jablonski and Raup (1995) for the Cretaceous–Tertiary turnover. A thorough phylogenetic analysis of these taxa may lead to an even further reduction in the number of apparent extinctions by allowing inferences to be made about the survival of clades. For example, *Conulus* became extinct at the end of the Maastrichtian but has the Paleocene genus *Neoglobator* as a sister group.

The same pattern of local extinction and replacement is repeated in other Cretaceous–Tertiary sections outside of Kazakhstan. Once again, if occurrences away from the studied area are considered, extinction rates are significantly reduced. In Denmark a 56 per cent. extinction across the Cretaceous–Tertiary boundary at the genus level (nine out of 16) is reduced to 25 per cent. (four



TEXT-FIG. 19. Range chart of echinoid species in the Maastrichtian and Paleocene of Mangyshlak, Kazakhstan (solid lines) and world-wide (thick dashed lines). (Thin dashed line denotes presence of species in the stage below.) Pa = nannoplankton zones NP1–2; Pb = nannoplankton zones NP3–4; Pc = planktic foraminifera zone P3; Pd = planktic foraminifera zones P4–P6 (Haq *et al.* 1987).



TEXT-FIG. 20. Possible scenarios for the Cretaceous–Tertiary boundary. Solid lines represent occurrences in the studied section; dashed lines represent occurrences elsewhere.

out of 16) if occurrences of taxa outside Denmark are considered, and in the Maastricht area, a loss of 68 per cent. of Maastrichtian genera (19 out of 28) drops to 39 per cent. (11 out of 28).

Can the patterns of taxonomic disappearance at Mangyshlak be explained by sampling alone? Text-figure 19 shows that diversity in the Mangyshlak sections is far greater in the Maastrichtian than in the Danian. This can be explained partially by the fact that two distinct facies types have been sampled in the Maastrichtian (chalk at Koshak and Kyzyslai and calcarenite at Sulukapy) compared with just one (chalk) in the Danian. But even if the three taxa found exclusively in the calcarenites of Sulukapy are eliminated, the diversity difference is still maintained (ten species in the

Maastrichtian and three in the Danian). This is not merely a function of more specimens being collected from the Maastrichtian. In fact, the numbers of Maastrichtian and Danian specimens are about equal with 33 specimens collected from Maastrichtian chalk and 35 specimens from the Danian.

The higher diversity fauna of the Maastrichtian chalk contains a sizeable proportion of regular echinoids which suggests relatively shallow water conditions. The Danian fauna, on the other hand, contains exclusively deep-water irregular forms. It therefore appears that an environmental shift in water depth with little lithological expression has occurred.

If the taxonomic turnover at the end of the Cretaceous had been brought about by some catastrophic event with no associated facies change, the Danian fauna would represent just a surviving percentage of the taxa present in the Maastrichtian (Text-fig. 20A; Hansen 1988). If however, a facies change alone had occurred over this time period, the pattern of survivorship would be very different (Text-fig. 20B). For example, if the Maastrichtian represented deposition in shallower water than the Danian, only species with large depth ranges would be present both below and above the boundary in the studied section. Shallow water forms would migrate or survive elsewhere whilst depth-tolerant species would migrate in from other localities in the Danian. Looking at global occurrence data, there would be no true extinctions. The sections at Mangyshlak appear to represent an intermediate situation (Text-fig. 20C) with a proportion of the taxa becoming extinct, others emigrating from the studied section and others still migrating in.

The study of the echinoid fauna in sections from the Mangyshlak Peninsula clearly demonstrates the problems of sampling and facies change encountered in the study of continuous boundary sections, however complete. Despite these difficulties, similar work needs to be done on other key sections of differing depositional setting and palaeolatitude to discover whether the patterns observed in Kazakhstan are repeated elsewhere. The study of these key sections and the determination of patterns of survivorship selectivity, both in these sections and from phylogenetic studies, will enable us to shed further light on the causes of the biological crisis at the end of the Cretaceous.

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