

Carrying on regardless: the echinoid genus *Cyclaster* at the Cretaceous–Tertiary boundary

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A taxonomic revision and subsequent cladistic analysis show that Maastrichtian and Palaeocene species of the genus *Cyclaster* are split into three clades. Members of all three are present before and after the Cretaceous–Tertiary boundary, demonstrating that the genus *Cyclaster* as a whole was unaffected by the crisis at the end of the Cretaceous. Unlike most spatangoids, *Cyclaster* has the characteristic crystallographic signature of a lecithotrophic larval stage. Further work on other groups will determine whether larval strategy affected survivorship at this time. □ *Echinoids, Cretaceous–Tertiary boundary, survivorship selectivity, phylogeny.*

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Despite the large amount of research time that has been invested in documenting and attempting to explain the biological turnover across the Cretaceous–Tertiary boundary, relatively little is known in detail about how the marine benthic macrofauna was affected. Simple taxon counts of echinoid species in the Maastrichtian and Palaeocene reveal that some groups did rather better than others over this time period, but is it possible to determine the biological or ecological traits that increase a taxon's chance of survival? Possible correlates fall into two broad categories: where they live (latitude, geographic range, water depth, sedimentary environment) and how they live (feeding strategy, larval strategy, life position in sediment).

To date, the detailed study of survivorship selectivity has concentrated on molluscan faunas. The most comprehensive studies, investigating a wide range of geographical and biological extinction patterns among molluscs at the K–T boundary, are those by Raup & Jablonski (1993), Jablonski & Raup (1995) and McClure & Bohonak (1995). As yet, there is little consensus about survival selectivity patterns recognized at the Cretaceous–Tertiary boundary.

For example, it has been suggested that taxa with a planktotrophic mode of larval development fared badly over the K–T boundary (Kennedy 1989, 1993; Gallagher 1991), associated with a collapse in primary productivity. In contrast, Jablonski (1986) recorded similar levels of

extinction in gastropods across the K–T boundary regardless of developmental strategy. Research into other groups of marine benthic macrofauna is necessary if patterns of selectivity are to be clarified.

This paper forms part of a project with the overall aim of investigating the patterns of survivorship selectivity across the Cretaceous–Tertiary boundary in holasteroid and spatangoid echinoids.

Taxonomic revision

Taxonomic disappearances due to artefacts of nomenclature (i.e. the naming of species solely on the basis of their occurrence in a particular stratigraphic level or geographic location) lead to pseudoextinctions and the inflation of extinction estimates. In order to avoid the problems of inconsistent taxonomic usage encountered in the literature, a thorough taxonomic revision is a prerequisite for all studies of biological turnover. Spatangoid echinoids with a characteristic three-gonopored apical disc and a subanal fasciole were included in this revision. In the existing literature, the nineteen nominal species were divided among three genera: *Cyclaster*, *Brissopneustes* and *Isopneustes* (see Table 1).

Despite being placed in separate families (*Cyclaster* in the Brissidae and *Brissopneustes* in the Micrasteridae), *Cyclaster* and *Brissopneustes* differ in their original defini-

Table 1. Species included in the taxonomic revision with details of locality and age.

Before revision	After revision	Age and locality
<i>Brissopneustes vilanovae</i> Cotteau, 1886	<i>Cyclaster vilanovae</i> (Cotteau, 1886)	Danian of Alicante (Spain) and Turkey.
<i>Isopneustes heberti</i> Nicklès, 1892	<i>Cyclaster heberti</i> (Nicklès, 1892)	Maastrichtian of Alicante (Spain).
<i>Isopneustes integer</i> Seunes, 1888	<i>Cyclaster integer</i> (Seunes, 1888)	Maastrichtian to Danian of French Pyrenees. Maastrichtian of Azerbaijan. Upper Maastrichtian to Lower Danian of northern Caucasus and Transcaspian region. Lower Danian of Georgia and Kazakhstan. Danian of Madagascar and Denmark.
<i>Isopneustes munieri</i> Seunes, 1888		
<i>Brissopneustes danicus</i> Schlüter, 1897		
<i>Cyclaster bruennichi</i> Ravn, 1927		
<i>Brissopneustes decaryi</i> Lambert, 1933		
<i>Cyclaster pygmeus</i> Rouchadze, 1940		
<i>Isopneustes aturicus</i> Seunes, 1888	<i>Cyclaster aturicus</i> (Seunes, 1888)	Danian of French and Spanish Pyrenees. Mid to Upper Danian of northern Caucasus and Transcaspian region. Lower to Upper Danian of Georgia.
<i>Brissopneustes schwetzkovi</i> Poslavskaya & Moskvina, 1960		
<i>Isopneustes gindrei</i> Seunes, 1888	<i>Cyclaster gindrei</i> (Seunes, 1888)	Danian of French Pyrenees. Lower Maastrichtian of Santander and Tremp (Spain). Upper Maastrichtian of Bidart (France). Mid Danian of northern Caucasus and Transcaspian region. Maastrichtian to Danian of Georgia.
<i>Cyclaster pyriformis</i> Cotteau, 1863 [<i>nomen nudum</i>]		
<i>Brissopneustes suecicus</i> Schlüter, 1897	<i>Cyclaster suecicus</i> (Schlüter, 1897)	Danian of Denmark and Sweden.
<i>Cyclaster pfenderae</i> Lambert, 1936	<i>Cyclaster pfenderae</i> Lambert, 1936	Lower Maastrichtian to Danian of Madagascar.
<i>Cyclaster platornatus</i> Kutscher, 1978	<i>Cyclaster platornatus</i> Kutscher, 1978	Lower Maastrichtian of Isle of Rügen and Maastricht area.
<i>Cyclaster galei</i> Jeffery, 1997a	<i>Cyclaster galei</i> Jeffery, 1997a	Uppermost Maastrichtian of Kazakhstan.
<i>Brissopneustes ruegensis</i> Kutscher, 1978	<i>Cyclaster ruegensis</i> (Kutscher, 1978)	Lower Maastrichtian of Isle of Rügen.
<i>Cyclaster beduinus</i> de Stefani, 1913	hemiasterid	Mid to Upper Maastrichtian of Libya.
<i>Cyclaster berberus</i> de Stefani, 1913	hemiasterid	Mid to Upper Maastrichtian of Libya.

tions 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 the Brissidae. As the presence of a peripetalous fasciole has been demonstrated to be an impersistent character, this practice is no longer sufficient by itself for family placement. Other differences between the Micrasteridae and Brissidae include an ethmophract apical system and mesamphisternous plastron structure in the micrasterids compared to 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, with the 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 appli-

cable to post-Cretaceous species. *Isopneustes* Seunes is thus synonymized with *Cyclaster*.

The revised taxonomy of the genus *Cyclaster* is summarized as follows:

Order. – Spatangoida Claus, 1876

Family. – Micrasteridae Lambert, 1920

Genus. – *Cyclaster* Cotteau, in Cotteau & Leymerie, 1856

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

Synonyms. – *Brissopneustes* Cotteau, 1886 [type species *Brissopneustes vilanovae* Cotteau, 1886, by original designation]; *Isopneustes* Seunes, 1888 (*non Isopneustes* Pomel, 1883).

Phylogenetic analysis

The occurrence of numerous non-monophyletic taxa in the literature indicates that traditional taxonomic practice, resting on the idiosyncrasies of the individual taxonomist, does not always reflect genuine biological groupings and processes. For example, the last appearance of a non-monophyletic taxon in the fossil record may correspond to a true biological extinction. Equally, it may just reflect a change in nomenclature, or pseudoextinction, and obscure lineage continuity. Thorough phylogenetic analysis may lead to a reduction in the number of appar-

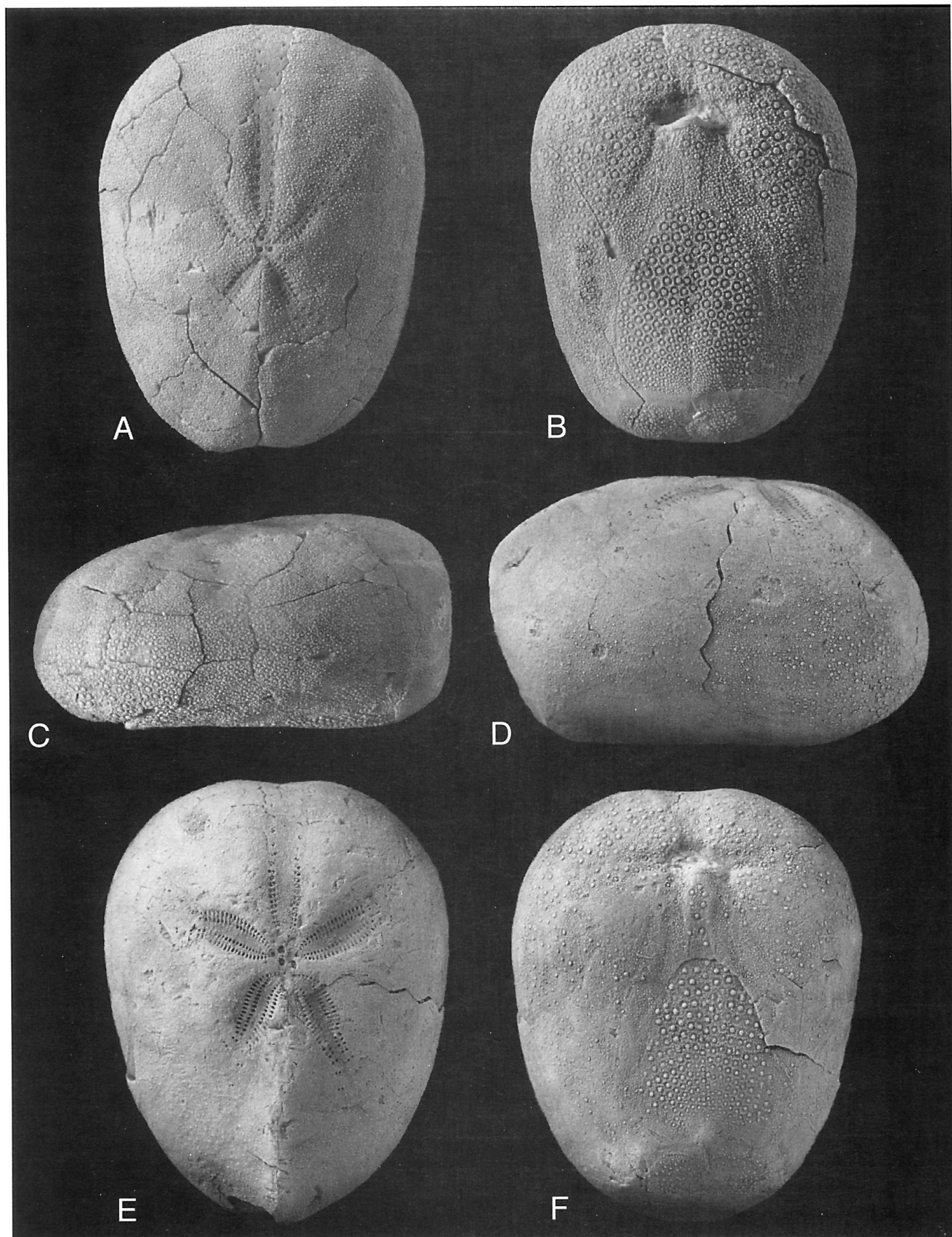


Fig. 2. □A–C. *Cyclaster galei* Jeffery; The Natural History Museum, London BMNH EE5575 holotype; Uppermost Maastrichtian of Kazakhstan. □D–F. *Cyclaster aturicus* (Seunes); BMNH EE6068; Danian of Navarra, Spain. All $\times 2$.

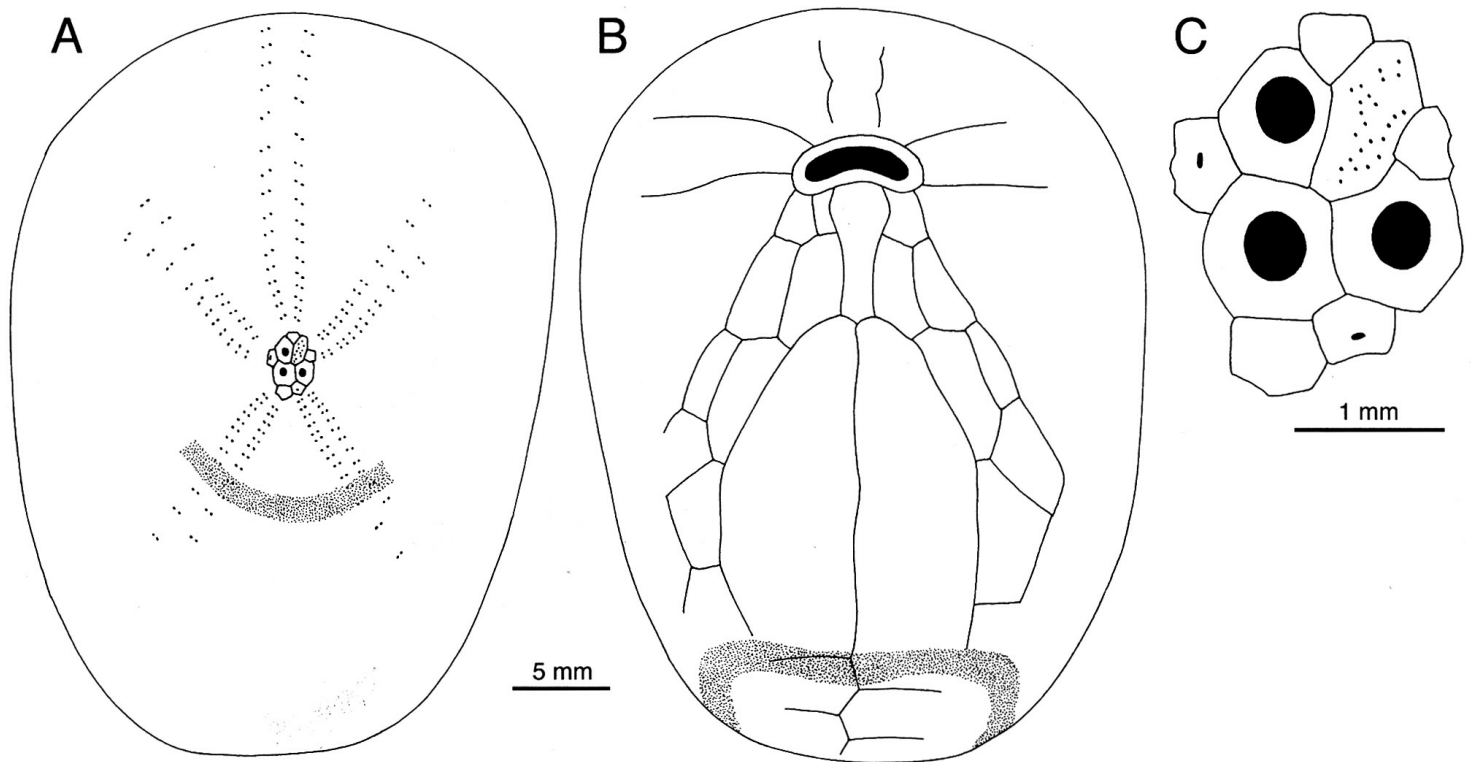


Fig. 3. Camera lucida drawings of *Cyclaster galei* Jeffery; BMNH EE5575 holotype; Uppermost Maastrichtian of Kazakhstan. □A. Apical view showing position and extent of peripetalous fasciole. □B. Oral view showing plastron plating. □C. Apical disc plating.

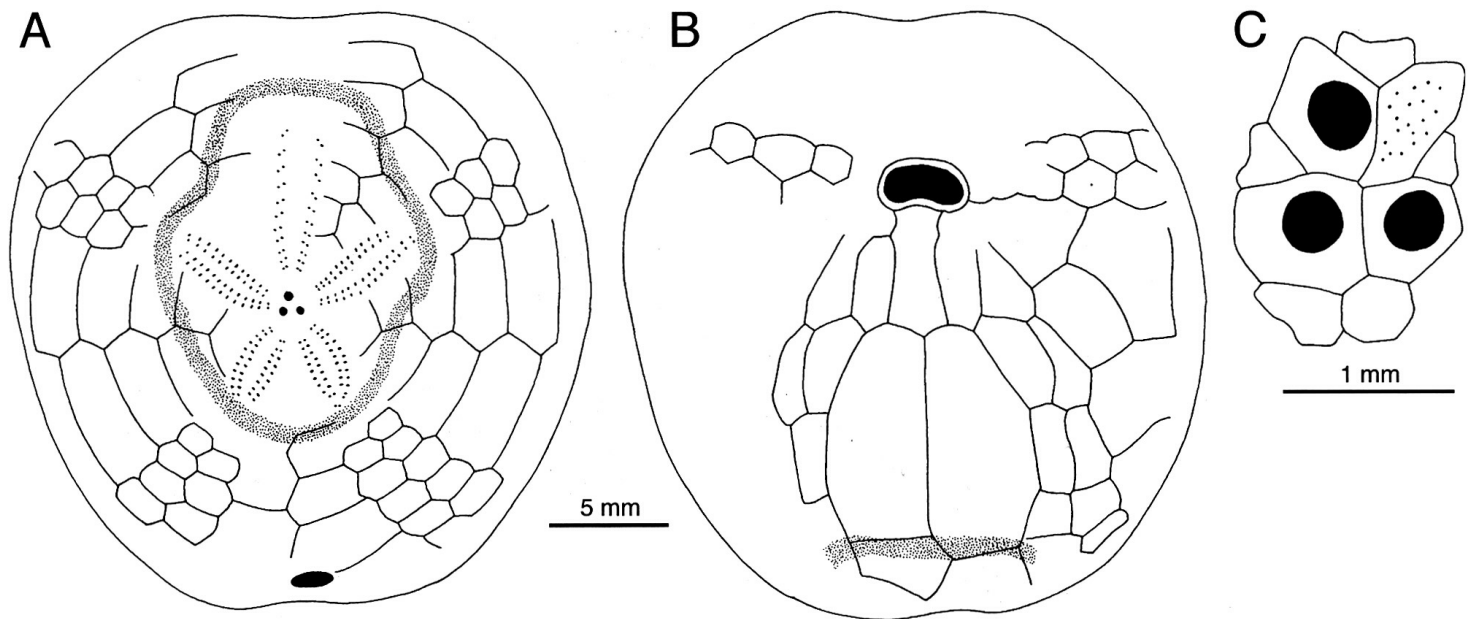


Fig. 4. Camera lucida drawings of *Cyclaster pfenderae* Lambert; Muséum National d'Histoire Naturelle, Paris (Lambert Collection) (no specimen number); Lower Maastrichtian of Madagascar. □A. Apical view showing extent of peripetalous fasciole. □B. Oral surface showing plastron plating. □C. Apical disc plating.

retained by the parent throughout development to the juvenile stage.

Almost nothing is known about the evolutionary history of developmental patterns in marine invertebrates, yet it is widely accepted that reproductive strategy is closely linked with a number of biogeographic and macroevolutionary correlates such as geographic range, spe-

cies longevity and survival at mass extinction events (Jackson 1974; Shuto 1974; Scheltema 1977; Hansen 1978, 1980, 1982, 1983; Jablonski 1986; Erwin 1990; Gili & Martinell 1994; Emlet 1995). Non-planktotrophs are thought to be less susceptible during mass extinctions because they are not dependent on phytoplankton for their nutrition, and therefore a crash in oceanic produc-

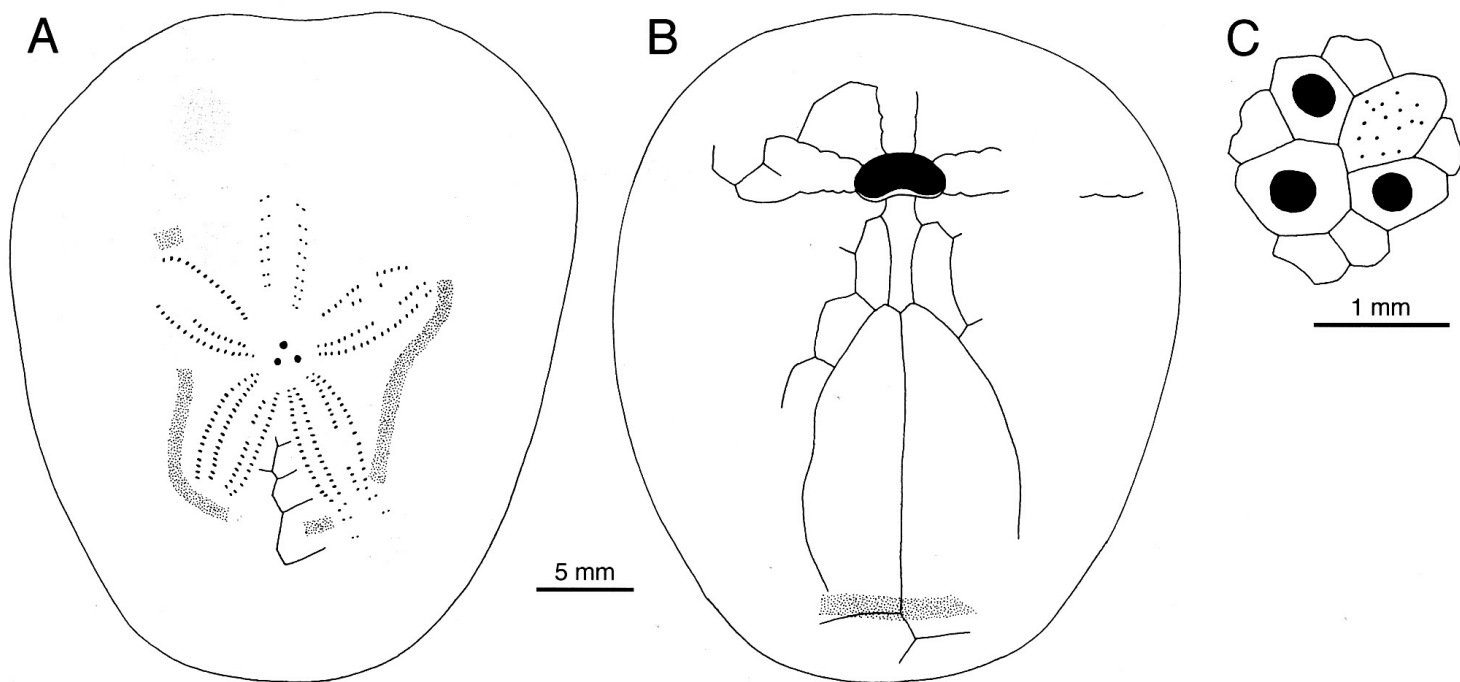


Fig. 5. Camera lucida drawings of *Cyclaster heberti* Nicklès; Museu de Geologia, Barcelona (no specimen number); Maastrichtian of Alicante, Spain. □A. Apical view showing extent of peripetalous fasciole. □B. Oral surface showing plastron plating. □C. Apical disc plating.

tivity would have little effect on them. In fact, larval strategy has been proposed as the explanation for the survival of the nautiloids (with a lecithotrophic larval stage) and the demise of the ammonites (with a planktotrophic larval stage) at the end of the Cretaceous (Landman 1984; Kennedy 1989, 1993; Gallagher 1991; Sheehan *et al.* 1996), the persistence of trilobites with a benthic larval stage during the Late Ordovician (Chatterton & Speyer 1989), and the decimation of bivalves and brachiopods at the end-Permian mass extinction (Erwin 1990). However, no correlation between survivorship and larval type has been found for taxa during the Late Devonian (McGhee 1996) or for gastropod molluscs at the K–T boundary (Jablonski 1986; Valentine & Jablonski 1986).

Methods of inferring non-planktotrophy in echinoids

Echinoids are unusual among marine invertebrates in that developmental mode (planktotrophy vs. non-planktotrophy) can be deduced simply and unambiguously from the adult skeleton. Three methods of inference are known, applicable to both Recent and fossil taxa. Brooded development may be recognized by the presence of depressed areas, or marsupia, on the adult test where offspring are sheltered during development (Kier 1967, 1969; McNamara 1994). Extreme sexual dimorphism in gonopore size (Kier 1967, 1968, 1969; Emlet 1989) can also be used to infer non-planktotrophy in sea urchins,

since in some taxa the female has bigger gonopores to accommodate the large yolky eggs produced. The third method hinges on the fact that the mode of larval development determines the orientations of crystallographic axes in the adult apical disc (Emlet 1985, 1988, 1989). In species with planktotrophic, feeding larvae, four of the genital plates form from elements of the larval skeleton and retain the crystallographic orientation of the calcite rod that was present in the larva. In two of these plates (G3 and G5), the *c*-axis is almost tangential to the plate surface. The remaining three plates have a different crystallographic signature, more or less perpendicular to the plate surface. In irregular echinoids, where there is no fifth genital plate, the crystallographic orientation of genital plate 3 is critical in inferring larval strategy. For lecithotrophic, non-feeding larvae where all the adult skeletal plates are formed *de novo*, all genital plates show a similar, perpendicular crystallographic orientation.

Lecithotrophy in *Cyclaster*

It has been demonstrated that non-planktotrophy in echinoids is a geologically recent phenomenon with few pre-Tertiary examples (Jeffery 1997b). However, *Cyclaster* is one lineage where non-planktotrophic forms are known from the latest Cretaceous (Jeffery 1997b). The two species of *Cyclaster* (*C. integer* and *C. vilanovae*) for which *c*-axis orientations have been determined both show the crystallographic signature characteristic of a lecithotrophic larval stage (Fig. 6). All species of *Cyclaster* exam-

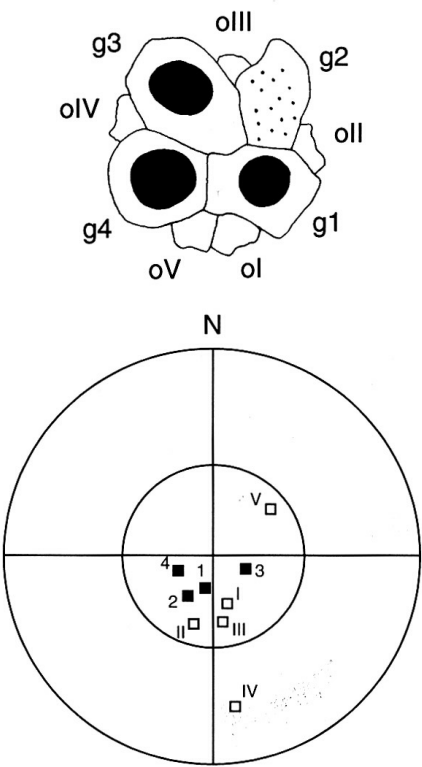


Fig. 6. Camera lucida drawing of the apical disc and stereographic projection of *c*-axes of genital and ocular plates in the apical system for *Cyclaster vilanovae* (Cotteau). Genital plate traces are shown as solid squares; ocular plate traces as open squares.

ined contain individuals with large gonopores taking up most of the genital plate area (see Figs. 3C, 4C, 5C). In addition, specimens of *Cyclaster integer* and *Cyclaster pfenderae* show sexual dimorphism in gonopore size, and similar dimorphism has also been reported for *Cyclaster platornatus* (Jagt & Michels 1990).

What happened to *Cyclaster* at the K–T boundary?

Representatives of all three clades of *Cyclaster* (rectangular, ovate and ‘coffin-shaped’) are present in both Maastrichtian and Palaeocene strata (Fig. 7). It appears that all three groups passed across the Cretaceous–Tertiary boundary; there was not just one survivor among the Maastrichtian species of *Cyclaster* that subsequently gave rise to new species in the early Tertiary. In fact, species diversity is approximately equal below and above the boundary (Fig. 7).

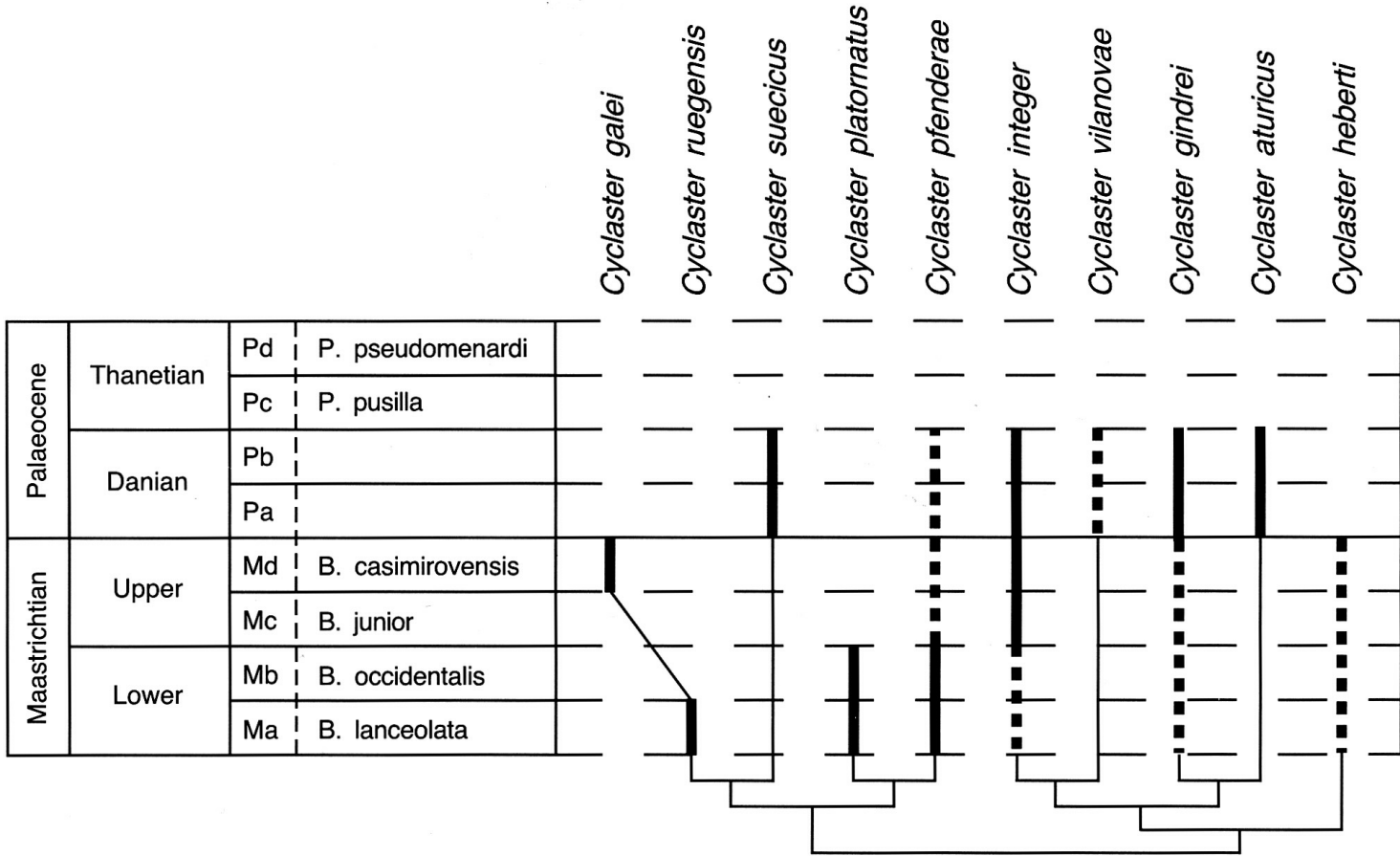


Fig. 7. Stratigraphic distribution of Maastrichtian and Palaeocene species of *Cyclaster* (thick lines) and inferred phylogenetic tree (thin lines) based on the cladogram presented above. Stratigraphically constrained occurrences are shown as solid lines; occurrences in stage (e.g., ‘Maastrichtian’) or substage (e.g., ‘Lower Maastrichtian’) are shown as thick dashed lines. Maastrichtian subdivisions are based on belemnite zones (Christensen 1990, 1996). Pa = nannoplankton zones NP1–2; Pb = nannoplankton zones NP3–4; Pc = planktic foraminifera zone P3; Pd = planktic foraminifera zones P4–6 (Haq et al. 1987).

Cyclaster, a genus with a lecithotrophic mode of larval development, survived the biological crisis at the end of the Cretaceous. Further work on other groups of atelostomate echinoids with differing life habits and geographic and environmental occurrences will determine whether larval strategy or some other correlate affected survivorship at this time.

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Appendix 1

Characters used in the phylogenetic analysis. Asterisks indicate ordered characters.

- 1 Width of test as percent of test length: 0=<75; 1=>75.
- 2 Shape in plan view: 0=rectangular; 1=tapered; 2=ovate.
- 3 Height of test as percent of test length: 0=<55; 1=>55.
- 4* Anterior margin: 0=convex; 1=flat to slightly notched; 2=distinctly notched.
- 5* Divergence of anterior paired petals: 0=<100°; 1=100–120°; 2=>120°.
- 6* % length to ambitus of anterior paired petals: 0=<40; 1=40–60; 2=>60.
- 7* % length to ambitus of posterior paired petals: 0=<35; 1=35–48; 2=>48.
- 8 Relative length of anterior to posterior petals: 0=<1.2; 1=>1.2.
- 9 Sunkeness of petals: 0=virtually flush; 1=noticeably depressed.
- 10 Pores in paired petals: 0=small and circular; 1=circular anteriorly and elongate posteriorly; 2=elongate.
- 11 Width of poriferous zone: 0=narrower; 1=equal; 2=broader than area between pore zones.
- 12 Posterior upper surface: 0=non-carinate; 1=carinate.
- 13 Relative length to width of labral plate: 0=<2.5; 1=>2.5.
- 14 Shape of labral plate: 0=not tapered posteriorly; 1=tapered posteriorly.
- 15 Extent of labral projection as percent of mouth length: 0=<33; 1=>33.
- 16 Peristome rim: 0=narrow; 1=prominent.
- 17 Width of mouth as percent of test width: 0=<16; 1=>16.
- 18 Position of mouth from anterior margin as percent of test length: 0=<20; 1=>20.
- 19 Mouth: 0=not invaginated; 1=invaginated.
- 20 Peripetalous fasciole: 0=absent; 1=incomplete; 2=complete.
- 21 Subanal fasciole: 0=absent; 1=present.
- 22 Tuberculation: 0=normal; 1=pustular.
- 23 Position of apical disc as percent of test length: 0=<40; 1=>40.
- 24 Number of gonopores: 0=4; 1=3.

Appendix 2

Character matrix for the ten species of *Cyclaster* plus *Isaster aquitanicus* and the outgroup *Micraster leskei* (indicated by an asterisk).

<i>*Micraster leskei</i>	1	1	1	1	1	1	1	1	2	0	1	0	0	0	0	1	0	0	1	0	1	0
<i>Cyclaster aturicus</i>	1	1	1	2	2	1	1	0	1	2	2	1	1	1	0	0	0	0	0	0	1	0
<i>Cyclaster galei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	
<i>Cyclaster gindreii</i>	1	1	1	2	2	1	0	1	0	2	2	1	1	0	0	0	0	0	?	1	0	
<i>Cyclaster heberti</i>	1	1	0	1	1	1	1	1	1	2	2	1	1	1	1	0	1	0	2	1	0	
<i>Cyclaster integer</i>	1	1	1	1	1	1	0	0	1		1	1	1	1	0	1	0	0	2	1	0	
<i>Cyclaster pfenderae</i>	1	2	1	0	1	1	1	1	1	2	2	0	0	0	0	1	0	1	0	2	1	
<i>Cyclaster platornatus</i>	1	2	0	0	0	0	0	1	1	2	2	0	0	0	0	1	1	1	0	2	1	
<i>Cyclaster ruegensis</i>	1	0	0	0	1	0	0	0	0		0	0	0	?	0	0	1	0	0	1	0	
<i>Cyclaster suecicus</i>	1	0	1	0	2	1	1	0	0		0	0	1	0	0	1	1	1	0		1	
<i>Cyclaster vilanovae</i>	1	1	1	1	1	1	0	1	2		2	1	1	1	0	0	1	0	0	1	1	
<i>Isaster aquitanicus</i>	1	2	1	0	2	2	2	0	0	2	2	0	0	1	0	0	1	0	0		1	