

The morphology, ontogeny, and inferred behaviour of the deep-sea echinoid *Calymne relictata* (Holasteroidea)

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The deep-sea holasteroid *Calymne relictata* was first described from a few fragments discovered by the HMS ‘Challenger’ in the Bermuda abyssal plain more than a century ago. In addition to re-examining the type material, we describe herein new specimens from unpublished material collected between 3720 and 4860 m during three scientific expeditions that took place on both sides of the North Atlantic between 1966 and 1991. The new material includes juvenile and adult specimens in sufficiently good preservational state to allow a full redescription, including all types of appendages, some of which have never been described. These new observations confirm the atypical characteristics of *C. relictata*, including test morphology and spines that have no equivalent in other extant taxa. We explore in detail characteristics of this species that were almost impossible to interpret previously. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 155, 630–648.

ADDITIONAL KEYWORDS: appendages – Calymnidae – functional morphology – spines – systematics.

INTRODUCTION

The deep-sea is the largest contiguous habitat on Earth, covering more than 60% of its surface. This habitat provides a variety of extreme environments and situations to analyse, as it is much more multifaceted than previously thought (Gage & Tyler, 1991). Many deep-sea forms have drastically modified their physiology, morphology, or behaviour to cope with high pressures (Seibert, 2002), darkness (Douglas, Partridge & Marshall, 1998), extreme temperatures (from cold bottoms to warm hydrothermal vents [Segonzac, De Saint Laurent & Casanova, 1993; Lee, 2003]), oxygen depletion (Levin, 2003), or scarcity of resources (Corbari, Sorbe & Massabuau, 2005). Bizarre fishes (Heezen & Hollister, 1971), cirrate octopuses (Roper & Brundage, 1972), swimming elapodid holothurians (Ohta, 1985), or the recently discovered armoured sea snail (Warén *et al.*, 2003) are emblematic of peculiar morphologies present in the

deep-sea. Such oddities are illustrative of adaptive strategies, including exaptations (Gould & Vrba, 1982). However, they may also suggest a release of selective competition among organisms (David, 1990), thereby allowing the expression of morphologies that may have been counter-selected in other environments.

Echinoids contribute significantly to this list of highly transformed animals. Among these are the Holasteroidea, an almost exclusively deep-sea order of irregular urchins. Bottle- and amphora-shaped pourtalesiids are probably the most unusual of all sea urchins (David, 1988; Saucède, Mooi & David, 2004). Not only do holasteroids exhibit strange morphologies but they have also developed some of the most extreme behaviours encountered in echinoids. Examples include the internally brooding *Antrechinus* (Mooi & David, 1993) and the symbiont-laden *Cystocrepis* (David *et al.*, 2003b).

Calymne relictata Thomson, 1877 was dredged from the Bermuda abyssal plain more than a century ago, during the HMS ‘Challenger’ cruise. The original material consisted only of a few fragments briefly

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described in the ‘Challenger’ reports (Thomson, 1877; Agassiz, 1881). These same fragments were recently redescribed by Smith (2004), providing an accurate but limited description of the test architecture. However, no precise depictions of the appendages (spines and pedicellariae) exist.

Previous treatments of *C. relictata* hinted at an atypical morphology departing even from that of other deep-sea holasteroids. However, this work was unable to say anything about *Calymne*’s mode of life (Lovén, 1883; Mortensen, 1907, 1950; Smith, 2004). During the ‘Atlantis’ cruise (1966), additional material was collected in the same geographic area in which the original material was found, as well as in other parts of the North Atlantic (Soviet cruises ranging from 1983 to 1991). This new material (Table 1) included juveniles and adults in sufficiently good preservational state to allow a full redescription of *C. relictata*, including all types of appendages. With the new material, we are able to add considerably to our understanding of divergent morphology of deep-sea echinoids. Therefore, we can explore in detail characteristics of this species that were almost impossible to interpret previously, and to propose an interpretation of its behaviour and habits.

MATERIAL AND METHODS

In addition to re-examining the type material, we studied six juvenile specimens and isolated fragments collected in 1966 from the Bermuda area during the ‘Atlantis’ cruise. These specimens were identified by R.H. Chesher, but never published. In addition, we had access to all the specimens collected by 0.25 m² grab during two Russian cruises in 1983 and 1991 on both sides of the North Atlantic (Fig. 1, Table 1).

Terminology of external appendages and test features is that of Mooi & David (1996). Spines, pedicellariae, and other external features were examined and drawn using the methods of Mooi & David (1996) and David & Mooi (2000).

SYSTEMATIC DESCRIPTION

Several very delicate specimens of *Calymne* were taken in an almost complete state during the Russian cruises. The excellent condition of this material is attributed to the fact that the 0.25 m² grab took specimens still enveloped in the cushioning ambient substrates.

FAMILY CALYMNIDAE MORTENSEN, 1907

In the most recent revision of holasteroid echinoids, Smith (2004) identified a clade, Calymnidae, comprising the Recent genera *Calymne* and *Sternopatagus* as

Table 1. Complete listing of all known specimens of *Calymne*. Except for the syntypes (NHM 81.11.22.46), all specimens were hitherto unpublished. *type material

Cruise	Station date	Sampling area	Depth	Sampling device	Institution catalogue number	Material [length]
HMS ‘Challenger’	Station 54 27.05.1873	‘north of the Bermudas’ (Mortensen, 1950)	4846 m	–	Natural History Museum, London NHM 81.11.22.46	*2 fragmented adult specimens [23 mm; 28 mm]
RV ‘Atlantis II’ cruise 24	Station 122 21.08.1966	North of Bermuda lat: 35°05.0’N–35°52.0’N long: 64°57.5’W–64°58.0’W	4833 m	Epibenthic trawl	Museum of Comparative Zoology, Harvard MCZ 8571	6 juvenile specimens [1.3–11.3 mm] 2 fragmented adult specimens [30 mm; 40–50 mm] 1 adult specimen [28 mm]
RV ‘Akademik Kurchatov’ cruise 37	Station 3787 25.07.1983	NW of Amper Seamount lat: 35°50.5’N long: 13°00.3’W	4860 m	Grab [layer: 0–50 mm]	Shirshov Institute of Oceanology, Moscow	1 juvenile specimen [13.8 mm]
RV ‘Akademik Mstislav Keldysh’ cruise 23	Station 2462 03.07.1991	Newfoundland Basin lat: 41°45.08’N long: 49°55.85’W	3720 m	Grab [layer: 0–50 mm]	Shirshov Institute of Oceanology, Moscow	1 juvenile specimen [13.8 mm]

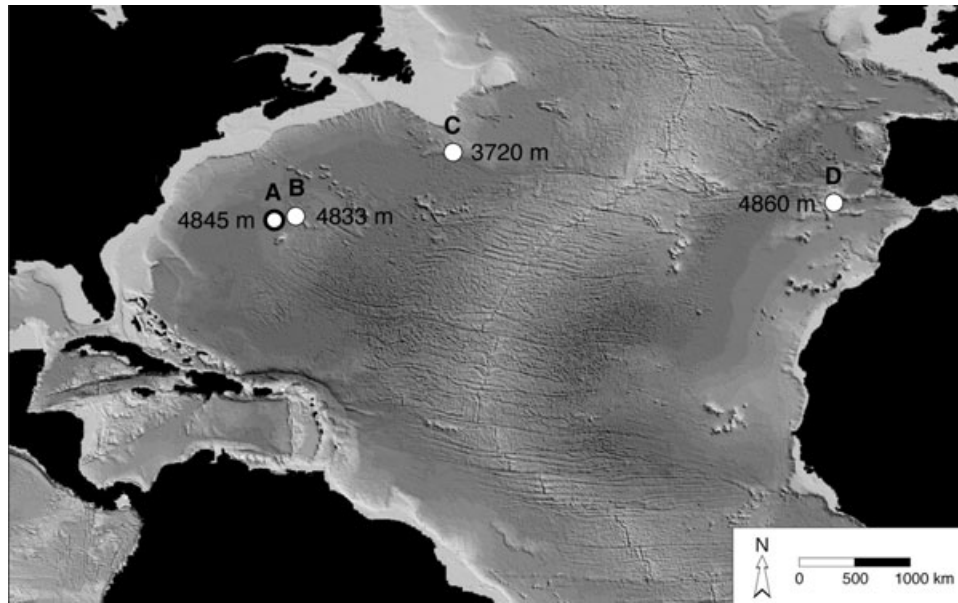


Figure 1. Map of northern Atlantic Ocean showing localities and depths from which *Calymne relicta* has been collected. A, type locality of specimen in Natural History Museum, London. B, R/V 'Atlantis II' cruise 24, station 122. C, R/V 'Akademik Mstislav Keldysh', cruise 23, station 2462. D, R/V 'Akademik Kurchatov', cruise 37, station 3787.

well as the fossil genera *Pseudoffaster*, *Sanchezaster*, and *Chelonechinus*. Some of the relationships among those taxa were already supported by the phylogenies proposed by David (1988). However, these placements were based on gross morphology and plate architecture, and did not take into account appendages that can be of the utmost importance (Mortensen, 1907). Moreover, some features of *Calymne* lead us to question the phylogeny proposed by Smith (2004) and the composition of the family Calymnidae. The genera referred by Smith (2004) to the family Calymnidae differ very significantly from each other in numerous characters. Examples of heterogeneous expressions of character states within the family include, but are not restricted to: peristome flush with the test or at the end of a deep groove; marginal fasciole well developed or absent; apical system disjunct or not; ambulacra with single or paired pores; test thin or thick; plastron continuous or disjunct. That these extremes in such basic characters can exist in a single clade is, to say the least, somewhat perplexing. Therefore, for the moment we will follow Clark (1917, 1925), Mortensen (1907, 1950) and Wagner & Durham (1966) in regarding *C. relicta* as the only species in the family Calymnidae, which is characterized by: (1) a meridosternous plastron; (2) amphiplacous anterior interambulacra (in interambulacra 2 and 3, the first plate is followed by a pair of plates); (3) a well-developed marginal fasciole; (4) a peristome flush with the test; (5) ambulacra with single pores; (6) highly specialized spines (as described below).

GENUS *CALYMNE* THOMSON, 1877

Diagnosis

Test of adults very high, ovoid in aboral view, and compressed laterally with low ambitus; anterior end rounded without frontal groove; posterior end almost vertically truncated. Large spoon-shaped spines present on plastronal area; frills of large paddle-shaped spines around periproct and aborally on the posterior end; subanal tuft of large pointed spines.

Other significant features are important in identification of the genus but are present in other holasteroids and therefore not diagnostic for *Calymne* alone. These are as follows. Orthosternous plastron with small labrum in contact with sternal plate; interambulacra 1 and 4 meridoplacous, interambulacra 2 and 3 amphiplacous in adults; anterior and posterior pairs of genital plates separated by pair of ocular plates; two gonopores on genital plates 2 and 3. Uniporous ambulacra. Peristome flush with test; periproct supramarginal, located at top of posterior face. Marginal orthofasciole crossing plates 5.a.4 and 5.b.5. Rostrate pedicellariae of three types; ophicephalous pedicellariae umbrella-shaped; triphyllous pedicellariae present; tridentate and globiferous pedicellariae absent.

Genotype and only known species: *Calymne relicta*.

CALYMNE RELICTA THOMSON, 1877

Calymne relicta – Thomson, 1877: 397, figs 102–103; Agassiz, 1881: 155–157, pls XXXIV, XXXIX 24–26,

XL 63–65, XLIII 24, XLIV 47, 48; Lovén, 1883: 90; Mortensen, 1907: 53–54, 86, text-fig. 7, pls X 5, 6, 30; Clark, 1917: 125; Clark, 1925: 188; Mortensen, 1950: 127–131; Mooi & David, 1996: figs 9p, 12k; Smith, 2004: 146–149, text-fig. 7.

Diagnosis

As for the genus.

RESULTS

GENERAL FEATURES AND PLATE ARCHITECTURE

Size

Juveniles collected during the R/V 'Atlantis' cruise (MCZ 8571) range between 1.3 and 11.3 mm in length. Test lengths of two adult specimens (30.0 mm and between 40.0 and 50.0 mm respectively) were estimated from fragments (MCZ 8571). The adult from the R/V 'Akademik Kurchatov' cruise was 28.0 mm long, 23.2 mm wide, and 25.0 mm high. The young specimen from the R/V 'Akademik Mstislav Keldysh' cruise was 13.8 mm long. As in most deep-sea holasteroids, the test is very thin and extremely fragile.

Colour

Either dry (after fixation or preservation) or wet (still in ethanol) the test is beige, tube feet are darker beige, primary spines are white, and miliary spines are translucent. However, the test and spines of the specimen collected by the 'Challenger' were described as being pale green (Agassiz, 1881; Clark, 1925).

Shape of the test

The test of adults is high, ovoid in aboral view, and compressed laterally, with a low ambitus (Fig. 2C, D). In contrast, the lateral view shown by Agassiz (1881: plate 34, test length (TL) of about 30 mm) is low, and therefore departs from that of our specimens. This can be accounted for by the fact that Agassiz's figure was compiled from fragments of different specimens and not likely to be an accurate reconstruction in all respects. A low profile is more typical of a juvenile specimen. Maximum width is approximately half-way along the anterior-posterior axis, but posterior to the peristome and the apical system (Fig. 2A, B). The anterior margin of the test is gently rounded and smoothly joins the domed aboral surface, which extends posteriorly in a broad, aboral ridge (Fig. 2E). Maximum height is about two-thirds of the length towards the posterior of the test, where the aboral surface forms a broad, barely distinguishable bulge. The posterior is vertically truncate except for a weakly developed rostrum below the ambitus. The oral surface is flat in the anterior region, but is

developed into a wide keel in the posterior part along the midline. The anterior, unpaired ambulacrum is slightly sunken adorally, with this trough shallowing near the anterior margin until it is flush with the rest of the test at the ambitus.

Apical system

In adult specimens the apical system is more or less elongate, but with considerable alteration of the typical holasteroid pattern [apical plates from left and right sides joining along the midline to form a biserial pattern, as described in Mooi & David (1996)]. In *Calymne*, the posterior genitals (1 and 4) and posterior oculars (I and V) are stretched along the midline of the apical surface. The posterior genitals can even be uniserially arranged (Fig. 3A). In the anterior part of the apical system, genital 3 may be separated from ocular IV by plates of interambulacrum 3. Such a pattern is reminiscent of that in *Plexechinus* and *Urechinus* (Mooi & David, 1996). In all the juvenile specimens examined (up to 11.3 mm long), apical plates are biserially arranged and organised according to the typical holasteroid pattern (Fig. 3B). Therefore, in *Calymne*, apical structures become progressively stretched and redistributed during ontogeny. The overall pattern and degree of stretching differ among specimens, and do not seem dependent on test size alone. The same phenomenon has been observed in several species of deep-sea holasteroids (Saucède *et al.*, 2004; Smith, 2004). Gonopores are present only on genital plates 2 and 3; posterior genitals lack pores. Genital plate 2 is the largest genital and is perforated by a few hydropores.

Peristome and periproct

The peristome is small, circular, slightly depressed, and tilted to face somewhat anteriorly. It is situated anteriorly, distant from the anterior edge by about 20% of the test length. The peristomial membrane contains numerous small platelets, with the mouth opening slightly displaced toward the posterior margin of the peristome (Fig. 4A). The periproct is longitudinally ovate, high on the posterior surface. The adoral margin of the periproct is bounded by interambulacral plates 5.a.7/5.b.8 and the aboral margin by plates 5.a.10/5.b.10 (Fig. 4B, D).

Ambulacra and interambulacra

Ambulacra are all similar and flush with the test, except for the aforementioned oral portion of ambulacrum III. Aborally, ambulacral plates are large and similar in size to the interambulacral plates (that is, there are no traces of petaloids) (Fig. 4C). Tube feet are mounted on minute unipores, situated near the centre of the ambulacral plates. Distal to the phyllopodia near the mouth, tube feet are rudimentary,

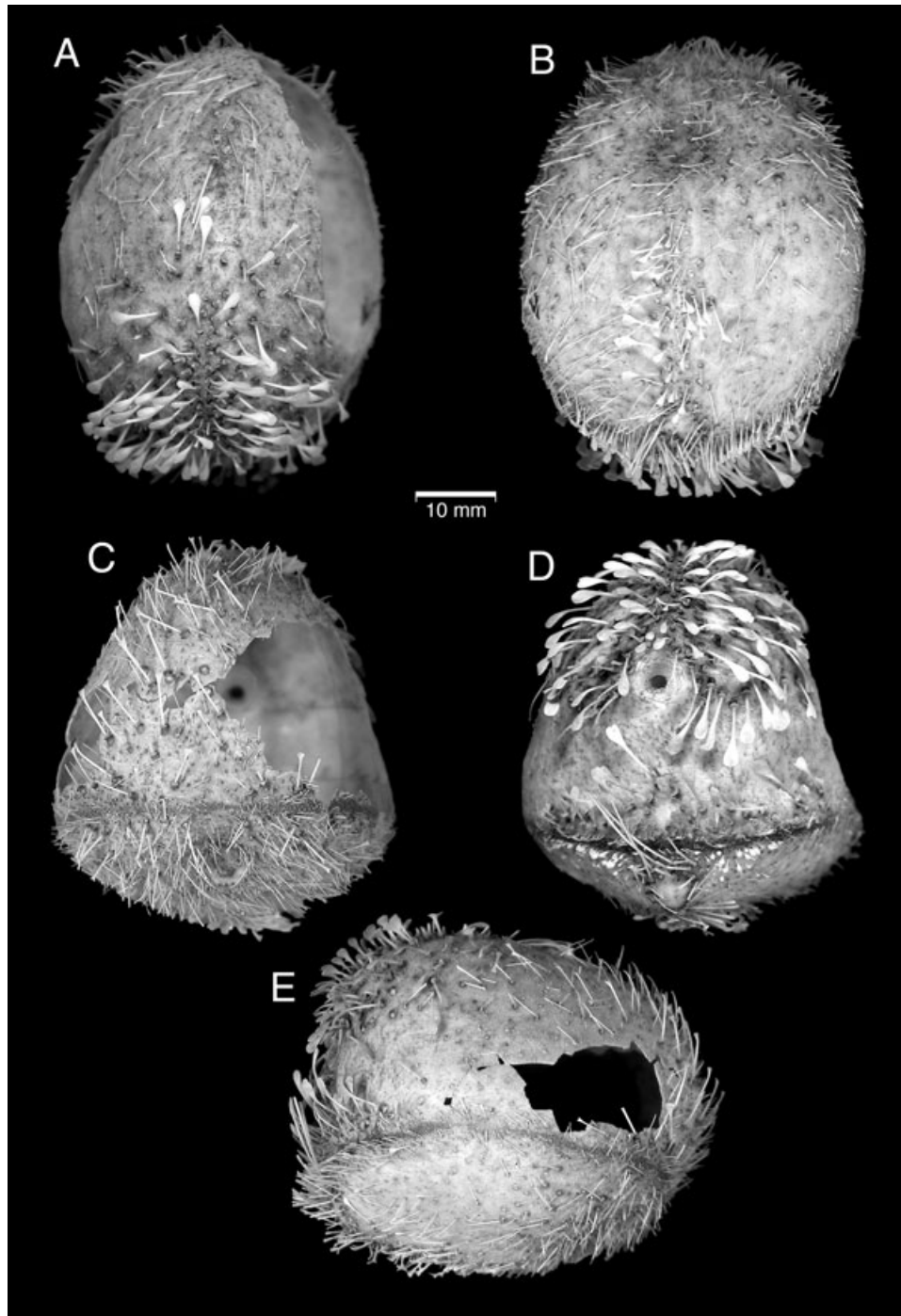


Figure 2. Specimen from R/V 'Akademik Kurchatov' cruise 37, station 3787. A, aboral surface. B, oral surface. C, anterior surface. D, posterior surface. E, right side.

appearing in preserved material as small, darkened knobs. Proximal to the peristome, the tube feet on the basicoronal ambulacral plates are developed into penicillate phyllopodia, each of which possesses about ten rudimentary digitations.

The plating in interambulacrum 5 is orthosternous (Fig. 4A). The labral plate (5.1) is followed by a single,

large sternal plate (5.b.2); both plates are always in contact. Laterally, the labrum contacts the first or second ambulacral plate, and the sternal plate reaches the second or third ambulacral plate. The sternal plate is followed by a pair of elongate, symmetrical episternal plates (5.a.2 and 5.b.3) then by a pair of elongate and non-alternating post-episternal

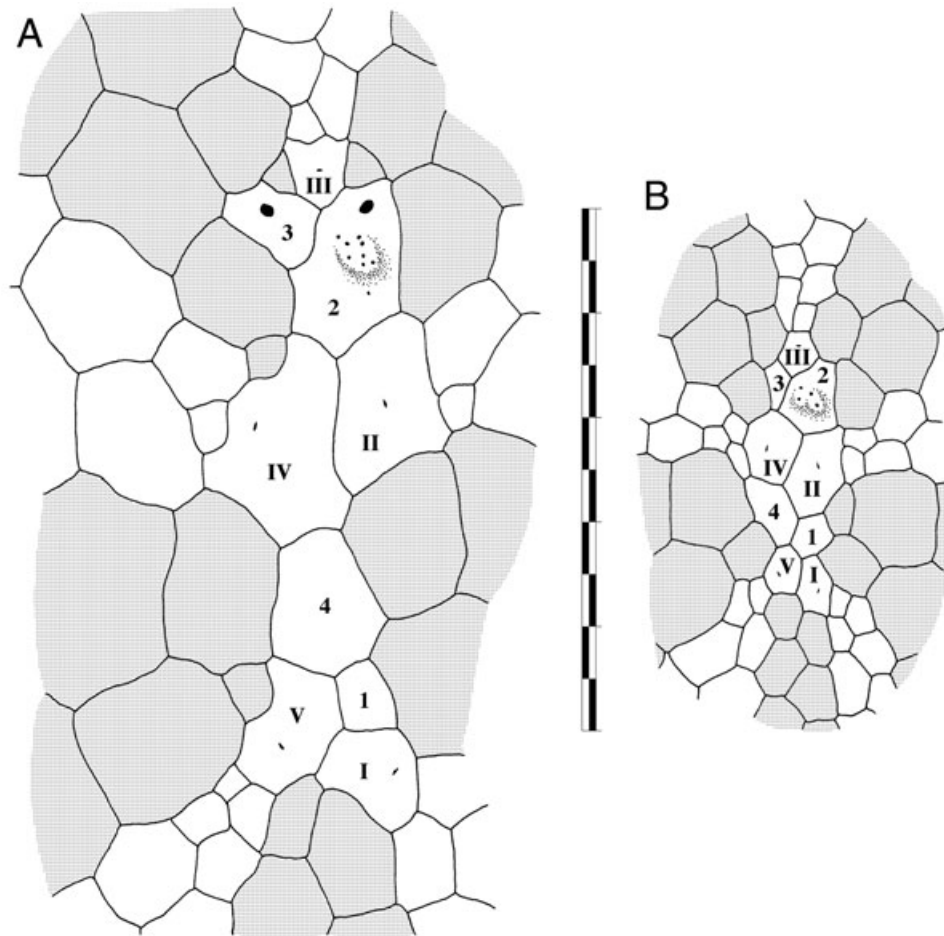


Figure 3. Apical system plate architecture of *Calymne relictata* (MCZ 8571) from R/V 'Atlantis' cruise 24, station 122, anterior towards top of page, interambulacral plates shaded, apical plates labelled according to Lovén's system. A, adult specimen approximately 30 mm long. B, juvenile specimen (lacking gonopores) 11.3 mm in test length.

plates (5.a.3 and 5.b.4), at which point the plates alternate. The plate pattern in interambulacra 1 and 4 is meridoplacous (plates 1.1 and 4.1 followed by a single plate). Interambulacra may be disjunct (Fig. 4A): interambulacral plates 1.1 and 1.b.2 disjunct (ambulacral plates I.b.2 and II.a.2 in contact) and interambulacral plates 4.1 and 4.b.2 disjunct (ambulacral plates IV.b.2 and V.a.2 in contact). The plating in interambulacra 2 and 3 is amphiplacous: plates 2.1 and 3.1 are followed by biserially arranged and regularly alternating plates.

APPENDAGES

Spine morphology

Spines are more diverse in size and shape than in any of the known holasteroids. Ten different types can be identified, including primary spines, miliary spines, and clavulae (spines of the fasciole) (see Mooi & David, 1996; David & Mooi, 2000 for terminology).

Primary spines include four types of long, slender spines (L1–L4) and four different types of spatulate spines (S1–S4). In all types of spines, the shaft is longitudinally striated by ribs that run from the tip almost to the base, where the spine is progressively more expanded and finally surrounded by distinct buttresses which flare out into the more or less enlarged and asymmetric milled ring. In spines of the L-type, the milled ring is slightly asymmetric, a little enlarged on the concave side of the curved shaft or bent extremity of the spine. In contrast, spines of the S-type are characterized by highly asymmetric rings, greatly enlarged on the convex side of the curved extremity of the shaft. The different types of spines are diversified and distributed on the test as follows [spine lengths are taken from the adult specimen from the R/V 'Akademik Kurchatov' cruise (station 3787)].

Spines of type L1 are up to 8.0 mm long. They are smooth and the same diameter for nearly their entire

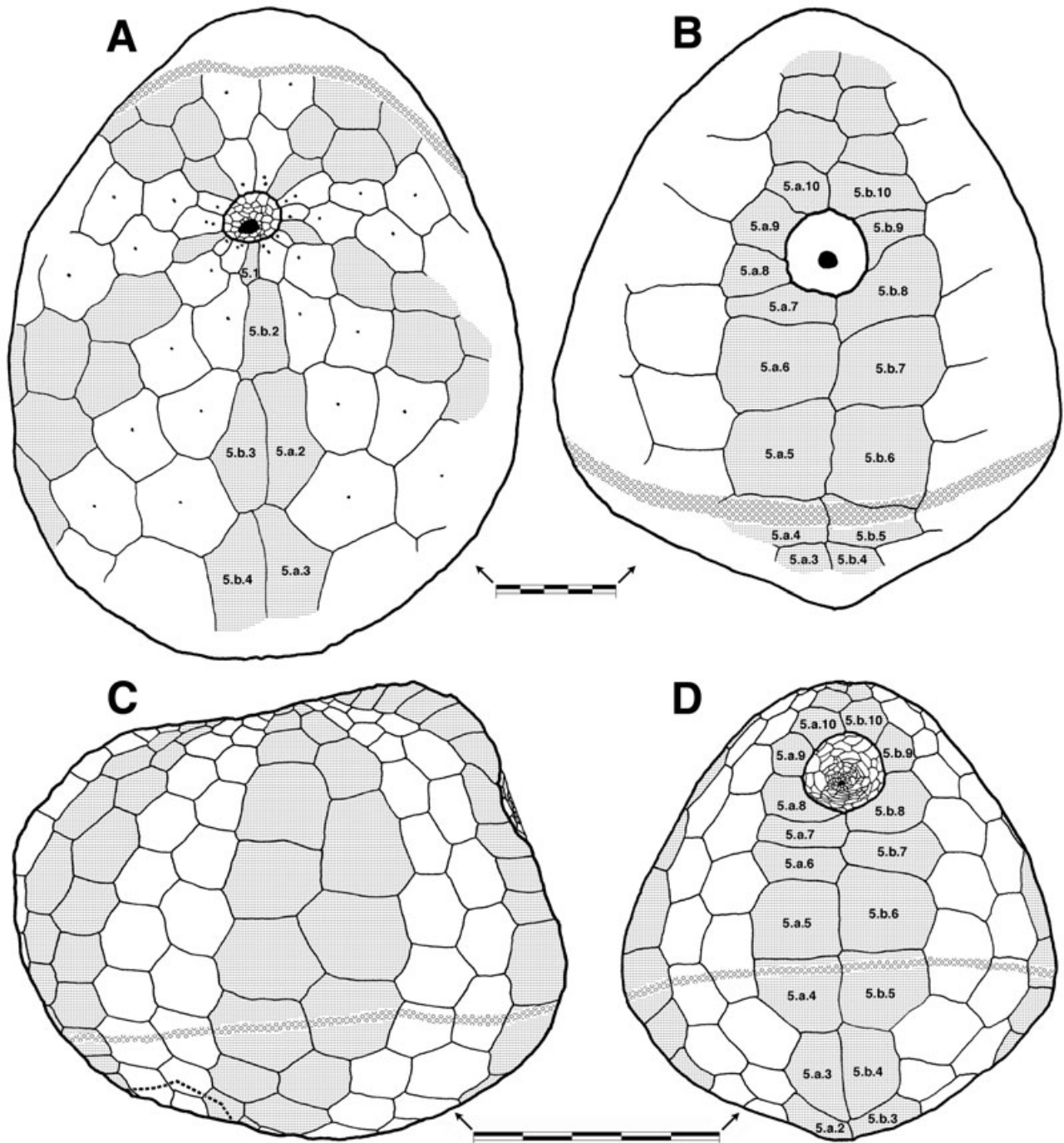


Figure 4. Plate architecture of *Calymne relict*. For each, the fasciole is indicated by bands of small, open circles, the interambulacra are shaded, mouth and anal openings are black, some plate sutures are omitted because they were not visible on the specimen. The plates of the posterior interambulacrum are numbered according to Lovén's rule. Scale bars are 5 mm long. A, oral surface of adult specimen from R/V 'Akademik Kurchatov' cruise 37, station 3787, anterior towards top of page. B, posterior surface of specimen in (A). C, left side of specimen from MCZ 8571, R/V 'Atlantis' cruise 24, station 122, position of mouth indicated by dashed line. D, posterior surface of specimen in (C), viewed slightly more from the oral surface than view shown in (B).

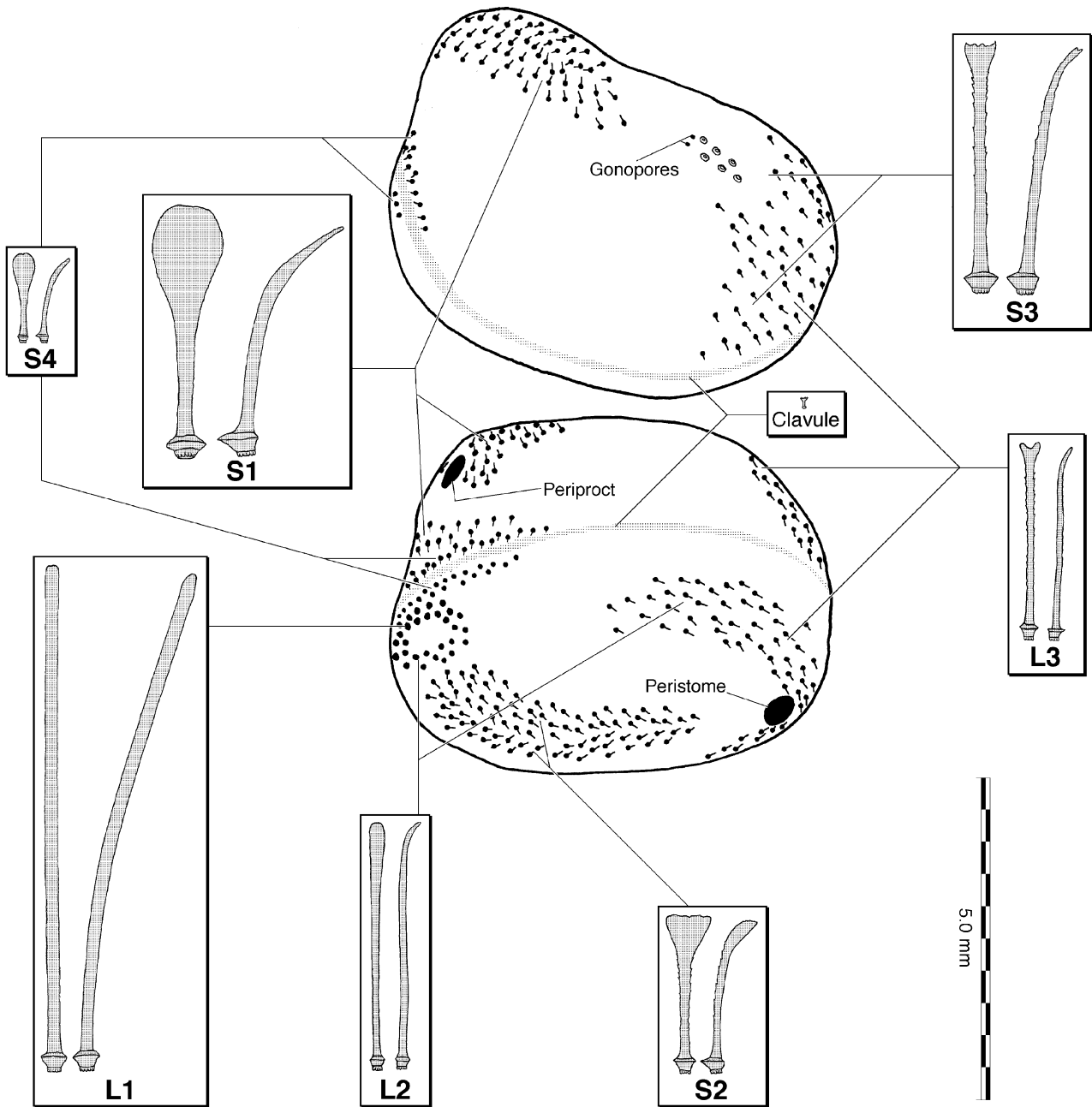


Figure 5. Location of spine types on *Calymne relictata* plotted on specimen from R/V 'Akademik Kurchatov' cruise 37, station 3787. For each view of entire specimen, the orientation of the power stroke as suggested by tubercle asymmetry is indicated by the direction of the small lines leading away from the dot. The upper drawing of the entire specimen is an oblique view from the anterior-dorsal, anterior to the right. The lower drawing of the entire specimen is an oblique view from the posterior-ventral, anterior to the right. Shaded bands indicate the position of the fasciole. For each spine drawing (except for the clavule), the image on the left is a 'frontal' view, the one on the right is a 'side' view. Scale bar at lower right is for the spines, which are all drawn to scale.

length, slightly curved, with a rounded tip. These spines are located on the posterior end of the test, just beneath the marginal fasciole, where they are curved upwards (Fig. 5). The spines are set into a circular

arc, bounding adapically the small posterior rostrum. In the adapical part of the anterior ambulacrum, five large and closely packed tubercles are arranged in two straight lines, with two tubercles on the left side

of the test and three on the right side. Unfortunately, we were unable to observe the spines that once articulated on these adapical tubercles in adults. Only the base of a single one of these spines (on an adapical tubercle) is preserved and shows that the spine was large. However, in a juvenile (station 2462, cruise 23 of the R/V 'Akademik Mstislav Keldysh'), a spine is preserved on one of these adapical tubercles; it is smooth and narrows gradually from its base to the flattened and slightly widened tip. At 49% of the test length, this is the longest spine on this specimen. It is more than a third longer than the L1 spines located beneath the marginal fasciole.

Spines of type L2 are about 4.0 mm long, with a smooth shaft and a slightly bent tip shaped into a flattened, oar-like terminus. The L2 spines are common on the oral, apical, and posterior surfaces of the test (Fig. 5). Posteriorly, they are present just distal to the plastron, where they form a half circle along the lower part of the posterior rostrum, bending upward. They change progressively into L1 spines towards the upper part of the half circle (described above); from this point they are present all over the oral surface, bending towards the anterior except on the posterior ambulacra in which L2 spines tend to be smaller, with their tips bending posteriorly. In the aboral region, they are located antero-laterally, and are bent posteriorly.

Type L3 spines are 2.5 to 3.0 mm long, and have a flattened, curved, and bifid terminal widening. The distal part of the shaft is thorny on the two sides of the bifid tip (Fig. 6A, B). L3 spines are present on the oral, aboral, and anterior surfaces of the test (Fig. 5). They are bent posteriorly in aboral regions and anteriorly in the adoral area.

Type L4 spines are short, with a length ranging between 1.5 and 2.0 mm. They have a pointed, slightly bent tip. The shaft is smooth at the base and thorny towards and on the concave side of the bent tip (Fig. 6C). L4 spines are scattered all over the test, except posteriorly. The tip is bent forward on the anterior and adoral parts of the test, and backward on the posterior and apical parts.

Spines of type S1 are up to 4.1 mm in length and are distinctly paddle-shaped (Fig. 6D), with a curved and broad tip (up to 1.0 mm wide). The entire spine is smooth. S1 spines are distributed on the posterior and aboral sides of the test into two distinct series (Fig. 5). The first series is a posterior, narrow band located just above the marginal fasciole. This series widens below the periproct and is separated by a 'naked' area (covered only by miliary spines) from the second series, which is a set of densely packed S1 spines that extends to the lateral edges of the periproct and aborally onto the posterior curvature of the test. These closely spaced S1 spines form a con-

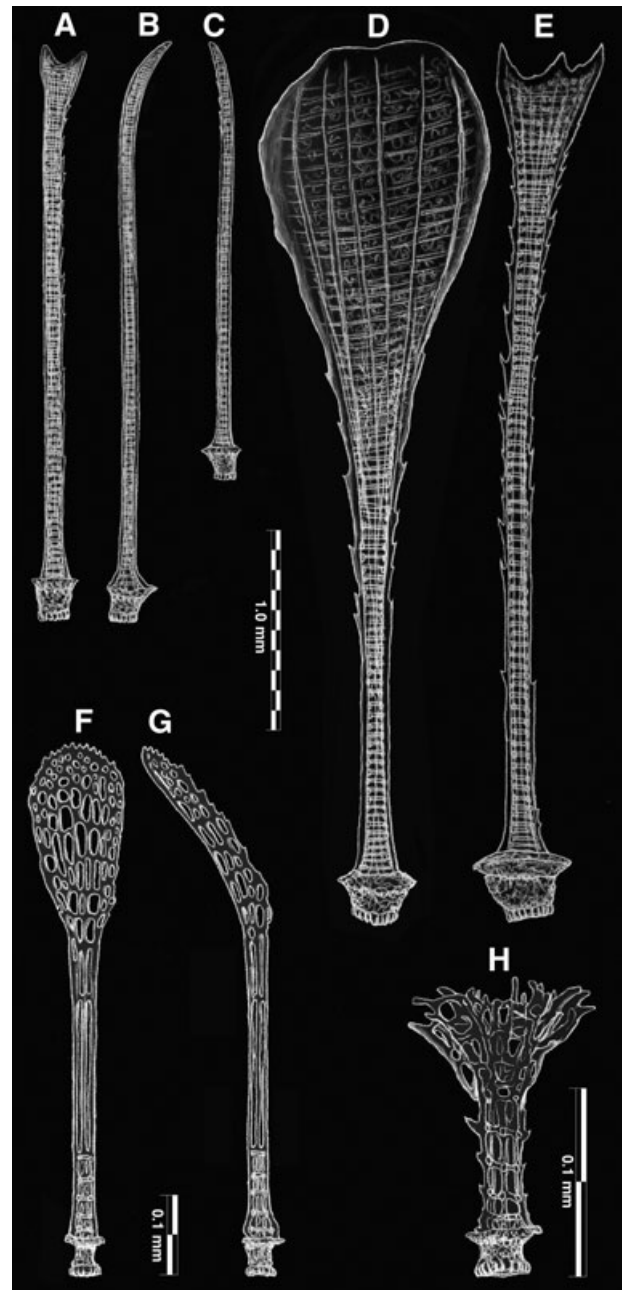


Figure 6. Drawings of spines of *Calymne relictta*, depicted as viewed with transmitted light microscopy. Scale bar at uppermost refers to (A)–(E), at lower left to (F) and (G), at lower right to (H). A, 'frontal' view of type L3. B, 'side' view of type L3. C, 'side' view of type L4. D, 'frontal' view of type S1. E, 'frontal' view of type S3. F, 'frontal' view of miliary. G, 'side' view of miliary. H, clavule from fasciole.

spicuous posterior tuft (Fig. 2D). In the first series, spine curvature is orientated upward while shafts of the second series are curved downward, radiating from the posterior edge of the aboral surface, where the test forms a broad, low bulge.

Spines of type S2 are thick and short, ranging between 2.7 and 2.8 mm in length. The tip is spatulate, concave, and truncated to form a shape like the proximal half of a spoon's ladle. The margin of the spatulate terminus is slightly serrate. The shaft is smooth on its convex side, and thorny on the other surfaces. S2 spines are present exclusively on the plastron, with the tips curved posteriorly (Fig. 5).

Spines of type S3 are about 4.0 mm long and possess a concave, terminal widening with a serrated margin. The shaft is smooth on the convex side, but thorny elsewhere (Fig. 6E). S3 spines are located on the anterior face of the test from the apical system to the oral surface, and are abundant above the marginal fasciole (Fig. 5). All these spines are curved upward above the marginal fasciole. However, adorally, they are orientated backward.

Spines of type S4 are small, spatulate spines about 1.5 mm long. They are located on the posterior part of the test, both above and below the marginal fasciole (Fig. 5). Those located above the fasciole are curved so as to point upward, whereas those below are pointed downward.

Miliary spines have a long and very slender shaft which terminates in a broad, flattened expansion (Fig. 6F, G). They are bent just at the point where the shaft starts flattening. As Mortensen (1907: 54) pointed out: 'miliary spines have the point widened so as to form a broad, fenestrated plate, finely serrate along the outer edge'. Miliary spines are present all over the test. However, they are especially abundant on the aboral surface, above the marginal fasciole. In contrast, they are rare on the oral surface and on the sides of the test.

Clavulae have a short shaft that terminates in very broad, crown-shaped terminal expansion (Fig. 6H). These expansions can be as wide as 0.6–0.8 times the length of the clavulae. The marginal fasciole is well developed and easily distinguished, with up to eight series of regularly arranged clavulae. Miliary tubercles that support these clavulae are very distinct from other miliaries of the test and form a true orthofasciole (*sensu* Néraudeau, David & Madon, 1998). The fasciole follows the ambitus, delineating the boundary between the oral and aboral surfaces, and passes well below the periproct (Figs 2D, 5). In adult specimens, the fasciole passes over the second pair of plates in ambulacrum III (plates III.a.2 and III.b.2) and over interambulacral plates 5.a.4 and 5.b.5 beneath the periproct (Fig. 4A, B). In interambulacrum 5, the position of the fasciole is the same in juvenile and adult specimens, but in ambulacrum III its position differs with ontogeny (see below).

Pedicellariae and sphaeridia

As in previous studies on other species of holasteroids (Mortensen, 1950; Mooi & David, 1996; David & Mooi, 2000), rostrate, triphyllous, and ophicephalous pedicellariae were identified. However, in *Calymne*, tridentate and globiferous pedicellariae were not found.

Calymne is distinguished by well-developed rostrate pedicellariae which vary in shape and size, and which are apparently more numerous in adult (station 3787) than in juvenile specimens (station 2462). Mortensen (1907, 1950) recognized two different types of rostrate pedicellariae. However, we could distinguish four types according to their size, relative length and width of the distal part of the blade, number and size of terminal teeth, and morphology of the basal part. Type 1 rostrate pedicellariae have valves about 0.4 mm in length, and a width/length (W/L) ratio (W/L of valve) of about 0.7 (Fig. 7A). Valves have a short middle constriction and a wide blade with about ten large, undifferentiated teeth. Margins of the basal part are serrated and a few thorns are developed on the stem (Fig. 7B). Type 1 rostrates are located on the oral surface and around the periproct. Type 2 rostrates have valves about 0.25 to 0.4 mm long, with a long, slender middle part and a relatively narrow blade with about ten large, undifferentiated teeth (Fig. 7C). The W/L ratio is about 0.5, and the distal part is longer than the basal part. Margins of the base are smooth as is the stem. Type 2 rostrates are found mainly on the aboral surface. Type 3 rostrates differ from type 2 only in possessing a wider blade with about 20 small, undifferentiated teeth (Fig. 7D). Type 4 rostrates are rare, found only near the peristome, and consist of minute valves about 0.2 mm long, with a W/L ratio of about 0.5.

Ophicephalous pedicellariae are found on both adult and juvenile specimens. They are especially numerous on the aboral side of the juvenile specimen collected by the R/V 'Akademik Mstislav Keldysh' (Station 2462). Ophicephalous pedicellariae have an elongated distal part of the valve, with a contrastingly very narrow, smooth proximal area, and a highly serrate, parasol-shaped terminal margin with about 16 downward-directed, needle-like teeth (Fig. 7E). The stems of these ophicephalous pedicellariae are extremely truncated, and less than 30% of the length of the valves themselves. The umbrella-shaped pedicellariae of *Calymne* are comparable to those observed in the Pourtalesiidae (Mooi & David, 1996). Some differences exist, however: *Echinocrepis* has short valves; *Cystocrepis* and *Ceratophysa* have medium-length valves; and *Echinosisgra* and *Pourtalesia* have long valves (Mironov, 1973).

Triphyllous pedicellariae were found around the peristome and above the periproct, and differ from ophicephalous and rostrate in having a long, muscu-

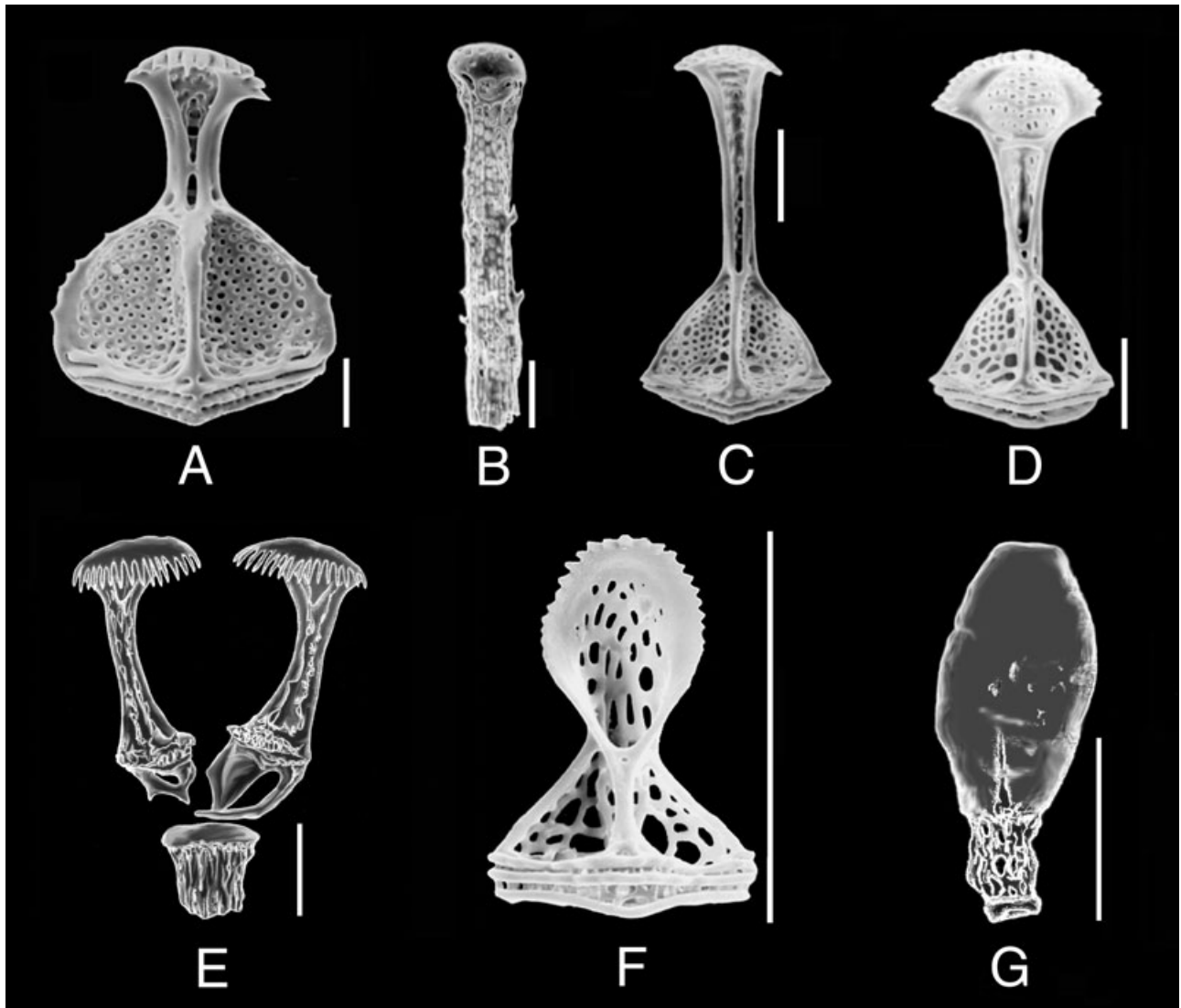


Figure 7. Pedicellariae of *Calymne relict*. A, scanning electron micrograph (SEM) of interior view of type 1 rostrate valve. B, SEM of interior view of type 1 rostrate stem. C, SEM of interior view of type 2 rostrate valve. D, SEM of interior view of type 3 rostrate valve. E, drawing of two of the three valves of an opificephalous pedicellaria showing position in life relative to the stem. F, SEM of interior view of triphyllous valve. G, drawing of sphaeridium. Scale bars 0.1 mm.

lar, hollow, fluid-filled neck between the valves and the stem. In *Calymne* the neck is one to three times the length of the valves. The valve is short and has evenly spaced, very small teeth, all of which are approximately the same size. The tip of the valve is rounded (Fig. 7F).

Smooth, slightly elongate sphaeridia (Fig. 7G) occur around the peristome, one or two per plate. In the posterior ambulacra, sphaeridia can be found distal to the peristome up to the fourth ambulacral plate.

ONTOGENETIC DATA

During cruises of the R/V 'Atlantis' and 'Akademik Mstislav Keldysh', entire, undamaged juveniles

ranging between 1.3 and 13.8 mm long were collected. The size range, as well as the presence of very early stages of growth represented by the smallest specimens, permit analysis of the morphological changes occurring during postlarval growth of *Calymne relict*.

The earliest stages (Fig. 8A) to which we had access were collected by the R/V 'Atlantis II', and represent a just-postlarval imago that is somewhat elongated and comparable to young, early postmetamorphic *Echinocardium cordatum* (Gordon, 1927) and *Pourtalesia miranda* (David, 1987). At this stage, the periproct is still partly enclosed by the apical system, reminiscent of adult early Jurassic Irregularia (Jesionek-Szymanska, 1959; Saucède, Mooi & David,

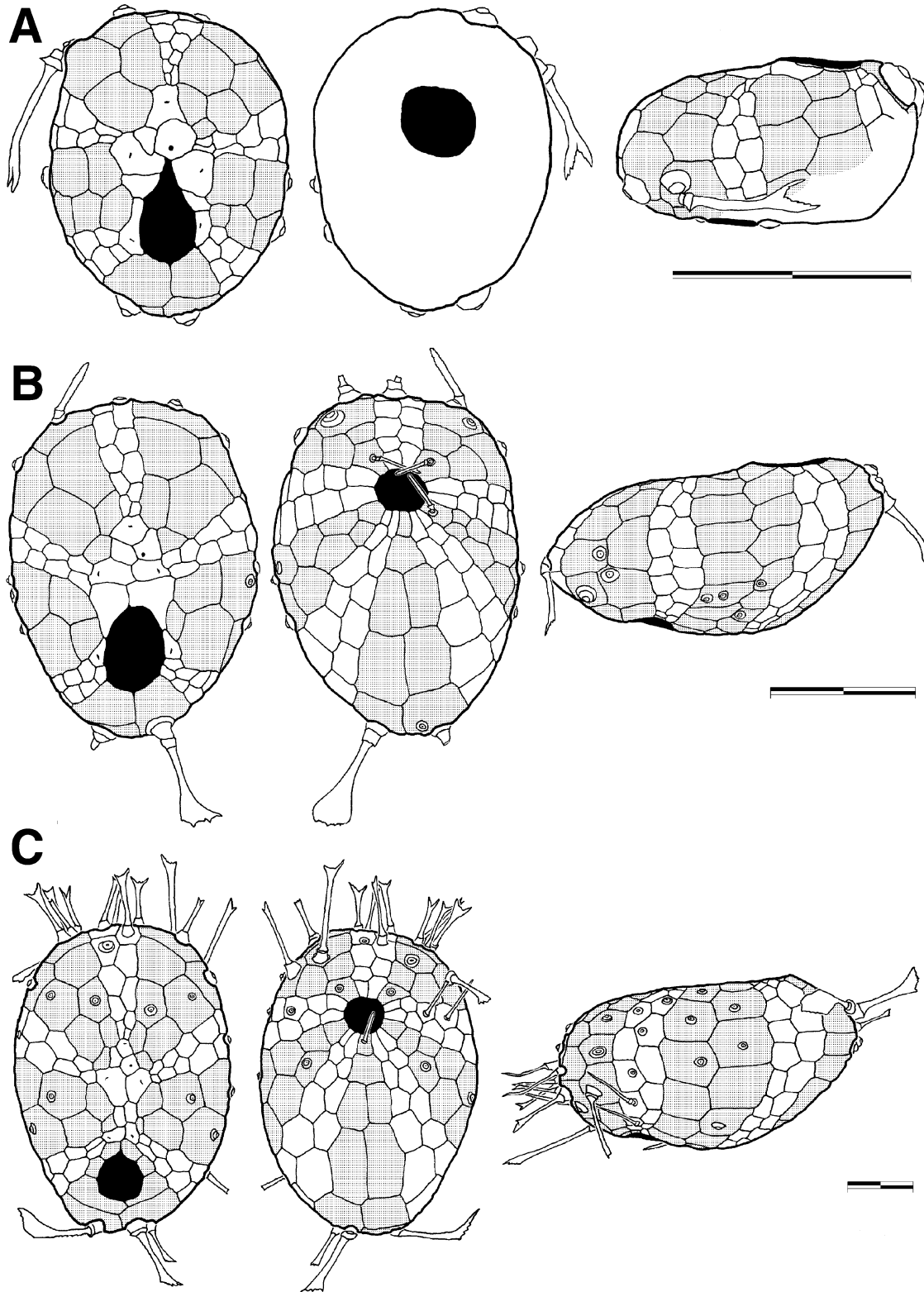


Figure 8. Ontogeny of *Calymne relictata* from MCZ 8571, R/V 'Atlantis' cruise 24, station 122. For each set of drawings, from left to right: apical view, oral view, and left side. The periproct and peristome are in black, and the interambulacral plates are shaded. In some specimens, the sutures are omitted because they were not discernible, and only primary tubercles are shown (some still with spines attached). All scale bars are 1 mm long. A, just-postlarval imago. B, very small juvenile. C, larger juvenile with periproct separated from apical system.

2007). The peristome is already in a slightly anterior position. Large bifid spines are present at the ambitus on the anterior edge.

At sizes of about 2.5 mm (Fig. 8B), the test is more elongated. The apical side is flattened, whereas the oral side is swollen behind the peristome. The periproct is still partly enclosed by the posterior part of the apical system, which is displaced posteriorly; it is separated from the peristome by about six plates. The plastron is conspicuously orthosternous, the labrum being in contact with a single sternal plate, while the other interambulacra are still all amphiplacous. Large tubercles encircle the test at the ambitus. Large spatulate spines (of S1 or S2 types) are present posteriorly; bifid spines occur anteriorly.

Although the general shape of the test does not change, important architectural changes occur by the time the young *Calymne* reaches 5.0 mm in length (Fig. 8C). The periproct is now separated from the apical system by one pair of interambulacral plates, and the apical system itself is configured in the typical holasteroid pattern. On the oral surface, the paired posterior interambulacra (1 and 4) remain meridoplacous. Large tubercles are now present in all regions of the test except the plastronal area. Numerous bifid spines adorn the anterior part of the test, while spatulate spines occur posteriorly. There is still no trace of a fasciole. Marginal spination seems completely undifferentiated and it has not been possible to identify any clavulae that might correspond to early stages of fasciole formation.

At 10.0 mm, the test profile has drastically changed, being much more elevated and less elongated (Fig. 4C, D). Changes occur almost exclusively on the upper part of the test and can be related to the high rate of production of new plates in the posterior interambulacrum (5), the periproct now being separated from the apical system by six pairs of plates. The periproct occupies an upper position on the vertical, posterior face. The oral surface remains relatively unchanged. A well-developed marginal fasciole is clearly visible all around the test (it crosses interambulacrum 5 on plates 5.a.4/5.b.5, and ambulacrum III on plates III.a.4/III.b.4); the clavulae are distinct, and have the characteristic crown-shaped tips. Hence, the fasciole forms when the test is between 5 and 10 mm long according to processes which still remain to be precisely identified.

Further development builds upon the previous trends with only minor modifications. The oral surface becomes more flat and parallel with the aboral surface. The apical system continues to elongate and eventually becomes disjunct. In ambulacrum III, the fasciole is shifted lower, passing over plates III.a.2 and III.b.2 in adults, whereas in interambulacrum 5, the position exhibited in earlier stages is maintained.

HABITAT

Determination of the physical environment in which specimens of *C. relictata* have been collected is a prerequisite for any behavioural interpretation. In particular, the nature of the sea bottom is a determinant factor in the ecology of irregular echinoids (Nichols, 1959a; Smith, 1980a; Kanazawa, 1992; Telford & Mooi, 1996). *Calymne* is an exclusively deep-sea form with a known depth range of 3720 to 3860 m. Characteristics of the sea bottom are precisely known only for station 2462, cruise 23 of the R/V 'Akademik Mstislav Keldysh'. The sediment is compact, viscous, dark-grey with dark-brown spots, and composed of clays and silts with the addition of numerous sand grains. The carbonate (CaCO₃) content is between 24.0 and 25.5%, comprising mostly foraminiferans and coccoliths. Some biogenic siliceous inclusions are present. The associated fauna includes hexactinellids, bryozoans, and polychaetes. More generally, the deep-sea bottom is soft with a superficial thixotropic layer of deep-sea marine snow covering the mud itself. Marine snow is made up of macroaggregates particularly rich in organic matter (bacteria, dead phyto- and zooplankton, faecal pellets) sinking from the upper layers of the water column. Marine snow is a major nutrient delivery system to the deep-sea benthic fauna (Turley, 2002).

DISCUSSION

SPINE MORPHOLOGY AND ACTION

Relationships among spine morphology, location, and function have been studied in detail in spatangoids (Nichols, 1959a; Kier & Grant, 1965; Chesher, 1968; Smith, 1980a, b; Kanazawa, 1992). A major precept of these works is that the preferred direction of the power stroke of spines can be deduced from the direction in which areoles (area around tubercles at which spine muscles insert) are enlarged and displaced (Nichols, 1959a; Smith, 1980a; Kanazawa, 1992).

In *Calymne*, the aboral surface is densely covered by miliary spines, but primary spines are relatively sparse over most of this surface (particularly on the sides of the test) except for the posterior region. This low spine density is typical of deep-sea epifaunal holasteroids. In contrast, aboral spines are more densely distributed in infaunal, irregular echinoids living in muddy substrates. This is the case for the extant deep-sea burrowing spatangoids *Aceste belidifera*, *Aeropsis rostrata*, *Hemiaster expergitus*, and *Brisaster latifrons* (Smith, 1980a; David & Sibuet, 1985; Kanazawa, 1992). In the latter species, the aboral spine canopy is implicated in maintaining the ceiling of burrows and in keeping a free space for ciliary currents between the test surface and the

sediment much as in other burrowing Irregularia (Mooi, 1986).

In *Calymne*, five large tubercles are grouped just anterior to the apical system on the adapical plates of ambulacrum III, indicating the presence of five large spines. In burrowing spatangoids (e.g. *Echinocardium cordatum* and *Moira atropos*), large apical spines are raised to form an upwardly directed tuft that helps to maintain the apical funnel that allows water to enter and oxygenate the burrow. Moreover, apical funnel-building tube feet are present for compaction and mucus-plastering activity of the apical tuft (Nichols, 1959a; Kanazawa, 1992). However, when these echinoids are exposed on the sea bottom, these long apical spines no longer form an erect tuft but lie flattened posteriorly over the aboral surface and the apical system (Smith, 1980a).

In *Calymne*, apical and funnel-building tube feet are absent, and the low density of spines suggests that aboral food collection is not a primary function of the apical spination. In our opinion, the biserial arrangement of the five apical tuft spines in *Calymne* is not consistent with maintenance activity at the base of a funnel. Instead, our observations suggest that the long apical spines over the two gonopores probably function as a protective canopy.

The anteriormost, or frontal surfaces of *C. relictata* are densely populated by several types of spines, including types L2, L3, and S3 (Fig. 2C). All are about the same length, and are more or less mixed together. Throughout this region, smaller primary spines (L4) are present in between the larger spines. Starting at the apical system, the arrangement consisting of one large spine per plate continues down ambulacrum III, but the five large apical spines are replaced by S3 spines that are in turn replaced by smaller L3 spines at the ambitus. S3 spines are also replaced laterally by the L3 type (Fig. 5). Above the fasciole, the areoles of all the frontal primary spines are enlarged aborally, indicating a downward power stroke, whereas spines located below the fasciole are constructed so as to perform an antagonistic, aborally directed stroke (Fig. 5).

Infaunal spatangoids tend to have frontal spines that are used for excavating or scraping on the facing wall of a burrow, and it is thought that the general motion of the spines is in a horizontal stroke (Gale & Smith, 1982; Kanazawa, 1992). Strokes in opposite directions on either side of a fasciole exist in some spatangoids (e.g. *Brissopsis lyrifera*, Smith, 1980a), but in these cases, the peripetalous fasciole is located far above the ambitus and spine morphology is completely different from that observed in *Calymne* (Smith, 1980a; Hollertz & Duchêne, 2001). In *Calymne*, L2, L3, and S3 spines have widened tips – an uncommon feature in scraping spines. Frontal

spines of the oddly shaped, deep-sea mud-burrower *Aceste bellidifera* are enlarged at their tips as well, but differ from those of *Calymne* in exhibiting a probably horizontal power stroke.

Latero-dorsal spines are represented by spine types L2, L3, and L4, which are sparsely distributed (Fig. 5). Generally, these spines are used in burrowing species to support the top of the burrow and maintain a space for water circulation (Gale & Smith, 1982; Kanazawa, 1992). In *Calymne*, the shape and low density of latero-dorsal spines are not suited for such a function. Similarly placed spines in epifaunal spatangoid species are involved in defence and/or righting of the test (Kanazawa, 1992), but they tend to be more robust than those observed in *Calymne*.

When the test is viewed directly at the posterior bulge, the spatulate spines radiate outwards from either side of the mid-line in two wide frills separated by a region of aligned or ‘combed’ spines (Fig. 2A, D). In these frills, all spines of type S1 (either located on the apical side or more posteriorly, around the periproct) have areoles that are asymmetrically enlarged in a direction converging on the highest point of the test, which corresponds to the aforementioned posterior bulge (Fig. 5). Therefore, S1 spines of the posterior frills are constructed to move in such a way as to converge on the posterior bulge of the test. That is, there is a posteriorly directed movement of aboral spines and an aborally directed movement of lateral and posterior spines. This arrangement is very unusual and probably unique in echinoids.

Calymne's orthofasciole is wide (eight miliary rows) and bears strongly differentiated clavulae (Fig. 6H). By analogy with spatangoids, it is likely that this orthofasciole is involved in water circulation over the test, a water current being generated by the epithelial ciliation especially developed along the clavulae. The ciliary current maintains a flow of oxygenated water close to the test, sweeps the surface of the test clean, and forces waste and other unwanted material under the test (Nichols, 1959a; De Ridder & Lawrence, 1982). In some species, this current may provide food particles as well (De Ridder & Lawrence, 1982). Currents can be reinforced by the ciliary action of miliary spines that are densely distributed aborally (Nichols, 1959a; Stephenson, 1963; Smith, 1980a). In spatangoids, clavulae are also implicated in mucus secretion by glands present in the epithelium of the clavulae to help shield the test surface from the ambient sediment (Nichols, 1959b). In *Calymne*, nothing is known about the mucus-secreting properties of the crown-shaped clavulae, which are very different in shape from clavulae in which mucus-secreting cells have been detected (Nichols, 1959b).

Marginal fascioles are uncommon in Recent sea urchins. Unfortunately they occur in animals for

which no direct knowledge of their behaviour is known (e.g. the spatangoids *Linopneustes excentricus*, *L. spectabilis*, and *Pericosmus macronesius*, and the holasteroid *Sternopatagus sibogae*). Some Cretaceous species also have marginal fascioles (*Infulaster*, *Hagenowia*, *Offaster*, and *Pseudoffaster*). The fossil holasteroids *Infulaster* and *Hagenowia* supposedly lived almost completely buried in carbonaceous mud, although their fasciole was in a marginal position and was morphologically less specialized than that of *Calymne* (Gale & Smith, 1982).

Posteriorly, the fasciole and the spine types S1 and S4 that border it on both sides (Fig. 5) display a pattern similar, although not at the same places on the test, to that in the deep-sea, mud-dwelling spatangoid *Aceste bellidifera*. In that species, large and small spatulate spines, very similar in shape to S1 and S4 spines of *Calymne*, are organised in two parallel bands on each side of a peripetalous fasciole, with the largest spines turned outward on the distal side of the fasciole. In burrowing spatangoids, spines surrounding the fasciole seem to transfer mucus towards the aboral and lateral surfaces of the test (Smith, 1980a). The situation is not completely the same in *Calymne*, as S1 and S4 spines are not distributed all along the fasciole, but only along its posterior portion. Therefore, it is likely that a mucous veil cannot be formed all over the test. If this is among their functions, S1 and S4 spines could be involved in developing a mucous coating specifically for the posterior part of the test. This would implicate these spines in isolating the test surface of the posterior region from the surrounding sediment.

The subanal tuft of *Calymne* includes spines that are curved gently upward, and lower spines (L2) with flattened extremities (Figs 2E, 5). In spatangoids, the subanal tuft is associated with a funnel used as a sanitary drain into which a cleansing ciliary current is directed (Smith, 1980a; De Ridder & Lawrence, 1982). In most burrowing species, this subanal sanitary drain is also associated with a subanal fasciole, which is absent in *Calymne*. However, the sector of the marginal fasciole near the tuft is likely to play a role similar to that of the subanal fasciole of spatangoids. Therefore, the subanal tuft of *Calymne* suggests the existence of a subanal funnel, further implying that this region of the test is below the sediment surface for at least some of the time.

The plastron of *Calymne* is covered by large, asymmetric tubercles bearing S2 spines (Fig. 2B). In spatangoids, plastronal spines are generally spatulate, and tend to be wider in mud- than in sand-dwellers (Smith, 1980a). However, they are rarely widened to such an extent as in *Calymne* (Fig. 6D). Similar spatulate spines are also present in the deep-sea spatangoids *Aeropsis rostrata* and *Aceste bellidifera*,

although they are slightly different in shape. Plastron spines are involved in locomotion (Nichols, 1959a; Stephenson, 1963; Smith, 1980a).

Calymne is unique among holasteroids and spatangoids because the asymmetric enlargement of areoles and the orientation of S2 spine curvatures imply a surprising but unmistakable preferred stroke toward the front of the test (Fig. 5). This unusual orientation is the reverse of that normally seen in spatangoid plastronal regions. Plastronal spines push backward in all species, generally in an oar-like movement, causing forward locomotion (Nichols, 1959a; Stephenson, 1963; Fischer, 1966; Smith, 1980a; Kanazawa, 1992). In *Calymne*, plastronal spines seem to make the test move or tilt backward, at least temporarily.

Calymne's ventro-lateral spines are sparse and represented by types L2, L3, and L4 (Fig. 5). In spatangoids with large, locomotory, plastronal spines, ventro-lateral spines are generally used to move sediment upward and/or backward from beneath the test (Smith, 1980a; Kanazawa, 1992). When burrowing spatangoids are exposed at the surface of the sediment, ventro-lateral spines are also used for rapid burial (Kier & Grant, 1965; Kanazawa, 1992, 1995; Hollertz & Duchêne, 2001).

The tips of L2 and L3 spines are widened and curved forward, an orientation compatible either with a frontward scraping stroke (primary or preferred stroke) or a backward propulsive thrust (secondary stroke). In the latter case, the propulsive thrust would make the test move forward, at least for some of the time. A propulsive function of ventro-lateral spines has been observed in some spatangoids (e.g. *Lovenia elongata*) in which plastronal spines are reduced in number and size and cannot provide an effective thrust. In those spatangoids, both locomotion and excavation are performed by ventro-lateral spines (Kanazawa, 1992).

IS CALYMNE EPIFAUNAL OR INFAUNAL?

Recent holasteroids are all deep-sea forms and consequently little is known about their behaviour (but see Southward *et al.*, 1976; Rice *et al.*, 1979; David & Sibuet, 1985; Lauermaun & Kaufmann, 1998; David *et al.*, 2003b). Nevertheless, functional and ecological interpretations have been reliably deduced from studies of functional anatomy (Mironov, 1975, 2008). There are, of course, problems with this approach for some groups. These are exemplified by the case of soft-bodied 'regular' echinoids, the echinothurioids, which have fleshy aboral spines. Few could have speculated accurately about the functions of these spines without direct observations (Emson & Young, 1998).

Morphology-based interpretations of the mode of life of atypical irregular echinoids such as *Calymne*

are necessarily hypothetical, and require confirmation by vehicle-based direct observation (Southward *et al.*, 1976; David & Sibuet, 1985; Lauermaun & Kaufmann, 1998). Fortunately, in irregular sea urchins, many characteristics of the test permit inferences concerning their behaviour and *Calymne* is no exception. When morphological characters are considered, comparisons with analogous (and sometimes even homologous) structures found in spatangoids – the closest relatives of holasteroids (Mintz, 1968; Smith, 1984) – take functional analysis from the realm of speculation to that of testable hypotheses. Correlations between actual behaviour of spatangoids and their functional morphology have been studied in detail and continue to provide reliable results supported by ecological observations (Nichols, 1959a; Kier & Grant, 1965; Chesher, 1968; Smith, 1980a, b; Kanazawa, 1992).

We feel that observations such as the ones provided above concerning the test and appendages permit robust, testable hypotheses regarding the mode of life of echinoids, because so many of their vital functions, such as locomotion, burial, respiration, and excretion are directly related to skeletal characteristics (Smith, 1984). The most significant morphological features of *Calymne* that might inform these hypotheses are: the high arch of the test when viewed in profile, the anterior placement of the mouth, the relatively high placement of the periproct on the posterior face of the test, the occurrence of a marginal fasciole, plastral spines with an apparent reverse power stroke, a subanal tuft, and posterior spine frills on either side of an aboral, posterior bulge in the test.

The first step in interpreting *Calymne*'s behaviour is to determine its living position relative to the sea floor. The only robust data we have concern one young specimen found within the first 5 cm of the upper sediment layer in station 2462, cruise 23 of the R/V 'Akademik Mstislav Keldysh'. Unfortunately, this is not sufficient to determine with precision *Calymne*'s living position. The problem is confounded by the fact that juveniles of some echinoids can exploit levels in the sediment different from those of their corresponding adults. In addition, interpretations of the position in life for *Calymne* in particular are made more difficult because seemingly incompatible characters occur together: specialized spines evocative of burrowing forms co-occur with general features unsuited for a permanent infaunal position. From that, it is necessary to consider several hypotheses regarding *Calymne*'s mode of life and ability to burrow.

Calymne is characterized by a high test profile (Fig. 2C–E). Such a high, inflated test camber is found in other extant deep-sea holasteroids such as the pourtalesiid genera *Echinocrepis* and *Cystocrepis*, and in fossils such as *Echinocorys*, all of which have

been observed or inferred to be epifaunal, or at most, shallow burrowers (Stephenson, 1963; Mironov, 1975, 2008; Southward *et al.*, 1976; Lauermaun & Kaufmann, 1998; David *et al.*, 2003b). Moreover, the epifaunal lifestyle is a common behaviour among holasteroids, although the fossil genus *Infulaster*, with its exceptional morphology, has been interpreted to be infaunal (Gale & Smith, 1982). Among spatangoids, most species are burrowers, with the exception of certain epifaunal deep-sea species (e.g. *Linopneustes murrayi*, *Genicopatagus affinis*) which evolved high test profiles and ambulacra with less well-developed petaloids (Mortensen, 1950; Fischer, 1966; Smith, 1980b; Kanazawa, 1992; David *et al.*, 2003a). These morphological features have been interpreted to be correlated with an evolutionary return from an infaunal habit to life at the surface of the sea floor (Fischer, 1966; Kanazawa, 1992).

A high test profile and a sparse aboral spine canopy seem incompatible with complete burrowing. Moreover, the anterior ambulacrum of mud-burrowers is distinguished by the presence of specialized organs and structures involved in nutrition and burrowing: penicillate tube feet and/or an oral groove with specialized spines (De Ridder, Jangoux & De Vos, 1987). In *Calymne*, the absence of such specialized structures in the anterior ambulacrum is congruent with an epifaunal hypothesis. The presence of a marginal fasciole suggests that *Calymne* is partly buried, at least up to the ambitus just above the fasciole. Concomitantly, the low marginal position of *Calymne*'s fasciole does not support a completely infaunal mode of life either. Generally, spatangoid burrowers that lack an aboral fasciole can live buried only in gravels or coarse sands, whereas all mud-burrowers possess an aboral fasciole (Smith, 1980a). Therefore, while the functional significance of marginal fasciole remains poorly understood, the absence of an aboral fasciole in *Calymne* prevents us from suggesting that this echinoid is a deep burrower. The presence of a subanal tuft as well as of spatulate spines on both sides of the fasciole (on the posterior side) reinforces the hypothesis of partial burrowing. Taking into account the upper frills of large spatulate spines at the posterior of the test, the direction of stroke, and the considerably enlarged S1 spines, we suggest a function related to sediment or particle (deep-sea marine snow) transfer over the posterior part of the test or more likely, to a pushing action against the sediment.

INFERRED BEHAVIOUR

Most benthic deep-sea animals cannot, energetically speaking, 'afford' a sessile lifestyle. In fact, most of the adaptations to the abyssal benthic lifestyle seem

directed towards enhanced mobility in order to exploit opportunistically the occasional rich marine snowfall or patchy distributions of otherwise sparse nutrients. This principle is manifested in several diverse echinoderms: swimming elasipodid holothuroids 'leaping' from place to place (Ohta, 1985); swimming aspidochirote holothuroids undulating above the bottom (Rice *et al.*, 1979); other holothuroids that can walk on enlarged podia (pers. observ.); crawling crinoids (Fujita, Ohta & Oji, 1987); and fast-moving, lightly constructed echinothurioid sea urchins with hooves on their spines (Emson & Young, 1998).

These observations reinforce the likelihood that *Calymne* is epifaunal. However, any such hypothesis of an epifaunal lifestyle must also accommodate the unorthodox position of the fasciole and two groups of spines. First, the occurrence of a marginal fasciole and of a subanal tuft implies that *Calymne* might live partly buried, the flat oral surface shallowly ploughing the sea floor, mouth-first. In this interpretation, the subanal tuft may be used to stabilize the test on the unstable deep-sea mud. Second, the function of the upper-posterior frills of large spines is difficult to envisage in the context of well-known echinoid behaviours. A superficial examination might lead to a first hypothesis involving cleaning of the test or a covering reaction, but this would depart significantly from all direct observations made on other deep-sea holasteroids (Rice *et al.*, 1979; David *et al.*, 2003b). A second hypothesis would suggest that the frills help overturned specimens to right themselves. Although it might seem unusual to evolve a specialized spination for this purpose alone, this hypothesis is supported by the shape of the test. It is very high, and therefore likely to be unstable in nearly any current regime, and lacks robust lateral spines that would otherwise perform this righting function. This hypothesis could also explain the spatulate shape of the spines, which is ideally suited for pushing against sediment.

The forward motion of *Calymne* almost undoubtedly results from the coordinated strokes of L2 and L3 spines located on the oral surface. In these spines, curvature is orientated forward, allowing efficient contact and thrust upon the substrate. During locomotion, plastral S2 spines can rest perpendicular to the test without producing any forward stroke, but would participate in stabilizing the test. The shallow burial could be accomplished by the combined strokes of plastral (S2) spines, frontal spines (S3), and ventro-lateral L2 and L3 spines. In this scenario, while ventro-lateral spines excavate that part of the sediment located beneath the test, their action is assisted by a slight rocking movement of the test. This movement, facilitated by the thixotropy of the substrate, would be achieved by the antagonistic and coordinated actions of plastral and frontal spines.

These spines would tilt the test alternatively forward through action of the forward stroke of plastral spines, and then backward by the downward stroke of frontal spines. Rocking movements have already been observed in *Brissopsis lyrifera* and wedge-shaped spatangoids that rock while burrowing in muddy substrates (Kanazawa, 1992; Hollertz & Duchêne, 2001). If we accept that *Calymne* is partially infaunal, we might envisage that it uses the phyllopodia to gather and transfer food from the relatively rich upper marine snow layers to the anteriorly placed mouth. One might even suggest that as *Calymne* does so, it is tilted upward to bring the mouth closer to the upper layers. This rocking behaviour could in fact help to orientate the animal to initiate this 'tilted ploughing'.

In *Calymne*, the combination of atypical morphological characters is a challenge to the functional morphological approach, particularly given the lack of detailed knowledge of deep-sea environments. Nevertheless, such morphological inference for function should not be the domain of palaeontology alone. For extant organisms that inhabit environments that remain relatively unexplored, it is necessary to develop hypotheses and even predictions concerning behaviour in order to develop a context for the unusual morphologies these animals represent. With further data from direct deep-sea observation, the soundness of such analyses can only be improved.

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