A NEW MARSUPIATE CIDAROID ECHINOID FROM THE MAASTRICHTIAN OF ANTARCTICA

by DANIEL B. BLAKE *and* WILLIAM J. ZINSMEISTER

ABSTRACT. *Almucidaris durhami* is a new genus and species of cidaroid echinoid from the Maastrichtian (Late Cretaceous) of Seymour Island, Antarctic Peninsula. The species is unique in that the genital plates of the female are expanded and hollowed to form marsupia. The incidence of brooding in invertebrates, including echinoderms, increases with latitude and apparent stress; stressful conditions might have contributed to the evolution of *A. durhami*.

SEYMOUR Island, in the Antarctic Peninsula, has been the source of an extraordinary diversity of superbly preserved late Mesozoic and early Cenozoic fossils (Feldmann and Woodburne 1988). None of these many fossils is better preserved or more elegant than a specimen of the new cidaroid echinoid described here; the new species is important for more than the aesthetic value of its holotype, however, because the genital plates of the female were much enlarged to form deep brood chambers. Taxonomically diverse brooding echinoids, including cidaroids, are known from numerous other occurrences, and these shed some light on the evolution of brooding in *Almucidaris durhami* gen. et sp. nov.

BROODING IN ECHINOIDS

The biology of brooding in echinoderms was reviewed by Lawrence (1987), and a taxonomic survey of brooding echinoids was provided by Philip and Foster (1971). Lawrence (1987, p. 264) defined brooding as '...the association of embryos and juveniles with an adult, usually the female parent'. The definition is broad, and includes simple presence of the juveniles on the surface of the parent, without structural differentiation. Brooding increases probability of offspring survival at a cost of decreased fedundity and dispersal, and increased reproductive effort. Although brooding has been reported from all living echinoderm classes (except the Concentricycloidea), it is not common, indicating that costs tend to outweigh benefits. In echinoids, brooding always is external, with the young present either in marsupia or distributed among the spines without parent structural differentiation.

Within echinoderms, brooding is found in different trophic groups, but as with marine invertebrates in general, it increases with latitude. Seventeen of the eighteen known species of Antarctic echinoids are brooders (Magniez 1983), some occurring intertidally on subantarctic islands under conditions of considerable physical stress (Lawrence 1987). Brooding also is known from lower latitudes; Gladfelter (1978) described it in the shallow-water infaunal Caribbean cassiduloid *Cassidulus caribbearum*, for example. The test of *C. caribbearum* is unmodified and the young are carried among the aboral spines.

Barker (1985) studied reproductive behaviour in the modern brooding cidaroid *Goniocidaris umbraculum* from the deep (95 m) continental shelf off New Zealand. Laboratory studies showed that brooding in this species begins with the urchins partially burying themselves in bryozoan shell debris. Oocytes are passed along the ambulacra by means of ciliary and tube foot action from the gonopore to the peristomial region. The oocytes are buoyant, and both their buoyancy and the oral spines help hold as many as 60 oocytes at the peristome. After 47–55 days, juveniles begin to migrate from the peristome to the bases of the spines on the oral side of the adult. Field data suggest the

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annual breeding cycle takes place over nearly a six month period, with juveniles remaining with the parents for approximately four months. The smallest individuals recovered with juveniles were under 18 mm in diameter.

Associated juveniles can be quite numerous; Magniez (1980) found the mean egg and juvenile number per female to be 27·3, with a maximum of 109, in a population of 315 females of the schizasterid spatangoid *Abatus cordatus* from Kerguelen Island.

Barker (1985) found controlling factors on brooding to be uncertain in *Goniocidaris*, which has a well defined annual breeding cycle. He suggested that photoperiod or nutrient accumulation might be important but that bottom temperature showed only a relatively minor 4 °C range of variation. This author further noted that the urchins do not feed during brooding; movement of the lantern might be sufficient to dislodge the eggs from the peristome. Partial burial might reduce risk of egg loss as well as provide a stable environment for the young. The range of *G. umbraculum* partially overlaps that of the broadcast spawning euechinoid *Pseudechinus huttoni* and both graze on the bryozoan *Cinctipora elegans*; however, competition was concluded not to have been involved with brooding in *G. umbraculum* because of the limited overlap of ranges. Hendler and Franz (1982) suggested brooding in the asteroid *Leptasterias* is a cold adaptation and not a result of competition; Barker (1985) preferred a temperature hypothesis for the origin of brooding in *G. umbraculum.*

Several living brooding cidaroids, including *Goniocidaris corona* (Barker 1968), *G. umbraculum* (D. L. Pawson pers. comm.), and *Austrocidaris canaliculata* (Philip and Foster 1971) carry young around the apical system; juveniles of other species are found at the peristome, protected by the primary spines. In *Austrocidaris*, a sunken median furrow is present in both ambulacra and interambulacra, and young can cling to the apical surface. The enlarged genital-plate marsupia of *Almucidaris* gen. nov. are unique.

De Ridder and Lawrence (1982) reviewed the literature on food resources of echinoids; available data on cidaroids were largely drawn from Mortensen (1928), whose observations were based primarily on gut contents. Cidaroid food consists of a diversity of bottom materials, including foraminifers, bryozoans, sponges and other generally smaller particles.

STRATIGRAPHIC OCCURRENCE OF *ALMUCIDARIS DURHAMI*

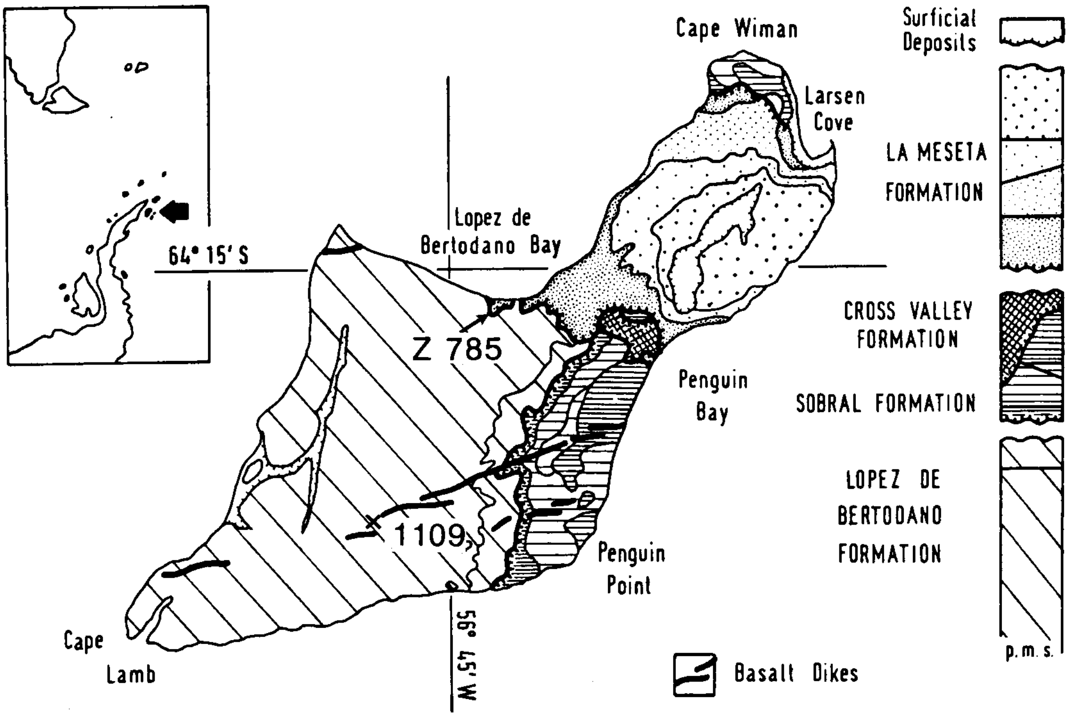
The holotype was collected from the Maastrichtian portion of the Lopez de Bertodano Formation of Seymour Island, Antarctic Peninsula (Text-fig. 1). The formation consists of approximately 1200 m of sandy siltstones and siltstones with numerous concretionary horizons. Although the invertebrate fauna is moderately diverse and well preserved, the abundance of individuals within any given interval is not great. Fragmentary echinoid material is abundant at a number of horizons; however, the holotype is the only known complete individual.

The specimens of *Almucidaris durhami* gen. et sp. nov. were collected from a 25 m interval of medium grey siltstone 320 m below the K/T boundary. Extensive bioturbation characterized by *Bergaueria* and Phycodes-like structures have destroyed all primary bedding structures. The absence of any primary sedimentary structures and the intensely bioturbated nature of the sediments suggest that the environment of deposition of this horizon was below wave base in a mid or outer shelf setting.

Although the fossils from the siltstone are not abundant, the fauna is exceptionally diverse (35 taxa) for the Lopez de Bertodano Formation, and remarkably well preserved. The composition of the invertebrate fauna from this siltstone interval differs markedly from that of the rest of the Lopez de Bertodano Formation by the presence of a large number of small gastropods that have not been encountered elsewhere in the formation. The molluscan fauna from the Antarctic Cretaceous generally is characterized by relatively large, thick-shelled species; the occurrence of many small, thin-shelled taxa indicates an unusual local facies not seen elsewhere in this unit.

BROODING IN *ALMUCIDARIS DURHAMI*

Although a number of aboral brooders are known among echinoids, peristomial brooding is



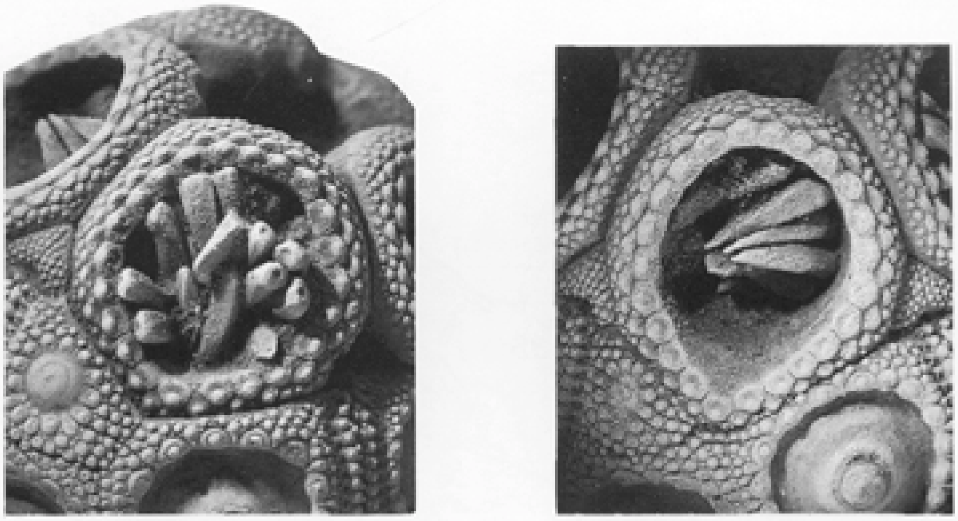
TEXT-FIG. 1. Geological locality map of Seymour Island, Antarctic Peninsula. The Lopez de Bertodano Formation is Cretaceous and Paleocene; that part of it in which the echinoid material was found is Maastrichtian. The Sobral and Cross Valley Formations are Paleocene, and the La Meseta is Eocene in age.

dominant; the latter provides more protection, but probably interferes with the parent's feeding. In contrast, the genital-plate marsupia of *A. durhami* (Text-fig. 2) provided effective protection yet they would not have impaired feeding. A second advantage of brood chambers in the genital plates was that oocytes could be transferred from the interior to them with little chance of loss. Many echinoid marsupia are formed by depressions in the test, and although all marsupia in echinoids are topologically external, they can utilize a significant percentage of the volume of the interior; the raised marsupia of *A. durhami* provided enclosed space without decreasing the parent's internal volume.

Almucidaris durhami, like *Goniocidaris umbraculum*, apparently lived below wave base, and therefore the adaptive value of marsupia in *A. durhami* was not directly related to variation in shallow-water conditions, although as in *Goniocidaris*, perhaps availability of nutrients was important.

Size at which juveniles become independent varies among species, but space is quite limited within the marsupia of *A. durhami*. Barker (1985) illustrated juveniles of *G. umbraculum* clinging to the spines of the adult; these had a test diameter of about 3 mm, and diameter including spines was approximately 6 mm. Perhaps juveniles of *A. durhami*, like those of *G. umbraculum*, moved onto the spines of the adult during ontogeny, freeing marsupial space for younger individuals. Sequentially overlapping broods are known in *Cassidulus caribbearum* (Gladfelter 1978).

Cidaroid taxonomy has proven difficult, in part because of individual variation and lack of agreement on phylogenetically significant characters. Smith and Wright (1989) provided a historical survey of cidaroid taxonomy, a revised classification, and a phylogenetic reconstruction. Their system is followed here, along with the taxonomic treatment of Philip (1963, 1964).



TEXT-FIG. 2. *Almucidaris durhami* gen. et sp. nov., holotype USNM 446322, two marsupia with spines displaced from scrobicular rings into the chambers, both ×6.

SYSTEMATIC PALAEONTOLOGY

Class ECHINOIDEA Leske, 1778
Order CIDAROIDA Claus, 1880
Family CIDARIDAE Gray, 1825
Subfamily CIDARINAE Gray, 1825
Tribe CIDARINI Gray, 1825
Genus ALMUCIDARIS gen. nov.

Type species. Almucidaris durhami sp. nov.
Etymology. Almus (L.); fostering, nourishing, cherishing; in reference to the brooding behaviour.

Diagnosis. Cidarinid with large genital plates forming deep marsupia, at least in females; ambulacral column pore rows strongly sinuous; podial pairs inclined perradially, not conjugate; interambulacral plates of adult with densely arranged tubercles, plate sutures closed by tubercles.

Almucidaris durhami sp. nov.

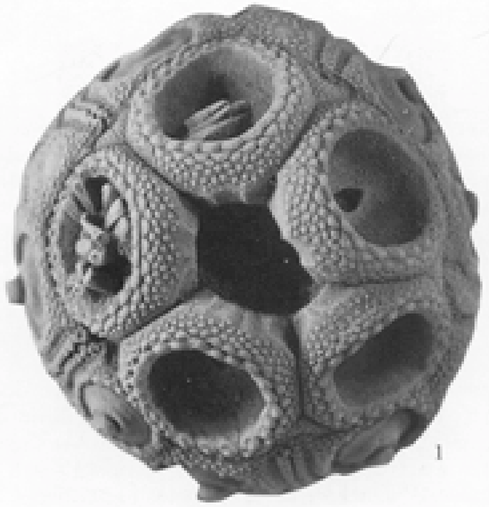
Plate 1, figs 1–6; Text-fig. 2

Material. Available material consists of one complete test (holotype, United States National Museum [USNM] 446322), the base of a second, and 25 test fragments, the latter ranging from single plates to nearly complete interambulacra with portions of adjacent ambulacra (paratypes USNM 446323-446348). Small spines are associated with the complete specimen and the base. Four isolated marsupial plates are included among the 25 fragments. Maastrichtian, Upper Cretaceous, Seymour Island, Antarctic Peninsula.

EXPLANATION OF PLATE 1

Figs 1–6, *Almucidaris durhami* gen. et sp. nov., holotype, USNM 446322, Maastrictian, Seymour Island, Antarctic Peninsula. 1, aboral view, note large facets for periproctal plates, gonopore, and spines collapsed into marsupia, ×2. 2, ambulacral detail, ×6. 3 and 4, stereo pair, lateral views, ×2. 5, oral view, ×2. 6, ambulacral detail, specimen is partially separated along perradial suture, ×6.

PLATE 1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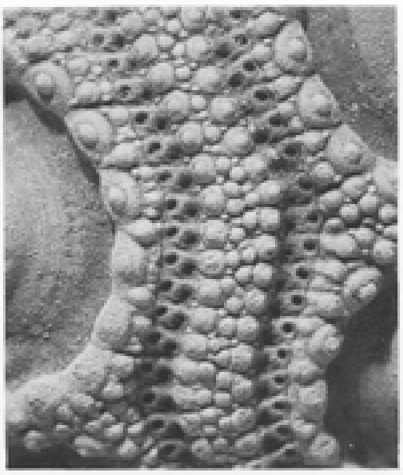
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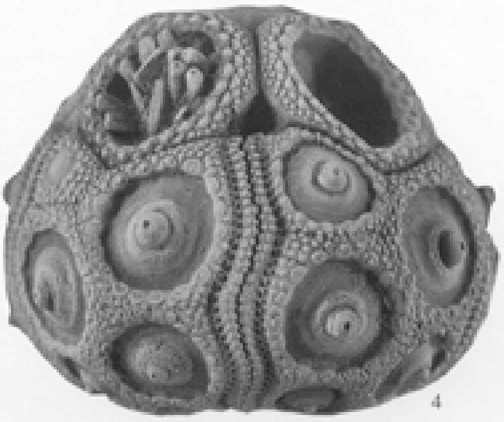
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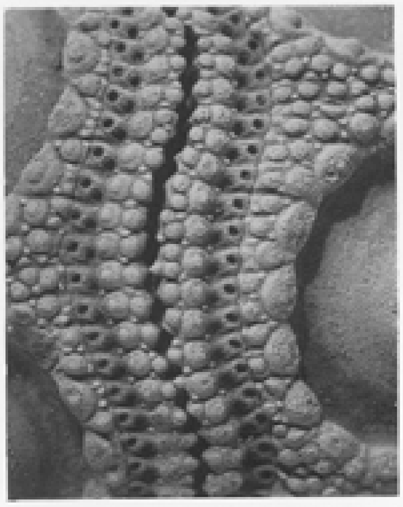
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BLAKE and ZINSMEISTER, *Almucidaris*

Etymology. The species is named in honour of Dr J. Wyatt Durham.

Diagnosis. As for the genus.

Description. The diameter of the holotype is 35 mm and the height is 21 mm; the height of the corona and genital ring together are 30 mm. The corona is somewhat flattened, with the apical ring forming a prominent, peaked aboral profile. The periproctal outline is elongate pentameral, with a length of 9 mm and a breadth of 7 mm; all periproctal plates were lost but large articular surfaces on the genital plates demonstrate that periproctals were large. The genitals are much enlarged, approximately 14–15 mm (vertical dimension) by 13–14 mm. They contain open hemispherical marsupial chambers which are approximately 10 by 8·5 mm; chamber openings are directed laterally and aborally. A genital pore is present at the base of each chamber; it is approximately 2 mm in length. The outer surface of the genital plate is covered by closely spaced tubercles which diminish in size away from the enlarged scrobicular ring; the scrobicular ring and the next lateral ring have rounded crescentic depressions which are directed toward the chamber, thus allowing spines to be deflected over the chamber opening. Oculars are triangular but indented at their bases; their breadth is approximately 4 mm and height is 3·5 mm. Oculars are covered by closely spaced tubercles of uniform size. Apical ring plate boundaries are incised and they are neither pitted nor have areas bare of tubercles. Ambulacra are strongly sinuous throughout. Ambulacral width at the ambitus is 10–11 % of test diameter, with the combined pore zones forming nearly one-half of the ambulacral width. Ambulacral pores are uniserial and pairs are inclined, with the perradial member of the pair lower than the adradial. Pores are not conjugate; the interporal partition is slightly broader than the width of a single pore. A clearly defined furrow extends from below the perradial pore to the lower edge of the ossicle; the groove is gradually lost toward the adradial pore. The perradial end of the plate has a single enlarged tubercle occupying the full plate height; one or two vertically aligned smaller perradial tubercles also are present, and on some ossicles, one or two additional small miliary tubercles are fitted among the perradial series. Most tubercles other than those of the enlarged series are absent near the peristome and periproct. Perradial sutures are not bare or pitted. Each interambulacral column consists of four or five plates, and all but perhaps one or two of the most recently-added plates have functional tubercles. The height and width of the plates are approximately equal, or the width is the slightly greater dimension. Primary tubercles are large with areoles of only the smallest adoral plates being confluent. The scrobicular series of slightly larger plates are tangent; plates ambitally and adapically in the series have closely arranged miliary tubercles separating the neighbouring scrobicular series. Sutural boundaries are not incised or bare, although scattered small pits are present. Areoles are deeply incised, occupying approximately 75 % of the plate width at the ambitus. Mamelon diameter is 15–20 % of plate width and most are perforate, although some adoral mamelons are imperforate or their condition was not preserved; they are weakly crenulate. Scrobicular tubercle series are clearly enlarged, with a distinct mamelon and a small crescentic depression toward the areole. Peristomial diameter is approximately 40 % of test diameter; the lantern is unknown. Spines of genital plates are cuneate in cross-section, and therefore they were closely fitted in life; they have longitudinal beaded ribbing.

Available isolated coronal fragments and plates (paratype specimens) add relatively little, in part because the surfaces of most have been abraded by wind and dust. The largest interambulacral plate is 19 by 13 mm, and that of an ambital interambulacral plate on the holotype is 11 by 10 mm, suggesting plate growth was anisometric. If test diameter was proportionate to ambital plate width, a diameter of at least 60 mm was attained. One adoral plate has a clearly crenulate tubercle. Although isolated, four marsupiate genitals were recovered, but no dimorphic examples were found. A basal test fragment retains a number of cuneate scrobicular spine fragments similar to those of the genitals, again indicating a closely fitted, protective arrangement.

Remarks. *Almucidaris* is assigned to the Cidarinae (sensu Smith and Wright 1989) based on the presence of well defined perforate tubercles; it is assigned to the Cidarini based on presence of well developed adapical tubercles and the presence in adults of tubercles obscuring plate sutures, and weakly developed sutural pits. Positive evidence on subtribal affinities is lacking, although pore pairs are neither conjugate or subconjugate and therefore *Almucidaris* does not belong to the Phyllacanthina. Smith and Wright (1989) noted that although the Cidarini is distinguished by pedicellariae and intestinal plate characters not found in fossils, some constituent genera can be traced back to the Lower Cretaceous; *Almucidaris* is similar to such genera as *Prionocidaris* sensu Smith and Wright (1989), and *Phyllacanthus* sensu Philip (1963). It differs from both in the nature of the pore pairs, and from the latter in the nature of the scrobicular spine bases (less strongly differentiated in *Almucidaris*) and the presence of marsupia. It is unlike *Prionocidaris* (but similar to *Phyllacanthus*) in the development of test tubercles.

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