



# Bathyal sea urchins of the Bahamas, with notes on covering behavior in deep sea echinoids (Echinodermata: Echinoidea)



David L. Pawson\*, Doris J. Pawson

National Museum of Natural History, Smithsonian Institution, WA DC 20013-7012, USA

## ARTICLE INFO

Available online 24 January 2013

### Keywords:

Echinodermata  
Echinoidea  
Bathyal  
Covering  
Bahamas  
Caribbean

## ABSTRACT

In a survey of the bathyal echinoderms of the Bahama Islands region using manned submersibles, approximately 200 species of echinoderms were encountered and documented; 33 species were echinoids, most of them widespread in the general Caribbean area. Three species were found to exhibit covering behavior, the piling of debris on the upper surface of the body. Active covering is common in at least 20 species of shallow-water echinoids, but it has been reliably documented previously only once in deep-sea habitats. Images of covered deep-sea species, and other species of related interest, are provided. Some of the reasons adduced in the past for covering in shallow-water species, such as reduction of incident light intensity, physical camouflage, ballast in turbulent water, protection from desiccation, presumably do not apply in bathyal species. The main reasons for covering in deep, dark, environments are as yet unknown. Some covering behavior in the deep sea may be related to protection of the genital pores, ocular plates, or madreporite. Covering in some deep-sea species may also be merely a tactile reflex action, as some authors have suggested for shallow-water species.

Published by Elsevier Ltd.

## 1. Introduction

During the years 1983–1989, a collaborative effort involving the National Museum of Natural History (NMNH), Smithsonian Institution, Washington DC, and the Harbor Branch Oceanographic Institution, Inc. (HBOI), Fort Pierce, Florida, resulted in a series of dives in Harbor Branch's *Johnson-Sea-Link* submersibles (JSL-I and JSL-II) around the Bahamas in bathyal depths. The main objective of these dives was to study the composition and biology of the echinoderm fauna of the region. Approximately 200 species of echinoderms were encountered and documented. Thirty three species of echinoids, none of them new to science, were photographed and videotaped, and voucher specimens were collected.

Some aspects of the biology of the sea urchins proved to be of special interest. We were astonished to find that even in bathyal depths some species exhibited so-called covering behavior (covering reaction, covering response, heaping, masking), which has been reported only once in the deep sea, as far as we can determine (Levin et al., 2001). David et al. (2003) reported on “conveying” by another deep-sea species of sessile or sedentary organisms which may merely have settled on the host animals. Typically, covering involves coordinated action on the part of the tube feet and spines (Millott, 1955, 1956) to heap debris on the upper surface of the

body. The pedicellariae apparently do not play a significant role in the process of covering, or in retention of the debris (Reese, 1966; Coppard et al., 2010). In shallow-water taxa the debris usually consists of shells, or seagrass, and other material picked up from the ocean floor, and it may frequently include pieces of drift algae that come in contact with the urchin, and are captured by the tube feet. In the deep sea, debris may include shell fragments, bryozoan colonies, pteropod skeletons—apparently, whatever is readily available to the animal.

In this paper, we list the species of echinoids encountered in the bathyal of the Bahamas, along with their depth ranges, and identify the species that cover themselves. Covering in the deep-sea is discussed, and compared and contrasted with covering in shallow-water species.

## 2. Materials and methods

For the Bahamas study, the research group comprised John E. Miller (Leader), Harbor Branch Oceanographic Institution, Inc.; Gordon Hendler, formerly Smithsonian Institution and then, from 1985, Los Angeles County Museum of Natural History; Porter M. Kier and David L. Pawson, Smithsonian Institution. Under an agreement between the Smithsonian Institution and Harbor Branch Oceanographic Institution, Inc., the submersibles *Johnson-Sea-Link I* and *II* were made available to us between 1983 and 1989. A total of 106 dives were made, 102 in daylight hours and 4 at night, at a variety of

\* Corresponding author. Tel.: +1 202 633 1757.  
E-mail address: [pawsond@si.edu](mailto:pawsond@si.edu) (D.L. Pawson).

sites around the Bahamas, to a maximum depth of approximately 765 m. Habitats where echinoderms flourished were commonly steep rocky slopes with a thin veneer of sandy sediment, and small almost-flat plains with deeper soft sediments.

During the Bahamas investigations, for each echinoderm of interest encountered, attempts were made to briefly videotape the subject and its surroundings, with the scientist/observer providing a contemporaneous commentary. Several 35 mm still color photographs were also taken. As desired, voucher specimens were collected for further study in the laboratory and eventual incorporation into reference collections at the National Museum of Natural History, Smithsonian Institution, and Harbor Branch Oceanographic Institution, Inc. Details of collection data for the species listed here can be found at <http://collections.nmnh.si.edu/search/jiz> or at the Oceanographic Museum, Florida Atlantic University Harbor Branch Oceanographic Institute, Fort Pierce, Florida.

Recently, we have participated in the Smithsonian Institution's Deep Reef Observation Project (DROP) using the submersible *Curasub* in June 2011 (4 dives) and in August 2012 (2 dives) to study echinoderms at Curacao, Netherlands Antilles, down to depths of approximately 305 m. At Curacao, individuals of *Conolampas sigsbei* were observed and collected and, in August 2012, were maintained alive in aquaria for approximately 36 h while a variety of experiments related to the covering reaction were conducted. Unfortunately, the animals were moribund and unresponsive, and the experiments were unsuccessful.

### 3. Results

Thirty three species of echinoids were found around the Bahamas in bathyal depths. An annotated list of echinoids is presented in Table 1. There were no new taxa; all echinoid species had been previously described from various areas of the Caribbean. This result was unexpected, because several new taxa were found in all other classes of Echinodermata. Species which typically burrow were, of course, seldom encountered. For burrowing species listed below, the only evidence of the species' presence in the area was in the form of a dead test on the sediment surface.

#### 3.1. Incidence of covering behavior in bathyal Bahamas Sea Urchins

##### 3.1.1. Three species exhibited covering behavior

*C. sigsbei* (A. Agassiz) (Fig. 1A and B). This relatively common species was photographed or videotaped *in situ* on 9 dives, at depths of 272–464 m, but it was observed and ignored, or merely briefly noted, on many other dives. All individuals documented by imagery were covered with a topknot of coarse debris. In many cases (see Fig. 1A and B) pieces of debris were in the process of being carried up the ambulacra towards the apex of the test. Unfortunately, *Conolampas* was not reported or documented on any of the four night dives that were made. Consequently, we were not able to determine if *Conolampas* dropped its cargo of debris at night.

At Curacao, Netherlands Antilles, in June 2011 and in August 2012, in dives on the *Curasub*, we observed a total of about 100 individuals of this species at depths of 274–305 m, almost always carrying a cover of coarse debris. In our 2012 dives, we were surprised to find that, in a population of about 40 individuals, 8 were not covered. We were unable to investigate this seemingly abnormal behavior, but we noted that the fine sediment on which these animals were sitting seemed to be remarkably homogeneous in texture, lacking conspicuous larger pieces of debris. All of the individuals that were covered carried only a topknot of small pieces of debris. Perhaps the few naked individuals had not

**Table 1**

Bathyal Bahamas echinoids documented during dives of the JSL submersibles, 1983–1989.

	<sup>a</sup> Depth range (m)	Covered?
<b>Order Cidaroida</b>		
<i>Cidaris abyssicola</i> (Agassiz, 1869)	633–723	No
<i>Cidaris blakei</i> (Agassiz, 1878)	577–902	No
<i>Cidaris rugosa</i> (Clark, 1907)	658–788	No
<i>Calocidaris micans</i> (Mortensen, 1903)	226–624	No
<i>Histocidaris nuttingi</i> (Mortensen, 1926)	618–624	No
<i>Histocidaris sharreri</i> (Agassiz, 1880)	732–868	No
<i>Histocidaris purpurata</i> (Thomson, 1872)	903	No
<i>Stylocidaris lineata</i> (Mortensen, 1910)	240–630	No
<i>Tretocidaris bartletti</i> (Agassiz, 1880)	212–305	No
<b>Order Echinothurioida</b>		
<i>Araeosoma belli</i> (Mortensen, 1903)	272–709	No
<i>Araeosoma fenestratum</i> (Thomson, 1872)	703–834	No
<i>Hygrosoma petersii</i> (Agassiz, 1880)	403	No
<i>Phormosoma placenta</i> (Thomson, 1872)	231–768	No
<b>Order Salenioida</b>		
<i>Salenia goesiana</i> (Loven, 1874)	314–616	No
<b>Order Aspidodiadematoida</b>		
<i>Aspidodiadema jacobyi</i> (Agassiz, 1880)	411–696	No
<b>Order Diadematoida</b>		
<i>Centrostephanus longispinus rubicingulus</i> (Clark, 1921)	54–58	No
<b>Order Arbacioida</b>		
<i>Coelopleurus floridanus</i> (Agassiz, 1872)	291–404	No
<b>Order Camarodonta</b>		
<i>Gracilechinus tyloses</i> (Clark, 1912)	778	No
<i>Lytechinus euerces</i> (Clark, 1912)	244–458	Yes/no <sup>b</sup>
<i>Genocidaris maculata</i> (Agassiz, 1869)	99	Unknown <sup>c</sup>
<b>Order Clypeasteroida</b>		
<i>Clypeaster cyclopilus</i> (Clark, 1941)	394–487	No
<i>Clypeaster subdepressus</i> (Gray, 1825)	226–378	No
<b>Order Spatangoida</b>		
<i>Aceste bellidifera</i> (Thomson, 1877)	569	Buried
<i>Agassizia excentrica</i> (Agassiz, 1869)	453–455	Buried
<i>Brissopsis atlantica</i> (Mortensen, 1907)	613–624	Buried
<i>Heterobrissus hystrix</i> (Agassiz, 1880)	237–614	No
<i>Linopneustes longispinus</i> (Agassiz, 1878)	231–700	Buried <sup>d</sup>
<i>Palaeobrissus hilgardii</i> (Agassiz, 1880)	598–698	Yes/no <sup>e</sup>
<i>Paleopneustes cristatus</i> (Agassiz, 1873)	265–592	No
<i>Paleopneustes tholoformis</i> (Chesher, 1968)	236–645	No
<i>Pleurobrissus grandis</i> (Gmelin, 1788)	392–409	Buried
<i>Plethotaenia angularis</i> (Chesher, 1968)	618–645	Buried
<b>Order Echinolampadoida</b>		
<i>Conolampas sigsbei</i> (Agassiz, 1878)	272–540	Yes

<sup>a</sup> Depth ranges given here are those encountered during the program of Bahamas submersible dives. For broader depth ranges of most species, see Serafy (1979) and Pawson et al. (2009).

<sup>b</sup> In *Lytechinus euerces*, some individuals were covered, and some were not.

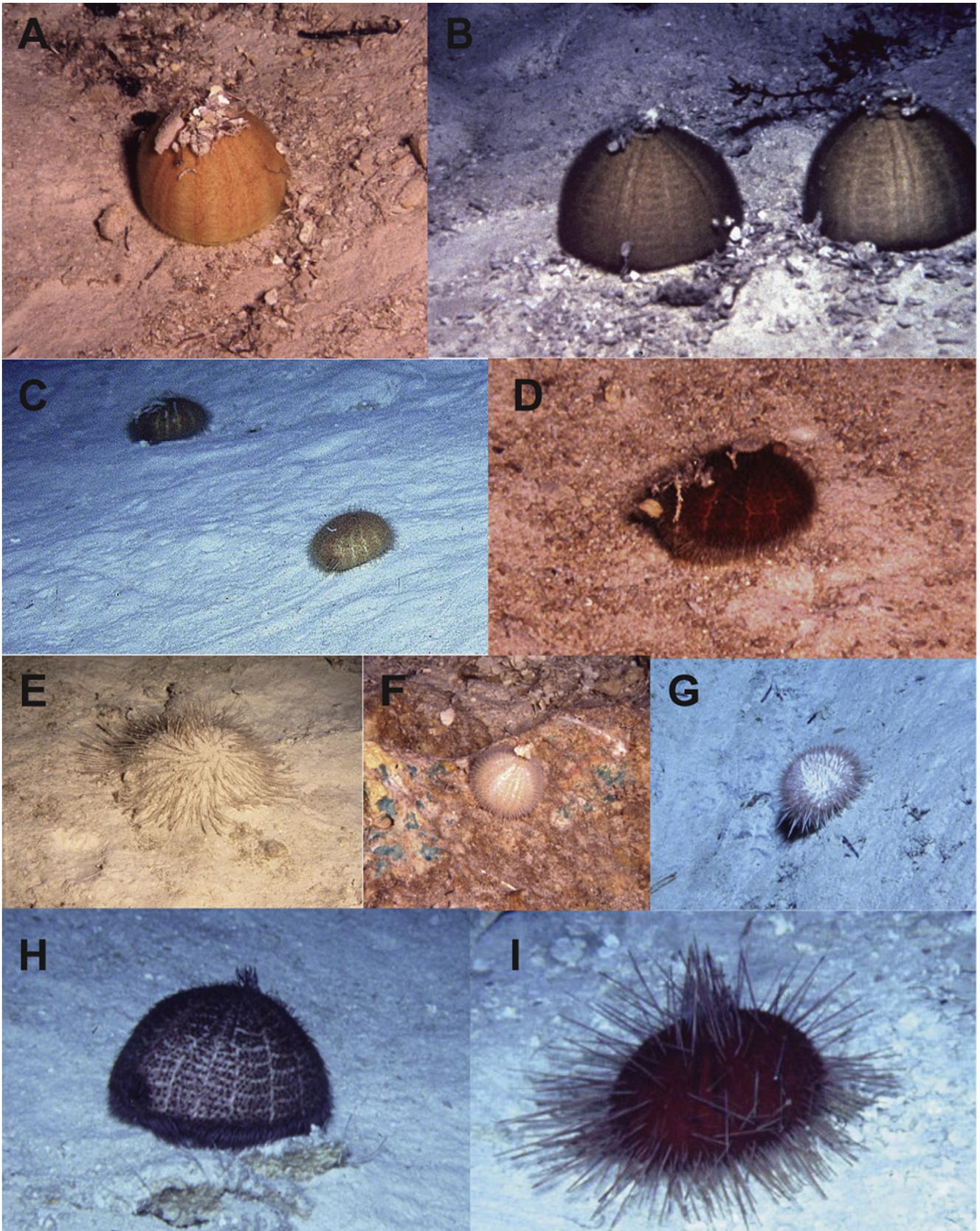
<sup>c</sup> This species is of such small size (ca. 10 mm diameter) that it could not be readily observed, whether covered or uncovered, from the submersible. It is possible that *Genocidaris maculata*, like its close relatives, covers itself.

<sup>d</sup> *Linopneustes longispinus* was observed at times to be partially buried.

<sup>e</sup> In *Palaeobrissus hilgardii*, some individuals were partially covered, and some were not.

yet come into contact with debris of a size sufficient to cover themselves.

*Palaeobrissus hilgardii* (A. Agassiz) On Dive JSL-I-1707 two individuals were photographed (Fig. 1C) at a depth of 608 m, and on Dive JSL-I-2009 one was photographed (Fig. 1D) at a depth of 611 m. Two of these three individuals carried a few pieces of debris on the upper surface of the body, and the third was essentially naked, with one piece of debris placed on or near its left posterolateral petal.



**Fig. 1.** Some bathyal echinoids from the Bahamas. (A) *Conolampas sigsbei*, Dive JSL-I-1502, 473 m. (B) *Conolampas sigsbei*, Dive JSL-I-1501, 535 m. (C) *Palaeobrissus hilgardi*, Dive JSL-I-1797, 608 m. (D) *Palaeobrissus hilgardi*, Dive JSL-I-2009, 611 m. (E) *Linopneustes longispinus*, Dive JSL-I-2258, 561 m. (F) *Lytechinus euerces*, Dive JSL-I-2006, 326 m. (G) *Gracilechinus tylodes*, Dive JSL-II-813, 778 m. (H) *Paleopneustes cristatus*, Dive JSL-I-1703, 563 m. (I) *Heterobrissus hystrix*, Dive JSL-I-1703, 563 m. Reproduced with permission from the Smithsonian Institution and Harbor Branch Oceanographic Institution, Inc.

*Lytechinus euerces* (H.L. Clark) (Fig. 1F). This species was photographed or videotaped *in situ* on five dives. On four of these dives (JSL-I Dives 1357, 1504, 1706 and 2006), at depths of 303–309, 323, 299 and 326 m respectively, the individuals were at least partially covered with debris, including in one case a small rock fragment (Fig. 1F). At a depth of 565 m (JSL-II Dive 1502), two individuals carried no cover at all. On Dive 1504, at 323 m, all of the submersible's lights were turned off to subjectively determine how much natural light was reaching this depth. In his video commentary, Porter Kier (personal communication) noted “a clear outline of the bottom could be seen”.

### 3.2. Notes on behavior of some other Bahamas echinoids

*Linopneustes longispinus* (A. Agassiz) (Fig. 1E). This species was documented on 6 dives, at depths of 527–782 m. In some cases, individuals were partially buried, as in Fig. 1E, covered with a thin veneer of fine sediment. Other individuals were found with scattered fragments of sediment on their tests.

*Paleopneustes cristatus* (A. Agassiz, 1873), documented on 8 dives, at depths of 265–592 m (Fig. 1H), *Paleopneustes tholoformis* (Chesher, 1968), documented on 6 dives, at depths of 236–645 m, and *Heterobrissus hystrix* (A. Agassiz, 1880), documented on 14 dives, at depths of 237–614 m (Fig. 1I). These species were common, often present in “herds” comprising scores of individuals. Unlike the species discussed above, these never carried debris on the upper surface of their tests, even though the two *Paleopneustes* species had relatively short spines, somewhat similar to those of *C. sigsbei*. It was notable, though, that in these three species, the apical spines were found to be converging, forming a tuft above the apical system (see Fig. 1H and I), as if in a protective mode. In *P. cristatus*, the apical spines are seen to be longer than other spines on the upper surface of the test (Fig. 1H), a fact noted by Chesher (1968); in *P. tholoformis* the apical spines are not notably longer than others.

## 4. Discussion

In terms of composition, the bathyal echinoid fauna of the Bahamas presents no surprises. Most of the species we encountered are reasonably common in many areas of the Caribbean. Six Bahamas species are not yet known from the Gulf of Mexico (Pawson et al., 2009), but they are expected to occur there.

Covering behavior in shallow-water sea urchins, mostly members of the order Camarodonta, has attracted the interest of biologists since classical Greek and Roman times, according to Harvey (1956). Pliny, and later Camerarius (1654), commented on covering, and both suggested that sea urchins covered themselves with stones as a storm approached, to provide ballast and prevent rolling of the animals during heavy wave action. James (2000) and Dumont et al. (2007) showed that for some species, covering can indeed be related to wave action, and in some cases the degree of covering is size-dependent, smaller individuals – being more susceptible to turbulence – covering to a relatively greater extent than larger individuals.

Modern research on sea urchin covering essentially began with Schmidt (see Brehm, 1884), and continues to the present day. Of particular interest have been the works of Millott (1956, 1965, 1966), Raup (1962) and Dambach and Hentschel (1970), and these have led to a spate of publications in recent years. The covering reaction seems to have attracted special interest because the reasons for covering appear to be complex, and the covering itself seems to be aimed at achieving a variety of results. Covering as a means of reducing or avoiding incident light has been proposed by Von Uexküll (1899), Dubois (1914), Mortensen (1943a,b), Cuénot

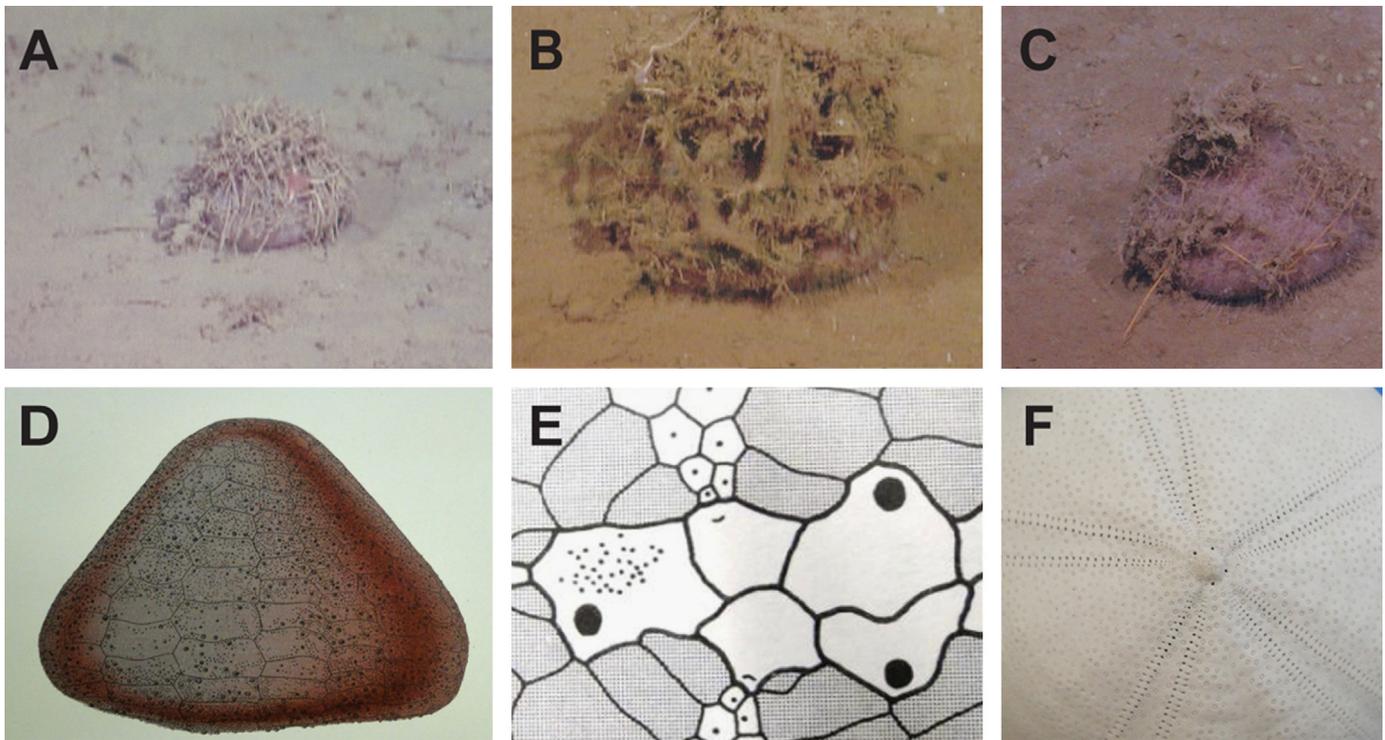
(1948), Millott (1956), Raup (1962), Kehas et al. (2005), Crook and Barnes (2001), Crook (2003), and others. Covering to specifically avoid ultraviolet light has been demonstrated for some species by Lees and Carter (1972), Adams (2001), Verling et al. (2002), and Dumont et al. (2007). Dix (1970) observed covering as a means of food (drift algae) stockpiling in the New Zealand species *Evechinus chloroticus*. The suggestions of Boone (1925) that covering in *Lytechinus variegatus* functioned as a predator-avoiding disguise, and also as camouflage as the echinoid sought prey, were discounted by Mortensen (1943a) and others, and Dumont et al. (2007) found no evidence that presence of predators affected covering behavior in *Strongylocentrotus droebachiensis*. However, Dayton et al. (1970) and Amsler et al. (1999) showed that in *Sterechinus neumayeri* covering increased the probability of surviving an attack by predatory sea anemones. Covering as a form of chemical defense has been suggested by a few investigators, including Dayton et al. (1970) for *S. neumayeri*, and for a deep-sea species, *Cystechinus loveni*, by Levin et al. (2001) (see below).

Dambach and Hentschel (1970) and Lawrence (1976) have provided some evidence to suggest that covering can be merely a reflex response to the presence of debris close to, and in contact with, the test and spines of echinoids. Given all of these documented complexities, it is not surprising that several recent authors (see Verling et al., 2004) have concluded that covering is not merely a response to a single extraneous cue, but it is instead a response to several biotic and abiotic factors.

### 4.1. Covering in deep-sea echinoids, especially *C. sigsbei*

It is usually assumed (Millott, 1956) that covering behavior is displayed only in shallow-water regular echinoids, most of them living in relatively exposed habitats. In the two published deep-sea records that we could find, Levin et al. (2001) documented astonishing covering in an abyssal species, the urchinid *C. loveni*, in the northeastern Pacific at a depth of 3088 m, and David et al. (2003) reported “conveying behavior” in the abyssal pourtalesiid *Cystocrepis setigera* off Peru at a depth of approximately 2500 m. In the latter case, the diverse cargo of organisms may have settled upon the echinoid, rather than being actively accumulated; this may be characterized as “passive covering”. The covering in *Cystechinus* is discussed below.

Of the three bathyal Bahamas species now known to exhibit covering behavior, *C. sigsbei* is the most surprising, for it was observed in the Bahamas to be almost always covered, even at depths approaching 800 m. No other members of the Order Echinolampadoida are known to cover themselves. In *Conolampas*, the tube feet are well-developed, each arising from double pores in the test, and they run in double bands from the ambitus to the apex (Fig. 2F). Short spines are numerous in ambulacra and interambulacra. In Fig. 1B, debris is being moved up two ambulacra in the individual on the left. Mortensen (1948, p. 305) has noted that *some* of the tube feet are equipped with “a large sucking disk”. A cursory examination by us in Curacao in 2011, and again in 2012, revealed that many of the tube feet on the upper surface have rounded tips; we found no feet with terminal disks. Presumably, all of the tube feet on the upper surface of the body, whether they possess disks or lack them, have adhesive properties (Flammang, 1996; Santos et al., 2005), and they can cling to pieces of debris, small and large, for varying periods of time. Further study of the tube feet in this species is in progress. It is evident, though, that *Conolampas*, using its tube feet and spines, is capable of moving quite substantial pieces of debris to its apex (see Fig. 1A), and retaining them in place. We collected these sea urchins at Curacao on one occasion in August 2012, using a manned submersible. Two specimens were “shoveled” from the seabed in a collecting net. In this process, both individuals were



**Fig. 2.** (A–E) *Cystechinus loveni*, northeastern Pacific. (A) 35.81°N, 122.57°W, 6/21/2006, 3266.42 m, ©2006 MBARI. (B) 45.40°N, 126.72°W, 8/27/2006, 2817.98 m, ©2006 MBARI. (C) 41.00°N, 127.55°W, 8/27/2005, 3270.5 m, ©2005 MBARI. (D) Bare test, showing sparsely scattered tubercles, after Agassiz (1869). (E) Apical area of bare test, showing single pores for tube feet, and three genital pores. After Mooi and David (1996). Reproduced with permission. (F) *Conolampas sigsbei*, apical region of bare test, showing double pores for tube feet.

tilted towards the submersible at an angle of at least 60 degrees from horizontal; we could clearly observe these individuals for several minutes, and we noted that not one of the numerous pieces of debris on top of both urchins was dislodged during the collecting and tilting.

Covering in *Conolampas* is clearly not a means of stockpiling food, avoiding desiccation, affording camouflage, avoiding temperature extremes, or of providing some sort of mechanical or chemical defense against predators. *Conolampas* commonly occurs on steep rocky slopes; can covering provide some ballast, to help prevent the animal from rolling down the slope? We believe that this is not the case, for two reasons: firstly, the weight of the covering material is negligible relative to the weight of the live animal, and it would not represent significant ballast. Secondly, *Conolampas* has a flat bottom, and a low center of gravity. Using the mechanical arm of the submersible, we have tried on several occasions to tip *Conolampas* over, and it is almost impossible; the animal always very promptly falls back onto its flat oral surface. Some form of additional ballast to improve stability is probably not needed.

It seems unlikely that deep-sea covering is light-related, as has been demonstrated for many shallow-water species. Ultraviolet radiation in sunlight has been shown to be a significant factor in covering by Adams (2001) and Verling et al. (2002) and others, but UV radiation rapidly becomes attenuated when sunlight enters seawater, and essentially disappears by a depth of 20 m (Jerlov, 1950; McFarland, 1986). In clear tropical waters, objects on the seafloor can be vaguely seen by the human eye at depths in excess of 300 m but, in this almost-dark twilight zone, why do some sea urchin species need to cover, and some not? Unfortunately, we have no night-time records, but we assume that in *Conolampas* the cover is retained at night, in contrast to shallow-water species such as *Triploneustes ventricosus*, which sheds its burden at night and picks it up again in the morning (Kehas et al.,

2005, and others). In relation to shedding of cover, Chen and Soong (2010) described “uncovering” behavior in *Toxopneustes pileolus* at spawning time (29 May, 2009); when ready to spawn this species drops its extensive cover, and then releases its gametes. Presumably covering was resumed upon completion of spawning. Mortensen (1943a) asserted, incorrectly, that this species did not cover itself.

Dambach and Hentschel (1970), with support from Lawrence (1976) suggest that covering is a merely reflexive tactile response to the presence of debris—“reflexive walking” as Dambach and Hentschel put it. Given that the usual causes of covering in shallow-water species do not seem to apply to deep-sea species, perhaps covering behavior in *Conolampas* is simply a reflexive action.

In the case of other urchins observed to “cover” in the Bahamas, we can do no more than record what we have observed. In the few records of *L. euerces*, we note that specimens found at depths of 299–326 m were all partially covered, and that the single specimen at 565 m was naked. Is this phenomenon somehow related to ambient light? *P. hilgardi* was found (Fig. 1C and D) with debris on its upper surface. This debris may have fallen onto these individuals from the steep slopes above, some may have drifted along and become entangled in the spines and tube feet, and some may have been picked up by the animal. Our observations on these species offer little in the way of answers to questions raised.

Finally, we observed the tendency of some echinoid species to “clump” their apical spines (Fig. 1H and I) with their distal extremities converging, a response of a type similar to that described as the shadow reaction in *Diadema* (Yoshida, 1966) and other sea urchins. We are not sure if this clumping is a full-time behavioral trait, or a rapid response to the slowly approaching submersible, with its lights and bow-wave. Our observations from a submersible and in the laboratory at Curacao in August 2012 suggest that the spine-clumping is not induced by the

submersible. Clumping was observed in a short-spined (Fig. 1H) as well as a long-spined (Fig. 1I) species; perhaps the clumping of spines is a form of protection for the genital pores, ocular pores, or madreporite. It is possible that, in *Conolampas*, which lacks elongated apical spines, the covering behavior serves simply to protect these apical pores. Further laboratory experiments using live *Conolampas* in varying physical conditions might help to provide some answers, and suggest directions for future research. In the meantime, the larger questions about covering in these bathyal species remain unanswered.

#### 4.2. Covering in *C. loveni*

Levin et al. (2001) described a specimen of the urchinoid echinoid *Cystechinus loveni* (Agassiz, 1898) (formerly *Urechinus loveni*) from the Gulf of Alaska, carefully collected in a tube core at a depth of 3088 m, which carried an astonishingly diverse cargo of living and dead protists. Levin et al. reasoned that the usual causes adduced for covering in shallow-water species do not apply to *Cystechinus*, but perhaps the covering in this species provides a chemical camouflage, or a change in specific gravity to reduce transport by currents.

Recent images of the same species, from other localities in the northeastern Pacific, are presented here (Fig. 2A and C). These images provide some new information in relation to covering in this species. As no naked individuals of *Cystechinus* have been observed *in situ*, it can be assumed that this species is always transporting a diverse population of protists. Some other species of surface-dwelling irregular echinoids that live in the same abyssal area, such as *Echinocrepis rostrata* (Mironov, 1973; Vardaro et al., 2007), appear in contrast to be always naked.

The bulk of the covering organisms listed by Levin et al. could theoretically have drifted and settled upon the echinoid, and grown there, without any assistance from the echinoid. Given the fact that *Cystechinus* has only sparsely scattered spines (Fig. 2D), and few tube feet, which arise from single podial pores (Fig. 2E) in the skeleton (test) rather than the more common double pores, it might be suggested that this animal is not well-equipped to actively pick up materials from the seabed and pass them to its upper surface using coordinated movements of its spines and tube feet, as in shallow-water taxa (Millott, 1966). Two facts help to contradict this idea: first, the tube feet, despite their small size and the single podial pores in the skeleton (test), have terminal disks (Smith, 1980), and they presumably can attach to, and pass, small objects upwards. Second, and most importantly, Levin et al. note that in their specimen the cargo included “four pebbles of basalt or clinker”. Clearly these pebbles did not drift and contact the urchin; they must have been actively picked up and held in place. This is indeed “active covering”. In the absence of additional evidence, we can only speculate upon the speculations of Levin et al. (2001) on the role of covering in *C. loveni*. We cannot agree that the covering provides an increase in specific gravity sufficient to help “anchor” the animal in the event of an increase in current speed; indeed, the covering raises the profile of the animal, presumably making it more susceptible to disturbance by currents. The notion of a “chemical camouflage”, briefly suggested by Levin et al., presumably aimed at deterring or misleading potential predators, is persuasive, despite the fact that other, related, echinoids in the area are apparently always naked.

#### Acknowledgments

DLP is most grateful to John E. Miller, Gordon Hendler, and Porter M. Kier, treasured colleagues and lifelong friends, for the wonderful experience of field work in many parts of Florida and

the Caribbean, especially the many dives in the *Johnson-Sea-Link* submersibles. Partial support for this research was provided by a Smithsonian Regents' Fellowship, the Smithsonian Marine Station at Fort Pierce, the NMNH's Small Grants program, and by Harbor Branch Oceanographic Institution, Inc.

Colleagues at Scripps Institution of Oceanography, Inc., have kindly provided access to collections of animals, and to still and video imagery. We thank Ken Smith (now at MBARI), Greg Rouse, and Harim Cha for their help. At Monterey Bay Aquarium Research Institute, Linda Kuhn has been especially helpful.

In June 2011, and again in August 2012, we made a total of six dives at Curacao, in the *Curasub*, based at Substation Curacao, to depths of approximately 305 m. These dives were part of the Smithsonian Institution's Deep Reef Observation Project, organized and led by Dr. Carole Baldwin (NMNH). We thank Dr. Baldwin, and Mr. Adriaan “Dutch” Shrier, owner of Substation Curacao, for enabling our participation in this project. We also thank the National Museum of Natural History's Small Grant Program for financial support, and Cristina Castillo for valuable assistance.

We are grateful to Cheryl Ames for assistance with the illustrations, and to Dr. Andreas Kroh and an anonymous reviewer for their very helpful comments on an earlier version of this paper.

We thank Dr. Paul Tyler of the University of Southampton for his friendship over many years, and for his pioneering and inspiring role in the study of deep-sea echinoderms.

#### References

- Adams, N.L., 2001. UV radiation evokes negative phototaxis and covering behavior in the sea urchin *Strongylocentrotus droebachiensis*. *Mar. Ecol. Prog. Ser.* 213, 87–95.
- Agassiz, A., 1869. Preliminary report on the echini and star-fishes dredged in deep water between Cuba and the Florida Reef, by L.F. de Pourtales, Assist. U.S. Coast Survey. *Bull. Mus. Comp. Zool. Harvard* 1 (9), 253–308.
- Agassiz, A., 1872. Revision of the Echini. *Mem. Mus. Comp. Zool. Harvard* 3, 1–762.
- Agassiz, A., 1873. The Echini collected on the Hassler Expedition. *Bull. Mus. Comp. Zool. Harvard* 3 (8), 187–190.
- Agassiz, A., 1878. Report on the Echini. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the United States Coast Survey Steamer Blake, Lieut.-Commander C.D. Sigsbee, U.S.N., Commanding. II. *Bull. Mus. Comp. Zool. Harvard* 5 (9), 185–196.
- Agassiz, A., 1880. Preliminary report on the Echini. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the United States Coast Survey Steamer Blake, Lieut.-Commander C.D. Sigsbee, U.S.N., Commanding. *Bull. Mus. Comp. Zool. Harvard* 8 (2), 69–84.
- Amsler, C.D., McClintock, J.B., Baker, B.J., 1999. An Antarctic feeding triangle: defensive interactions between macroalgae, sea urchins, and sea anemones. *Mar. Ecol. Prog. Ser.* 183, 105–114.
- Boone, L., 1925. Echinodermata from tropical East American seas. *Bull. Bingham Oceanogr. Collect.* 1 (4), 1–22.
- Brehm, A.E., 1884. *Merveilles de la Nature*. Bailliére, Paris.
- Camerarius, J., 1654. *Symbolorum et Emblematum ex re Herbaria Desumptorum Centuria IV, Una Collecta*. Frankfurt.
- Chen, A., Soong, K., 2010. “Uncovering” behavior at spawning of the trumpet sea urchin *Toxopneustes pileolus*. *Zool. Stud.* 49 (1), 9.
- Chesher, R.H., 1968. The systematicws of sympatric species in West Indian spatangoids: a revision of the genera *Brissopsis*, *Plethotaenia*, *Palaeopneustes*, and *Saviniaaster*. *Stud. Trop. Oceanogr. (Miami)* 7, 1–165.
- Clark, H.L., 1907. The Cidaridae. *Bull. Mus. Comp. Zool. Harvard* 51 (7), 163–230.
- Clark, H.L., 1912. Hawaiian and other Pacific Echini. The Pedinidae, Phymosomatidae, Stomopneustidae, Echinidae, Temnopleuridae, Strongylocentrotidae, and Echinometridae. *Mem. Mus. Comp. Zool. Harvard* 34 (4), 205–383.
- Clark, H.L., 1921. Report on the Echinoidea Collected by the Barbados-Antigua Expedition from the University of Iowa in 1918. *Univ. Iowa Stud. Nat. Hist* 9 (5), 103–121.
- Clark, H.L., 1941. The echinoderms (other than holothurians). Reports on the scientific results of the Atlantis expeditions to the West Indies. *Mem. Soc. Cubana Hist. Nat* 15 (1), 1–154.
- Coppard, S.E., Kroh, A., Smith, A.B., 2010. The evolution of pedicellariae in echinoids: an arms race against pests and parasites. *Acta Zool.* 20, 1–24.
- Crook, A.C., 2003. Individual variation in the covering behaviour of the shallow water sea urchin *Paracentrotus lividus*. *Mar. Ecol.* 24 (4), 1–22.
- Crook, A.C., Barnes, D.K.A., 2001. Seasonal variation in the covering behaviour of the echinoid *Paracentrotus lividus* (Lamarck). *Mar. Ecol.* 22 (3), 231–239.
- Cuénot, L., 1948. In: Pierre-P. Grassé, G. (Ed.), *Traité de Zoologie*, vol. 2. Masson, Paris, p. 137.

- Dambach, M., Hentschel, G., 1970. Die Bedeckungsreaktion von Seeigeln. Neue Versuche und Deutungen. *Mar. Biol.* 6, 135–144.
- David, B., Magniez, F., Villier, L., de Wever, P., 2003. Conveying behavior of the deep sea pourtalesiid *Cystocrepis setigera* off Peru. In: Féral, J.-P., David, B. (Eds.), *Echinoderm Research*. Swets and Zeitlinger, Lisse, pp. 253–257. In: Féral, J.-P., David, B. (Eds.), *Echinoderm Research*. Swets and Zeitlinger, Lisse, pp. 253–257.
- Dayton, P.K., Robilliard, G.A., Paine, R.T., 1970. Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. In: Holdgate, M.W. (Ed.), *Antarctic Ecology*, vol. 1. Academic Press, London, pp. 244–258.
- Dix, T.G., 1970. Covering response of the echinoid *Evechinus chloroticus* (Val.). *Pac. Sci.* 24 (2), 187–194.
- Dubois, R., 1914. Action de la lumière sur les Echinodermes. *C. R. Int. Congr. Zool.* 9, 148.
- Dumont, C.P., Drolet, D., Deschênes, I., Himmelman, J.H., 2007. Multiple factors explain the covering behaviour in the green sea urchin, *Strongylocentrotus droebachiensis*. *Anim. Behav.* 73 (6), 979–986.
- Flammang, P., 1996. Adhesion in echinoderms. In: Jangoux, M., Lawrence, J.M. (Eds.), *Echinoderm Studies*, vol. 5. Balkema, Rotterdam, pp. 1–60.
- Gmelin, J.F., 1788. *Linnaei Systema Naturae* 13 (6), 3200.
- Gray, J.E., 1825. An attempt to divide the Echinida, or sea eggs, into natural families. *Ann. Phil.* 26, 423–431.
- Harvey, E.B., 1956. *The American Arbacia and other Sea Urchins*. Princeton University Press, Princeton, New Jersey, pp. 1–298.
- James, D.W., 2000. Diet, movement, and covering behavior of the sea urchin *Toxopneustes roseus* in rhodolith beds in the Gulf of California, México. *Mar. Biol.* 137, 913–923.
- Jerlov, N.G., 1950. Ultra-violet radiation in the sea. *Nature* 166, 111–112.
- Kehas, A.J., Theoharides, K.A., Gilbert, J.J., 2005. Effect of sunlight intensity and albinism on the covering response of the Caribbean sea urchin *Tripneustes ventricosus*. *Mar. Biol.* 146, 1111–1117.
- Lawrence, J., 1976. Covering response in sea urchins. *Nature* 262, 490–491.
- Lees, D.C., Carter, G.A., 1972. The covering response to surge, sunlight, and ultraviolet light in *Lytechinus anamesus* (Echinoidea). *Ecology* 53, 1127–1133.
- Levin, L.A., Gooday, A.J., James, D.W., 2001. Dressing up for the deep: agglutinated protists adorn an irregular urchin. *J. Mar. Biol. Assoc. UK* 81, 881–882.
- Lovén, S., 1874. Etudes sur les Echinoidées. *Svenska. Vetenskapsakad. Handl* 11 (7), 1–91.
- Mortensen, T., 1903. Echinoidea (Part I). *Danish Ingolf-Exped* 4 (1), 1–193.
- Mortensen, T., 1907. Echinoidea (Part II). *Danish Ingolf-Expedition* 4 (2), 1–200.
- Mortensen, T., 1910. On some West Indian echinoids. *Bull. U.S. Nat. Mus.* 74, 1–31.
- Mortensen, T., 1926. A new West Indian cidarid. *Univ. Iowa Stud. Nat. Hist* 11 (7), 5–8.
- McFarland, W.N., 1986. Light in the sea—correlations with behaviours of fishes and invertebrates. *Am. Zool.* 26, 389–401.
- Millott, N., 1955. The covering reaction in a tropical sea urchin. *Nature* 175, 561.
- Millott, N., 1956. The covering reaction of sea-urchins. I. A preliminary account of covering in the tropical echinoid *Lytechinus variegates* (Lamarck), and its relation to light. *J. Exp. Biol.* 33 (3), 508–523.
- Millott, N., 1965. In: Bainbridge, R., Evans, G.C., Rackham, O. (Eds.), *The Enigmatic Echinoids*. Blackwell, Oxford, pp. 265–291.
- Millott, N., 1966. Coordination of spine movement in echinoids. In: Booloottian, R.A. (Ed.), *Physiology of Echinodermata*. John Wiley and Sons, New York, pp. 465–486.
- Mironov, A.N., 1973. New deep-sea echinoid species of the genus *Echinocrepis* and distribution patterns of the family Pourtalesiidae (Echinoidea, Meridosternina). *Tr. Shirshov Inst. Oceanol.* 91, 240–247.
- Mooi, R., David, B., 1996. Phylogenetic analysis of extreme morphologies: deep-sea holasteroid echinoids. *J. Nat. Hist.* 30 (6), 913–953.
- Mortensen, T., 1943a. A Monograph of the Echinoidea. III, 2. Camarodonta I. Reitzel, Copenhagen.
- Mortensen, T., 1943b. A Monograph of the Echinoidea. III, 3. Camarodonta II. Reitzel, Copenhagen.
- Mortensen, T., 1948. A Monograph of the Echinoidea. IV, 1. Holecypoida, Cassiduloidea. Reitzel, Copenhagen.
- Pawson, D.L., Vance, D.J., Messing, C.G., Solis-Marin, F.A., Mah, C.L., 2009. Echinodermata of the Gulf of Mexico. In: Felder, D.L., Camp, D.K. (Eds.), *Gulf of Mexico: Origin, Waters, and Biota*. Texas A&M University Press, College Station, Texas, pp. 1177–1204.
- Raup, D.M., 1962. The phylogeny of calcite crystallography in echinoids. *J. Pal.* 36 (4), 793–810.
- Reese, E., 1966. The complex behavior of echinoderms. In: Booloottian, R.A. (Ed.), *Physiology of Echinodermata*. John Wiley and Sons, New York, pp. 157–218.
- Santos, R., Gorb, S., Jamar, V., Flammang, P., 2005. Adhesion of echinoderm tube feet to rough surfaces. *J. Exp. Biol.* 208, 2555–2567.
- Serafy, D.K., 1979. Echinoids (Echinodermata: Echinoidea). *Mem. Hourglass Cruises* 5 (3), 1–120.
- Smith, A.B., 1980. The structure, function, and evolution of tube feet and ambulacral pores in irregular echinoids. *Palaeontology* 23 (1), 39–84.
- Thomson, C.W., 1872. On the Echinoidea of the Porcupine dredging expeditions. *Proc. Roy. Soc. London* 20, 491–497.
- Thomson, C.W., 1877. *The voyage of the Challenger. The Atlantic; a preliminary account of the general results of the exploring voyage of H.M.S. Challenger during the year 1873 and the early part of the year 1876*. Macmillan, London, 424 pp.
- Vardaro, M.F., Parmley, D., Smith, K.L., 2007. A study of possible “reef effects” caused by a long-term time-lapse camera in the deep north Pacific. *Deep-Sea Res.* 1 (54), 1231–1240.
- Verling, E., Crook, A.C., Barnes, D.K.A., 2002. Covering behaviour in *Paracentrotus lividus*: is light important? *Mar. Biol.* 140, 391–396.
- Verling, E., Crook, A.C., Barnes, D.K.A., 2004. The dynamics of covering behaviour in dominant echinoid populations from American and European west coasts. *Mar. Ecol.* 25 (3), 191–206.
- Von Uexküll, J., 1899. *Die Physiologie des Seeigelstachels*. *Z. Biol.* 39, 73.
- Yoshida, M., 1966. Photosensitivity. In: Booloottian, R.A. (Ed.), *Physiology of Echinodermata*. Interscience, New York, pp. 435–464.