

Echinoids of the Pacific Waters of Panama: Status of knowledge and new records

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Abstract: This paper is primarily intended as a guide to researchers who wish to know what echinoid species are available in the Bay of Panama and in the Gulf of Chiriqui, how to recognize them, and what has been published about them up to 2004. Fifty seven species of echinoids have been reported in the literature as occurring in the Pacific waters of Panama, of which I have collected and examined 31, including two species, *Caenopedina diomediae* and *Meoma frangibilis*, that have hitherto only been mentioned in the literature from single type specimens. For the 31 species I was able to examine, I list the localities in which they were found, my impression as to their relative abundance, the characters that distinguish them, and what is known about their biology and evolution. Not surprisingly, most available information concerns abundant shallow water species, while little is known about deep water, rare, or infaunal species. Rev. Biol. Trop. 53(Suppl. 3): 147-170. Epub 2006 Jan 30.

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The eastern Pacific waters of Panama extend roughly from 9°01' N, 82°52' W to 6°50' N, 77°54' W (Fig. 1). They comprise two embayments, separated by the Azuero Peninsula: (1) The Bay of Panama, which contains the Pearl Island Archipelago and (2) the Gulf of Chiriqui, which contains various island complexes, with Islas Coiba, Cebaco, Ladrões, Secas and Contreras, being the most prominent. Though depths within the two bays are shallower than 200 m, the 1 000 m isobath passes within less than a kilometer from the shores of the Azuero and Burica Peninsulas and the island of Jicaron (Fig. 1). Oceanographic conditions of the area have been described by Forsbergh (1969), Glynn (1972, 1982), D'Croz *et al.* (1991), D'Croz and Robertson (1997), and Podesta and Glynn (2001). There are pronounced differences in the seasonality of thermal and trophic regimes of the two bays. Whereas the Gulf of Chiriqui is protected by high mountains from the trade winds out of the North, the Bay of Panama is exposed during

the dry season (December-April) to these strong winds. The winds push surface water to the South, and cause upwelling of cold, nutrient rich water, which greatly increases primary productivity, but also reduces surface temperatures from an average of about 26° to as low as 16°C. Possibly as a consequence of the low temperatures, certain ecologically important echinoderm species, such as *Acanthaster planci* (L.), though present in the Gulf of Chiriqui, do not enter the Bay of Panama (Glynn 1974).

The echinoid fauna of the Pacific coast of Panama (and the rest of the eastern Pacific) has been sampled and described during the past two centuries mostly as the result of the "Albatross" (Agassiz 1898, 1904), "Zaca" (H.L. Clark 1940), and Velero III (A.H. Clark 1939, H.L. Clark 1948) expeditions. Detailed information about the distribution of echinoderms of the region has been very ably synthesized and tabulated by Maluf (1988), who has rendered a tremendous service to echinoderm biogeographers by combing the entire literature

on eastern Pacific echinoderms and plotting the range of each species. Mortensen spent several months on the island of Taboga in the Bay of Panama in 1915, and, though he never published a specific work on the echinoderms of the region, he included the information he gathered on the distribution and larval development of the local echinoids in other publications (e.g. Mortensen 1921, 1928-1951). Boone (1928) listed observations on specimens of echinoderms from Islas Perlas, along with those from the Sea of Cortez, but occasionally confused the two areas, stating at one point that the type specimen of *Arbacia incisa* (A. Agassiz) comes from "Guaymas, Panama". A.H. Clark (1946) also treated specimens that came into his hands from Islas Perlas, but concentrated mostly on *Encope*, and described a new species, *E. wetmorei* A. H. Clark from the area. Chesher (1972) provided a list of eastern Pacific echinoids with presumed Atlantic "gemmates", i.e. species that were formed by the rise of the Isthmus of Panama. However, despite rather intense ecological and molecular

systematic study of certain species that occur off the southern shores of Panama, much of it motivated by the known time of the closure of the Isthmus, there is no work that contains detailed information on which echinoid species are likely to be found in any given locality of the Bay of Panama or of the Gulf of Chiriqui, or a summary of the systematic, phylogenetic, and ecological information that exists for each of them. My own work over the past 25 years on life histories and evolution of various species of echinoids has led me to seek populations and specimens in Panamanian waters. Here I attempt to summarize the information I have gathered about systematics and micro-distributions of Panamanian echinoid species in the course of this work, along with information that can be gleaned from the literature. This paper is primarily intended as a guide to researchers who may wish to know what echinoid species are available in the Bay of Panama and in the Gulf of Chiriqui, how to find them, how to recognize them, and what has been published about them up to 2004.

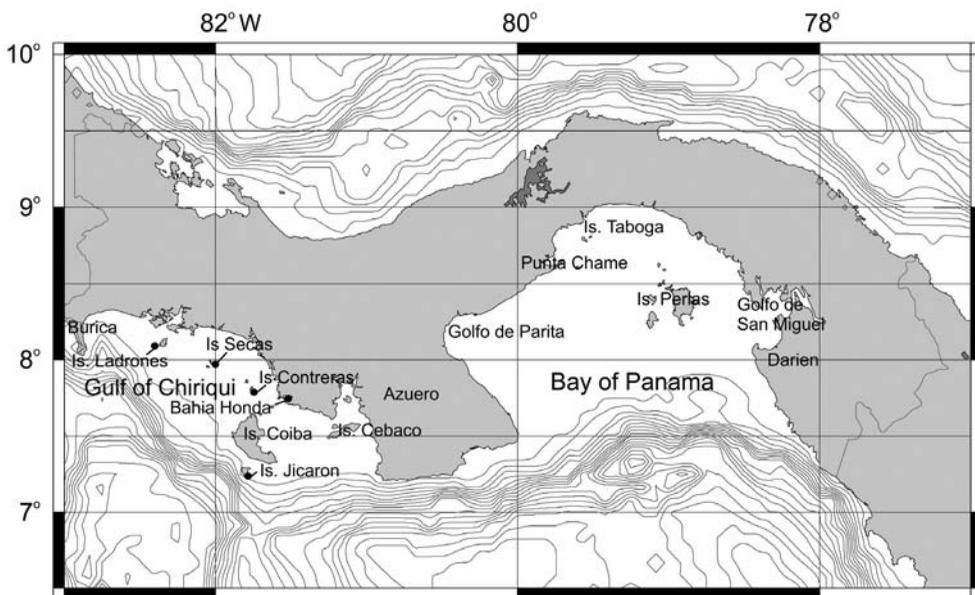


Fig. 1. Pacific waters of Panama: depth contours and main features. Localities are identified in the text in relation to the main features and by indicating their coordinates the first time they are mentioned.

Fig. 1. Aguas del Pacífico de Panamá: contornos de profundidad y características principales. Se identifican las localidades en el texto en relación con las características principales e indicando sus coordenadas en la primera vez que son mencionadas.

Records in the literature

Table 1 is excerpted from the information presented by Maluf (1988) for the entire eastern Pacific, so as to include only those species whose range includes Panama. As the Table indicates, 40 echinoid species are expected to occur in depths of < 100 m, and 17 species in deeper water, for a total of 57 species. For biogeographical purposes, it is important to distinguish those species for which there are actual records of specimen collection within Panamanian waters, from those for which collection records straddle Panamanian latitudes, but have not been documented as occurring in the area. There are seven species that fall in the latter category. Of these, *Kamptosoma asterias* (A. Agassiz), *Plesiodiadema horridum* (A. Agassiz), *Cystocrepis setigera* (A. Agassiz), *Pourtalesia tanneri* A. Agassiz, and *Homolampas fulva* A. Agassiz are deep water species, difficult to collect, and thus could well be located off Panama in future sampling. However, for two additional species, the inference that they are likely to occur in Panama would not necessarily be correct. *Centrostephanus coronatus* (Verrill) is a subtropical species, preferring the colder waters of California and of the Galapagos Archipelago. It has not been found in Panama, though it is apparently present in Costa Rica (J. J. Alvarado pers. com.). *Echinometra oblonga* (Blainville) was found North of Panama in Clarion and Socorro Islands (H.L. Clark 1948), in Angeles Bay, Baja California (Grant and Hertlein 1938), and in the Revillagigedos (Lessios *et al.* 1996), as well as South of Panama in the Galapagos (H.L. Clark 1948). H.L. Clark (1948) remarks on its absence at Isla del Coco, off Costa Rica, but McCartney *et al.* (2000) found individuals with mitochondrial DNA of this species at this island. It might, therefore, be thought reasonable that *E. oblonga* would also exist undetected in Panama. However, *E. oblonga* is a central and western Pacific species, the larvae of which are apparently able to occasionally breach the Eastern Pacific Barrier, and establish populations on the outer eastern Pacific islands. Like another echinoid, *Echinothrix diadema*

(L.), it seems to be confined to the outer islands of the eastern Pacific, without having established populations close to the mainland (Lessios *et al.* 1996, 1998).

In addition to the preceding species about which there may be doubt as to their presence in Panama, there are two species, the absence of which in Panama is almost certain. Maluf's (1988) records of *Lytechinus pictus* (Verrill), and its synonym, *L. anamesus* H.L. Clark, in Panamanian latitudes are based on H.L. Clark's (1948) mention of one specimen from Bahia Honda and one specimen from Gorgona Island, Colombia. Clark states that these may well be specimens of *L. panamensis* Mortensen, and this is very likely the case. Mitochondrial DNA sequences have shown that, though *L. pictus* cannot be distinguished from *L. anamesus* and though *L. panamensis* cannot be distinguished from *L. semituberculatus* (Valenciennes), the clade composed of the first two is quite distinct from the clade of the last two (Zigler and Lessios 2004). There is, therefore, no reason to assume the alternative explanation, that *L. pictus*, *L. anamesus* and *L. panamensis* are all one species. The second case of mistaken literature reports concerns *Caenocentrotus gibbosus* (L. Agassiz and Desor). Maluf (1988) indicates this species as occurring at 8°N, but none of the references she cites places it in any locality above the equator.

Maluf's (1988) compilation indicates that *Brissopsis columbaris* (Agassiz, 1898) is absent from Panama and the rest of Central America, because, based on a personal communication from A. Larrain, she considered it an invalid species, and thus assigned records of its presence by Agassiz (1898), Caso (1983), Grant and Hertlein (1938) and Mortensen (1928-1951) outside the Sea of Cortez to *B. pacifica* (A. Agassiz). Given that there is no treatment in the literature that suggests *B. columbaris* is not a valid species, I have preserved the name, even though I have otherwise based Table 1 on Maluf (1988). I have also added to the list *Mellita grantii* Mortensen and *Mellita notabilis* H. L. Clark, for which Maluf shows distributions that do not reach as far south as Panama, because

Harold and Telford (1990) report examining specimens from Panamanian beaches.

New records

In searching the intertidal during low tide, numerous SCUBA dives, two major dredging trips, and one expedition with the submersible "Sea Link" of the Harbor Branch Oceanographic Institution, I have located 31

echinoid species in the eastern Pacific waters of Panama. For each species, I summarize here my own observations as to its abundance, systematics, and biology in Panama, as well as articles that involve studies at Panama or from Panamanian specimens. For species that are hard to find, I list the exact locations of specimens that I or my colleagues have collected. The following list is arranged in the phylogenetic order shown in Table 1.

TABLE 1

List of echinoid species with published ranges that include the eastern Pacific waters of Panama, and depth ranges of species encountered by the author

CUADRO 1

Lista de especies de equinoideos con rangos publicados que incluyen las aguas del Pacífico oriental de Panamá, y profundidad de las especies encontradas por el autor

Species	Reports of presence in Panama	Reported depth range (m)	Depth for specimens examined (m)
Class Echinoidea			
Subclass Perischoechinoidea			
Superorder Megalopodacea			
Order Cidaroida			
Family Cidaridae			
<i>Aporocidaris milleri</i>	1	300-3937	
<i>Centrocidaris doederleini</i>	1	91-550	198-300
<i>Eucidaris thouarsii</i>	1	0-150	0-15
<i>Hesperocidaris asteriscus</i>	1	2-183	66
<i>Hesperocidaris dubia</i>	1	64-205	72-196
<i>Hesperocidaris panamensis</i>	1	55-274	?
<i>Hesperocidaris perplexa</i>	1	13-1500	60
Subclass Eucechinoidea			
Superorder Diadematacea			
Order Echinothuroidea			
Family Echinothuriidae			
<i>Araeosoma leptaleum</i>	1	1063	740
<i>Tromikosoma hispidum</i>	1	1820-2763	
<i>Tromikosoma panamense</i>	1	2054-3334	
Order Diadematoidea			
Family Diademataidae			
<i>Astropyga pulvinata</i>	1	0-90	10-37
<i>Centrostephanus coronatus</i>	1	0-125	

TABLE 1 (Continued...)
List of echinoid species with published ranges that include the eastern Pacific waters of Panama, and depth ranges of species encountered by the author

CUADRO 1 (Continúa...)
Lista de especies de equinoideos con rangos publicados que incluyen las aguas del Pacífico oriental de Panamá, y profundidad de las especies encontradas por el autor

Species	Reports of presence in Panama	Reported depth range (m)	Depth for specimens examined (m)
<i>Diadema mexicanum</i>	1	0-113	1-18
<i>Kamptosoma asterias*</i>	1	2988-4950	
Family Aspidodiadematidae			
<i>Plesiodiadema horridum*</i>	1	1625-3241	
Order Pedinoidea			
Family Pedinidae			
<i>Caenopedina diomedeeae</i>	1	837-3382	723-933
Superorder Echinacea			
Order Saleniodida			
Family Salniidae			
<i>Salenocidaris miliaris</i>	1	1200-3058	
Order Arbacioidea			
Family Arbaciidae			
<i>Arbacia stellata=A. incisa</i>	1	0-90	0-10
<i>Dialithocidaris gemmifera</i>	1	3193-3279	
Order Temnopleuroidea			
Family Toxopneustidae			
<i>Lytechinus panamensis</i>	1	5-10	10
<i>Lytechinus pictus+</i>	1	0-300	
<i>Toxopneustes roseus</i>	1	0-55	5-25
<i>Tripneustes depressus</i>	1	0-73	2-15
Order Echinoida			
Family Echinometridae			
<i>Coenocentrotus gibbosus+</i>	1	0-9	
<i>Echinometra oblonga*</i>	1	0-34	
<i>Echinometra vanbrunti</i>	1	0-53	0-6
Superorder Ganthostomata			
Order Clypeasteroida			
Family Clypasteridae			
<i>Clypeaster europacificus</i>	1	0-402	66-100
<i>Clypeaster ochrus</i>	1	0-162	
<i>Clypeaster rotundus</i>	1	0-91	

TABLE 1 (Continued...)
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Species	Reports of presence in Panama	Reported depth range (m)	Depth for specimens examined (m)
<i>Clypeaster speciosus</i>	1	0-128	
Family Mellitidae			
<i>Encope micropora</i>	1	0-82	0-17
<i>Encope perspectiva*</i>	1	9-27	
<i>Encope wetmorei</i>	1	9-54	
<i>Mellita grantii</i>	4	0-3	10
<i>Mellita kanakoffi</i>	1	?	0-6
<i>Mellita longifissa</i>	1	0-60	0-6
<i>Mellita notabilis</i>	4	?	
<i>Mellitella stokesii</i>	1	0-6	0-10
Superorder Atelostomata			
Order Cassiduloida			
Family Cassidulidae			
<i>Rhyncolampas pacificus</i>	1	7-134	0-24
Order Holasteroida			
Family Urechinidae			
<i>Urechinus naresianus</i>	1	755-4400	
Family Pourtalesiidae			
<i>Cystocrepis setigera*</i>	1	2875-3436	
<i>Pourtalesia tanneri*</i>	1	1450-2454	
Order Spatangoida			
Family Hemiasteridae			
<i>Hemiaster tenuis</i>	1	980-4027	
Family Schizasteridae			
<i>Agassizia scrobiculata</i>	1	0-62	0-30
<i>Brisaster latifrons</i>	1	20-1900	
<i>Moira atropos clotho</i>	1	0-160	10-16
Family Aeropsidae			
<i>Aeropsis fulva</i>	1	1455-5200	
Family Brissidae			
<i>Brissopsis pacifica</i>	1	9-3279	

TABLE 1 (Continued...)
List of echinoid species with published ranges that include the eastern Pacific waters of Panama, and depth ranges of species encountered by the author

CUADRO 1 (Continúa...)
Lista de especies de equinoideos con rangos publicados que incluyen las aguas del Pacífico oriental de Panamá, y profundidad de las especies encontradas por el autor

Species	Reports of presence in Panama	Reported depth range (m)	Depth for specimens examined (m)
<i>Brissopsis columbaris</i>	2,3	899-1271	
<i>Brissus obesus</i>	1	0-45	5-6
<i>Meoma frangibilis</i>	1	55	96
<i>Meoma ventricosa grandis</i>	1	0-200	30-76
<i>Metalia nobilis</i>	1	0-18	5-6
<i>Plagiobrissus pacificus</i>	1	6-137	7
Family Lovenidae			
<i>Homolampas fulva*</i>	1	3665-4500	
<i>Homolampas hastata</i>	1	1785-2100	
<i>Lovenia cordiformis</i>	1	0-201	29

*: species with ranges that straddle Panama, but for which no published records of actual presence in Panama exist. +: Published range is incorrect, and unlikely to include Panama. Reference abbreviations: 1: Maluf (1988) and references therein. 2: Agassiz (1898). 3: Boone (1926). 4: Harold and Telford (1990).

ORDER CIDAROIDA

Centrocidaris doederleini

(A. Agassiz, 1898)

The extremely wide ambulacral areas, naked apical system, long and narrow genital plates, and the short and extremely slender primary spines are characteristics of this species that set it apart from the species of *Hesperocidaris*. All specimens I examined had strikingly red-purple poriferous zones. They were all collected in dredge hauls near Isla Montuosa in the Gulf of Chiriqui at 7°25.26' N, 82°15.11' W, at a depth of 198 m, and at 7°25.65' N, 82°15.10' W, at a depth of 300 m.

Eucidaris thouarsii

(Valenciennes, 1846)

This is the only representative of the Perischoechinoidea with a depth range limited to shallow water in the eastern Pacific. Though

in overall appearance it is very reminiscent of its Atlantic geminate, *E. tribuloides* (Lamarck), it has diverged morphologically to a sufficient degree to be morphometrically distinct (Lessios 1981a). The most easily visible difference between the two is coloration of the secondary spines, gray in *E. tribuloides*, brown in *E. thouarsii*. The two species are also distinct in isozymes (Lessios 1979, 1981a, Bermingham and Lessios 1993), in restriction fragment patterns of its mitochondrial DNA (Bermingham and Lessios 1993), and in DNA sequence of its cytochrome oxidase I (COI) mitochondrial gene (Lessios *et al.* 1999). It was formerly thought that the eastern Pacific islands and the mainland shared the same species of *Eucidaris*. However, COI sequences and protein electrophoresis showed that *Eucidaris* at Galapagos, Isla del Coco, and the Clipperton Atoll is a separate phylogenetic entity from *Eucidaris* at Panama or Mexico. Döderlein (1887) had

described *Eucidaris* from the Galapagos islands as a separate species, *E. galapagensis*, based primarily on the prevalence of club spines in populations at this archipelago. H. L. Clark (1907) stated that there are no characters to distinguish *E. galapagensis* from *E. thouarsii* and conveyed Döderlein's "present opinion" that "*galapagensis* should be regarded as a variety of *thouarsii*". Mortensen (1828-1951) correctly pointed out that club spines is an unreliable specific character and synonymized *E. galapagensis* with *E. thouarsii*. Even though the phylogenetically distinct entity discovered by Lessios *et al.* (1999) was not restricted to the Galapagos, and even though it did not exhibit the morphological characters used by Döderlein to designate it as a different species, they revived the name *E. galapagensis* for the island form. A morphological study of *E. thouarsii* and *E. galapagensis* is needed to establish non-molecular characters that distinguish between the two. *Eucidaris* populations in Galapagos are characterized by high population density of large-sized individuals that are conspicuously aggregated in open, unprotected areas, whereas Panamanian populations are composed of individuals of much smaller size that tend to be cryptic (Glynn *et al.* 1979). These, however, are not characteristics that can be ascribed to their being different species, because populations at Isla del Coco resemble mainland ones in average size, population densities and tendency to hide, yet genetically belong to *E. galapagensis*. As one of the findings of Glynn *et al.* (1979) was that *Eucidaris* in the Galapagos fed mostly on *Pocillopora*, Lawrence and Glynn (1984) studied the absorption of animal tissue by this carnivorous echinoid. Egg diameter of *E. thouarsii* in Panama is 91.06 μm (Lessios 1990), and displays no significant variation through time (Lessios 1987). The early stages of larval development of *E. thouarsii* were described by Mortensen (1921) and the entire larval phase through metamorphosis by Emler (1988).

E. thouarsii is common in rocky intertidal and subtidal areas and among coral branches of *Pocillopora* reefs in the Bay of Panama and

the Gulf of Chiriqui. It is always found under rocks, in reef interstices, or wedged in crevices, never out in the open, presumably because of the danger of predation by large labrid, balistid and diodontid fish, which are common in both areas. The primary spines are often encrusted with orange sponges.

Hesperocidaris asteriscus

H.L. Clark, 1948

This species can be distinguished from the other species of *Hesperocidaris* by the naked margins of genital and ocular plates, which result in a distinct star-shaped outline, the lower number of spines on genital plates that leave the apical system more naked than those of *H. dubia*, and its pinkish-brown coloration, all characters that fit H.L. Clark's (1948) description. In Panama it appears to be locally abundant, though patchily distributed. More than 80 specimens were brought up in a single dredge haul North of Isla Montuosa at 7°30.40' N, 82°15.1' W, at a depth of 66 m, but the species was not encountered anywhere else.

Hesperocidaris dubia

(H.L. Clark, 1907)

This species is characterized by its slightly raised apical system thickly covered with spines and by its secondary spines which have a whitish-greenish margin and a purple stripe running through the middle. Its primary spines have 13-14 longitudinal ridges of tubercles (one more than the upper limit mentioned by Mortensen 1928-1951), which distinguishes it from *Hesperocidaris panamensis* (A. Agassiz), which has more than 16. *H. dubia* appears to be the most common deep water cidaroid in Pacific Panamanian waters. Like *H. asteriscus*, it is locally very abundant, with hundreds of specimens coming up on a single haul, but unlike the former, it seems to also be widespread over many areas. It was obtained in the Gulf of Chiriqui, east of Isla Coiba at 7°16.29' N, 81°16.29' W at a depth of 103 m (and also 7°13.49' N, 81°23.03' W at a depth of 114 m); west of Isla Coiba at 7°23.60' N, 82°02.13' W, at a depth of 72.5 m (and also at 7°28.26' N,

82°10.04' W, at a depth of 108 m), west of the Azuero Peninsula at 7°13.93' N, 81°24.08' W, at a depth of 110 m (and also at 7°27.0' N, 81°59.00' W, at a depth of 107 m); and next to Isla Montuosa at 7°28.0' N, 82°15.0' W, at a depth of 110 m. It was also observed and collected by submersible near Isla Ladrões, at 7°50.435' N, 82°28.656' W, at a depth of 196 m. In the Gulf of Panama it was collected west of Islas Perlas at 7°42.00' N, 79°15.00' W, at a depth of 133 m (and also at 7°59.3' N, 79°15.00' W, at a depth of 99 m); in the Golfo de San Miguel at 7°53.0' N, 78°239' W at a depth of 71 m; and off the Darien at 8°11.0' N, 79°25.00' W at a depth of 157 m.

Submersible observations carried out off Isla Ladrões in 1995 indicated that individuals of this species are perched on top of rocks that project off the sediment of the slope. A study of the evolution of sea urchin retroviral-like retrotransposable elements (SURL) based on the DNA sequences of their reverse transcriptase (Gonzalez and Lessios 1999) showed that *H. dubia* shares a lineage of SURL elements with *H. panamensis* (A. Agassiz) and with *Eucidaris*, and that this lineage is basal to that of all other echinoids. Thus, the elements contained in *H. dubia* must have been coevolving with their host, the Perischoechinoidea, starting at a time that predates their split from the Euechinoidea.

Hesperocidaris panamensis
(A. Agassiz, 1898)

I have examined only one specimen of this species, collected by F. Rodriguez in 1995 off Isla Ladrões at a depth that was not recorded. I have followed Mortensen (1928-1951) in identifying it as *H. panamensis*, because its ambital primary spines had 18 ridges of tubercles but were not flattened at the distal end, and because its secondary spines were white-green and lacked the purple stripe characteristic of *H. dubia* and *H. perplexa* (H.L. Clark).

Emlet (1995) deduced from crystallographic patterns of adult apical plates that *Hesperocidaris panamensis* has a feeding, planktonic larva. Gonzalez and Lessios (1999) found in their reconstruction of genealogy of

SURL elements that *H. panamensis*, in addition to the SURL lineage it shares with *H. dubia* and *Eucidaris*, also contains a lineage that is otherwise found only in camarodont sea urchins. Thus, there appears to have been a fairly recent horizontal transfer event of retroviral-like elements between the lineages that lead to *H. panamensis* and the lineages that lead to the camarodonts.

Hesperocidaris perplexa
(H.L. Clark, 1907)

I obtained only one specimen of this species between Isla del Rey and the Darien at 8°13.61' N, 78°38.3' W at a depth of 60 m. It measures 4.1 cm in horizontal diameter, has the distally flattened ambital spines which, according to Mortensen (1928-1951), sets this species apart from the other species of *Hesperocidaris*, and has 18 series of ridges of tubercles on its primary spines. The secondary spines have a median purple stripe, similar to that of *H. dubia*.

ORDER ECHINOTHUROIDA

Araeosoma leptaleum

A. Agassiz and H.L. Clark, 1909

Two specimens of this species were located walking on bottom ooze by the submersible "Sea Link" at a depth of 740 m off Montuosa (7°27.022' N, 82°18.671' W) in 1995. They possessed the inversely conical "hoof" on their oral primary spines, characteristic of this species.

The lineage leading to the SURL elements of *Araeosoma leptaleum* also shows evidence of horizontal transfer, this time with the SURL lineage of the cidaroid *Prionocidaris bispinosa* (Lamarck) (Gonzalez and Lessios 1999). How such transfers occur by these retroviral elements during the history of echinoids is unknown.

ORDER DIADEMATOIDA

Astropyga pulvinata
(Lamarck, 1816)

This spectacularly colored diadematoid cannot be mistaken for any other species. The

skin over the test and the anal cone are usually beige colored with prominent, turquoise, iridescent spots arranged in vertical series, and the spines are banded. A star-shaped outline of darker brown or violet color runs down the test. The anal cone can also be gray. Mortensen (1928-1951) also mentions greenish specimens from Isla Taboga and remarks on the distinct coloration of the brown specimens he obtained at the Perlas, which apparently he was intending to describe as a separate species (see Mortensen 1921), though intergradation of color morphs and lack of any other diagnostic characters subsequently convinced him to recognize them as a separate variety. I have not seen *A. pulvinata* in Taboga, but the 60 specimens I have collected in Isla Changame (8°56' N, 79°31' W), not far from Taboga, were all beige, though the anal cone was sometimes green. *A. pulvinata* appears to reach a smaller size than its Atlantic congener *A. magnifica* A. H. Clark; the largest specimens I have examined were approximately 5 cm in horizontal test diameter. The test of *A. pulvinata* is more raised than that of *A. magnifica*. The morphological differences between the two species are such, that Mortensen (1928-1951) suggested that their split must have pre-dated by a significant amount of time the rise of the Isthmus of Panama, but Chesher (1972) has included them in the list of geminate species. Spines of *Astropyga* that penetrate human flesh cause the same painful reactions as those of *Diadema* and *Echinothrix*. It is unclear whether *Astropyga* ectoderm contains naphthaquinone pigments, or other toxins similar to the ones that may cause pain and irritation in wounds received from *Diadema* (Lessios 1983).

A. pulvinata is moderately abundant in the Bay of Panama and the Gulf of Chiriqui. Single individuals can be found infrequently on coral rubble or sand, but in one locality, Changame, the population was so dense in April, 1987 that 60 individuals could be collected without depleting the number of animals present. Even though Mortensen (1928-1951) says that *A. pulvinata* is found on hard substrates, the ones at Changame were present on sand, at a depth of approximately 10 m. I have also obtained

specimens at Islas Perlas west of Isla Mongo-Mongo at 8°32.71' N, 79°05.35' W in water 23 m deep, and at 8°31.37' N, 79°05.79' W in water 24 m deep, and in the Gulf of Chiriqui at Isla Uva (Fig. 1, 7°48' N, 81°45' W) at 10 m, at Isla Canal de Afuera, Bahia Honda (7°56' N, 81°37' W) at 7 m, and near Islas Secas, 8°00.03' N, 82°2.30' W, at 26 m.

The mean diameter of *Astropyga pulvinata* eggs is 89.47 µm (Lessios 1990). The early stages of its larval development have been described by Mortensen (1921). Mortensen (1928-1951) mentions that one specimen he collected was parasitized by the gastropod *Mucronalia*. There has been horizontal transfer between retrotransposons of *A. pulvinata* and those of the sand dollar *Clypeaster* (Gonzalez and Lessios 1999).

Diadema mexicanum

A. Agassiz, 1863

This is the most abundant and best studied echinoid in the Bay of Panama and in the Gulf of Chiriqui, encountered frequently in large numbers under rocks, corals and (in greatest densities) on the dead sides of *Pocillopora* reefs. In Taboga and Taboguilla, rocks under which *Diadema* is hiding can be easily spotted by the pinkish halo surrounding them, presumably as the result of its grazing activities, which leave a visible veneer of coralline algae. During the day, the coloration of adult *D. mexicanum* is black with blue vertical lines, but at night the color becomes gray. Juveniles have banded spines. Mortensen (1928-1951) stated that if it weren't for their geographical separation, *D. mexicanum* and the Atlantic *D. antillarum* Philippi would have never been designated as separate species, a statement for which he was criticized by Mayr (1954). As a matter of fact, and despite the data given by Chesher (1972) for this purpose, it is almost impossible to identify specimens from the two sides of the Isthmus of Panama without locality information. Multivariate discriminant functions have some degree of success in classifying individuals into one of the two species when they are built on specimens from the same

localities as the unknowns (Lessios 1981a), but fail when the function is built on the basis of individuals collected in one area, and the unknown specimens of the same species come from another. *D. antillarum* and *D. mexicanum* can also not be distinguished on the basis of isozymes (Lessios 1979, 1981a, Bermingham and Lessios 1993), and harbor SURL elements with identical DNA sequences in their reverse transcriptase (Gonzalez and Lessios 1999). However, they are more distinct in mitochondrial DNA than *D. antillarum* is from the Indo-Pacific species *D. savignyi* (Audouin) Michelin and *D. paucispinum* A. Agassiz (Lessios 2001, Lessios *et al.* 2001), and, most important, their monthly reproductive cycles are 15 days out of phase (Lessios 1984). If the latter characteristic is genetically fixed, *D. antillarum* and *D. mexicanum* are good biological species, because they would be unable to interbreed, even if the geographical barrier between them were removed (Lessios 1984, 2001).

In the Bay of Panama, *D. mexicanum* reproduces from August to November (Lessios 1981b), spawning at full moon (Lessios 1984). Its average egg diameter is 69.54 μ m (Lessios 1990), and egg size does not vary significantly between months and localities (Lessios 1987). The length of its larval life in the laboratory is 42 days (Emler 1995). In the Gulf of Chiriqui, Eakin (1988) documented intense interactions between *D. mexicanum* and the damselfish *Stegastes acapulcoensis* (Fowler), which excludes the former from its territories by biting its spines and occasionally lifting entire sea urchins in its mouth and spitting them outside the territory. In 1983, *D. mexicanum* remained unaffected by the mass mortality that devastated its Caribbean congener *D. antillarum* (Lessios *et al.* 1984, Lessios 1988). As a matter of fact, *D. mexicanum* seems to have benefitted by the coral mortality imposed by the ENSO event to increase its population densities in 1983 by more than 20-fold, possibly as the result of larger reef areas occupied by algae (Glynn 1988). The denser populations have resulted in a three-fold increase in rates of reef

bioerosion, except inside damselfish territories (Eakin 1988, Glynn 1988).

ORDER PEDINOIDA

Caenopedina diomedea

Mortensen, 1939

The single specimen from which Mortensen (1939) described the species appears to remain as the only published record of its existence, because Maluf (1998) records the entire species range as Punta Mala (7°23' N, 80°09' W) where it was taken by the "Albatross". Agassiz (1898) mentioned it along with other "Albatross" specimens of *Porocidaris milleri* (A. Agassiz), which elicited Mortensen's (1928-1951) remark that "evidently he [Agassiz] cannot have examined it very carefully". I obtained six specimens, collected by the submersible "Sea Link" in the Gulf of Chiriqui, not far from the type locality. Of these, one was deposited at the California Academy of Sciences, and I am grateful to R. Mooi for its identification. I examined the other five. One came from Banco Hanibal (7°21.429' N, 82°04.583' W, 733 m deep), and the rest from around Isla Jicarita, three from 7°11.590' N, 81°51.023' W, 900-933 m deep, and one from 7°11.784' N, 81°50.897', 723 m deep. They ranged from 2.2 to 2.5 cm in horizontal diameter, and they conformed to Mortensen's (1928-1951) detailed description. The coloration of the spines was always white, but the test was covered with small purple dots, which varied in density between specimens, so that some appeared almost completely white, but one was almost completely purple. Mortensen's type specimen lacked intact primary spines, but I can verify his speculation that this species does not show any evidence that they widen towards their ends, as they do in *C. cubensis* A. Agassiz. The good preservation of the specimens also makes strikingly prominent the fact that spines on the apical system are confined to the adapical edge of the plates, so that the periphery of the periproct appears to bear a ring of spines. Mortensen (1928-1951) also mentions that the genital pores of his type specimen were actually

slits, which he said “indicates the specimen to be a male”. Based on this character, four of my specimens are females, with regular, round genital pores, and one is a male.

The submersible also photographed two of the animals *in situ*, which provides the first direct observation of their habitat. One was perched on the side of a rock, the other was actually walking on what appears to be soft sediment on a slope but more likely is a sediment-covered rock (Fig. 2). *Caenopedina diomedieae* is another species in which retrotransposons show evidence of horizontal transfer, as they belong to the same clade as those of the camarodont *Caenocentrotus gibbosus* (Gonzalez and Lessios 1999).

ORDER ARBACIOIDA

Arbacia stellata

(Blainville?, 1825; Gmelin 1788)

= *A. incisa* (A. Agassiz, 1863)

The only shallow water arbacioid species in Panama, it is readily distinguishable by the large naked aboral areas and the cover of the anus by triangular plates. Its color can be black particularly in juveniles, but in larger specimens it is reddish, with conspicuous spots that run in a star-shape down the test. This is a rather rare

species in Panama, never reaching densities that are regularly seen in other places in the eastern Pacific, such as the Gulf of Fonseca. The single locality where it could be located reliably some twenty years ago was in the intertidal of Punta Paitilla (8°56' N, 79°31' W) in Panama City, but it seems to have succumbed to pollution, because the city's main sewer empties close to this area. Like Mortensen (1921) in 1915, I have only been able to obtain juveniles around Taboga, and the same is true at Isla Uva in the Gulf of Chiriqui. I have found adults in the Islas Perlas at Isla Pacheca (8°40' N, 79°03' W, 5 m) and Isla Contadora (8°37' N, 79°02' W), and it has also been dredged in the Golfo de San Miguel off the Darien (8°11.0' N, 79°25.00' W, 10 m).

An unfortunate fact about the name of this species is that it is not certain whether *Echinus stellatus* of Blainville and of Gmelin is the same species as *Echinocidaris incisa* of A. Agassiz (Mortensen 1928-1951). It is, therefore, not certain which of the two names has priority. Mortensen favored *A. stellata*, as a name that had received ample use. Since then, publications have tended to use *A. incisa* when the specimens came from Baja California and the Sea of Cortez (e.g. Brusca 1980, Metz *et al.* 1998, Buenrostro *et al.* 1998), and *A. stellata*

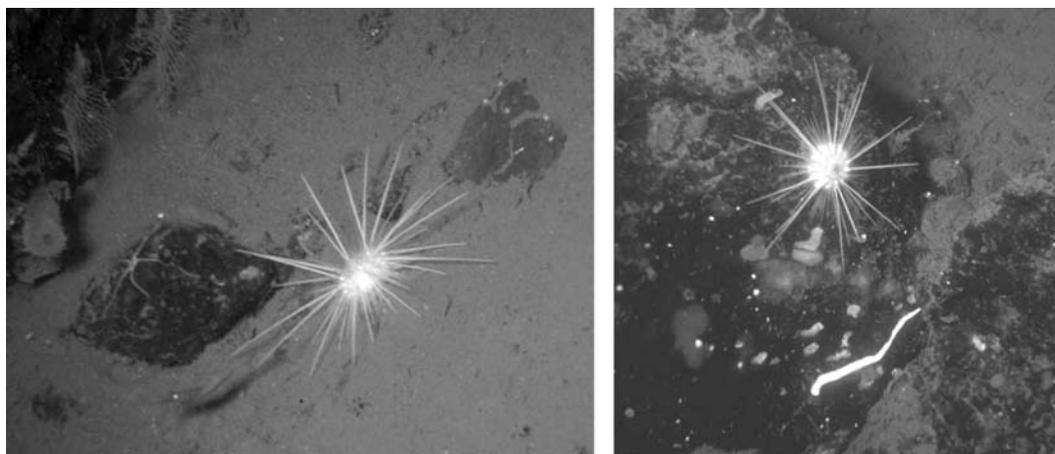


Fig. 2. Photographs of *Caenopedina diomedieae* on sediment-covered and bare rock taken by the submersible “Sea Link” off Isla Jicarita at 953 m, and off Banco Hanibal at 812 m respectively.

Fig. 2. Fotografías de *Caenopedina diomedieae* en una cubierta de sedimento y roca pelada tomada por el sumergible “Sea Link” en la Isla Jicarita a 953 m, y en el Banco Hanibal a 812 m respectivamente.

when they came from elsewhere in the species range (e.g. Mortensen 1921, Lessios 1990, Emler 1995). To someone unfamiliar with the uncertainty of the name, this would imply the existence of two allopatrically distributed species, which is not the case.

Curiously, considering the difficulty of locating it in the field, *Arbacia stellata* is the only echinoid which settles from larvae in sea water tanks at the Naos Marine Laboratory of the Smithsonian Institution in Panama. This may be because, coming from a small egg (66.78 µm average diameter, Lessios 1990), the larvae may be able to pass through sediment filters. Nevertheless, such successful settlement implies that larvae are present in the water column, which agrees with the fact that Mortensen (1921) was able to obtain them in plankton tows. Either there are as yet unlocated high density populations of this species in the Bay of Panama, or else the larvae are especially long-lived and arrive from far away places. Larvae of this species settle in the laboratory after 22 days (Emler 1995), and have been figured in Emler *et al.* (2002). Mortensen (1928-1951) considered that *A. stellata* was not the geminate species of the Atlantic *A. punctulata* (L.), reserving this relationship for *A. spatuligera* (Valenciennes), which is found off the West coast of S. America. Metz *et al.* (1998) studied the evolution of bindin and cytochrome oxidase I of this species and suggested that *A. punctulata* and *A. stellata* speciated before the rise of the Isthmus of Panama, but did not resolve the issue of the Pacific sister species of *A. punctulata*, because their phylogenies did not include *A. spatuligera*. All that can be said at the moment is that the mitochondrial DNA divergence of *A. stellata* and *A. punctulata* seems to be slightly higher than that of other species that are presumed to have been split by the completion of the isthmus, but not by so much as to definitively rule out this possibility (Lessios *et al.* 2001).

ORDER TEMNOPLEUROIDA

Lytechinus panamensis

Mortensen, 1921

This is the most enigmatic shallow water echinoid in Panamanian waters. It was initially described in a four-line footnote by Mortensen (1921) from specimens he obtained in Taboga, where it was apparently abundant enough to allow him to obtain gametes and raise the early stages of the larvae. He later provided a full description in his monograph, but except for being included in lists by Chesher (1972) and by Maluf (1988), and a mention that its development is through a feeding larva (Emler 1995), this was the last time this species appeared in any publication until Zigler and Lessios's (2004) inclusion in the phylogeny of *Lytechinus*. Despite many efforts to locate it, including a week-long dredging and diving cruise devoted specifically to this species, I have only seen two specimens, collected by A. Herrera off Isla Saboga at the Perlas Archipelago (8°38' N, 79°03' W) in 1987. Zigler and Lessios's (2004) phylogeny included DNA from one of these specimens, which places the cytochrome oxidase I of *L. panamensis* squarely among sequences of *L. semituberculatus* (Valenciennes). Given this result, its apparent rarity and small size (ca 2 cm horizontal diameter) raise the question of whether *L. panamensis* might represent juvenile individuals of *L. semituberculatus* that occasionally settle in the Bay of Panama from larvae that come from the South [its existence in Clarion (Mortensen 1928-1951) being doubtful (Maluf 1988)]. Though I have only seen adults of *L. semituberculatus*, I doubt that this is the case. For one thing, the individuals obtained by Mortensen (1921) in Taboga had viable gametes, which would suggest that they were past the age of first reproduction. For another, there are definite morphological differences between *L. panamensis* and

L. semituberculatus (Mortensen 1928-1951), including coloration (light brown in the former, green in the latter). The other possibility that would explain the rarity of *L. panamensis* in Panama has been raised by H.L. Clark (1925) and Mortensen (1928-1951). They speculated that *Lytechinus* from the mainland of Peru and of Ecuador are not *L. semituberculatus*, as was previously thought, but rather *L. panamensis*. If so, larvae from these places may occasionally arrive in the Bay of Panama and establish transient populations of individuals that persist to adulthood but do not receive regular recruitment, so they subsequently disappear. It is, of course, quite possible that stable populations of *L. panamensis* may also exist in Panama, but have not yet been located.

In color, adult size, and overall outline of the test, *L. panamensis* resembles the Caribbean *L. williamsi* Chesher, which is the reason that Chesher (1972) listed them as members of a geminate pair. Zigler and Lessios (2004), however, have found that each is a member of the two major clades of *Lytechinus*, one Atlantic and one Pacific, and thus, there is no special relationship between the two species.

Toxopneustes roseus
(A. Agassiz, 1863)

This large (adult horizontal diameter 12 cm), pink sea urchin with unmistakable, large globiferous pedicellariae covering the whole test and protruding past the short spines cannot be mistaken for any other species. In Panama it is moderately abundant in the coral rubble that accumulates at the bottom of *Pocillopora* reefs, but it may be hard to find, because during the day it burrows under the bits of coral, as it does in the Sea of Cortez (James 2000). Juveniles are even harder to find. In the two small (1.2 and 2.4 cm horizontal diameter) specimens I have been able to collect, the globiferous pedicellariae, though present, are not nearly as prominent as they are in the adults. Also the test, which in adults is somewhat raised, in the juveniles tends to be flatter. I have collected *T. roseus* in the Bay of Panama at Isla Taboguilla (8°47' N, 79°30' W, 10 m), and in the Perlas Archipelago at Isla

Pacheca, (8°40.18' N, 79°02.76' W, 6-15 m), at Isla Saboga (8°37' N, 79°03' W, 5 m), at Punta Cocos, Isla del Rey (8°13' N, 78°54' W, 5 m). In the Gulf of Chiriqui I have found it at Isla Uva, (7°48.60' N, 81°45.5' W, 25 m).

Diameter of eggs of this species is 101.72 µm (Lessios 1990). Larvae from plankton tows are described by Mortensen (1921).

Tripneustes depressus

A. Agassiz, 1863 = *T. gratilla* (L., 1758)

This large (adult horizontal diameter 14 cm) species is almost never encountered in the Bay of Panama (two specimens encountered off Isla Pacheca) and is found only occasionally in the Gulf of Chiriqui (two specimens at Uva Island and one at Jicarita). It is, however rather abundant at Jaque (7°31' N, 78°10' W), close to the Colombian border. Its globose test is dark gray or dark brown, almost black, and the spines are white and very short.

It is certain that this species should be synonymized with the Indo-Pacific *T. gratilla*. The extreme morphological similarity between the two species was remarked upon by H. L. Clark (1912) and by Mortensen (1928-1951). Zigler and Lessios (2003a) found that bindin DNA sequences of *T. depressus* and *T. gratilla* are phylogenetically intermingled, and Lessios *et al.* (2003) found identical cytochrome oxidase I haplotypes extending from the eastern Pacific all the way to the Indian Ocean. Gonzalez and Lessios (1999) found retrotransposons with identical reverse transcriptase DNA sequences in *T. depressus* and *T. gratilla*. Thus, larvae of this species appear to be able to cross the Eastern Pacific Barrier on a regular basis, and the resulting adults appear to be able to fertilize individuals of the local populations. Interestingly, the blue form of *T. gratilla* that is not uncommon in the central and western Pacific, does not appear to be present in the eastern Pacific, at least not in Panama, Isla del Coco and the Galapagos, where I have collected.

Tripneustes in the Gulf of Chiriqui has small (79.16 µm in diameter) eggs (Lessios 1990). Its bindin molecule does not show any evidence of selection (Zigler and Lessios

2003a). The identity of the retrotransposons of *T. depressus* and *T. gratilla* was ascribed by Gonzalez and Lessios (1999) to horizontal transfer, but subsequent knowledge from cytochrome oxidase I (Lessios *et al.* 2003) and from bindin (Zigler and Lessios 2003a) indicates that it is clearly the result of previously unsuspected gene flow.

ORDER ECHINOIDA

Echinometra vanbrunti

A. Agassiz, 1863

E. vanbrunti is the most common echinoid in the Panamanian rocky intertidal, occupying crevices, tide pools and the underside of rocks in areas where there is little sediment. Morphologically it is the most distinct species of *Echinometra*, visibly differing from the Atlantic *E. lucunter* (L.) and *E. viridis* A. Agassiz and the Central Pacific-Indo-West Pacific *E. oblonga*, *E. insularis* H.L. Clark, and the *E. mathaei* (Blainville) complex by its flat test, by the nearly circular outline of the ambitus, and by its very thin spines. Indeed, it looks so different from other species of *Echinometra* that at various times it has been placed in nine other genera (see references in Mortensen 1928-1951). Cytochrome oxidase I DNA sequences, however, show that it is nested within the phylogeny of *Echinometra* as an outgroup of the two Atlantic species, whereas all the other species of the genus form a clade deeply divided from these three (McCartney *et al.* 2000). The cytochrome oxidase I phylogeny also agrees with isozymes (Lessios 1979, 1981a, Bermingham and Lessios 1993) that *E. vanbrunti* split from the two Atlantic species, presumably as the result of the completion of the Isthmus of Panama, before they split from each other, despite the fact that in multivariate morphometrics it is more similar to *E. lucunter* than to *E. viridis* (Lessios 1981a).

Like *Diadema mexicanum*, *Echinometra vanbrunti* in the Bay of Panama reproduces from August to November, though in one locality the gonads are still in the process of being built up until September (Lessios 1981b). The

mean diameter of its egg is 72.40 μm (Lessios 1990), but size varies significantly between months and years (Lessios 1987). The eggs of this species can be readily fertilized by those of *E. viridis* and of *E. lucunter* and its sperm can fertilize eggs of *E. viridis*, but not those of *E. lucunter* (Lessios and Cunningham 1990, McCartney and Lessios 2002). This parallels amino acid replacements seen in bindin, presumably because this male molecule tracks changes that evolve in egg receptors (McCartney and Lessios 2004). Larvae of this species settle after 18 days in the laboratory (Emlet 1995).

ORDER CLYPEASTEROIDA

Clypeaster europacificus

H.L. Clark, 1914

This species can be easily distinguished from other species of *Clypeaster* by its concave interradial margins that give it a pentagonal appearance, its straight, narrow petals with pore series that do not converge distally and by the fact that the periproct is situated in a distinct notch at the posterior margin. It is rather abundant in Panamanian waters. In the Bay of Panama I have found it southwest of Islas Perlas (7°57.99' N, 79°16.55' W, 100 m, and also 7°58.79' N, 79°15.16' W, 100 m), west of Islas Perlas (7°59.3' N, 79°15.00' W, 99 m), off the Azuero Peninsula (7°50.00' N, 79°45.00' W, 76 m), and off the Darien (7°53.0' N, 78°23.9' W, 71-74 m). In the Gulf of Chiriqui I found it off Isla Montuosa (7°30.40' N, 82°15.1' W, 66 m, and 7°28.0' N, 82°15.0' W, 96 m). This is a large species. The largest specimen in my collection measures 13.8 cm, but H.L. Clark (1948) mentions individuals 20.2 cm long. One very small specimen (1.2 cm long) is round. Mortensen (1928-1951) remarks that his smallest specimen is 77 mm long and has genital pores, while that figured by H.L. Clark (1914) is 60 mm long and lacks genital pores, from which he concludes that the pores must develop between these sizes. In examining approximately 100 specimens, I have found individuals as small as 44 mm with

genital pores and as large as 54 mm without, sothere is some variation in the size of first sexual maturity. All individuals shorter than 42 mm lacked genital pores.

Encope micropora

L. Agassiz, 1841

This large (ca 15 cm adult size) *Encope* can be distinguished from *E. wetmorei* A. H. Clark and *E. perspectiva* L. Agassiz (neither of which I found in Panama) by the position of its unpaired lunule, most of which projects posterior to the petals. The color is dark olive. This species is rather abundant in the intertidal of Playa Veracruz (8°53' N, 79°34' W) among more plentiful individuals of *Mellitella stokesii* (L. Agassiz) and at Punta Chame (8°79' N, 79°41' W), but is otherwise not easy to find. In addition to these places, I have also found it in the Perlas Archipelago at Isla del Rey in (8°15.054' N, 78°54.344' W, 10 m; 8°17.30' N, 78°50.32' W, 15 m; and 8°17.32' N, 78°53.03' W, 16.7 m) and Isla San Jose (8°19.18' N, 79°06.97' W). Mortensen (1921) described the larvae of *E. micropora*, but was unable to raise them to metamorphosis.

Mellita grantii

Mortensen, 1948

The distribution of this species was until 1990 believed to reach only as far south as 26°N (Maluf 1998), but Harold and Telford (1990) reported specimens from unspecified localities in the Bay of Panama. My only collection of what I presume to be this species consists of eight small (< 2 cm wide) individuals collected at the Golfo de San Miguel (8°11.0' N, 79°25.00' W, 10 m). The highest point of the test is at the apical system, and the periproct is located half way between the mouth and the posterior lunule, which distinguishes *M. grantii* from *M. longifissa* Michelin (Harold and Telford 1990). The unpaired posterior lunule does not reach the apical system, which distinguishes *M. grantii* from *M. kanakoffi* Durham. Lack of deep pressure drainage canals, leaving the edges of the lunules looking straight, distinguish *M. grantii* from *M. notabilis* H. L. Clark. If these

small specimens do not belong to *M. grantii*, they must belong to an undescribed species of *Mellita*. Eight dead tests of larger individuals that definitely belong to *M. grantii* were encountered at Playa Venado.

A cladistic analysis of morphological characters of *Mellita* by Harold and Telford (1990) placed *M. grantii* as sister to *M. longifissa*, and, indeed, Mortensen (1928-1951, 1948) described the species from a single specimen that he separated out of *M. longifissa*.

Mellita kanakoffi

Durham, 1961

This is the most often encountered species of *Mellita* on the Pacific side of Panama. Harold and Telford (1990) mention examining 64 specimens of *Mellita notabilis* from "Playa Lajas" in Panama from D. Dexter's private collection. I have examined 67 specimens of *Mellita* from Las Lajas (8°10' N, 81°52') in Chiriqui, collected between 1998 and 2004, and they all belonged to *M. kanakoffi*. They all fit Harold and Telford's description, with the high point of the test being anterior to the apical system, a long unpaired posterior lunule reaching almost to the apical system, widely divergent food grooves, and no evidence of deep pressure channels at the margin of the ambulacral lunules. In Panama there is more than one beach called "Las Lajas", so it is possible that Dexter's specimens do not come from the same locality. *M. kanakoffi* was also collected in the intertidal at Isla Caña (7°23.80' N, 80°20.00' W), on the south side of the Azuero Peninsula, at Punta Chame, at Puerto Armuelles (8°16.25' N, 82°51.70' W) and at Playa Monagre (8°00' N, 80°82' W) on the east side of the Azuero. Judging by the specimens I have seen, a good field character for distinguishing *Mellita kanakoffi* from *M. longifissa* is the position of the thicket of oral primary spines between food grooves on the posterior half of the test. Because the food grooves are so divergent in *M. kanakoffi*, the thicket of spines runs from the mouth to the margin at an angle half way between ambulacral lunules. In *M. longifissa*, the spines appear to be surrounding the posterior ambulacral lunules.

The color of *M. kanakoffi* varies from gray-green to yellow-brown.

In Harold and Telford's (1990) phylogeny, *M. kanakoffi* is sister to *M. notabilis* on a clade that is sister to the one composed of *M. longifissa* and *M. grantii*.

Mellita longifissa

Michelin, 1858

This is the second most abundant species of *Mellita* in Panama. It has been found intertidally at Punta Chame and at Playa Gorgona (8°32' N, 79°51' W). It can be distinguished by its extremely long unpaired posterior lunule, which is almost touching the apical system, and (from *M. kanakoffi*) by its narrowly divergent food groves. The color of the specimens I have examined was olive-green.

Mellitella stokesii

(L. Agassiz, 1841)

This species was formerly assigned to the genus *Encope*, and there is good evidence for retaining in this genus (R. Mooi, pers. com), but for the sake of consistency, I have followed Maluf (1998) in recognizing *Mellitella* as a valid genus. *M. stokesii* can be locally abundant. My specimens come from the intertidal of Playa Veracruz, from Rodman at the mouth of Panama Canal (8°55' N, 79°33' W), from Playa el Saldo (8°11.00' N, 80°28.50' W) near Aguadulce, from Playa Monagre, and it has also been dredged at Ensenada Carachine (8°11' N, 78°25' W) in the Golfo de San Miguel at a depth of 10 m, which extends its depth range by a few meters (Table 1). This is a small species; the largest specimens in my collection are 5.2 cm long. The posterior ambulacral lunules are almost always open, even in juveniles, which immediately distinguishes this species from *Mellita* and from *Encope micropora*. The unpaired posterior lunule reaches anteriorly only to the end of the petals. H.L. Clark (1914, 1925) considered *Mellitella stokesii* to be the juvenile of *Encope micropora*, but, as Mortensen (1928-1951) points out, this is very unlikely, as genital pores in *M. stokesii* appear at a size of

approximately 2.5 cm, whereas *E. micropora* specimens of even 7.5 cm (the largest recorded size of *M. stokesii*) lack such pores.

The ecology of *Mellitella stokesii*, unlike that of the rest of the Pacific Panamanian sand dollars, has received considerable attention, thanks to the efforts of Dexter (1977). She documented the high density of this species in the mid-intertidal of Playa Venado (as high as 65 individuals per m²) and found that juveniles recruit throughout the year. The life expectancy is less than a year. Its egg diameter is 106.70 µm (Lessios 1990). *M. stokesii* has the shortest bindin molecule known to date, with only 193 amino acids in its mature region (Zigler and Lessios 2003b).

ORDER CASSIDULOIDA

Rhyncholampas pacificus

A. Agassiz, 1863

This species appears in Maluf (1988) as *Cassidulus pacificus*, but I have followed Mooi (1990) in placing it in the genus *Rhyncholampas*. Though its habit of burrowing in sand makes it hard to spot while diving, it has come up in enough dredge hauls to justify the conclusion that it is fairly abundant. It has been found in the intertidal of Playa Bique (8°53.00' N, 79°39.60' W) and at Islas Perlas, near Isla del Rey (8°14.972' N, 78°54.517' W, 13.5 m; and also 8°17.30' N, 78°50.32' W, 15 m), north of Isla San Jose (8°19.180' N, 79°06 973' W, 18 m; and also 8°19.037' N, 79°06.897' W, 14.5 m), north of Isla Viveros (8°29.794' N, 78°57.6' W, 15 m) and at multiple locations north of Isla Gibrালেон (8°31.075' N, 79°03.588' W, 8 m; 8°31.37' N, 79°05.79' W, 24 m; 8°31.93' N, 79°05.60' W, 23 m; 8°32.63' N, 79°05.09' W, 24 m; 8°32.83' N, 79°04.97' W, 18.8 m). It is the only cassiduloid in Panama, so there is no difficulty in its identification. It can get rather large; the largest specimen in my possession is 6.7 cm long. Its color is white mottled with green spots. As Mooi (1990) has noted, nothing is known about the biology of this species.

ORDER SPATANGOIDA

Agassizia scrobiculata
Valenciennes, 1846

Unlike all the previous species, which can be fairly easily assigned to genus, the Spatangoida are confusing, so that identification even at the family level is difficult and requires extensive reference to the taxonomic literature. For this reason, I have included a key that should help assign specimens to species that are known to be present in Panama (Table 2).

Even though H.L. Clark (1948) says that this species was the most infrequent of the spatangoids encountered by the Vellero III, it is actually fairly common in shallow water in the Bay of Panama. I have found it at Rodman, at Playa Venado, and at the Islas Perlas around Isla Pacheca (8°40.23' N, 79°02.64' W, 27 m; 8°40.39' N, 79°02.78' W, 20 m; 8°39.76' N,

TABLE 2
Key to the species of Spatangoida of the Pacific waters of Panama, based on characters given by Mortensen (1928-1951) and Chesher (1970)

CUADRO 2
Clave para las especies de Spatangoida de las aguas del Pacifico de Panamá, basada en caracteres dados por Mortensen (1928-1951) y Chesher (1970)

1	Test globose, length, width, and height almost equal to each other	2
	Test height much less than width	3
2	Test abruptly truncated posteriorly, depth range >900 m	<i>Hemiaster tenuis</i>
	Test rounded posteriorly, depth range <160 m	4
3	Test long and cylindrical, oral side rounded, length <4.5 cm, depth range >1000 m	<i>Aeropsis fulva</i>
	Test more or less flattened, ovoid rather than cylindrical	5
4	Anterior petals sunken very little or none at all	<i>Agassizea scrobiculata</i>
	Anterior petals very visibly sunken and narrow	<i>Moiria atropos clotho</i>
5	Frontal notch present	6
	Frontal notch absent	7
6	Apical system with 3 genital pores	8
	Apical system with 4 genital pores	9
7	Large, bilobed subanal fasciole	<i>Brissus obesus</i>
	Narrow subanal fasciole	<i>Metalia nobilis</i>
8	Large sunken areoles on aboral side, test conspicuously narrower posteriorly	10
	No large areoles, tubercles fine and uniformly-sized, anterior ambulacrum deeply sunken and very long	<i>Brisaster latifrons</i>

TABLE 2 (Continued...)
 Key to the species of *Spatangoida* of the Pacific waters of Panama, based on characters given by Mortensen (1928-1951) and Chesher (1970)

CUADRO 2 (Continua...)
 Clave para las especies de *Spatangoida* de las aguas del Pacífico de Panamá, basada en caracteres dados por Mortensen (1928-1951) y Chesher (1970)

9	Large sunken areoles on aboral side, outline of test conspicuously narrower posteriorly	<i>Lovenia cordiformis</i>
	No large large areoles, outline of test more or less ovoid	11
10	Only one large tubercle per series within the peripetalous fasciole in each of the posterior ambulacra	<i>Homolampas hastata</i>
	Several large primary tubercles within the peripetalous fasciole	<i>Homolampas fulva</i>
11	Large tubercles (and long spines) on aboral side, ambulacra flush with the test	<i>Plagiobrissus pacificus</i>
	No large tubercles on aboral side on aboral side, ambulacra conspicuously sunken	12
12	Peripetalous fasciole forms a sharp angle anteriorally of the anterior ambulacra	13
	Peripetalous fasciole bends gently at a distance from the anterior ambulacra	14
13	Peristome with 8-10 oral pores in lateral phyllode, test strong and heavy	<i>Meoma ventricosa grandis</i>
	Peristome with 5-6 oral pores in lateral phyllode, test very fragile	<i>Meoma frangibilis</i>
14	Posterior petals divergent, posterior end of test sloping outwards, so that periproct is visible when test viewed from above, peripetalous fasciole does not bend inward behind anterior petals	<i>Brissopsis columbaris</i>
	Posterior petals parallel, posterior end of test vertical, so that periproct is not visible when test viewed from above, peripetalous fasciole bends inward behind anterior petals	<i>Brissopsis pacifica</i>

79°01.94' W), around Isla Pedro Gonzalez (8°22.70' N, 79°04.9' W, 21 m; 8°25.220' N, 79°06.435' W), around Isla Pachequilla (8°40.36' N, 79°02.77' W, 7 m), around Isla Contadora (8°38.685' N, 79°01.898' W, 30 m) and around Isla del Rey (8°17.30' N, 78°50.32' W, 15 m; 8°27.43' N, 78°51.31' W, 15.7 m). This is a small species; the largest specimen in my possession is 2.6 cm long. Its globose test distinguishes it from all other shallow water spatangoids in Panama except *Moiria*, from which it differs in lacking a deep frontal notch

and sunken anterior petals (Table 2). The sternum is very wide and covered with spines that widen distally. The labrum is so inconspicuous, that it is hard to find the mouth in specimens that are covered with spines. The posterior petals are very short. The color is usually white, but in a few specimens from the Perlas the test is brown and only the spines are white.

The retrotransposons of *Agassizia scrobiculata* group with those of *Plagiobrissus* and *Brissopsis*, without any suggestion of a horizontal transfer (Gonzalez and Lessios 1999).

Moira atropos clotho
(Michelin, 1855)

This species appears to prefer fine, muddy sediments, which I have not sampled extensively, so I have collections from only two places, the Golfo de Parita (8°19' N, 80°17' W, 10 m) and north of Isla del Rey (8°30.00' N, 78°55.90' W, 16 m). The largest specimen is 3.3 cm. long. They are all white.

Moira from the eastern Pacific was previously accorded specific status, but Chesher (1972) was unable to find any valid characters to distinguish it from its Atlantic counterpart *M. atropos* (Lamarck) and suggested that the former is only a geographical subspecies of the latter. H.L. Clark (1948) says that the sunken anterior petal of *Moira atropos clotho* "presumably serves as a brood pouch for the young", but Mortensen (1928-1951) points out that *Moira atropos atropos* in the Atlantic is known to have a typical spatangoid echinopluteus, so it is unlikely that *M. atropos clotho* broods its young. The bindin of *M. atropos clotho* is interesting in that it contains glycine-rich repeat regions that have otherwise only been seen in the order Echinoida, and are missing from the other sampled orders of the Echinoidea (Zigler and Lessios 2003b).

Brissus obesus
Verrill, 1867

I have found this rather rare species buried in sand bottoms surrounded by coral and rocks at the Perlas Islands at Isla San Telmo (8°16.50' N, 78°51.00' W, 6 m) and at Isla Pacheca (8°39.8' N, 79°03.10' W, 5 m). The longest specimen in my collection is 3.5 cm. It appears to inhabit the same habitat as *Metalia nobilis* Verrill, from which it can be distinguished by the shape of its subanal fasciole (Table 2).

Fragmentary information about the larval development of *Brissus obesus* is given by Mortensen (1921)

Meoma ventricosa grandis
Gray, 1851

The large size of adult specimens, its sunken petals, large periproct, and robust test

make this species easy to distinguish from other genera of spatangoids in Panama. Densities of *M. ventricosa grandis* do not appear to be nearly as high in the Bay of Panama and the Gulf of Chiriqui as those of *M. ventricosa ventricosa* (Lamarck) in the Caribbean. Solis-Martin *et al.* (1997) reported similar differences in population densities of the two subspecies between the Pacific and Atlantic coasts of Mexico. *M. ventricosa grandis* has come up in dredging in the Gulf of Chiriqui near Isla Cavada (7°58.00' N, 82°02.40' W, 30 m), and in the Bay of Panama next to the Darien (7°50.00' N, 79°45.00' W, 76 m). The largest specimen was 17 cm long, and was dark brown. Both Mortensen (1928-1951) and Chesher (1970) point out that the Pacific *Meoma* has a darker color than the Atlantic one, but one specimen in my collection from the Gulf of Chiriqui has a light, ochre color.

M. ventricosa grandis, like *Moira atropos clotho*, was formerly accorded specific status, but was demoted to a subspecies of its Atlantic counterpart by Chesher (1970). Mitochondrial DNA sequencing suggests that genetically, as well as morphologically, the members of the amphiamerican pair of *Meoma* have diverged less than those of other pairs of echinoid species split by the Isthmus of Panama (Lessios *et al.* 2001). Mortensen (1921) was able to obtain some larvae of *M. ventricosa grandis*, but they did not develop past the first stage.

Meoma frangibilis
Chesher, 1970

Meoma frangibilis was described from a single specimen from the Bay of Panama by Chesher (1970), but has not been reported again in the literature, except by inclusion in Kier and Lawson's (1978) index of echinoids. A dredge haul in the Gulf of Chiriqui, west of Isla Montuosa at 8°28.0' N, 83°15.0' W at a depth of 96 m in November 2000 brought up three new specimens. They measure 4.45 cm, 4.28 cm and 1.40 cm in length, and they undoubtedly belong to the genus *Meoma*, because they have a frontal notch, sunken petals, flat oral side, a large periproct, and their peripetalous fasciole makes the characteristic sharp bend

anterior to the anterior paired ambulacra (Table 2). The oral area of the smallest specimen is damaged, but in the larger two specimens the lateral phyllode has 6 pores. The test is very fragile, not at all like that of *Meoma ventricosa grandis*. The anal area of one of the larger specimens is also damaged, but in the other two a complete subanal fasciole is clearly visible. Thus, these three specimens fit the description of *M. frangibilis*, and quadruple the number of known specimens of this species.

Chesher (1970) suggested that *Meoma frangibilis* was most closely related to the W. African *M. cadenati* Madsen, another species known only from its single type specimen.

Metalia nobilis

Verrill, 1867

This species was collected in exactly the same localities at Isla Pacheca and Isla San Telmo as *Brissus obesus*, at the same depth under the sand. As Mortensen (1928-1951) points out, the phyllodes of *Metalia* are conspicuous, and the labrum is broad and short, as in *Brissus*. Indeed, had it not been for *Metalia*'s shield-shaped subanal fasciole, so distinct from the bilobed one of *Brissus*, there would have been no reason to suspect that two different genera were present. It would be interesting to sample various areas to determine the proportion of individuals that belong to each genus and to determine whether there is any fine-level distinction between the habitats they occupy. As they both seem to prefer rather coarse sand accumulating between rocks and corals, such sampling could only be done by divers.

Plagiobrissus pacificus

H.L. Clark, 1940

I have only been able to collect one small (1.7 cm in length) specimen of this species Northeast of Isla Contadora, at 8°35.733' N, 79°01.186' W, at a depth of 7 m. The frontal notch is faintly developed, but the peripetalous fasciole that runs parallel to the edge of the test, without curving inwards between the petals, and the large tubercles and curved spines on

the aboral side indicate that this is a juvenile of *P. pacificus*.

H.L. Clark (1940) in his description of this species remarked on its correspondence with the Caribbean *Plagiobrissus grandis* (Gmelin), and implied that this is another species pair created by the rise of the Isthmus of Panama. Mortensen (1928-1951), on the other hand, maintains that *P. pacificus* is more closely related to *P. costae* (Gasco) from the Mediterranean and W. Africa.

Lovenia cordiformis

A. Agassiz, 1872

I have only collected this species around Isla Pedro Gonzalez, north of the island at 8°26.20' N, 79°16.46' W at 13 m depth, and southeast of the island at 8°22.70' N, 79°04.09' W at 29 m depth. Its posteriorly tapering test and large, deeply sunken areoles make it easy to identify. My largest specimen is 3 cm long. The test is white or brown. The long aboral spines are as long as the test and banded with violet and white.

Concluding remarks

The state of knowledge of Pacific Panamanian echinoids, and indeed, those of the entire tropical eastern Pacific parallels that of echinoids in other areas of the world, including regions closer to major research universities. The basic taxonomic work has been more or less completed, but information regarding the mode of development, life histories, general ecology, and evolution of most species is lacking. It exists only for the most abundant shallow water species, such as *Eucidaris thouarsii*, *Diadema mexicanum*, *Tripneustes depressus*, *Echinometra vanbrunti* and *Mellitella stokesii*. Compared with what is known about their Caribbean counterparts (reviewed in Hendler *et al.* 1995), the Panamanian Pacific species have received less attention. If this paper helps promote research on some of the more difficult to find species by indicating localities where they can be collected and means by which they can be identified, it will have served its purpose.

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RESUMEN

La intención principal de este trabajo es de servir como una guía para aquellos investigadores que deseen saber cuáles especies de equinoideos están presentes en la bahía de Panamá y en el Golfo de Chiriquí, como reconocerlos, y que se ha publicado sobre ellos hasta el año 2004. Se informa de 57 especies de equinoideos para las aguas del Pacífico Panameño, de las cuales he recolectado y examinado 31, incluyendo dos especies, *Caenopedina diomedieae* y *Meoma frangibilis*, mencionados hasta ahora en la literatura a partir de un único ejemplar tipo. De las 31 especies que he podido examinar, menciono las localidades en las cuales fueron halladas, mis impresiones de su abundancia relativa, las características que las distinguen, y qué se conoce sobre su biología y evolución. No es de sorprender que la mayoría de la información sea concerniente a las especies someras más abundantes, mientras que se sabe poco de las especies de aguas profundas, escasas e infaunales.

Palabras claves: Pacífico Oriental, erizos de mar, Bahía de Panamá, Golfo de Chiriquí, sistemática.

REFERENCES

Agassiz, A. 1898. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer “Albatross” during 1891, Lieut. Commander Z.L. Tanner, U.S.N., Commanding. XXIII. Preliminary report on the

Echini. Bull. Mus. Comp. Zool. Harvard University 32: 71-86.

Agassiz, A. 1904. The Panamic deep sea Echini. Report XXXII on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands. Mem. Mus. Comp. Zool. Harvard College 31: 1-243.

Berminham, E.B. & H.A. Lessios. 1993. Rate variation of protein and mtDNA evolution as revealed by sea urchins separated by the Isthmus of Panama. Proc. Natl. Acad. Sci. USA 90: 2734-2738.

Boone, L. 1928. Echinoderms from the Gulf of California and the Perlas Islands. Bull. Bingham Oceanogr. Coll., Yale Univ. 2: 1-14.

Brusca, R.C. 1980. Common Intertidal Invertebrates of the Gulf of California. 2nd Edition. Univ. Arizona, Tucson. 513 p

Buenrostro, C.E.C., H.R. Bonilla & O. A. Covarrubias. 1998. The echinoderms (Echinodermata) of Cabo Pulmo reef, Pacific of Mexico. Rev. Biol. Trop. 46: 341-343.

Caso, M.E. 1983. Los Equinoideos del Pacifico México. Parte 3. Orden Cassiduloida y Spatangoida. Anal. Centro Ciencias Mar Limnol., Mexico, Publ. Esp. 6: 1-200.

Chesher, R.H. 1970. Evolution in the genus *Meoma* (Echinoidea: Spatangoida) and a description of a new species from Panama). Bull. Mar. Sci. 20: 731-761.

Chesher, R.H. 1972. The status of knowledge of Panamanian echinoids, 1971, with comments on other echinoderms. Bull. Biol. Soc. Wash. (2) 139-158.

Clark, A.H. 1939. Echinoderms (other than holothurians) collected on the presidential cruise of 1938. Smithsonian Misc. Coll. 98: 2-24.

Clark, A.H. 1946. Echinoderms from the Pearl Islands, Bay of Panama with a revision of the Pacific species of the genus *Encope*. Smithsonian Misc. Coll. 106: 1-11.

Clark, H.L. 1907. The Cidaridae. Bull. Mus. Comp. Zool. Harvard College 51: 165-230.

Clark, H.L. 1912. Hawaiian and other Pacific Echini. Pedinidae, Phymosomatidae, Stomopneustidae, Echinidae, Temnopleuridae, Strongylocentrotidae and Echinometridae. Mem. Mus. Comp. Zool. Harvard College 34: 209-383.

Clark, H.L. 1914. Hawaiian and other Pacific Echini. The Clypeasteridae, Arachnoididae, Laganidae, Fibulariidae and Scutellidae. Mem. Mus. Comp. Zool. Harvard College 46: 1-78.

- Clark, H.L. 1925. A catalogue of the recent sea urchins (Echinoidea) in the collection of the British Museum (Natural History). Oxford Univ. Press, London. 250 p.
- Clark, H.L. 1940. Eastern Pacific Expeditions of the New York Zoological Society. XXI. Notes on Echinoderms from the west Coast of central America. *Zoologica* 25: 331-352.
- Clark, H.L. 1948. A report of the echini of the warmer eastern Pacific, based on the collections of the *Veleiro III*. Allan Hancock Pacific Expeditions 8: 225-252.
- D'Croz, L., J.B. Delrosario & J.A. Gomez. 1991. Upwelling and phytoplankton in the Bay of Panama. *Rev. Biol. Trop.* 39: 233-241.
- D'Croz, L. & D.R. Robertson. 1997. Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama, p. 2053-2058. *In* H.A. Lessios & I.G. Macintyre (eds.). *Proc. 8th Int. Coral Reef Symp.* Smithsonian Tropical Research Institute, Balboa, Panama.
- Dexter, D.M. 1977. A natural history of the sand dollar *Encope stokesi* L Agassiz in Panama. *Bull. Mar. Sci.* 27: 544-551.
- Döderlein, L. 1887. Die Japanischen Seeigel. I. Familie Cidaridae und Saleniidae. E. Schweizerbart'sche Verlagshandlung, Stuttgart. 59 p.
- Eakin, C.M. 1988. Avoidance of damselfish lawns by the sea urchin *Diadema mexicanum* at Uva Island, Panama. *Proc. 6th Inter. Coral Reef Symp.* Townsville 2: 21-26.
- Emlet, R.B. 1988. Larval form and metamorphosis of a "primitive" sea urchin, *Eucidaris thouarsi* (Echinodermata: Echinoidea: Cidaroida), with implications for developmental and phylogenetic studies. *Biol. Bull.* 174: 4-19.
- Emlet, R.B. 1995. Developmental mode and species geographic range in regular sea urchins (Echinodermata: Echinoidea). *Evolution* 49: 476-489.
- Emlet, R.B., C.M. Young & S.B. George. 2002. Phylum Echinodermata: Echinoidea, p. 531-551. *In* C.M. Young, M.A. Sewell & M.E. Rice (eds.), *Atlas of Marine Invertebrate Larvae*. Academic Press, New York.
- Forsbergh, E.D. 1969. On the climatology, oceanography and fisheries of the Panama Bight. *Inter-Amer. Trop. Tuna Comm. Bull.* 14: 49-385.
- Glynn, P.W. 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panama. *Bull. Biol. Soc. Wash.* (2) 13-30.
- Glynn, P.W. 1974. The impact of *Acanthaster* on corals and coral reefs in the eastern Pacific. *Env. Cons.* 1: 295-304.
- Glynn, P.W. 1982. Coral communities and their modifications relative to past and prospective Central American seaways. *Adv. Mar. Biol.* 19: 91-132.
- Glynn, P.W. 1988. El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea* 7: 129-160.
- Glynn, P.W., G.M. Wellington & C. Birkeland. 1979. Coral reef growth in the Galapagos: limitation by sea urchins. *Science* 203: 47-48.
- Gonzalez, P. & H.A. Lessios. 1999. Evolution of sea urchin retroviral-like (SURL) elements: evidence from 40 echinoid species. *Mol. Biol. Evol.* 16: 938-952.
- Grant, U.S.I.V. & L.G. Hertlein. 1938. The West American Cenozoic Echinoids. *Univ. Calif. Pub. Math. and Phys. Sci.* 2: 1-225.
- Harold, A.S. & M. Telford. 1990. Systematics, phylogeny and biogeography of the genus *Mellita* (Echinoidea, Clypeasteroidea). *J. Natur. Hist.* 24: 987-1026.
- Hendler, G., J.E. Miller, D.L. Pawson & P.M. Kier. 1995. Sea stars, sea urchins, and allies: echinoderms of Florida and the Caribbean. *Smithsonian Inst. Press, Washington.* 390 p.
- James, D.W. 2000. Diet, movement, and covering behavior of the sea urchin *Toxopneustes roseus* in rhodolith beds in the Gulf of California, Mexico. *Mar. Biol.* 137: 913-923.
- Kier, P. M. & M. H. Lawson. 1978. Index of living and fossil echinoids. *Smithsonian Contr. Paleobiol.* 34: 1-182.
- Lawrence, J.M. & P.W. Glynn. 1984. Absorption of nutrients from the coral *Pocillopora damicornis* (L.) by the echinoid *Eucidaris thouarsi*. *Comp. Biochem. Physiol. [A]*. 77A: 111-112.
- Lessios, H.A. 1979. Use of Panamanian sea urchins to test the molecular clock. *Nature* 280: 599-601.
- Lessios, H.A. 1981a. Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the Isthmus of Panama. *Evolution* 35: 618-634.
- Lessios, H.A. 1981b. Reproductive periodicity of the echinoids *Diadema* and *Echinometra* on the two coasts of Panama. *Jour. Exper. Mar. Biol. Ecol.* 50: 47-61.

- Lessios, H.A. 1983. Los erizos de mar panameños, las lesiones que causan y su tratamiento. *Rev. Medica Panamá* 8: 56-71.
- Lessios, H.A. 1984. Possible prezygotic reproductive isolation in sea urchins separated by the Isthmus of Panama. *Evolution* 38: 1144-1148.
- Lessios, H.A. 1987. Temporal and spatial variation in egg size of 13 Panamanian echinoids. *Jour. Exper. Mar. Biol. Ecol.* 114: 217-239.
- Lessios, H.A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annu. Rev. Ecol. Syst.* 19:371-393.
- Lessios, H.A. 1990. Adaptation and phylogeny as determinants of egg size in echinoderms from the two sides of the isthmus of Panama. *Amer. Natur.* 135: 1-13.
- Lessios, H.A. 2001. Molecular phylogeny of *Diadema*: Systematic implications, p. 487-495. In M. Barker (ed.), *Echinoderms 2000*. Proc. 10th Int. Echinoderm Conf. Swets and Zeitinger, Lisse.
- Lessios, H.A. & C.W. Cunningham. 1990. Gametic incompatibility between species of the sea urchin *Echinometra* on the two sides of the Isthmus of Panama. *Evolution* 44: 933-941.
- Lessios, H.A., J.D. Cubit, D.R. Robertson, M.J. Shulman, M.R. Parker, S.D. Garrity & S.C. Levings. 1984. Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs* 3: 173-182.
- Lessios, H.A., B.D. Kessing, G.M. Wellington & A. Graybeal. 1996. Indo-Pacific echinoids in the tropical eastern Pacific. *Coral Reefs* 15: 133-142.
- Lessios, H.A., B.D. Kessing & D.R. Robertson. 1998. Massive gene flow across the world's most potent marine biogeographic barrier. *Proc. R. Soc. Lond. Ser. B.* 265: 583-588.
- Lessios, H.A., B.D. Kessing, D.R. Robertson & G. Paulay. 1999. Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution* 53: 806-817.
- Lessios, H.A., B.D. Kessing & J.S. Pearse. 2001. Population structure and speciation in tropical seas: Global phylogeography of the sea urchin *Diadema*. *Evolution* 55: 955-975.
- Lessios, H.A., J. Kane & D.R. Robertson. 2003. Phylogeography of the pantropical sea urchin *Tripneustes*: contrasting patterns of population structure between oceans. *Evolution* 57: 2026-2036.
- Maluf, L.Y. 1988. Composition and distribution of the central eastern Pacific echinoderms. Natural History Museum of Los Angeles County, Technical Reports 2: 1-242.
- Mayr, E. 1954. Geographic speciation in tropical echinoids. *Evolution* 8: 1-18.
- McCartney, M.A. & H.A. Lessios. 2002. Quantitative analysis of gametic incompatibility between closely related species of neotropical sea urchins. *Biol. Bull.* 202: 166-181.
- McCartney, M.A. & H.A. Lessios. 2004. Adaptive evolution of sperm bindin tracks egg incompatibility in neotropical sea urchins of the genus *Echinometra*. *Mol. Biol. Evol.* 21: 732-745.
- McCartney, M.A., G. Keller & H.A. Lessios. 2000. Dispersal barriers in tropical oceans and speciation of Atlantic and eastern Pacific *Echinometra* sea urchins. *Mol. Ecol.* 9: 1391-1400.
- Metz, E.C., G. Gómez-Gutiérrez & D. Vacquier. 1998. Mitochondrial DNA and bindin gene sequence evolution among allopatric species of the sea urchin genus *Arbacia*. *Mol. Biol. Evol.* 15: 185-195.
- Mooi, R. 1990. Living cassiduloids (Echinodermata: Echinoidea): a key and annotated list. *Proc. Biol. Soc. Wash.* (103) 63-85.
- Mortensen, T. 1921. Studies of the development and larval forms of echinoderms. G.E.C. Gad, Copenhagen. 253 p.
- Mortensen, T. 1939. New Echinoidea (Aulodonta), Preliminary Notice. *Vidensk. Meddel. Dansk Naturhist. Foren.* 103: 547-550.
- Mortensen, T. 1928-1951. A Monograph of the Echinoidea. C.A. Reitzel, Copenhagen.
- Podesta, G.P. & P.W. Glynn. 2001. The 1997-98 El Niño event in Panama and Galapagos: An update of thermal stress indices relative to coral bleaching. *Bull. Mar. Sci.* 69: 43-59.
- Solis-Martin, F.A., A. Laguarda-Figueras & A. Leija-Tristán. 1997. Morphology, systematics, and distribution of *Meoma ventricosa grandis* and *M. ventricosa ventricosa* (Echinodermata: Echinoidea: Brissidae) along Mexican coasts. *Proc. Biol. Soc. Wash.* (110) 301-309.
- Zigler, K.S. & H.A. Lessios. 2003a. Evolution of bindin in the pantropical sea urchin *Tripneustes*: Comparisons to bindin of other genera. *Mol. Biol. Evol.* 20: 220-231.
- Zigler, K.S. & H.A. Lessios. 2003b. 250 million years of bindin evolution. *Biol. Bull.* 205: 8-15.
- Zigler, K.S. & H.A. Lessios. 2004. Speciation on the coasts of the New World: phylogeography and the evolution of bindin in the sea urchin genus *Lytechinus*. *Evolution* 58: 1225-1241.